ASSESSING THE IMPACT OF CLIMATE CHANGE ON MANGROVE CRABS: THE ROLE OF ONTOGENETIC MACROPHYSIOLOGY AND SETTLEMENT IN THE PERSISTENCE OF CENTRAL AND MARGINAL POPULATIONS

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BRUCE PETRUS MOSTERT

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ABSTRACT

After a brief respite in the mid to late 20th century, macrophysiology has come to the fore in elucidating large scale ecological patterns and processes as physiological assumptions often form the backbone of many predictive theories associated with species distributions. Critically, macrophysiological patterns are valuable in explaining physiological variation across multiple scales and provide insights into the effects of climate change on populations spanning a wide range of latitudes. This can assist in predicting possible distribution expansions, contractions or shifts in light of current climate change scenarios. From this perspective, investigating intra- and inter-specific physiological responses to environmental stress may contribute to better understanding and predicting the effects of climate change on geographical ranges. Further, investigating the physiological effects to environmental stresses across ontogenetic stages allows for the identification of weak links within the lifecycle of a species. Additionally, determining settlement characteristics along a latitudinal cline provides integrated indications of the sustainability of populations, highlighting vulnerable regions in terms of repopulation of viable habitats. In this context, the present study aimed at establishing how temperature, in a physiological context, may affect reproductive biology of two species of mangrove crab, *Perisesarma guttatum* and *Uca urvillei* at the centre (Kenya) and edge (South Africa) of their distributional range along the east coast of Africa and highlight possible consequences for range distributions. A third species, *Neosarmatium africanum*, only in South Africa, was included to provide additional interspecies comparisons. Furthermore, settlement characteristics of brachyuran populations at the centre and edge of their distributional range were considered in order to determine how settlement may contribute to population persistence.

Physiological investigations at the centre and edge of distributional range and across ontogenetic stages (larvae, stage 2 and 4 embryos, non-gravid and gravid females) under the concept of oxygen and capacity limitation of thermal tolerance (OCLTT), revealed that, for both species, populations at the centre of their distribution (Kenya) were generally more robust to increasing temperatures and generally displayed greater physiological stability with increasing temperatures compared to their conspecifics in South Africa. Variability in physiological robustness between regions, did however, differ among ontogenetic stages and species but, overall, were evident throughout. Within and between regions, adaptation to oxygen extraction in both milieus (air or water) was displayed for present temperature conditions but aerial respiration largely alleviated increased thermal stress due to overcoming the limitations of reduced oxygen availability and diffusiveness in water for all bimodal ontogenetic stages. Brooding eggs proved to be a physiologically critical process with either heighted oxygen consumption for gravid females or collapse of physiological processes demonstrated by supressed oxygen consumption. The physiological cost of brooding eggs, referred to as maternal costs, was reflected in in both *Perisesarma guttatum* and *Uca urvillei* where, in most cases, maternal costs were negative. Again, aerial respiration was able to alleviated increased thermal stress, as shown by positive maternal costs indicating sustained maternal care, but this mechanism was species and regionally specific.

Settlement patterns differed between the edge and centre of distribution of the species studied. This difference was predominantly driven by zonal preference within the mangal and/or effects of new and full moon (lunar phase). Overall, settlement dynamics were more widely variable in South Africa, both spatially and temporally, than in Kenya.

Finally, empirical physiological data from ontogenetic stages present during the reproductive process (early and late stage embryos) and from non-gravid and gravid females were used in conjunction with data mined from the existing literature to parameterise an individual based model designed to simulate reproductive output at the centre and edge of distribution of *Perisesarma guttatum.* Physiological data indicate that, in terms of reproductive output across increasing temperatures, populations based at the centre of their distribution presently outperform their counterparts at the edge of the species' distribution, but reproductive output stagnated as temperature rose. Edge of distribution populations consistently increased reproductive output with increasing temperatures to eventually outperform centre of distribution populations at higher simulated temperatures.

Overall, results of the physiological and settlement studies suggest that with increased climate change there may be a contraction of distributional range of the study species from high latitudes to low latitudes, contrary to general poleward shifts/migrations seen in most species, with possible contractions of the entire ecosystem mirroring the disappearance of keystone mangrove macrofauna.

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CHAPTER 1

GENERAL INTRODUCTION

Species distribution and diversity patterns have been intriguing natural scientists since the advent of evolutionary theory (e.g. Darwin 1859, 1862, Wallace 1878). One of the most fundamental patterns observed in the natural world is the increase of biodiversity from high latitudes to the equator and this has been discussed in detail by a plethora of authors spanning decades of work which detail this pattern in marine and terrestrial environments, across animal phyla and encompassing biodiversity across millennia (e.g. Dobzhansky 1950, Fischer 1960, MacArthur 1965, Pianka 1966, 1989, Connell 1978, Rohde 1978a, b, 1980, Schall and Pianka 1978, Huston 1979, Krebs 1985, Stevens 1989, Rohde 1992, Gaston 1996, Rosenzweig 1992, 1995, Rosenzweig and Sandlin 1997, Forbes *et al*. 1999, Willig *et al.* 2003). Based on this work, an abundance of hypotheses have attempted to explain species distribution and diversity patterns along the latitudinal cline between the equator and the poles, but no single hypothesis adequately accounts for all such patterns (Rohde 1992, Gaston and Blackburn 2000, Willig *et al.* 2003). Rather, this suggests that patterns of species diversity and distributions are the result of interactions of a number of aspects (Willig *et al.* 2003). Notably, the physical environment mostly drives distribution patterns as it has hierarchal effects on biological functions ranging from molecules to ecosystems (Clarke 2003, Macpherson 2002, Somero 2010, Boucher-Lalonde *et al.* 2012) and understanding outcomes of climate change drivers will require an in depth understanding these hierarchal effects (Spicer and Gaston 1999, Ricklefs and Wikelski 2002, Wikelski and Cooke 2006, Brook 2008, Brook *et al.* 2008, Cooke and Suski 2008).

1.1 Climate change and distributional shifts:

Environmental factors strongly influence species distributions in both marine and terrestrial environments (Woodward and Williams 1987, Macpherson 2002, Boucher-Lalonde *et al.* 2012), indicating that climate has important implications in shaping past and future species distributions (Peterson *et al.* 2002, Parmesan and Yohe 2003, Root *et al.* 2003, Thomas *et al.* 2004a, b, Rosenzweig *et al.* 2008). Impacts of climate change are likely to vary geographically (Root *et al.* 2003, Parmesan and Yohe 2003, Thomas *et al.* 2004a, Parmesan 2007, Deutsch *et al.* 2008, Dillon *et al.* 2010, IPCC 2014a, b, c, d) and will depend on the specific sensitivities of species to changing conditions (Roessig *et al.* 2004, Harley *et al.* 2006, Munday *et al.* 2008). The marine realm is not an exception and studies have shown that marine species often respond to environmental factors associated with climate change by shifting their ranges (Perry *et al.* 2005, Parmesan 2006, Hiddink and Hofstede 2008, Mueter and Litzow 2008, Dillon *et al.* 2010). Range shifts may result in localised extinctions (e.g. Peterson *et al.* 2002, Dulvy *et al.* 2003, Cheung *et al.* 2009, Sinervo *et al.* 2010) or facilitate range expansion and the invasion of new habitats (e.g. Hiddink and Hofstede 2008, Cheung *et al.* 2009) which can possibly disrupt and alter ecosystems and their associated functions (Duffy 2003, Roessig *et al.* 2004, Worm *et al.* 2006, Cheung *et al.* 2009, Hoegh-Guldberg and Bruno 2010, Doney *et al.* 2012).

Species both at high latitudes and in equatorial regions are expected to be highly sensitive to climate change with the possibility of localised extinctions (Deutsch *et al.* 2008, Cheung *et al.* 2009, Dillon *et al.* 2010), and generally marine species distributions are predicted to shift polewards under the influence of climate change which will lead to an increase of species invasion producing greater richness at higher latitudes (Zacherl *et al.* 2003, Precht and Aronson

2004, Harley *et al.* 2006, Cheung *et al.* 2009). Further shifts are expected to affect polar species with distributions retreating back towards the poles as these species are generally less robust than their lower latitude counterparts (Somero and DeVries 1967, Peck *et al.* 2004), while sub polar regions are expected to experience greater invasions from low latitude regions (Cheung *et al.* 2009). Such shifts have been documented in the northern hemisphere particularly at the mid- to high- latitudes (Walther *et al.* 2002, Parmesan 2007, Rosenzweig *et al.* 2008) and under the present assumptions about climate change are not unexpected due to the high warming rates in these regions (Walther *et al.* 2002, Root *et al.* 2003, Rosenzweig *et al.* 2008). The varying rates of climate change and the complex responses of species that influence range expansions and contractions therefore require a global scale perspective to obtain a complete picture of the effects and repercussions of climate change. Underlying these predictions is a strong foundation in physiology, as biological impacts are likely to be mediated through physiology and metabolic rates (Pörtner *et al.* 2007, Tewksbury *et al.* 2008, Deutsch *et al.* 2008, Dillon *et al.* 2010).

1.2 The role of physiology in large scale patterns of distribution:

A promising facet that contributes to the understanding of species distributions and patterns is the study of physiology over large scales or macrophysiology (Chown *et al.* 2004, Chown and Gaston 2008, Gaston *et al.* 2009, Violle *et al.* 2014). During the first half of the 20th century, macrophysiology was common place as ecology and physiology were largely synonymous (e.g. Shelford 1911, Chapman 1931, Fox 1936, 1938, 1939, Fox and Wingfield 1937, Moore 1939, 1942, 1952, Scholander *et al.* 1953, Andrewartha and Birch 1954, Scholander 1955). In the latter half of the twentieth century however, large scale physiological ecology was rather side-lined (Kingsolver 1988) compared to the flourishing disciplines of molecular biology and biochemistry and their roles in elucidating the mechanisms and effects of physiology (Weibel

1997, Gaston *et al.* 2009). In the 21st century, there has been fresh interest in both large scale temporal and spatial physiological ecology initiating a call to re-establish macrophysiology (Chown and Gaston 1999, Spicer and Gaston 1999, Hoffmann *et al.* 2001, 2003, Chown *et al.* 2004, Osovitz and Hofmann 2007, Chown and Gaston 2008, Gaston *et al.* 2009, Stillman and Tagmount 2009), with the importance of short term and local studies still being emphasised (Brown and Maurer 1989, Lawton 1999, Walther *et al.* 2002, Gaston *et al.* 2009) as seen in the combination of small and large scale ecological approaches (Ricklefs 1987, Ricklefs and Schluter 1993, Brown 1995, Gaston & Blackburn 2000). The basis for this "new light" on macrophysiology was provided by reviews of the vast amount of early 20th century macrophysiological work in the latter half of the 20th century (e.g. Garland and Adolph 1991, Huey 1991, Spicer and Gaston 1999) forming an ideal platform from which studies into macrophysiology can be justified, especially in the more current context of climate change (Chown and Gaston 2008).

The merits of large scale studies have come to the fore in the identification and explanation of ecological patterns and processes (Brown 1995, Gaston and Blackburn 2000, Blackburn and Gaston 2003) and are often associated with physiological assumptions that back up these theories (Geist 1987, Stevens 1989, Gaston *et al.* 1998, Chown and Gaston 1999, Spicer and Gaston 1999, Clarke and Gaston 2006, Ghalambor *et al.* 2006, Millien *et al.* 2006, Kearney and Porter 2009) with further links to its evolutionary significance (Lovegrove 2000, 2001). Analyses of macrophysiological patterns are valuable in explaining physiological variation across multiple scales (Clarke and Johnston 1999, Chown *et al.* 2003). For example, the Rapoport effect, which applies to diverse taxa in both terrestrial and aquatic environments, targets the issue of an increase in species range with latitude (Rapoport 1975, Stevens 1989, Gaston *et al.* 1998). This effect is driven by the more variable (and/or alternation of extreme) climate towards the poles,

which is linked to broader physiological tolerances (Stevens 1989). This theory predicts that tropical species should have less physiological flexibility than their counterparts at higher latitudes (Stevens 1989, Willig *et al.* 2003, Chown *et al.* 2004). Quantitative links between macroecology and physiology were however relatively infrequent (Brown 1995, Kirkpatrick and Barton 1997, Clarke 2003, Bernardo *et al.* 2007), but amongst recent research, there are studies focused on the marine environment (e.g. Pörtner 2001, Pörtner and Knust 2006, Orr *et al.* 2005, Parmesan 2006), including the intertidal habitat (e.g. Helmuth *et al.* 2002, Place *et al.* 2008, Sunday *et al.* 2011). Importantly, it must be noted that, within the marine realm, large scale displacements are more likely due to changing physical conditions than simple expansion and contractions of distributions (Parmesan 2006), highlighting the importance of studying these systems. Smaller scale studies targeting possible variability of physiology in relation to geographic distribution are still relevant as they form the building blocks upon which macrophysiology is founded. Additionally, the mechanistic basis on which traits are constructed and linked to local environmental factors (e.g. temperature, precipitation, salinity, solar radiation, productivity) has been identified as a potential driver of spatial and temporal variability in physiological traits and so is essential in the consideration of large scale patterns and processes across scales (Chown *et al.* 2004, Gaston *et al.* 2009).

Considering the dynamic yet physiologically vulnerable nature of intertidal systems (see Helmuth *et al.* 2002, Somero *et al.* 2010), mangroves, which range from warm temperate, to subtropical and tropical environments, are obvious candidates to link macrophysiology and climate change studies. Mangrove ecosystems spanning the east coast of Africa provided an ideal platform to evaluate the physiological responses of cosmopolitan species to temperature change over many degrees of latitude. Due to tropical species living close to their thermal optima (Krockenberger *et al.* 2004, Somero 2005, Deutsch *et al.* 2008, Huey and Tewksbury 2009,

Dillon *et al.* 2010, Nguyen *et al.* 2011, Faulkner *et al.* 2014, Rummer *et al.* 2014), in Chapter 2, I propose that species in this region (Kenya) will be more vulnerable to climate change, experiencing greater physiological stress and more adversely affected by changing temperatures (shown by elevated oxygen consumption at higher temperatures). Meanwhile, I propose that, while temperate conspecifics will still be affected by increasing temperatures associated with climate change, the the elevation in oxygen consumption rates associated with increasing temperatures will be lower than for their tropical counterparts indicating that they are physiologically more robust than their tropical counterparts. In Chapter 3, I investigate settlement dynamics of mangal Brachyura in order to identify similarities or differences between centre (Kenya) and edge (South Africa) populations. Chapter 4 aims to use data collected in Chapter 2 to parametrise an individual-based computer model that deals with the reproductive output of mangrove crabs under changing temperature conditions.

1.3 Structure of thesis:

Comprised of three working chapters, the present thesis examined the metabolic response of two cosmopolitan brachyurans (*Perisesarma guttatum* and *Uca urvillei*) that exploit a bimodal breathing lifestyle within the mangrove ecosystem, taking advantage of oxygen uptake from both air and water. Several ontogenetic stages were targeted in the evaluation of metabolic response at both low latitude (Kenya) and high latitude (South Africa) regions to allow the examination of variation in physiological strategies across several life stages and the identification of possible physiological weaknesses (as shown by elevated oxygen consumption) under the influence of changing temperatures (Chapter 2). A third species, *Neosarmatium africanum*, was included in South Africa to further examine interspecific variability (Chapter 2). The important facet of settlement was also considered as this is a crucial process whereby new settlers are recruited in the existing population contributing to overall population dynamics and structure (Underwood

and Fairweather 1989, Flores *et al.* 2002, Papadopoulos *et al.* 2002, Anger 2006). In order to gather baseline information on the natural settlement rates of cosmopolitan species at key latitudes (centre and edge of distribution), the ultimate aspect of reproductive success, settlement, was monitored in the two regions over the reproductive season (Chapter 3). Lastly, using empirical data from chapter 2 and in-situ environmental profiles from each of the studied sites, an Individual Based Model (IBM) was designed and implemented to assess the effects of projected increasing in temperatures (IPCC 2014b, d), on the production and development of eggs at each of these localities (Chapter 4). Chapter 1 and 5 of the thesis cover the general introduction and synthesis of this research.

1.4 Overview on the system, region and species:

1.4.1 Importance of Mangrove Ecosystems:

Mangals are among the most biologically important and productive ecosystems globally, providing valuable ecosystem functions (Adams *et al.* 2004, Nagelkerken *et al.* 2008, Lee *et al.* 2014), including the stabilisation of shorelines, reducing the impacts of natural disasters such as tsunamis and hurricanes (Giri *et al.* 2011). Biologically, they provide significant refuge, breeding grounds and nurseries for birds, marine invertebrates, pelagic and marine fish (Adams *et al.* 2004, Giri *et al.* 2011). They contribute to coastal primary production, producing more than 2 tons ha^{-1} yr^{-1}, making them one of the most productive ecosystems and further contribute to food chains through detrital pathways (Snedaker 1978, Robertson 1996, Alongi 1998, Adams *et al.* 2004). Additionally, mangals and their associated sediments are estimated to sequester approximately 22.8 million metric tons of carbon annually (Giri *et al.* 2011), accounting for 11% of the total terrestrial carbon and 10% of the terrestrial dissolved organic carbon (DOC) exported to the ocean (Jennerjahn and Ittekot 2002, Dittmar *et al.* 2006). Economically, these unique

forests are important in providing building materials, firewood, enhancing water quality in estuaries and nearby coastal systems, fisheries and ecotourism (Ewel *et al.* 1998, Cole *et al.* 1999, Adams *et al.* 2004). Overall mangals are unique, integral parts of the coastal ecosystem, important both biologically and economically.

1.4.2 Global distribution of mangroves:

Mangals are conspicuously distributed throughout intertidal tropical and sub-tropical areas globally, usually between 30° N and 30° S latitude, and are occasionally present in warm temperate regions (Duke *et al.* 1998, Morrisey *et al.* 2010, Giri *et al.* 2011). They inhabit the land-sea interface, typically growing in sheltered intertidal areas that are submerged during high tide (Alongi *et al.* 1999). These systems are generally divided into two groups; the Atlantic East Pacific (AEP) and the Indo West Pacific (IWP) with the IWP having greater species richness (Duke *et al.* 1998). Overall, mangroves are estimated to cover between 13.7 to 15.5 million ha along the coasts of North and South America, Asia and Australia, while a further 3 million ha occur along the coasts of East and West Africa (Blasco *et al.* 1998, Adams *et al*. 2004, Giri *et al.* 2011), although some recent studies suggest that the total area in Africa has decreased and is now between 1.1 to 2.6 million ha (Wilkie and Fortune 2003, FAO 2007, Fatoyinbo and Simard 2013).

Temperature is one of the main environmental factors controlling the global distribution of mangroves (Duke *et al.* 1998, Morrisey *et al.* 2010, Saintilan *et al.* 2014). It is postulated that the latitudinal limits coincide with a mean monthly atmospheric temperature of 20°C during the coldest months of the year (Walsh 1974, Saintilan *et al.* 2014). Their distribution is however more accurately identified by the position of the 20°C isotherm in sea surface temperature (SST)

during winter, as this controls latitudinal limits in both the southern and northern hemispheres (Duke *et al.* 1998, Alongi 2009). The limits for different mangrove species can be uneven and the SST and atmospheric temperature effects may vary from each of the described limits for different species (Quisthoudt *et al.* 2012, 2013). Studies have identified annual thermal amplitudes of less than 5°C as being important in distribution patterns (Walsh 1974, Chapman 1975) and Ellison (2000) noted that latitudinal frost limits and the winter 16°C atmospheric isotherm were important in driving distributional limits in the South Pacific. Further literature suggests that a varying SST winter isotherm between 15 and 20°C limits the distribution of mangroves (Tomlinson 1986, Woodroffe and Grindrod 1991, Duke *et al.* 1998, Alongi 2002). In any event, there is clear agreement that temperature, in one form or another, is a limiting factor for the occurrence of mangroves.

Growth of some species is already inhibited at 5°C (Tomlinson 1986) and decreases in seedling growth of *Avicennia marina* have been recorded below temperatures of 15°C (Kao *et al.* 2004). Further literature indicates that this species shows negligible growth at 17°C (Steinke and Naidoo 1991). Frost has been shown to cause embolisms in the secondary xylem, killing trees (Stuart *et al.* 2007), causing premature death of leaves (Ellis *et al.* 2006), while temperatures from -3°C are known to cause death of *A. marina* (Sakai and Wardle 1978, Wardle 1985). An increase in latitude has been shown to correlate with decreased net primary production in some *Rhizophora* species, mortality of propagules and the occurrence of seedlings with damaged leaves (Krauss *et al.* 2008, Suwa and Hagihara 2008). Trees belonging to the genus *Avicennia* are amongst the few that show some frost tolerance (Stevens *et al.* 2006), making them among the most widely distributed species across latitudes (Saintilian *et al.* 2013).

The latitudinal distributions of mangroves along continental east and west coasts vary due to oceanic currents; cool western boundary currents often cause constriction of distributions due to unfavourable climatic conditions and limitation of propagule dispersal, while warm eastern boundary currents cause an expansion into higher latitudes (Chapman 1975, Duke 1992). These notable modifying factors are prominent along the west coasts of America and Africa, where there is an absence of mangroves south of 5°32′ and 12°20′ respectively. Along the east coast of Africa, mangroves make up an integral part of the coastal ecosystems and range from Egypt (28^{o} N) in the northeast of the continent to the southeast of South Africa (29^{o} S) (Fatoyinbo and Simard 2013). The northern latitudinal limits of mangroves along the Indian Ocean and Red Sea are restricted by factors such as temperature and aridity (Fatoyinbo and Simard 2013). Mean average rainfall of below 30 mm year $^{-1}$ along the west coast of Africa has also been shown to be important in restricting the distribution of mangroves (Saenger and Bellan 1995). Aridity is considered to be the second most important climatic factor restricting the distribution of mangroves as they require higher temperatures for survival in these conditions (Spalding *et al.* 1997, Saenger 1998, Quisthoudt *et al.* 2013). Other factors that influence distributional patterns of mangroves include nutrients, which are linked to underlying differences in geochemistry over latitudes (Lovelock *et al.* 2007), wave energy, salinity, pH, and duration of inundation by water (Morrisey *et al.* 2010).

Mangals consist of a range of functional forms, including trees, shrubs, a palm and a fern, all generally greater than half a meter in height. Compared to other high biomass tropical ecosystems such as coral reefs or tropical rainforests, they have considerably lower species richness (Ricklefs and Latham 1993). In order to survive in the harsh intertidal region, flora have a broad range of structural and functional adaptations (Duke *at al.* 1998). These adaptations include, but are not limited to, pneumatophores (e.g. *Avicennia* spp.), prop roots (e.g. *Rhizophora*

spp.), mechanisms for physiological salt exclusion (e.g. *Rhizophora* spp.) and/ or excretion (e.g. *Avicennia* spp.) and viviparous propagules (Passioura *et al.* 1992, Clarke and Allaway 1993, Kathiresan and Bingham 2001, Kitaya *et al.* 2002).

For the purpose of this study, East African mangroves were selected from their mid-distributional range in Kenya, specifically Gazi Bay and Shirazi Creek, while two mangrove systems were chosen from the southern edge of their distribution in South Africa, Mngazana and Mntafufu estuaries (MacNae 1963, Saenger and Bellan 1995, Spalding *et al.* 1997).

1.4.3 Kenya:

The Kenyan coastline experiences two distinct seasonal tropical monsoon cycles, with the southeast (SE) monsoon occurring between April and September while the northeast (NE) monsoon occurs between October and March (McClanahan 1988, Wakibia *et al.* 2006). The SE monsoon is characterised by strong winds, low air and water temperatures, low solar radiation and heavy rains (Wakibia *et al.* 2006). In contrast, the NE monsoon is a reversal of these variables (McClanahan 1988). Overall, there is a mean annual precipitation of approximately 1144mm and the mean monthly temperature ranges from 23.3 to 29.9°C while the mean annual temperature between 1931 – 1990 was 26.4°C (Lieth *et al.* 1999).

Gazi Bay (39º30'E, 4º22'S) is located on the southern coast of Kenya, 50 km south of Mombasa. The bay opens into the Indian Ocean through a 3.5 km wide mouth and is mostly shallow with a mean depth of 4 m (Kitheka and Mwashote 1997). Feeding into the 15 km^2 bay are two rivers, the Kidogoweni River at the north-west of the bay, which supports the majority of the mangroves, while the Mkurumuji River is on south-west side and supports a much less extensive

mangrove stand (Kitheka and Mwashote 1997). The catchments for the Kidogoweni River and the Mkurumuji River extend 30 km^2 and 164 km^2, respectively, into the Shimba Hills which receive an average rainfall of 900 mm $year^{-1}$. The mangrove forest contained within the bay covers approximately 7 km^2 and consists of all the mangrove species common to tropical east African mangroves: *Avicennia marina*, *Bruguiera gymnorrhiza* (L.) Lam., *Ceriops tagal* (Perr.) C.B. Robinson, *Heritiera littoralis* Dryand., *Lumnitzera racemosa* Willd., *Rhizophora mucronata*, *Sonneratia alba* Sm., *Xylocarpus granatum* Koen, *Xylocarpus moluccensis* (Lamk.) Roem and *Pemphis acidula* Forst (Cannicci *et al.* 2009, Richmond 2010). Shirazi Creek (39º25'E, 4º31'S) is located 12 km South of Gazi Bay and approximately 62 km from Mombasa and makes up part of the Shirazi-Funzi mangrove system fed by the Ramisi and Mwena Rivers which drain through the Mamuja and Vikurani Creeks, respectively (Cannicci *et al.* 2009). This mangrove system is made up of the same east African species found in Gazi bay except *P. acidula* is absent (Cannicci *et al.* 2009). In both these systems, *R. mucronata, C. tagal* and *A. marina* are the dominant species and make up approximately 70% of the mangrove (Spalding *et al*. 2010).

1.4.4 South Africa:

The area and species composition of South African mangroves are smaller and less diverse compared to those found in the tropics. South African mangroves generally consist of three species of tree: *Avicennia marina*, *Bruguiera gymnorrhiza* and *Rhizophora mucronata.* These species are not necessarily cold specialists, but rather have a wide latitudinal distribution (Morrisey *et al.* 2010). These mangroves are restricted to estuaries due to high energy wave action which prevents the establishment of open coast mangrove ecosystems (Quisthoudt *et al.* 2013). Wave action either prevents the establishment of propagules or creates delays between new shore creation and colonisation by mangroves (Clarke and Myerscough 1993, Alongi 2009).

Along the east coast of South Africa, mangroves are restricted to 37 estuaries covering approximately 1688 ha, and make up about 0.05 % of the total area of mangroves found in Africa (Adams *et al.* 2004). Mangroves distributed within estuaries further north, closer to the tropics, are larger than their more southern counterparts (Adams *et al.* 2004).

Out of the 37 estuaries hosting mangroves in South Africa two estuaries, Mngazana and Mntafufu were chosen on the basis that both contained relatively large mangrove stands, and are approximately 25 km apart and are estuaries considered to be close to the furthest southern limits of mangrove distribution. The Mngazana catchment covers 275 km^2 (Emmerson 2005) and the 5.3 km estuary which enters the subtropical section of Indian Ocean (29°25'E, 31°42'S) is rated as the third largest mangrove system in South Africa at 1.45 km^2 (Colloty 2000, Adams *et al.* 2004, Rajkaran *et al.* 2004). The 5 km long Mntafufu estuary is considered to host a medium sized mangrove stand in South African terms and is estimated to cover 12.4 ha (Adams *et al.* 2004) and enters the Indian Ocean at 29°38'E, 31°33'S. Both the Mngazana and Mntafufu systems have extensive intertidal flood plains which facilitate complex riverine forests with high tree densities (Adams *et al.* 2004). In these systems, *Avicennia marina* is the pioneer species on both the seaward and landward edges of the mangroves, *Bruguiera gymnorrhiza* forms a band between the stands of *A. marina*, while *Rhizophora mucronata* lines the channels running through the flood plains (MacNae 1963, Rajkaran and Adams 2012).

The Port St Johns area, which encompasses both estuaries, is subject to year round rainfall although greater precipitation is recorded during summer (November to January). Weather data for this area has been collected over 89 years (1920 – 2009) during which mean minimum temperatures range between 10.5 to 22.4°C while mean maximum temperatures are between 18.7

and 28.2°C, the average ± SE rainfall for this period is 115.6 ± 3.4 mm during summer while average ± SE winter rainfall was recorded at an 46.6 ± 3.1 mm (Rajkaran and Adams 2012).

1.4.5 Mangrove Fauna:

Mangals host a diverse array of macrofaunal assemblages that display a variety of lifestyles from marine to semi-terrestrial to fully terrestrial and include members from the Gastropoda, Brachyura, Insecta, Arachnida and Oligochaeta (Ravichandran and Wilson 2012, Vannini and Fratini 2012). The importance of these assemblages in mangrove ecosystem functioning has been revised over the past two decades (Cannicci *et al.* 2008, Lee 2008) and their role in ecosystem functioning and mangal structuring clarified (Smith 1987, Smith *et al.* 1991, Lee 1998, 2008, Kristensen and Alongi 2006, Cannicci *et al.* 2008, Kristensen 2008).

1.4.6 Importance of the Brachyura:

The fauna of mangal systems is dominated by brachyuran crabs, which have evolved to take advantage of the available marine, intertidal, terrestrial and arboreal habitats, exploiting several niches critical to mangrove ecosystem functioning (Hartnoll 1975, Jones 1984, Dahdouh-Guebas *et al.* 2002, Fratini *et al.* 2005, Duke *et al.* 2007, Mukherjee *et al.* 2012, Vermeiren and Sheaves 2012). The integral role of mangrove fauna in ecosystem functioning was highlighted in Australian mangals (Robertson 1986, Robertson and Daniel 1989, Micheli 1993) where mangrove brachyurans were shown to scavenge and bury up to 28% and 71 - 79% of leaf litter in the low and high intertidal zones respectively (Robertson 1986, Robertson and Daniel 1989). Crabs also feed extensively on detrital matter and primary production located in mangal sediments (Crane 1975). This highlights the importance of brachyurans in the trapping and converting of primary production and in transferring it to higher trophic levels, both within the

mangal and as exported larvae (Giddings *et al.* 1986, Robertson and Daniel 1989, Micheli 1993, Skov and Hartnoll 2002, Hartnoll *et al.* 2002). It is hypothesised that due to the deposit and carnivorous feeding preferences of the crab assemblages in the Atlantic East Pacific, their role in mangrove ecosystem functioning differs from those of the herbivorous Indo-West Pacific mangroves assemblages (Robertson 1988, McIvor and Smith 1995).

East African mangals are estimated to produce 17 tonnes $ha^{-1}yr^{-1}$ of primary production of which 80% is leaf litter (Shunula and Whittick 1999). The contribution to the detrital pathway in mangals by microalgae, phytoplankton and epiphytes is generally low (Alongi 1998), but the greater nitrogen content of algae suggest that this forms an important supply of organic nitrogen into mangal food webs (Newell *et al.* 1995, Kristensen 2008, Bouillon *et al.* 2008). The majority of the East African brachyuran assemblages are comprised of members from the Graspidae superfamily and the Ocypodidae family (Hartnoll 1975, Jones 1984). Grapsidae in particular, are voracious herbivores and the removal of leaf litter from African mangals is amongst highest in the world (Micheli *et al.*1991, Steinke *et al.*1993, Skov 2001, Ólafsson *et al.* 2002). Grapsids generally macerate, ingest and bury leaf litter, preventing loss of nutrients from the mangal and promoting decomposition (Emmerson and McGwynne 1992, Lee 1997). Ocypodids, in contrast, primarily feed on micro-algal mats and are generally located in open areas of the mangal where sunlight promotes algal growth (Nobbs 2003, Kristensen and Alongi 2006). Their feeding effects are confined to the upper few millimetres of the sediment (Dye and Lasiak 1986) that the crabs sort, consuming micro-algal cells, nematodes, and bacteria, while the residue is shaped into balls and placed back on the surface of the sediment (France 1998). Studies suggest fiddler crabs have profound effects on micro-algal and bacterial abundances (France 1998, Bouillon *et al.* 2002, Meziane *et al.* 2002, Reinsel 2004, Kristensen 2008) as well as meiofauna through predation, disturbance or competition for food (Schrijvers *et al.* 1995, Ólafsson and Ndaro 1997, Reinsel

2004, Weis and Weis 2004). Furthermore, the mixing of the sediment that occurs during the feeding process greatly alters microbial distribution and activity due to change in the chemistry of the upper 2cm of the sediment (Kristensen and Alongi 2006).

Members of the Graspidae and Ocypodidae further contribute to ecosystem functioning by burrowing extensively in the mangal, with significant effects on the topography and biogeochemistry of the sediments, emphasising the role of these species as ecosystem engineers (Smith *et al.* 1991, Mouton and Felder 1996, Botto and Iribarne 2000, Kristensen 2008). Additionally, the faecal matter of brachyurans contributes to secondary production via enhanced microbial activity (Lee 1997, Gillikin *et al.* 2001, Kristensen and Pilgaard 2001, Kristensen 2008). Furthermore, mangals have been highlighted as important feeding grounds with brachyurans and other invertebrates being a primary food source for mobile marine and terrestrial fauna, further reinforcing their crucial role in ecological functioning (Wilson 1989, Fry and Ewel 2003, Lugendo *et al.* 2006). Finally, very recent and novel findings suggest that the burrowing activity by mangrove associated crabs (Ocypodids) might influence directly and indirectly the productivity of mangroves by supplying oxygen to the roots, not only during ebbing tides, but also during tidal submersion (Cannicci *et al.* unpublished data).

1.4.7 Model species:

Perisesarma guttatum (Brachyura: Sesarmidae) (A. Milne Edwards, 1869):

Perisesarma guttatum is endemic to the east coast of Africa, spanning several degrees of latitude from Somalia to the Transkei region of South Africa, its distribution further extends across the Mozambique Channel to Madagascar (Kensley 1981, Vannini and Valmori 1981, Lago 1993a, Silva *et al.* 2010a). This species occupies the seaward fringe of the mangal (Macnae 1968, pers

obs) and is mostly associated with the root systems of *Rhizophora mucronata* (Cannicci *et al.* 1996). *P. guttatum* roam freely on the mangal floor, rarely constructing burrows, but rather sheltering in crevices, holes and prop roots; they typically feed on mangal leaves and any other available organic matter (Fratini *et al.* 2005, Silva *et al.* 2010a). Females reach sexual maturity at approximately 2 years of age (Flores *et al.* 2002) and in tropical regions breed year round (Gove and Mambonhe 2000, Skov 2001, Flores *et al.* 2002), while in temperate regions *P. guttatum* demonstrates seasonal breeding patterns (pers. obs.). The eggs are brooded through five stages on the underside of the female abdomen (Skov 2001, Simoni *et al.* 2013) and planktonic larvae are released during the ebb phase of new and full moon spring tides, as is typical of sesarmid species (Flores *et al.* 2002, Skov *et al.* 2005, Guerao 2011, 2012). Larvae spend approximately 22-25 days as pelagic larvae during which they morph through five zoeal stages and one megalopa stage (Lago 1993a). Recent phylogenetic and morphometric analyses have indicated that there are two divergent clades, the first being associated with populations in Kenya, Tanzania and northern Mozambique, while the second clade is present in southern Mozambique, (Inhaca Island and Maputo Bay) (Silva *et al.* 2010a) and presumably populations located further south, along the coast of South Africa. Although two divergent clades of *P. guttatum* have been identified along the east coast of Africa (Silva *et al.* 2010a), I do not expect this differing genetic diversity to confound the results of the study, as divergent physiological responses are expected at the centre and edge of the distributional range as populations will likely show adaptations to present climate conditions regardless of clade. Examples of different genetic lineages having different physiologies for mussels have been described by Zardi *et al.* (2011). Additionally, Silva *et al.* (2010a) were unable to determine whether the differentiation occurs due to a distinct break or is a result of clinal variation (Hebert *et al.* 2003, Silva *et al.* 2010a). Early studies of this species may also have confused *Perisesarma samawati* (which was described for the first time in

2004 by Gillikin and Schubart) for *P. guttatum.* In this study care was taken to identify and separate these two species to prevent confounding of results.

Neosarmatium africanum (Brachyura: Sesarmidae), previously *Neosarmatium meinerti* (De Man 1887):

In 2009 the phylogeography of *Neosarmatium meinerti* was investigated based on genetic and morphological traits throughout its geographical range producing a species complex with four evolutionary branches; African mainland, western Indian Ocean islands, south-eastern Asia, and northern Australia (Ragionieri *et al.* 2010). Subsequently, with the sequencing of mitochondrial genes, the African mainland complex was renamed *Neosarmatium africanum* which is distributed from Somalia to South Africa reaching parts of Madagascar (Ragionieri *et al.* 2012). *N. africanum* inhabits the upper intertidal region of estuaries and mangals where they are rarely submerged, they burrow up to 80cm into the sediment often reaching the water table (Skov 2001, Berti *et al.* 2008). Mangrove leaves form a large part of the diet, especially those of *Avicenna marina*, as well as small amounts of animal matter (Emmerson and McGwynne 1992, Dahdouh-Guebas *et al.* 1997, 1999), indicating that this species plays an integral role in the biochemical cycle in mangrove ecosystems (Skov and Hartnoll 2002). Furthermore, this species feeds intensively on mangrove propagules, highlighting its importance in mangal regeneration (Dahdouh-Guebas *et al.* 1998, Bosire *et al.* 2005). Breeding seasons for *N. africanum* vary along its latitudinal distribution. In Kenya, the breeding season is typically during the dry season between February and April, while in South Africa breeding occurs during the summer months of January and February (Emmerson 1994, 1999, Skov 2001, Skov *et al.* 2005). *N. africanum* broods eggs through five stages on the underside of its abdomen (Skov 2001) and releases pelagic larvae which include five zoeal stages and one megalopa stage (Lago 1989).

Uca urvillei (Brachyura: Ocypodidae) (A. Milne Edwards, 1852):

The distribution of *Uca urvillei* spans the east coast of Africa from Somalia to South Africa and it is present in Madagascar, coastal Pakistan and western coastal India (Vannini and Valmori 1981). Within the mangal, it is typically associated with open muddy areas between stands of *Rhizophora mucronata* and *Avicenna marina* where it is able to construct burrows, graze and filter sediment (Hartnoll 1975, Branch and Grindley 1979, Litulo 2005a). In tropical regions, *U. urvillei* is considered to breed year round (Litulo 2005a), while in temperate regions breeding occurs seasonally (Emmerson 1994, 1999). Females brood eggs on the underside of their abdomen through five stages until larval release which usual occurs during the spring high tides associated with new and full moon (pers. obs.). Although this species inhabits areas inundated with water twice daily, it tends to avoid submersion by foraging during low tides and retreating to its burrow during incoming tides, where it plugs the entrance with a disc of mud preventing submersion (Cannicci et al, unpublished data), as is common in fiddler crab species (de la Iglesia 1994).

1.4.8 Characterisation of the in-situ environmental conditions of model species habitat:

To characterise natural temperature and humidity variations experienced by brachyuran populations at their respective latitudinal distributions, ten temperature i-button loggers (Maxim integrated product, ColdChain Thermodynamics) were placed in water proof silicon capsules to prevent water damage and placed in areas inhabited by the model species. The loggers were haphazardly positioned both 1cm above and 20cm below the sediment surface in semi shaded conditions typical of mangal habitat. A further four i-button temperature and humidity loggers were placed approximately 1.5m above the sediment surface in each area. The temperature i-

button loggers were set to record temperature every 5 min for 15 days, while the temperature and humidity loggers recorded both temperature and humidity values for the same time intervals, after which the data were retrieved and the i-buttons reset. Data were downloaded with Cold Chain ThermoDymanimcs software (version 4.9 – Fairbridge Technology), and average temperature for each hour of each day was calculated. Tidal data were sourced from Wtide (version 3.1.7; www.wtide.com). All data were collected during field expeditions to each region limiting the available time for data collection. In Kenya, field expeditions corresponded to the northeast (NE) monsoon (McClanahan 1988, Wakibia *et al.* 2006). The NE monsoon is thought to be the equatorial equivalent to peak summer in South Africa. Both these periods correspond to the peak breeding season for the targeted study speciesi in this thesis. Data collection was further subject to the number of available i-button loggers, limiting data collection to specific periods at specific sites.

Gazi Bay mangal, Kenya

The environmental conditions of the zones inhabited by *Perisesarma guttatum* among the *Rhizophora mucronata* roots (Figure 1.1) and the open areas between *R. mucronata* trees which *Uca urvillei* typically inhabits (Figure 1.2) at Gazi Bay, were characterised over 47 days during the northeast monsoon season in Kenya (McClanahan 1988).

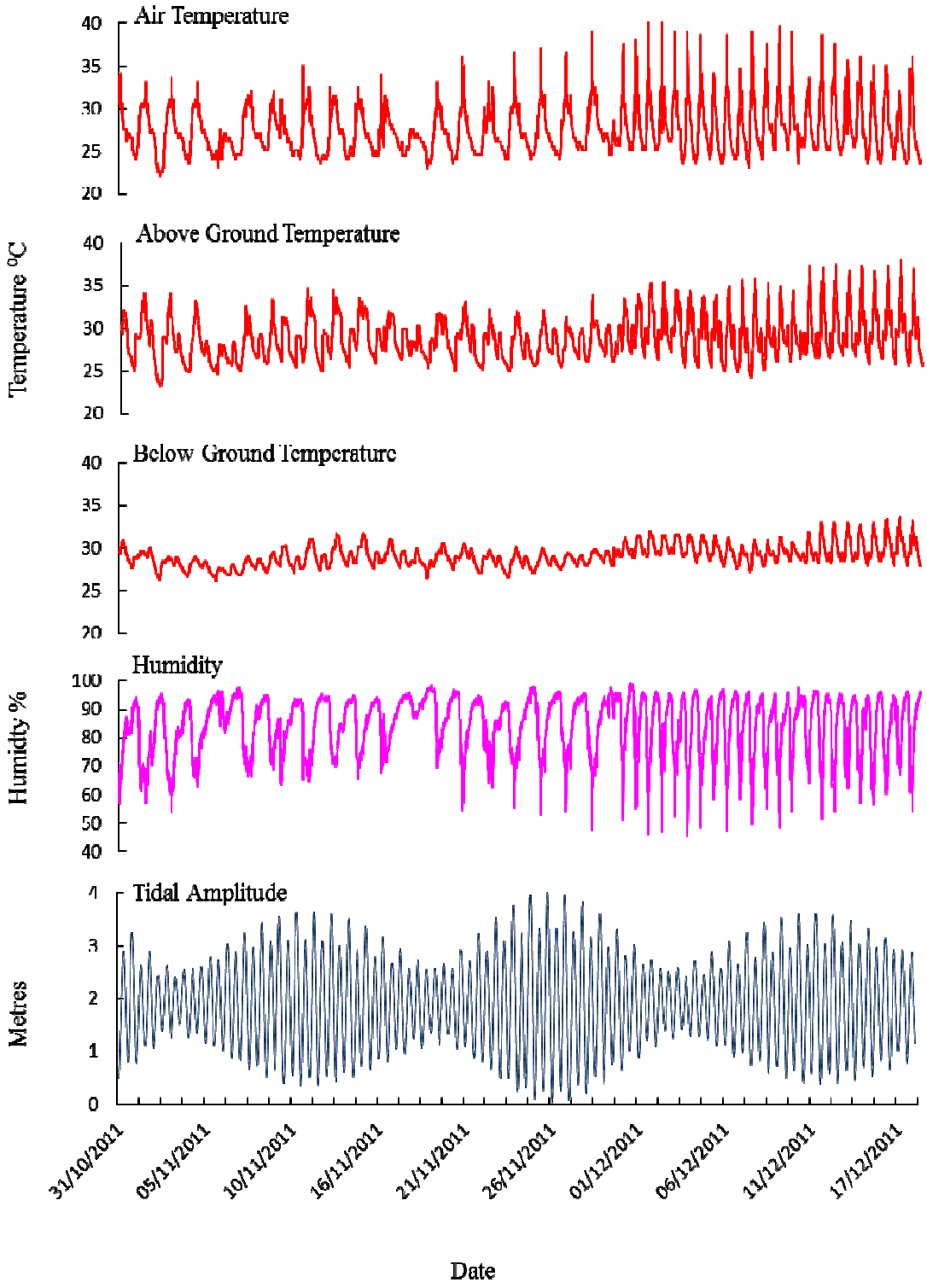

Figure 1.1: Temperature, humidity and tidal profile for the *Rhizophora mucronata* zone within the Gazi Bay mangal, which typically hosts *Perisesarma guttatum* and where *Uca Urvillei* are occasionally found. The profile was recorded between 31 October 2011 and 17 December 2011.

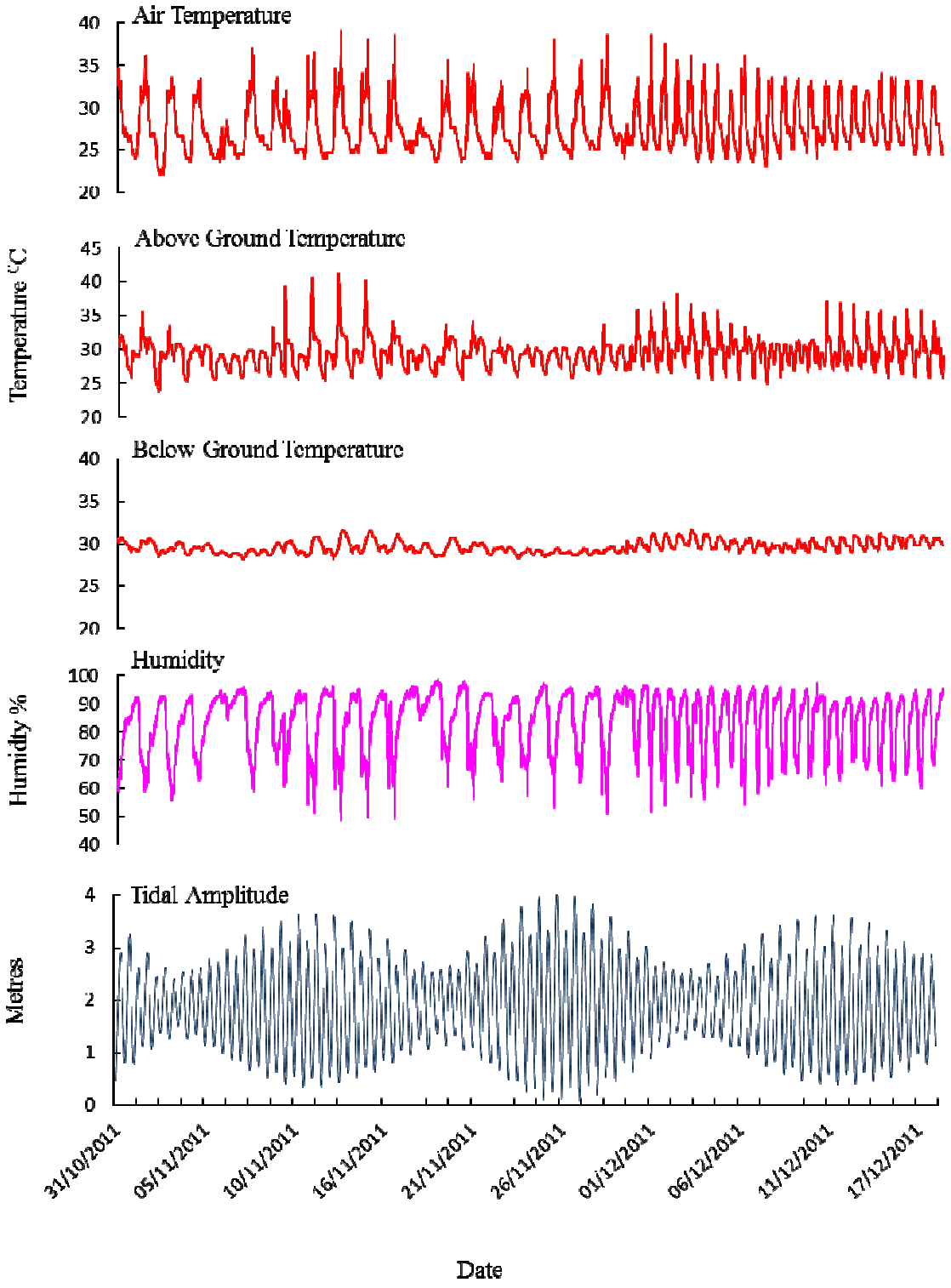

Figure 1.2: Temperature, humidity and tidal profile for the open areas within the *Rhizophora mucronata* zone at the Gazi Bay mangal, which typically hosts *Uca urvillei*. The profile was recorded between 31 October 2011 and 17 December 2011.

Mngazana estuary mangal, South Africa:

Over 27 days during the summer months of January and February at Mngazana estuary, South Africa the environmental conditions of the zones typically inhabited by the study species were characterised. These were the *Rhizophora mucronata* zone among the roots which is the typical habitat of *Perisesarma guttatum* (Figure 1.3), the open areas between *R. mucronata* trees where *Uca urvillei* are found (Figure 1.4) and along the high tide mark of the banks of the estuary where *Neosarmatium africanum* are located (Figure 1.5).

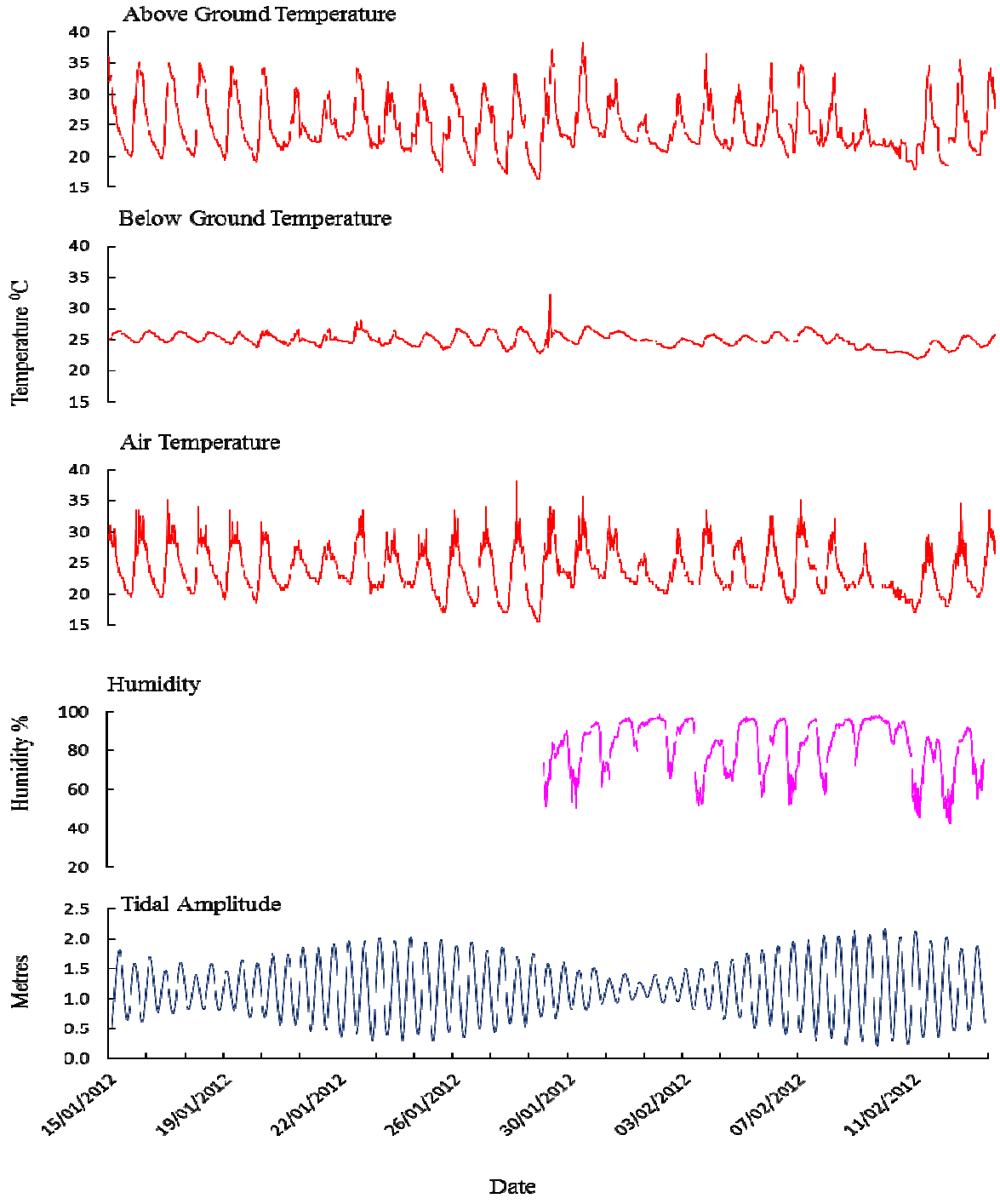

Figure 1.3: Temperature, humidity and tidal profile for the *Rhizophora mucronata* zone within the Mngazana estuary mangal, which typically hosts *Perisesarma guttatum.* The profile was recorded between 15 January 2012 and 11 February 2012.

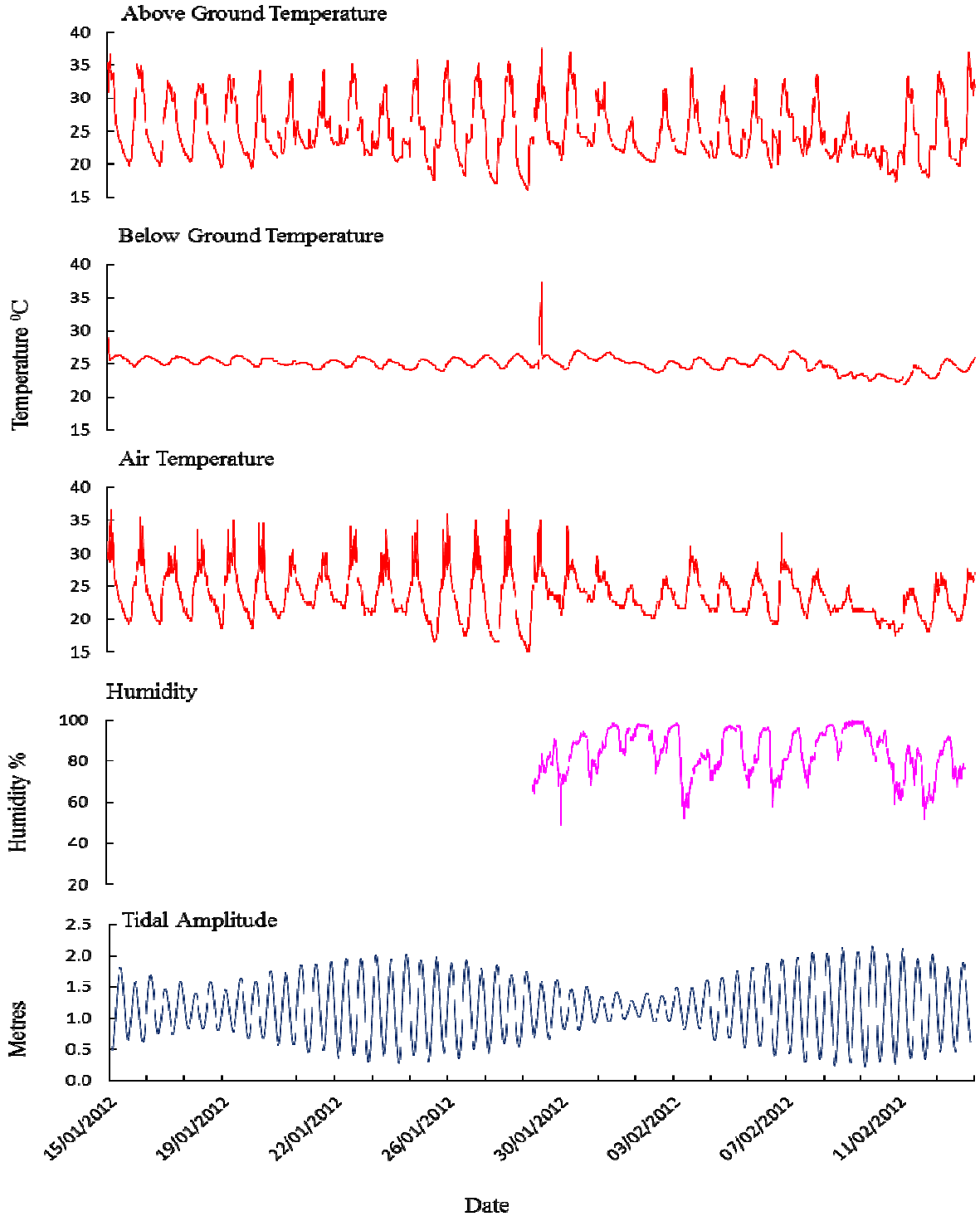

Figure 1.4: Temperature, humidity and tidal profile for the open areas within the *Rhizophora mucronata* zone at the Mngazana estuary mangal, which typically hosts *Uca urvillei*. The profile was recorded between 15 January 2012 and 11 February 2012.

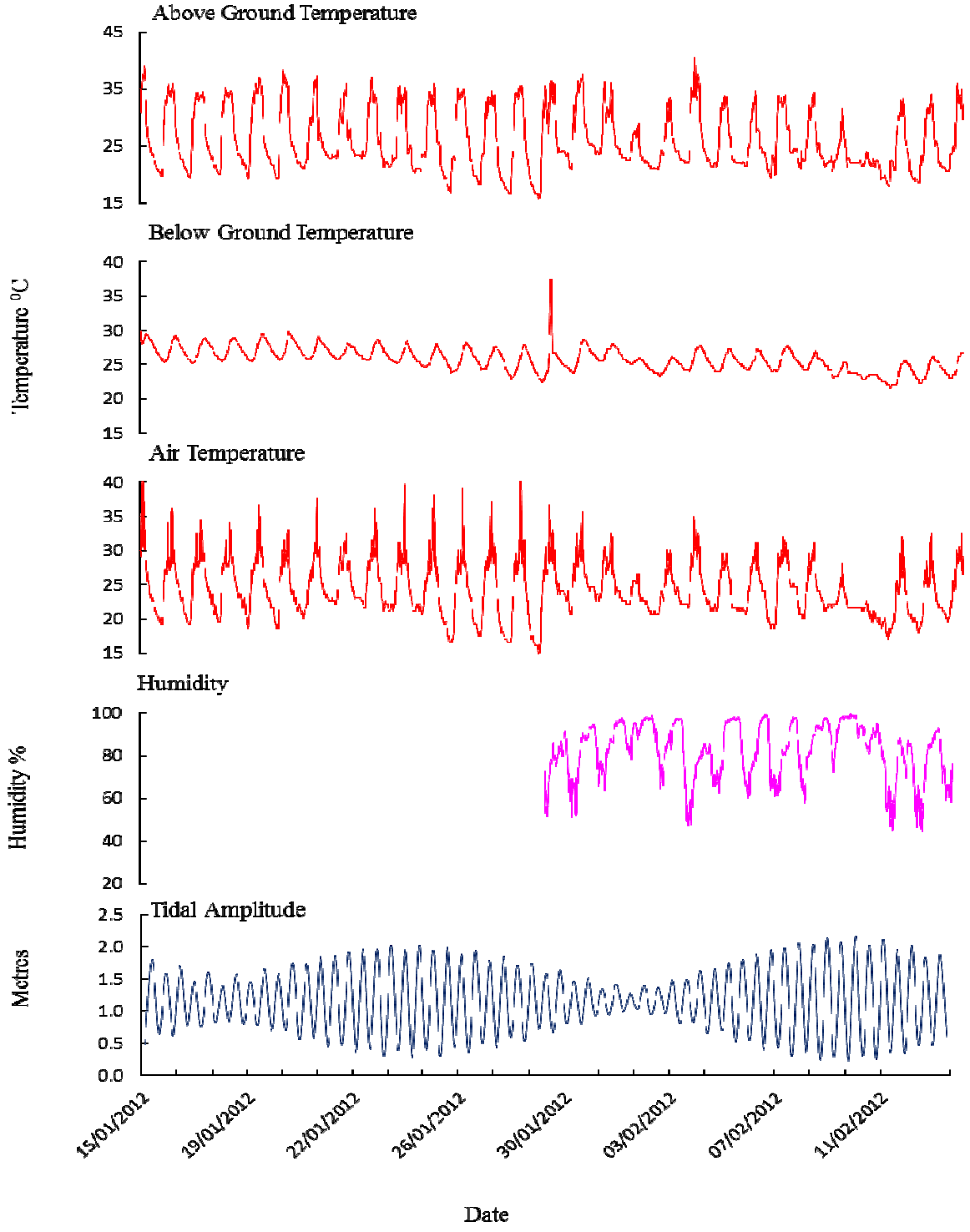

Figure 1.5: Temperature, humidity and tidal profile for the upper intertidal zone at the Mngazana estuary mangal, which typically hosts *Neosarmatium africanum.* The profile was recorded between 15 January 2012 and 11 February 2012.

CHAPTER 2

THERMAL SENSITIVITY AT THE CENTRE AND EDGE OF DISTRIBUTION RANGE: VULNERABILITY OF MANGAL MACROFAUNA TO GLOBAL CLIMATE CHANGE

2.1 Introduction:

Anthropogenically induced climate change significantly alters the physical and chemical aspects of ecosystems worldwide, affecting their functioning and structure (Walther *et al.* 2002, Deutsch *et al.* 2008, Hoegh-Guldberg and Bruno 2010, Doney *et al.* 2012). These changes have large scale biological effects such as driving pole-wards shifts in species distributions, varying population sizes and growth rates and restructuring community diversity and interactions (Somero 2010, Sunday *et al.* 2012). On a smaller scale, localised effects include, but are not limited to, variations in reproduction, foraging, inter- and intra-specific interactions, morphology, behaviour and physiology (Harley *et al.* 2006, Helmuth *et al.* 2006, Pörtner 2010).

While global climate change is recognised as an overarching process, its effects are not uniform on all ecosystems (IPCC 2014a, b, c, d). For example, in Africa, temperature increase at high latitudes is expected to be greater compared to increases at tropical latitudes (Deutsch *et al.* 2008, Dillon *et al.* 2010). Furthermore, while warming is expected in both terrestrial and marine

environments it will occur to different degrees in the two milieus (Deutsch *et al.* 2008, Dillon *et al.* 2010). Intertidal communities are particularly vulnerable to climate change as organismal fitness is significantly decreased by acute or episodic temperature changes that exceed an organism's thermal window (Hawkins *et al.* 2008, Cheung *et al.* 2009). Intertidal systems are further stressed, as the species within inhabit a narrow transition area between the marine and terrestrial environments and are thus affected by the complex interactions of a multitude of chemical and physical stressors (Alongi 2008, Nagelkerken 2008).

Oxygen and capacity limitation of thermal tolerance (OCLTT) has been suggested as a unifying principle to explain the sensitivity of terrestrial and aquatic ectotherms to thermal stress. Under this principle, the ability of an organism to extract oxygen from the environment and efficiently deliver it to its tissues is one of the key determinants of its thermal tolerance (Frederich and Pörtner 2000, Pörtner 2001, 2002, 2010, Mark *et al.* 2002, Melzner *et al.* 2006, Wittmann *et al.* 2008). During short or long term thermal stress at the high and low limits of the thermal window, responses in the respiration and circulatory systems fulfil the increased oxygen demands, however, when they can no longer cope with the increased demand, the organism's thermal tolerance is constrained by the onset of hypoxemia. Major thermal stress induces protective metabolic pathways such as the production of heat shock proteins (Morimoto *et al.* 1994, Hartl and Hayer-Hartl 2002, Hamdoun and Epel 2007), but eventually tissue anaerobiosis sets in compromising recovery and ultimately survival.

OCLTT predicts that the effects of thermal stress are alleviated by an increased supply of oxygen either by optimisation of respiratory mechanisms or by an increased supply from the environment, thus widening the thermal tolerance window. For example, the green crab *Carcinus maenas* exploits haemocyanin-bound oxygen reserves to alleviate thermal stress and widen its thermal tolerance window (Pörtner and Giomi 2013), while work on the Antarctic eelpout *Pachycara brachycephalum* demonstrated that hyperoxic water mitigates temperature induced loss of performance, allowing survival at higher temperatures compared to individuals exposed to normal oxygen conditions (Mark *et al.* 2002).

Oxygen is vastly more available in air than water and has a greater diffusiveness; breathing air conveys a distinct advantage to bimodal breathing organisms approaching their upper or lower thermal windows, allowing them to reduce the cost of respiration and extend their thermal tolerance (Pörtner 2001, 2010, Verberk *et al.* 2011, Giomi *et al.* 2014). This translates into an advantage when the organism's respiratory apparatus is optimised to extract oxygen from air (Farrelly and Greenaway 1994, Morris 2002, Giomi *et al.* 2014). Embryos also display the ability to exploit oxygen uptake from air and water (Cannicci *et al.* 2011, Simoni *et al.* 2011, Simoni *et al.* 2013), although brooding behaviour of brachyurans limits the supply of oxygen to eggs at the centre of the egg clutch and requires the female to undertake behaviours that adequately ventilate the brood mass (Woods 1999, Fernández *et al.* 2000, Fernández and Brante 2003).

The exploitation of both aquatic and aerial media for oxygen provision (bimodal breathing) has been documented in a variety of vertebrate and invertebrate phyla. Among vertebrates, the most extensive examples occur in fish with approximately 400 species relying on aquatic and aerial

media for oxygen provision to differing extents (Sayer and Davenport 1991, Brainerd 1994, Graham 1997, Aguilar *et al.* 2000, Ishimatsu *et al.* 2007), while among invertebrates, multiple taxa display bimodal breathing (e.g. Molluscs; Innes *et al.* 1984, Dye 1987, Fratini *et al.* 2001 and Annelids; Mill 1996). Crustacea have been particularly successful in utilising bimodal breathing to inhabit the aquatic-terrestrial boundary in marine and fresh water environments of temperate and tropical regions (Innes and Taylor 1986, Hartnoll 1988, Henry 1994, Cannicci *et al.* 1996, Gillikin and Schubart 2004, Schubart *et al.* 2006).

True crabs (Decapoda; Brachyura) are at the beginning of their terrestrial transition and have evolved a variety of novel and modified breathing, osmoregulatory and excretory pathways that enable them to take advantage of the terrestrial environment (Little 1983, 1990, Dejours 1988, Burggren 1992, Henry 1994, Weihrauch *et al.* 2004). Novel respiratory adaptations include gill sclerotisation, to prevent the collapse of the respiratory epithelia or the use of gill chambers as lungs (Farrelly and Greenaway 1994, Morris 2002, Giomi *et al.* 2014), while a shift from ammonia to uric acid in nitrogen excretion has proved pivotal in the terrestrialisation process (Bliss 1968, Burggren and McMahon 1988, Henry 1994). All extant marine brachyuran families, with terrestrial and semi-terrestrial species, have examples inhabiting mangals (Hartnoll 1988, Schubart *et al.* 2006) which exploit intertidal, supratidal and even arboreal habitats (Hartnoll 1975, Jones 1984, Dahdouh-Guebas *et al.* 2002, Fratini *et al.* 2005). Further, facilitating expansion into terrestrial environments have been adaptations to feeding behaviours (Cannicci *et al*. 1996, Erickson *et al*. 2003, 2004) and sensory systems (Cannicci *et al.* 2002, Zeil and Hemmi 2006).

Whilst adults are able to exploit the terrestrial environment to varying extents, reproductive aspects restrict true terrestrialisation and firmly tie the Brachyura to the aquatic environment (Anger 1995, Simoni *et al.* 2011). Females typically brood their eggs between the abdomen and carapace where they are fixed to pleopods by filaments until hatching (Fernández *et al.* 2002). This allows the female to protect, clean and maintain the embryos, but at the same time incurs metabolic costs (Bauer 1989, Fernández *et al.* 2000, Ruiz-Tagle *et al.* 2002, Fernández and Brante 2003). As it stands, fairly little is known about the biology of mangal brachyuran embryos (Cannicci *et al.* 2011), with information recently being published on a limited number of species (e.g. Simoni *et al.* 2011, Simoni *et al.* 2013). Although embryos of different species demonstrate varying degrees of terrestrialisation themselves, most still require water for the removal of metabolic waste and the facilitation of oxygen diffusion across the embryonic membrane (Cannicci *et al.* 2011, Simoni *et al.* 2011, Simoni *et al.* 2013), needs that are fulfilled by the ovigerous females. This necessity implicates a behavioural adjustment of both females and embryos into a bimodal breathing lifestyle, having to extract oxygen from air and water. Several East African mangrove Sesarmid species regularly perform such behaviour e.g. *Perisesarma samawati*, *Chiromantes ortmanni*, *Chiromantes eulimene Parasesarma leptosoma* and *Selatium elongatum* (Simoni *et al.* 2011, Cannicci *et al.* 2011, Simoni *et al.* 2013). Once hatched, larval development occurs predominantly in the aquatic environment further enforcing the aquatic ties in Brachyura (Anger 1995).

OCLTT has further been verified in crustacean larvae (e.g. Storch *et al.* 2009), as well as in small zooplankton (e.g. Seidl *et al.* 2005), and results obtained in the laboratory often effectively support the application of this theory to natural scenarios (Frederich and Pörtner 2000, Pörtner

2001, Mark *et al.* 2002, Melzner *et al.* 2006, Wittmann *et al.* 2008). Only recently has this principle been focused on bimodal breathing organisms (e.g. Giomi *et al.* 2014, Giomi *et al.* in press) and to a limited degree been explored over a latitudinal gradient using adults of conspecific species (Fusi *et al.* 2014). Additionally, this principle has not been applied to brooding bimodal breathing organisms where a mismatch in thermal tolerance between mother and embryo may have critical outcomes especially with the increasing temperatures associated with global climate change.

To verify the vulnerability of mangal crabs to climate change, I investigated the physiology of two intertidal crabs (*Perisesarma guttatum* and *Uca urvillei*) at the centre (Kenya) and edge (South Africa) of their distributions along East Africa. Specifically, I propose that ontogenetic life stages (females with and without eggs, 2^{nd} and 4^{th} stage embryos and larvae) at the centre of their distribution will experience greater physiological stress and to be more adversely affected by changing temperatures (shown by elevated oxygen consumption at higher temperatures) than at the edge of their distirbution. Furthermore, I propose temperate conspecifics will still be affected by increasing temperatures associated with climate change. However, the elevation in oxygen consumption rates associated with increasing temperatures will be lower than their tropical counterparts. Interspecies variability in oxygen consumption was also compared for these ontogenetic life stages at each locality using *Perisesarma guttatum* and *Uca urvillei* in Kenya and *Perisesarma guttatum*, *Uca urvillei* and *Neosarmatium africanum* in South Africa. The effect of brooding eggs on female physiology, hereafter termed maternal costs (MC), was also investigated over the same latitudinal scale.

2.2 Methods:

These experiments were conducted in two different countries at different times during the study on mangal brachyurans. As such, different oxygen consumption meters were used due to availability. Unfortunately, oxygen consumption meters were not available in each locality at the same time to perform baseline studies to confirm that the meters and methods produced comparable data. However, non-significant differences between Kenya and South Africa obtained at ambient temperature (27°C) using different VO_2 meters and methods verify that these results were in fact comparable. All oxygen meters used had built in temperature compensation software to adjust for dissolved oxygen available in water at different temperatures.

2.2.1 Oxygen consumption by larvae:

Gravid female *Perisesarma guttatum* and *Uca urvillei* were collected in Kenya and South Africa and additional gravid *Neosarmatium africanum* were collected in South Africa. For each species, embryonic stage of gravid females were assessed and females brooding 5^{th} stage eggs were placed in separate plastic containers containing rocks and aerated seawater. Females were typically kept in these holding tanks for 1-2 days before hatched larvae were released in to the water. Larvae of each species were then collected using a pipette and placed in separate temperature controlled holding tanks with aerated seawater set at 27°C. Two different techniques were used to measure oxygen consumption of larvae in South Africa and Kenya due to oxygen meter availability.

In South Africa, for each species, between 50 and 100 larvae were placed in a 2ml mass spectrometer vial filled with recently aerated seawater with an oxygen sensor spot glued to the inner wall, the vial was then sealed. A Fibre-optic oxygen meter (Fibox 3 with oxygen Micro-optode Type PSt3 PreSens, Regensburg, Germany), calibrated in air-equilibrated seawater (100%) and saturated sodium thiocyanate solution (0%) was used to measure the collective oxygen consumption of the larvae at 27°C. Measurements were taken until at least a decrease of 5% oxygen saturation was detected and it was ensured that the oxygen saturation never fell below 60% oxygen saturation, this period of time was approximately 1 hour. Larval movement was adequate to mix the water inside the chambers, allowing the linear recording of oxygen decline over time. This procedure was repeated between 10 and 20 times at each experimental temperature and new larvae were used for each trial. A control vial, filled with seawater, was used to quantify background oxygen changes, and oxygen consumption rates were adjusted accordingly. Once the experimental procedure was complete, the larvae were removed from the vials and placed in 5ml Eppendorf vials containing 70% ethanol for further measurements. The same experimental procedure was repeated along an increasing and decreasing temperature ramp whereby consumption rates were measured at each of the temperatures; 27°C /29°C /31°C /33°C /35°C and 25°C /23°C /21°C /19°C respectively. After each measurement the temperature of the holding tanks was altered accordingly along the stepwise ramps at a rate of $1°C \times h^{-1}$ until the next experimental temperature was reached and the measurement procedure repeated.

In Kenya, for each species, between 10 and 25 larvae were placed in a custom made 0.5 ml glass vial filled with recently aerated seawater. A glass electrode oxygen meter (Unisense with glass electrode, Regensburg, Germany), calibrated in air-equilibrated seawater (100%) and saturated

sodium thiocyanate solution (0%) was used to measure oxygen consumption of the larvae at 27°C. Measurements were taken until at least a 5% decrease of oxygen ($\mu mol*l^{-1}$) was detected. Larval movement within the chambers was adequate to mix the water inside the chambers, allowing the linear recording of oxygen decline over time. A control vial was used to quantify the background oxygen consumption, and oxygen consumption rates were adjusted accordingly. Once the experimental procedure was complete, larvae were removed from the vials and placed in Eppendorf vials containing 70% ethanol for further measurements. The experiments were run along a temperature ramp as above.

Overall, for each species, a minimum of 10 replicates were measured at each temperature in both South Africa and Kenya. As average oxygen consumption was measured for several larvae, accounting for body mass of individual larvae and their effects on metabolic rate was not possible. Therefore, the larvae in each vial were counted and the oxygen consumption rates were standardised to $nmol*larvae^{-1}*hr^{-1}$.

2.2.2 Oxygen consumption of stage 2 and stage 4 embryos:

Gravid female *Perisesarma guttatum* and *Uca urvillei* were collected in Kenya and South Africa. Gravid *Neosarmatium africanum* were only collected in South Africa. For each species, embryonic stage of gravid females were assessed and females brooding 2nd and 4th stage embryos were placed in temperature controlled holding tanks set at 27°C, with either a layer of moist sand or filled aerated seawater. Gravid females were kept under these conditions throughout the experimental procedure. Three different techniques were used to measure oxygen consumption

of 2nd and 4th stage embryos in both air and water for South Africa and Kenya due to oxygen meter availability.

In Kenya, only for oxygen consumption rates in water, between 100 and 500 eggs from a single brooding female were removed from the female's pleopods and immediately placed in a custom made 0.5 ml glass vial filled with recently aerated seawater. The Unisense glass electrode oxygen meter was used following the procedure described above to measure oxygen consumption of larvae. Once the experimental procedure was complete, eggs were removed from the vials and placed in 5 ml Eppendorf vials containing 70% ethanol for further measurements. A control vial filled only with aerated seawater was used to quantify background oxygen consumption, and oxygen consumption rates were adjusted accordingly.

In both Kenya and South Africa, to measure oxygen consumption rates in air and water, between 20 and 100 eggs were removed from a single brooding female and placed in Hamilton syringes set at 100µl. For experiments conducted in water, the syringes were filled with recently aerated seawater prior to the addition of eggs and sealed.For experiments in air, eggs were placed in the syringe and sealed. Fiber-optic oxygen microsensors (NTH-PSt1-L5lTF-PC3,1-NS 35x1,20-YOP, PreSens GmbH, 93053 Regensburg, Germany) combined with a TX2-A oxygen meter (PreSens) with integrated signal processing software were used to measure oxygen consumption of the eggs at 27°C. Prior to each experiment, optodes were calibrated in oxygen-free (solution of seawater and sodium dithionite) and air-saturated (bubbled) seawater. For water experiments, syringes were repeatedly manually inverted to ensure the eggs moved through the water column creating suitable mixing allowing the linear recording of the oxygen decline over time. A control

syringe was used to quantify the background oxygen consumption, and oxygen consumption rates were adjusted accordingly. Once the experimental procedure was complete, the eggs were removed from the syringes and placed in Eppendorf vials containing 70% ethanol for further processing.

In South Africa only, to measure oxygen consumption in air and water, between 100 and 500 eggs from a single brooding female were placed in 2ml mass spectrometer vials with oxygen sensor spots glued to the inner wall. For air experiments the vial was filled with either air while for water experiments the vial was filled with recently aerated seawater and was then sealed. Oxygen consumption rates were measured using the Fibox 3 oxygen meter as described above in the measurement of oxygen consumption by larvae.

All experimental procedures were repeated along an increasing and decreasing temperature ramp of 27°C /29°C /31°C /33°C /35°C and 25°C /23°C /21°C /19°C respectively. The temperatures of the gravid female holding tanks were altered accordingly along the stepwise ramps at a rate of $1°C \times h^{-1}$. For each species, a minimum of 8 replicates were measured at each temperature for each egg stage in both Kenya and South Africa. Experiments at each temperature typically lasted between one to two hours. As average oxygen consumption was measured for several eggs, accounting for body mass of individual eggs and their effects on metabolic rate was not possible. Lastly, the number of eggs were counted and the oxygen consumption rates was standardised to $nmol*larvae^{-1}*hr^{-1}$.

2.2.3 Oxygen consumption of gravid and non-gravid females:

In Kenya and South Africa gravid (fo) and non-gravid (f) female *Perisesarma guttatum* and *Uca urvillei* were collected and kept in plastic containers tilted to one side and partially filled with mangrove mud and fresh aerated seawater. Females of the same size range were collected in Kenya and South Africa. Further gravid and non-gravid *Neosarmatium africanum* were collected in South Africa only. Embryonic stage of gravid females was assessed prior to the experimental setup, only females brooding 4^{th} stage eggs were used for the experiment. Crabs were kept unfed for at least 24 hours before experimental setup. A single crab was then placed in each of nine custom-made intermittent flow Perspex chambers (0.5 litres) while a tenth chamber remained empty/or filled with water (depending on the medium tested) as a control. For aerial experiments, chambers containing crabs were closed and connected to air pumps to ensure a constant supply of oxygen. For aquatic experiments, chambers were filled with seawater and connected to circulation pumps from temperature controlled aerated seawater holding tanks. The chambers were of relatively low volume limiting the available space for the crabs to move. These chambers were then covered with aluminium foil to minimise visual stress, ensuring therefore a rest state of the specimens tested (Giomi *et al.* 2014, Fusi *et al.* 2014), and submerged in a water bath set at 27°C and left to settle for eight hours to reduce possible effects of handling stress.

After this acclimation period, the chambers were completely sealed by cutting off the supply of air or aerated seawater from the circulation pumps. An oxygen sensor spot glued to the inner wall of the chamber and a Fibox 3 Fibre-optic oxygen meter was used to measure oxygen consumption as described above. The movements of the crabs were adequate to mix the water inside the chambers allowing the linear recording of oxygen decline over time for experiments

conducted in water. Thereafter, the flow of either air or aerated seawater was returned to the chamber and the same experimental procedure was repeated along an increasing or decreasing temperature ramp of 27°C /29°C /31°C /33°C /35°C and 25°C /23°C /21°C /19°C. The temperature was altered along the stepwise ramps at a rate of 1°C × h^{-1}. Fresh gravid (fo) and non-gravid (f) crabs were used for each of the increasing and decreasing temperature ramps, with each individual being used for only one experiment (once, either increasing or decreasing ramp). The control chamber was used to quantify the background oxygen consumption, which was routinely less than 2-3% of the consumption recorded in water, and negligible in air in all cases. Following each experiment, the eggs from the brooding females were removed from the pleopods and stored in 70% ethanol for further measurements and the animal wet weight and volume were measured and recorded.

The clutch of removed eggs were separated from the pleopods and the number of eggs in each clutch counted. Oxygen consumption of each egg clutch was calculated by extrapolating from the consumption of a single stage 4 egg as calculated in the experiments for egg respiration described above to the entire clutch (C) by multiplying the number of eggs per clutch by the rate of a single stage 4 egg at the given experimental temperature. The oxygen consumption rates of gravid females (with clutches) were then adjusted by subtracting the calculated rate of the clutch (C) from the rate of gravid females (fo-C) giving just the rate for the adjusted gravid female ($fo_{(adjusted)}$). These rates were standardised to micromole oxygen consumed per gram of animal per minute ($\mu mol*g^{-1}*min^{-1}$) and used for the statistical analysis.

$fo_{(adjusted)} = fo - C$

2.2.4 Maternal Cost:

The cost of brooding eggs, maternal costs (MC), was calculated by subtracting non-gravid female (f) rates from adjusted gravid female rates as calculated above (fo – C);

MC = (fo – C) – f

2.3 Statistical Analysis:

2.3.1 Oxygen consumption of larvae:

As the oxygen consumption rates at 27°C for *Uca urvillei* larvae were abnormally high, indicating an error in the measurement of oxygen consumption at this temperature, the data point was excluded from the analysis. The possible effects of a 3-way interaction the factors "Region" (2 levels), "Species" (2 levels) and "Temperature" (8 or 9 levels depending on the species) on the oxygen consumption of the two species of brachyuran larvae (*Perisesarma guttatum* and *Uca urvillei*) were analysed with the Permutational Multivariate Analysis of Variance (PERMANOVA) add-on in PRIMER 6. As new groups of larvae were used in each experiment it was not possible to use a repeated measures design (Anderson *et al.* 2008). For this and all ensuing analyses, distance-based tests for homogeneity of multivariate dispersions (PERMDISP) were used to check for homogeneity within each factor. Unless otherwise stated, factors were fixed and orthogonal and variances were heterogeneous as there were no suitable transformations (PERMDISP, $P < 0.05$, untransformed data). All analyses were conducted on Euclidean distance matrices. Post hoc pairwise tests were performed when appropriate and all data are expressed as mean + standard error.

Oxygen consumption of a third species, *Neosarmatium africanum*, was considered in South Africa. 2-way PERMANOVA analyses testing the effects of the factors "Species" (3 levels) and "Temperature" (9 levels) were conducted for oxygen consumption of *Perisesarma guttatum, Uca urvillei* and *Neosarmatium africanum* larvae.

2.3.2 Oxygen Consumption of stage 2 and stage 4 embryos:

As new clutches of embryos were used in each experiment it was not possible to use a repeated measures design (Anderson *et al.* 2008). The possible effects of the factors "Region" (2 levels), "Species" (2 levels), "Temperature" (9 levels) and "Milieu" (Air vs water, 2 levels) on the oxygen consumption of stage 2 and stage 4 *Perisesarma guttatum* and *Uca urvillei* embryos were analysed separately, through a 4-way design, with the PERMANOVA add-on in PRIMER 6.

Again a third species, *Neosarmatium africanum*, was considered in South Africa. 3-way analyses, testing the effects of the factors "Species" (3 levels), "Temperature" (9 levels) and "Milieu" (2 levels) were conducted for oxygen consumption of stage 2 and Stage 4 *Perisesarma guttatum, Uca urvillei* and *Neosarmatium africanum* embryos.

2.3.3 Oxygen Consumption of gravid and non-gravid females:

As analyses comparing species yielded uninformative statistical results, species were analysed separately (Statistical tables comparing species are included in appendix 6.1). As the experimental crabs used to determine oxygen consumption were the same along one temperature ramp (either increasing or decreasing) during a single experiment, but different for each

combination of gravid/non-gravid (f/fo) and milieu (air/water), a repeated measures PERMANOVA 4-way design (Anderson *et al.* 2008) was used to test for the possible effects of the factors "Region" (2 levels), "Gravid/Non Gravid" (2 levels), "Milieu" (2 levels) and "Temperature" (9 levels in South Africa, 5 levels in Kenya). Experimental design was limited to 5 levels in Kenya as the decreasing temperature experiments could not be conducted due to time limitations during data collection.

2.3.4 Maternal Costs:

As analyses comparing species yielded uninformative statistical results species were analysed separately (Statistical tables comparing species are included in appendix 6.2). As the crabs used to determine the maternal costs along a temperature gradient were the same as those used to determine differences in oxygen consumption along the same temperature ramp, a repeated measures PERMANOVA 3-way design was used to test for the possible effects of the factors "Region" (2 levels), "Milieu" (2 levels) and "Temperature" (9 levels). Variances were homogeneous for "Region" and "Species" (PERMDISP, $P > 0.05$, untransformed data).

2.4 Results:

The interpretations of the results in this chapter are complex as most interactions in the ensuing analyses were significant. In the following section, probability levels refer to the results of Pairwise tests at an alpha level of 0.05 unless otherwise stated.

2.4.1 Perisesarma guttatum and *Uca urvillei* larvae in South Africa and Kenya:

Interactions among the factors Region, Species and Temperature had significant effects on the oxygen consumption rates of larvae compared between South Africa and Kenya (Table 2.1). Intraspecifically, the oxygen consumption of *Perisesarma guttatum* larvae differed significantly between regions at higher temperatures (27°C, 29°C, 31°C, 33°C 35°C) and at 23°C, where generally larvae from South Africa had greater rates than larvae from the Kenyan population (Figure 2.1A). Oxygen consumption rates at all temperatures, within *P. guttatum* and within country, were compared with one another giving 36 possible comparisons. Within South Africa there was fairly high variability between rates at different temperatures (26 significant differences of the possible 36 comparisons), while in Kenya there was less variability (6 significant differences of the possible 36 comparisons).

Uca urvillei consumption rates did not differ between South Africa and Kenya for comparisons at 19°C, 21°C, 23°C and 25°C (Pairwise test, $P > 0.05$). However, significantly greater rates were noted at 29°C, 31°C, 33°C and 35°C in South Africa than in Kenya (Figure 2.1B). Intraspecific and intraregional comparisons of *U. urvillei* within South Africa yielded a high variability along the experimental temperature range (19 significant differences of the possible 28 comparisons), while Kenya had low variability (8 significant differences of the possible 36 comparisons)

Within South Africa, oxygen consumption differed between the two species at 29°C, 31°C and 35°C (Figure 2.1A & B), where *Perisesarma guttatum* larvae had greater oxygen consumption

rates than *Uca urvillei*. In Kenya, rates only differed significantly between the two species at 23°C where *U. urvillei* had a higher rate than *P. guttatum* (Figure 2.1A & B).

Table 2.1: PERMANOVA on the oxygen consumption rates (nmol*larvae^{-1}*hr^{-1}) of *Perisesarma guttatum* and *Uca urvillei* larvae, comparing Kenya and South Africa. For this and following tables * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

		Oxygen Consumption Rate of larvae	
Source	d.f.	M.S.	Pseudo-*F*
Region = Re	1	1886.8	124.03***
Species = Sp	1	190.36	12.51***
Temperature = Temp	8	370.26	24.34***
Re x Sp	1	291.85	19.19***
Re x Temp	8	261.13	17.17***
Sp x Temp	8	417.76	52.22***
Re x Sp x Temp	7	41.13	2.70***
Residual	587	15.21	
Total	621		

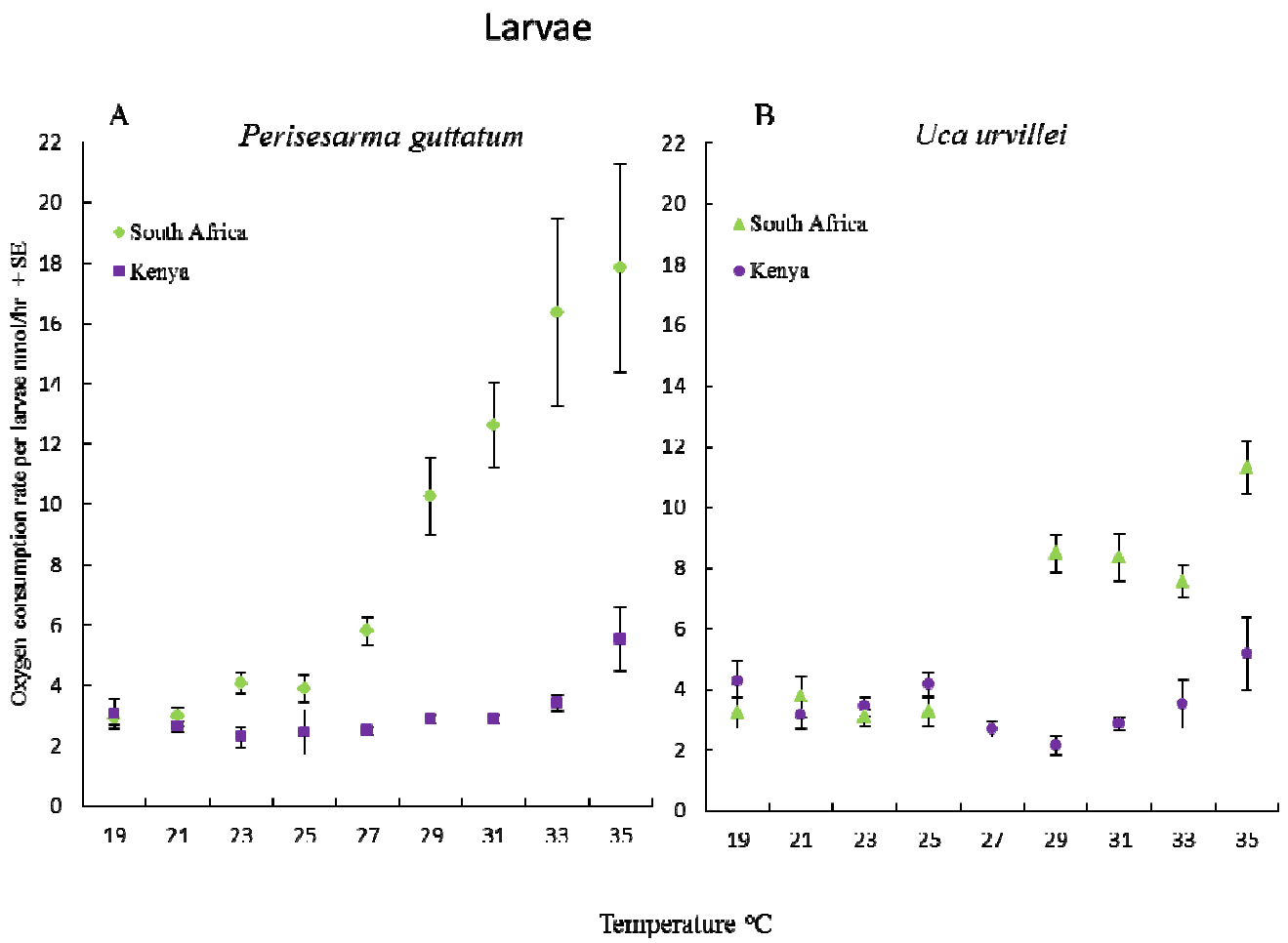

Figure 2.1: Average rates of oxygen consumption (nmol*larvae^{-1}*hr^{-1}) of (A) *Perisesarma guttatum* and (B) *Uca urvillei* larvae in South Africa and Kenya measured over a stepwise temperature ramp from 19°C to 35°C at 2°C intervals. All error bars represent standard errors (n = 10 – 30). The data point at 27°C for *U. urvillei* in South Africa was excluded due to an error during the measurement making this abnormally high.

2.4.2 Perisesarma guttatum, *Uca urvillei* and *Neosarmatium africanum* larvae in South Africa:

Within South Africa, an interaction of the factors Species and Temperature had significant effects on the oxygen consumption rates of larvae (Table 2.2). At 19ºC, 21ºC, 23ºC and 25ºC there was no difference in oxygen consumption among the three species (Figure 2.2). Thereafter, *Neosarmatium africanum* larvae consumed significantly less oxygen compared to *Perisesarma guttatum* and *Uca urvillei* (Figure 2.2) except for the comparison of *N. africanum* and *U. urvillei* at 33ºC (Figure 2.2). *P. guttatum* larvae had greater consumption rates than those of *U. urvillei* larvae between 29ºC and 35ºC; although these differences were only significant at 31ºC and 33ºC. Intraspecific comparisons of *U. urvillei* larvae yielded significantly different oxygen consumption rates for 19 of the 28 possible comparisons over the temperature range, while *P. guttatum* and *N. africanum* larvae had significantly different oxygen consumption rates for 26 and 14 of the 36 possible comparisons respectively.

2.4.3 Larvae Summary:

Differences between regions and species were generally evident at temperature greater than 27ºC, where South African larvae had greater oxygen consumption rates and were typical for both species. In Kenya, there was generally no difference between the two species while in South Africa differences among the three species were evident at higher temperatures. In Kenya, there was little variability in oxygen consumption rates with increasing temperature while in South Africa there was generally more variability with increasing temperatures.

Table 2.2: PERMANOVA tables on rates of oxygen consumption (nmol*larvae^{-1}*hr^{-1}) of *Neosarmatium africanum*, *Perisesarma guttatum* and *Uca urvillei* larvae in South Africa.

Oxygen consumption Rate			
Source	d.f.	M.S.	Pseudo-*F*
Species = Sp	2	683.82	30.90***
Temperature = Temp	8	517.71	23.39***
Sp x Temp	15	79.13	3.57***
Residual	350	22.13	
Total	375		

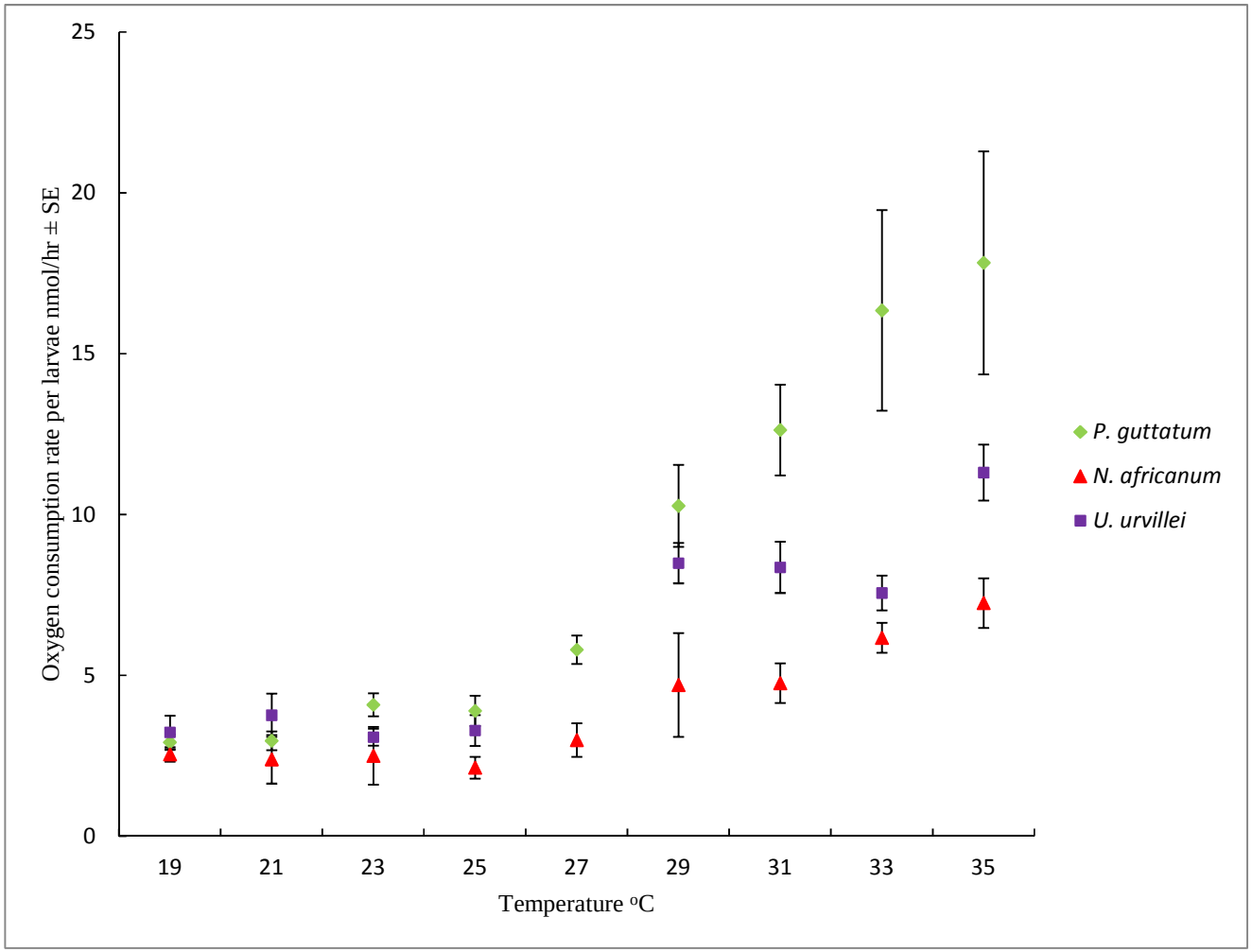

Figure 2.2: Average rates of oxygen consumption (nmol*larvae^{-1}*hr^{-1}) of *Neosarmatium africanum*, *Perisesarma guttatum* and *Uca urvillei* larvae in South Africa over a stepwise temperature ramp from 19ºC to 35ºC at 2ºC intervals. All error bars represent standard errors (n = 10 – 30).The data point at 27^{o}C for *U. urvillei* was excluded due to an error during the measurement making this abnormally high.

2.4.4 Perisesarma guttatum and *Uca urvillei* stage 2 embryos in South Africa and Kenya:

Significant interactions of the factors Species, Region, Air/Water and Temperature affected the rates of oxygen consumption of stage 2 embryos (Table 2.3). Between regions, oxygen consumption rates of *Perisesarma guttatum* embryos in air only differed significantly at 23ºC, with greater oxygen consumption rates recorded in embryos from South Africa than Kenya (Figure 2.3A). In general, oxygen consumption rates in air were greater in South Africa than Kenya, except for non-significant differences at 29ºC and 35 ºC (Figure 2.3A). *P. guttatum* stage 2 embryos in water exhibited significant differences in oxygen consumption between regions at all experimental temperatures except 19ºC, 23ºC and 25ºC. Rates were higher in Kenya than in South Africa between 19ºC and 25ºC while the trend reversed at 27ºC, where rates were greater in South Africa than in Kenya (Figure 2.3C).

Oxygen consumption rates of stage 2 embryos of *Uca urvillei* in air were significantly different between South Africa and Kenya at all but 2 experimental temperatures (19ºC and 27ºC). Rates of consumption were higher in South Africa at all temperature except 27ºC (Figure 2.3B). In water, there were no significant differences in rates of consumption between regions at 19ºC and 25ºC and Kenyan embryos had greater oxygen consumption rates than South African ones from 19ºC to 25ºC.Thereafter the oxygen consumption rates of South African embryos were greater than Kenyan stage 2 embryos (Figure 2.3D).

In South Africa, consumption rates of stage 2 embryos of *Perisesarma guttatum* did not differ between air and water at the lower temperatures of 19ºC, 21ºC and 23ºC, while the higher

experimental temperatures produced significantly different rates. In all cases except at 25ºC, consumption rates in water were greater than air (Figure 2.3A & C). In Kenya, rates were significantly different at all temperatures except at 19ºC and embryos in water consumed more oxygen than those in air in all cases (Figure 2.3A & C).

In South Africa, stage 2 embryos of *Uca urvillei* had significantly different oxygen consumption rates between air and water at 19ºC and between 27ºC and 35ºC. These rates were higher in water than in air except at 21ºC and 23ºC (Figure 2.3B & D). In Kenya, *U. urvillei* stage 2 embryos oxygen consumption rates were significantly higher in water than in air at all experimental temperatures (Figure 2.3B & D).

In South Africa, aerial oxygen consumption of stage 2 embryos did not differ between the two species. In water, however, rates of oxygen consumption significantly differed between the two species at 27ºC, 29ºC, 31ºC and 33ºC where *Perisesarma guttatum* had greater consumption rates than *Uca urvillei* (Figure 2.3C & D). Within Kenya, *P. guttatum* and *U. urvillei* largely showed no differences in oxygen consumption rates in air or water, with exceptions occurring at 29ºC in air and 33ºC and 35ºC in water.

Oxygen consumption rates of *Perisesarma guttatum* differed significantly among temperatures less often in air than water in both South Africa and Kenya, with 8 and 10 of 36 possible comparisons in air and 23 and 15 of 36 possible comparisons in water for South Africa and Kenya respectively. Of the 36 comparisons in air, stage 2 embryos of *Uca urvillei* showed differences for 16 in South Africa and 10 in Kenya while in water there were more differences

between temperatures for South Africa with 23 of 36 but the same amount In Kenya with 10 of 36 possible comparisons.

Table 2.3: PERMANOVA of rates of oxygen consumption (nmol*egg^{-1}*hr^{-1}) of stage 2 *Perisesarma guttatum* and *Uca urvillei* eggs in Kenya and South Africa.

	Oxygen consumption Rate		
Source	d.f.	M.S.	Pseudo-*F*
Sp	1	5077500	47.27***
Re	1	33079000	307.92***
Air/Water	1	64020000	595.95***
Temp	8	8047400	74.91***
Sp x Re	1	812750	7.57**
Sp x Air/Water	1	2468700	22.98***
Sp x Temp	8	503460	4.69***
Re x Air/Water	1	17207000	160.18***
Re x Temp	8	4540300	42.27***
Air/Water x Temp	8	5546000	51.63***
Sp x Re x Air/Water	1	2669900	24.85***
Sp x Re x Temp	8	478420	4.45***
Sp x Air/Water x Temp	8	878020	8.17***
Re x Air/Water xTemp	8	4653000	43.31***
Sp x Re x Air/Water x Temp	8	805960	7.50***
Residual	945	107430	
Total	1016		

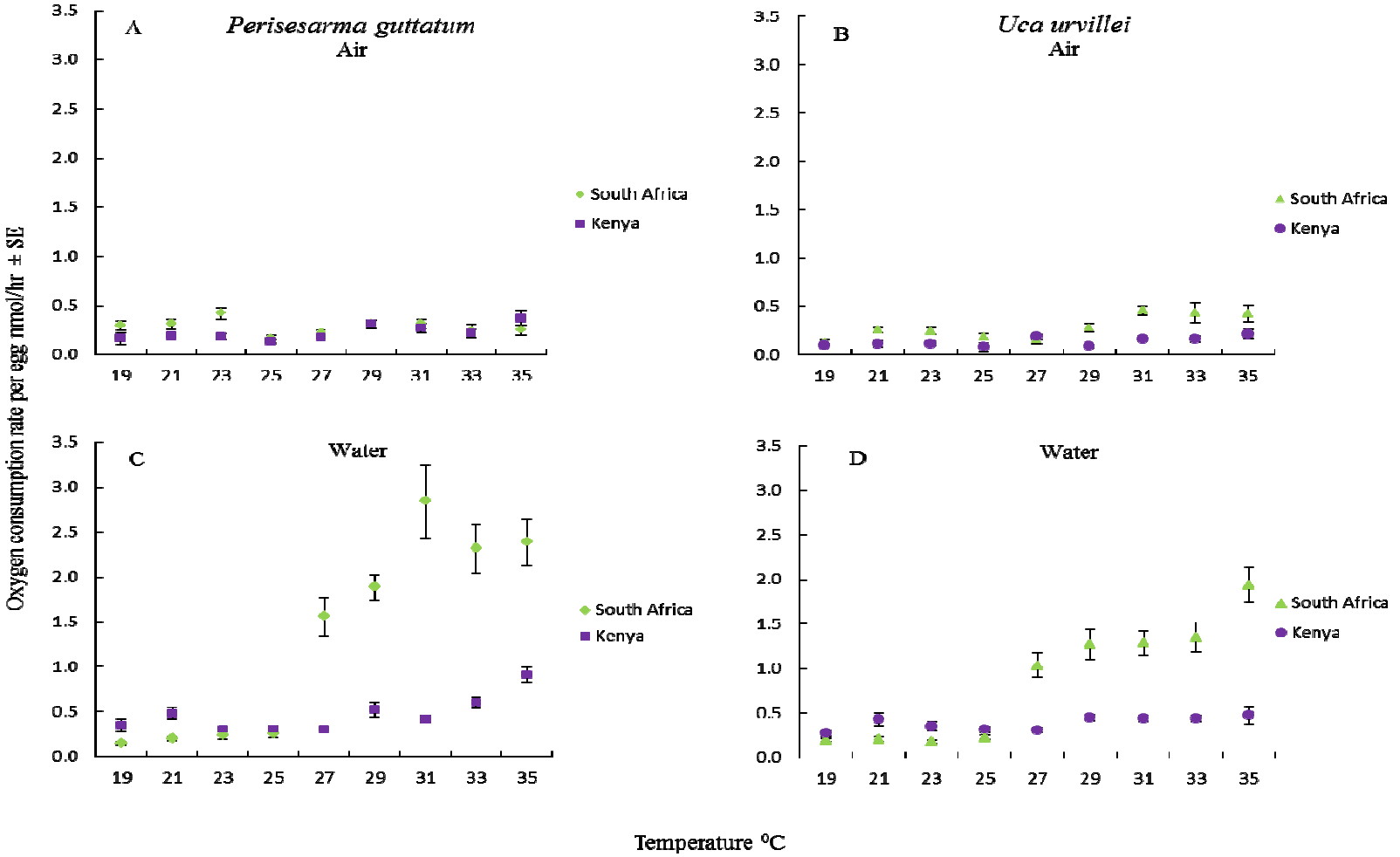

Figure 2.3: Average rates of oxygen consumption for stage 2 embryos (nmol*egg^{-1}*hr^{-1}) of (A) *Perisesarma guttatum* in air, (B) *Uca urvillei* in air, (C) *P. guttatum* in water and (D) *U. urvillei* in water in South Africa and Kenya measured over a stepwise temperature ramp from 19ºC to 35ºC at 2ºC intervals. All error bars represent standard errors (n = 5 – 15).

2.4.5 Perisesarma guttatum, Uca urvillei and *Neosarmatium africanum* stage 2 embryos in South Africa

Interactions among the factors Species, Air/Water and Temperature had significant effects on the oxygen consumption rates of stage 2 embryos in South Africa (Table 2.4). There were no differences in rates of oxygen consumption between stage 2 embryos of *Perisesarma guttatum* and *Uca urvillei* in air. *P. guttatum* generally had significantly lower oxygen consumption rates compared with *Neosarmatium africanum* (Figure 2.4A), as did *U. urvillei,* at low (19ºC and 23ºC) and mid-experimental (27ºC and 29ºC) temperatures (Figure 2.4A).

In water, *Perisesarma guttatum* stage 2 embryos had greater oxygen consumption rates than *Uca urvillei* at 27ºC, 29ºC, 31ºC and 33ºC (Figure 2.4B). Similarly, *P. guttatum* stage 2 embryos had significantly higher oxygen consumption than *Neosarmatium africanum* at almost all experimental temperatures (except 19ºC and 21ºC), with non-significant differences observed at 23ºC, 25ºC and 27ºC (Figure 2.4B). Significant differences of rates of oxygen consumption of stage 2 embryos of *N. africanum* and *U. urvillei* were noted at 21ºC, 23ºC, 31ºC 33ºC and 35ºC, with *U. urvillei*, showing greater rates of oxygen consumption than *N. africanum* at the higher experimental temperatures (Figure 2.4B). A possible switch respose with a large increase in oxygen consumption was detected between 25◦Cand 27◦C for all three species.

In South Africa, consumption rates of stage 2 embryos of *Perisesarma guttatum* were significantly different between air and water at all temperatures except 19ºC, 21ºC and 23ºC and consumption was generally greater in water except at 25ºC (Figure 2.4A & B). *Uca urvillei* exhibited significant differences between air and water at 19ºC and between 27ºC and 35ºC, in

all cases oxygen consumption was greater in water than air, except at 21ºC and 23ºC (Figure 2.4A & B). *Neosarmatium africanum* had significant differences in oxygen consumption rates between air and water at 23ºC, 29ºC and 33ºC (Figure 2.4), but no clear pattern emerged as to which temperature and milieu induced greater oxygen consumption rates (Figure 2.4A & B). Overall, significant intraspecific differences of oxygen consumption among temperature comparisons were scarcer in air compared with water; *P. guttatum* had 8 of 36 significant differences in air compared with 24 of 36 in water, *U. urvillei* and *N. africanum* each had 16 of 36 significant differences in air compared with 23 of 36 and 26 of 36 in water respectively.

2.4.6 Stage 2 embryo summary

Generally in air, *Perisesarma guttatum* had no significant differences in oxygen consumption between South Africa and Kenya at lower temperatures, while in water differences were evident across all temperatures. *P. guttatum* from South Africa generally had the highest consumption rates.

In both air and water oxygen consumption rates of *Uca urvillei* in South Africa were greater in South Africa than Kenya, except at lower temperatures in water.

Within Kenya, *P. guttatum* and *U. urvillei* largely showed no differences in oxygen consumption rates in air or water. In South Africa, differences between *U. urvillei* and *P. guttatum* were not evident in air, but both these species had lower rates than *Neosarmatium africanum*. In water, differences between *U. urvillei* and *P.guttatum* only became apparent at higher temperatures, but both these species generally had higher rates than *N. africanum.*

Table 2.4: PERMANOVA of rates of oxygen consumption (nmol*egg^{-1}*hr^{-1}) *Neosarmatium africanum, Perisesarma guttatum* and *Uca urvillei* for stage 2 embryos in South Africa.

Oxygen consumption Rate			
Source	d.f.	M.S.	Pseudo-*F*
Species = Sp	2	4.77E^{6}	11.28***
Air/Water	1	8.40E^{6}	19.87***
Temperature = Temp	8	1.24E^{7}	29.23***
Sp x Air/Water	2	5.53E^{6}	13.07***
Sp x Temp	16	1.36E^{6}	3.21***
Air/Water x Temp	8	2.21E^{6}	5.23***
Sp x Air/Water x Temp	16	9.23E^{5}	2.18**
Residual	665	4.23E^{5}	
Total	718		

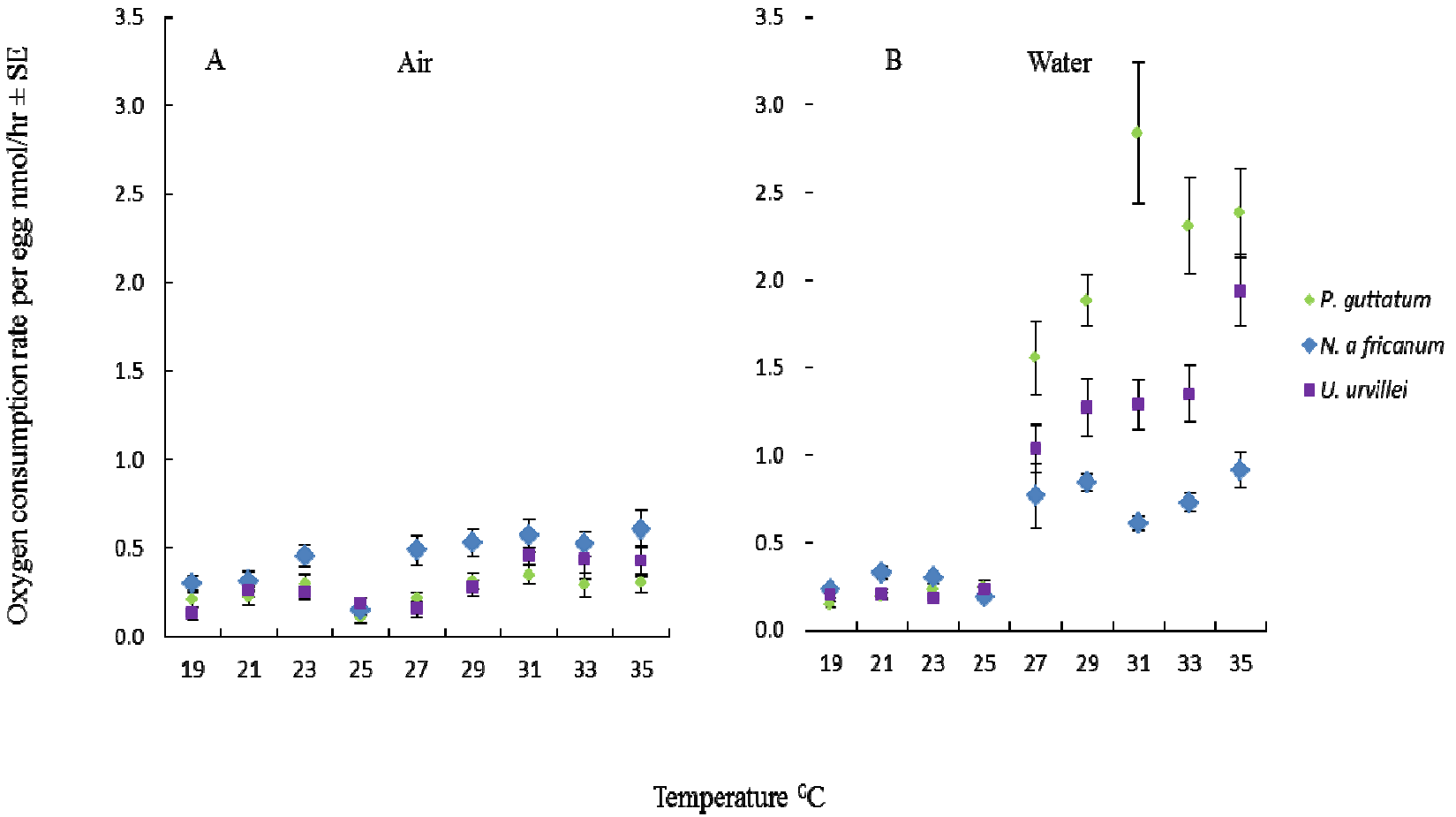

Figure 2.4: Average rates of oxygen consumption of stage 2 embryo (nmol*egg^{-1}*hr^{-1}) of *Perisesarma guttatum. Uca urvillei* and *Neosarmatium africanum* in (A) air and (B) water in South Africa over a stepwise temperature ramp from 19ºC to 35ºC at 2ºC intervals. All error bars represent standard errors (n = 5 – 15).

2.4.7 Perisesarma guttatum and *Uca urvillei* stage 4 embryos in South Africa and Kenya

Interactions among the factors Species, Region, Air/Water and Temperature had significant effects on the oxygen consumption rates of stage 4 embryos (Table 2.5). Comparison of rates of *Perisesarma guttatum* between South Africa and Kenya, exposed to air showed no significant differences at 25ºC, 27ºC, 31ºC and 33ºC though rates were greater in South Africa than Kenya at all temperatures except 35ºC (Figure 2.5A). In the comparison between regions, oxygen consumption rates of *P. guttatum* exposed to water, only showed a non-significant difference at 29ºC. Rates were greater in Kenya than South Africa between 19ºC and 25ºC and at 29ºC, while the trend reversed at 27ºC and between 31ºC and 35ºC, with rates greater in South Africa than in Kenya (Figure 2.5C). Stage 4 embryos of *Uca urvillei* exposed to air showed significant differences between regions at 19ºC, 21ºC, 23ºC, 29ºC and 31ºC and in all cases rates were greater in South Africa than Kenya (Figure 2.5B). Rates in water were significantly different between regions at all temperatures, with Kenya having greater oxygen consumption than South Africa between 19ºC and 25ºC, but lower oxygen consumption than South Africa for temperatures between 27ºC and 35ºC (Figure 2.5D).

Oxygen consumption was significantly greater in water than air for both *Perisesarma guttatum* (Figure 2.5A & C) and *Uca urvillei* (Figure 2.5B & D) in Kenya. Stage 4 embryos of *P. guttatum* in South Africa showed significant differences in oxygen consumption between air and water at all temperatures except 25ºC and oxygen consumption was significantly greater in water except at 19ºC, 21ºC and 23ºC (Figure 2.5A & C). Non-significant differences in oxygen consumption rates between air and water were noted for *U. urvillei* embryos in South Africa for 21ºC, 23ºC

and 25ºC, generally oxygen consumption was greater in water compared with air, except at 23ºC and 25ºC (Figure 2.5B & D).

At the higher experimental temperatures in South Africa (27ºC, 31ºC, 33ºC and 35ºC), there was no significant difference between *P. guttatum* and *U. urvillei* in air, while in water no significant differences were observed at 23ºC, 25ºC and 29ºC. In Kenya, no significant differences in oxygen consumption between species were noted mostly at the lower experimental temperatures (19ºC, 21ºC, 25ºC and 29ºC), while in water, non-significant differences spanned the entire experimental temperature range (19ºC, 21ºC, 23ºC, 31ºC and 35ºC). Of the 36 possible temperature comparisons of stage 4 embryos exposed to air, *P. guttatum* showed significant differences for 4 in South Africa and 22 in Kenya, while in water there were more significant differences between temperatures for South Africa with 28, but less in Kenya with 6 of the 36 possible temperature comparisons. *U. urvillei* stage 4 embryos showed more significant differences in South Africa with 19 and 25 in air and water respectively, compared with 2 and 12 in Kenya.

Table 2.5: PERMANOVA of rates of oxygen consumption (nmol*egg^{-1}*hr^{-1}) of stage 4 *Perisesarma guttatum* and *Uca urvillei* embryos in Kenya and South Africa.

	Oxygen consumption Rate		
Source	d.f.	M.S.	Pseudo-*F*
Sp	1	9434600	41.31***
Re	1	12981000	56.83***
Air/Water	1	110520000	483.90***
Temp	8	7635500	33.43***
Sp x Re	1	15877	0.07
Sp x Air/Water	1	1133800	4.96*
Sp x Temp	8	5671000	24.83***
Re x Air/Water	1	269860	1.18
Re x Temp	8	649880	2.85**
Air/Water x Temp	8	5474200	23.97***
Sp x Re x Air/Water	1	2674000	11.71***
Sp x Re x Temp	8	847590	3.71***
Sp x Air/Water x Temp	8	9278700	40.62***
Re x Air/Water xTemp	8	1467300	6.42***
Sp x Re x Air/Water x Temp	8	1541600	6.75***
Residual	926	211500000	
Total	997		

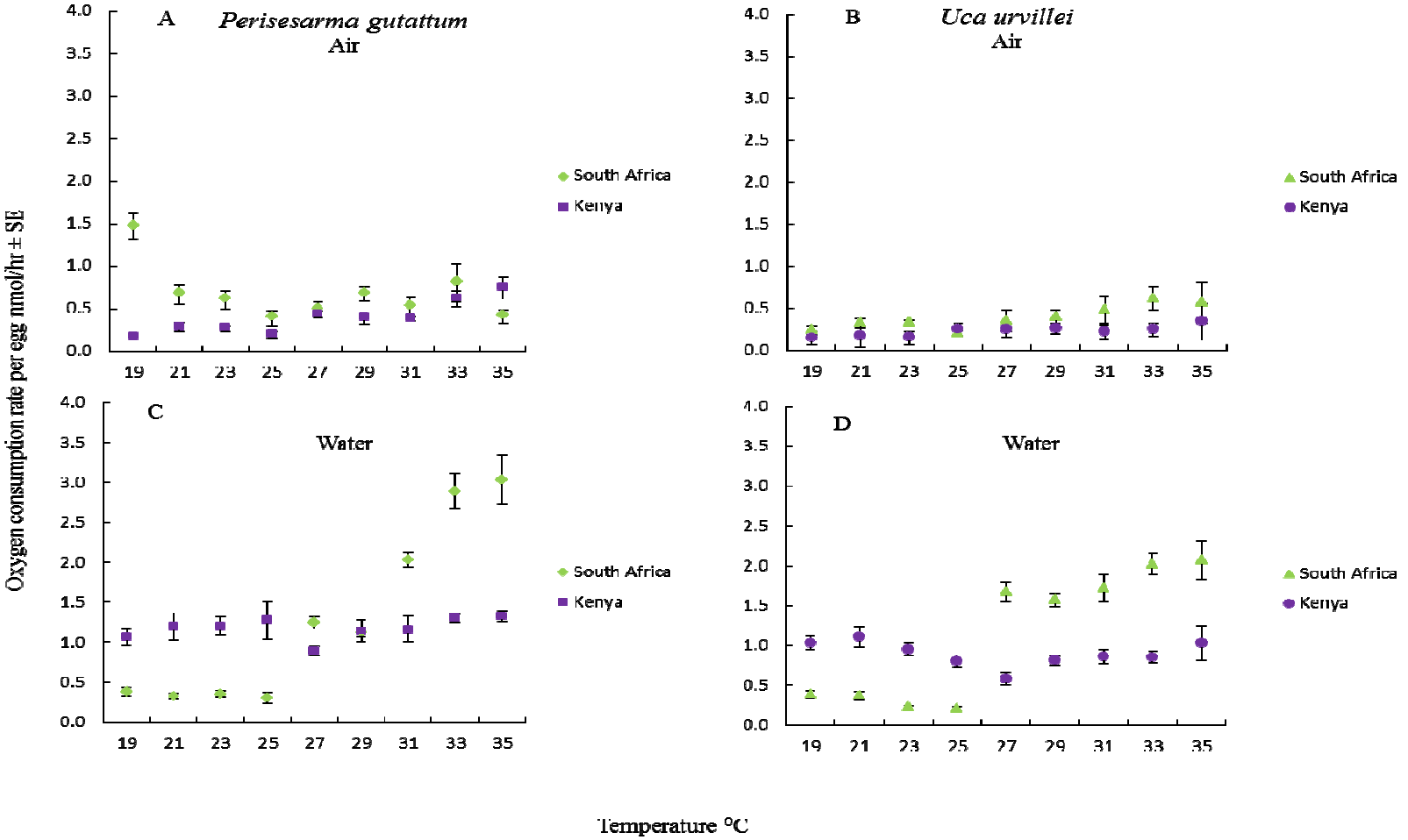

Figure 2.5: Average rates of oxygen consumption (nmol*egg^{-1}*hr^{-1}) for stage 4 embryos of (A) *Perisesarma guttatum* in air, (B) *Uca urvillei* in air, (C) *P. guttatum* in water and (D) *U. urvillei* in water in South Africa and Kenya measured over a stepwise temperature ramp from 19ºC to 35ºC at 2ºC intervals. All error bars represent standard errors (n = 5 – 15).

2.4.8 Perisesarma guttatum, Uca urvillei and *Neosarmatium africanum* stage 4 embryos in South Africa

Significant interactions of the factors Species, Air/Water and Temperature affected the oxygen consumption rates of stage 4 embryos tested in South Africa (Table 2.6). *Uca urvillei* stage 4 embryos exposed to air had significantly lower oxygen consumption rates than *Neosarmatium africanum* and *Perisesarma guttatum* at 19ºC to 27ºC and 19ºC to 25ºC and 29ºC respectively (Figure 2.6A). Thereafter, there was no difference in oxygen consumption rates between *U. urvillei* and either *P. guttatum* or *N. africanum*. *P. guttatum* and *N. africanum* stage 4 embryos had relatively similar oxygen consumptions rates in air. Differences were only noted at two temperatures, *P. guttatum* having higher consumption rates than *N. africanum* at 19ºC with the opposite trend at 25ºC (Figure 2.6A).

When exposed to water, differences in oxygen consumption rates among all three species were more evident. *Perisesarma guttatum* had significantly greater oxygen consumption rates than *Uca urvillei* at 23ºC, 33ºC and 35ºC, but significantly lower consumption at 27ºC and 29ºC (Figure 2.6B). Comparisons between *U. urvillei* and *Neosarmatium africanum* yielded only 3 non-significant differences, at 19ºC, 21ºC, and 25ºC respectively and generally *Uca urvillei* had greater oxygen consumption among the two species (Figure 2.6B). Oxygen consumption rates between *Perisesarma guttatum* and *Neosarmatium africanum* stage 4 embryos were significantly different at all experimental temperatures except 19ºC, 21ºC and 25ºC, and in all cases *Perisesarma guttatum* embryos had greater oxygen consumption than *N. africanum* (Figure 2.6B). A possible switch respose, with a large increase in oxygen consumption, was detected between 25◦Cand 27◦C in water for *P. guttatum, U. urvillei* and *N. africanum.*

Intraspecifically, *Perisesarma guttatum* had significantly different oxygen consumption rates at all experimental temperatures except 25ºC, consumption rates greater in air than water at 25ºC and below greater in water at 27ºC and above (Figure 2.6B). Aerial oxygen consumption in stage 4 embryos showed the least variation among temperatures, with only 4 of the 36 temperature comparisons yielding significantly different rates. In water, however, *Perisesarma guttatum* had a high variation in oxygen consumption rates over the experimental temperature range with 28 of the 36 temperature comparisons yielding significantly different rates. *Uca urvillei* had non-significant differences between air and water 21ºC, 23ºC and 25ºC, and generally oxygen consumption was greater in water except at 23ºC and 25ºC (Figures 2.6A & B). Significant differences over the experimental temperature range were detected in air and water in 18 of the 36 and 25 of the 36 temperature comparisons respectively. *Neosarmatium africanum* oxygen consumption rates in air and water were the most similar, with significant differences only at 21ºC, 23ºC and 25ºC. Variability in oxygen consumption in air was smaller than in water, with pairwise tests yielding significant differences at 12 and 21 of the 36 temperature comparisons respectively.

2.4.9 Stage 4 embryo summary

Generally, in air, *Perisesarma guttatum* in South Africa had greater oxygen consumption rates than in Kenya. In water, rates in Kenya were greater at low temperatures, but lower at temperatures above 27ºC.

In air, *Uca urvillei* generally had greater rates in South Africa than Kenya. In water rates were greater in Kenya at temperatures below 25ºC, but rates were lower in Kenya above this temperature.

In Kenya, oxygen consumption was generally greater in air compared with water for both species. In South Africa oxygen consumption was again generally greater in air compared with water for both species. In South Africa, *Neosarmatium africanum* embryos had similar consumption rates in air and water.

Table 2.6: PERMANOVA of rates of the oxygen consumption rates (nmol*egg^{-1}*hr^{-1}) for stage 4 embryos of *Neosarmatium africanum, Perisesarma guttatum* and *Uca urvillei* within South Africa.

Oxygen consumption Rate			
Source	d.f.	M.S.	Pseudo-*F*
Species = Sp	2	1.24E^{6}	38.07***
Air/Water	1	1.60E^{6}	4.93*
Temperature = Temp	8	1.29E^{7}	39.68***
Sp x Air/Water	2	1.79E^{6}	54.84***
Sp x Temp	16	2.18E^{6}	6.71***
Air/Water x Temp	8	3.28E^{6}	10.08***
Sp x Air/Water x Temp	16	1.65E^{5}	5.08***
Residual	624	3.26E^{5}	
Total	677		

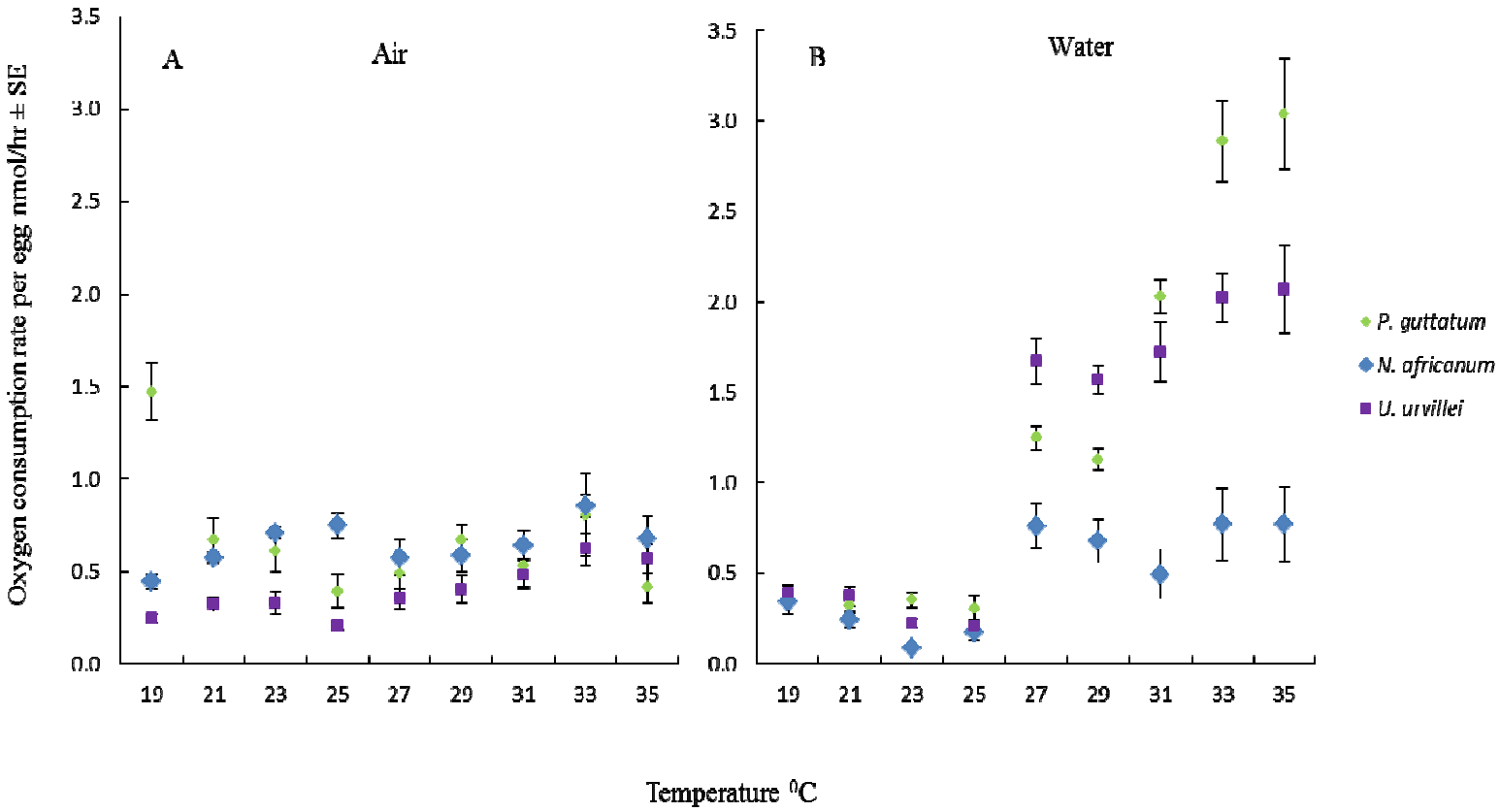

Figure 2.6: Average rates of oxygen consumption (nmol*egg^{-1}*hr^{-1}) stage 4 embryos of *Perisesarma guttatum*, *Uca urvillei* and *Neosarmatium africanum* in (A) air and (B) water in South Africa over a stepwise temperature ramp from 19ºC to 35ºC at 2ºC intervals. All error bars represent standard errors (n = 5 – 15).

2.4.10 Perisesarma guttatum and *Uca urvillei* gravid and non-gravid females in South Africa and Kenya

Significant interactions of the factors Region, Gravid/Non-gravid, Air/Water and Temperature affected the oxygen consumption rates of *Perisesarma guttatum* in South Africa and Kenya (Table 2.7). Non-gravid females had significantly lower rates in South Africa than Kenya at 33ºC in air. In water at 27ºC, rates in Kenya were significantly lower than those in South Africa. Gravid females differed at only 31ºC in air where South Africa had significantly lower oxygen consumption rates. In water, rates were significantly higher in Kenya than South Africa for all experimental temperatures. In South Africa, significant differences between non-gravid and gravid females were seen in air between 19ºC and 25ºC, with rates being lower for gravid females at 19ºC, but higher for gravid females at 21ºC, 23ºC and 25ºC. In water, differences between non-gravid and gravid females were noted at 25ºC, 31ºC, 33ºC and 35ºC, where rates for gravid females were greater than those of non-gravid females. In South Africa, rates differed significantly between air and water for non-gravid females at 19ºC, where rates in air were greater than those in water, while at 27ºC, 31ºC and 33ºC rates were greater in water. Gravid females had significant differences between rates in water and air at 19ºC, 31ºC, 33ºC and 35ºC, with rates being greater in air except at 19ºC. In Kenya, rates for non-gravid females were significantly greater in water than air at 31ºC and 35ºC, but were significantly greater in air at 33ºC. In Kenya, gravid females only had significantly greater rates in water than air at 29 ºC. For non-gravid females in South Africa, significant differences over the experimental temperature range were detected in air and water in 21 and 30 of the 36 temperature comparisons respectively. Gravid females in South Africa had less variation over the experimental temperature range with 15 and 3 significant differences of the 36 comparisons in air and water respectively. In Kenya, significant differences over the experimental temperature range were

detected in air and water for non-gravid females for 4 and 5 of the 10 temperature comparisons respectively, while for gravid females these values were 1 and 2 respectively.

Five significant 2-way interactions affected the oxygen consumption rates of non-gravid and gravid *Uca urvillei* females in South Africa and Kenya (Table 2.7). In the first 2-way interaction, the factors Region and f/fo condition affected oxygen consumption significantly. Non-gravid females did not differ significantly in oxygen consumption between South Africa and Kenya, but gravid females did. In both South Africa and Kenya, there were significant differences between non-gravid and gravid females. In the second two way interaction, the factors Region and Air/Water affected oxygen consumption rates. In both air and water, significant differences of oxygen consumptions rates between South Africa and Kenya were evident. The third significant interaction involved the factors f/fo and Air/Water. There was no significant difference between air and water for non-gravid females, but significant differences between air and water were evident for gravid females. In both air and water, oxygen consumption rates differed significantly between non-gravid and gravid females. A fourth significant interaction between the factors Air/Water and Temperature affected oxygen consumption rates. Consumption rates of *U. urvillei* differed between air and water at all experimental temperatures except 21ºC, 23ºC and 35ºC. *U. urvillei* had 9 significant differences of the 36 possible temperature comparison combinations over the experimental temperature range in air, while in water there was slightly less variation with 14 significant differences of 36. A significant interaction between the factors f/fo and Temperature affected oxygen consumption rates of non-gravid and gravid *U. urvillei.* Rates of oxygen consumption differed significantly between non-gravid and gravid females at 25ºC, 31ºC, 33ºC and 35ºC. Oxygen consumption rates of *U. urvillei* non-gravid and gravid females over the experimental temperature range were fairly variable with 14 and 19 significant differences out of 36 possible temperature comparisons respectively.

2.4.11 Gravid and non-gravid female summary:

Overall, oxygen consumption rates of *Perisesarma guttatum* differed very little between South Africa and Kenya for non-gravid females in air and water, and for gravid females in air, however, differences were evident in water. Within South Africa, differences between non-gravid and gravid females were evident for the lower temperatures in air and higher temperatures in water. In South Africa, differences between air and water were mostly at higher temperatures with rates being greater in water, while for gravid females, rates again were mostly different at higher temperatures, but were greater in air. Within Kenya, differences between non-gravid and gravid females were rarely evident in air, whereas in water, differences were evident at higher temperatures. Differences between air and water were evident at higher temperatures for non-gravid females, but were scarcer for gravid females. Overall, there was more significant variability over the experimental temperature range in non-gravid females compared to gravid females.

Pairwise statistical tests were not able to explain the significant two way interactions. Overall, significant differences between South Africa and Kenya were seen for gravid females and for pooled non-gravid versus gravid females oxygen in both air and water. Within both South Africa and Kenya, oxygen consumption rates differed significantly between non-gravid and gravid females and between air and water. Non-gravid females in general did not differ in oxygen consumption rates in air nor water, whereas gravid females did. In general, within both air and water oxygen consumption rates differed significantly between non-gravid and gravid females. Temperature generally affected oxygen consumption rates between air and water, while between non-gravid and gravid females differences were noted at higher temperatures. Over the experimental temperature range, there was relatively low variability in oxygen consumption

among females in air and water, but higher variability among both non-gravid and gravid females.

Table 2.7: PERMANOVA tables comparing the oxygen consumption rates (μmol*g^{-1}*min^{-1}) of gravid and non-gravid *Perisesarma guttatum* and *Uca urvillei* between Kenya and South Africa.

		Oxygen consumption Rate	
Source	d.f.	M.S.	Pseudo-*F*
Species = Sp	1	$2.22E^{-2}$	7.94**
Region = Re	1	0.43	153.7***
Air/Water	1	$1.10E^{-3}$	0.39
Condition (Gravid/Non-gravid) = Co	1	$9.50E^{-2}$	33.94***
Temperature = Temp	8	$5.43E^{-2}$	19.39***
Sp x Co	1	$1.44E^{-2}$	5.15*
Sp x Air/Water	1	0.10	37.09***
Sp x Temp	8	$1.75E^{-2}$	6.27***
Re x Co	1	0.48	169.84***
Re x Air/Water	1	$5.19E^{-2}$	18.562***
Co x Air/Water	1	$1.33E^{-2}$	4.74*
Co x Temp	8	$3.52E^{-2}$	12.57***
Sp x Co x Air/Water	1	$6.23E^{-2}$	22.25***
Re x Co x Air/Water	1	$4.19E^{-2}$	14.97***
Re x Co x Temp	4	$1.05E^{-2}$	3.77**
Co x Air/Water x Temp	8	$1.18E^{-2}$	4.21***
Sp x Re x Co x Air/Water	1	$6.40E^{-2}$	22.89***
Re x Co x Air/Water x Temp	4	$8.60E^{-3}$	3.07*
Residual	785	$2.80E^{-3}$	
Total	899		

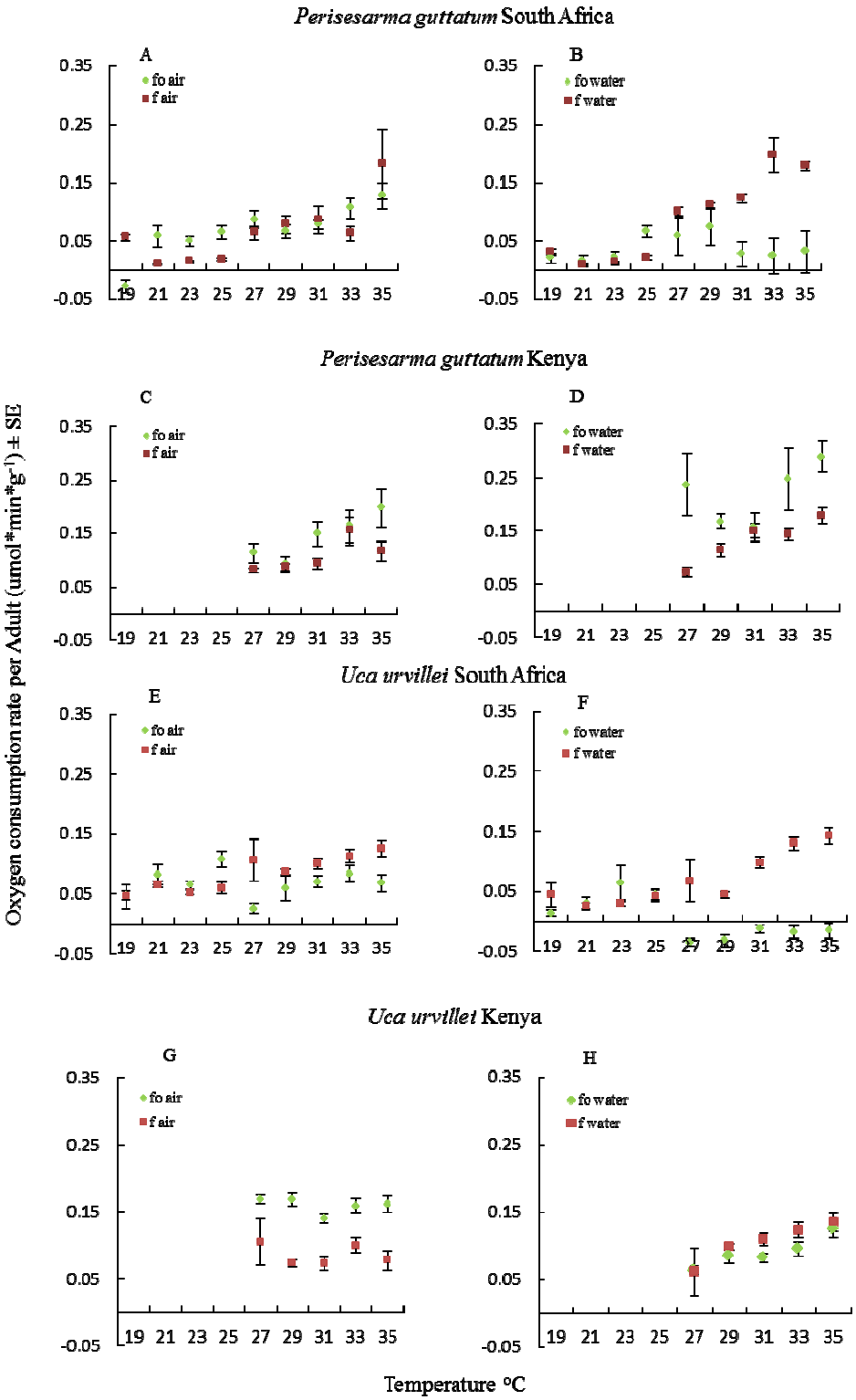

Figure 2.7: Average gravid and non-gravid oxygen consumption rates (µmol*g^{-1}*min^{-1}) of *Perisesarma guttatum* in South Africa in (A) air, (B) water, and in Kenya in (C) air and (D), and of *Uca urvillei* in South Africa in (E) air, (F) water, and in Kenya in (G) air and (H) over a stepwise temperature ramp from 19ºC to 35ºC at 2ºC intervals. All error bars represent standard errors (n = 5 – 15). Note that no measurements were made between 19ºC and 25ºC in Kenya (C & D).

2.4.12 Perisesarma guttatum and *Uca urvillei* maternal costs in South Africa and Kenya

Significant interactions of the factors Region, Air/Water and Temperature affected the maternal costs of *Perisesarma guttatum* in South Africa and Kenya (Table 2.8). In air, there was only a significant difference in maternal costs between South Africa and Kenya at 35ºC, with positive and negative maternal costs in Kenya and South Africa respectively. In water, significant differences between South Africa and Kenya were evident across all experimental temperatures, where Kenya had positive maternal costs compared to negative ones in South Africa. Significant differences in maternal costs between air and water were evident at 19ºC, 31ºC, 33ºC and 35ºC in South Africa, where maternal costs in water were negative. In Kenya, maternal costs in water were significantly higher than those in air at 27ºC and 29ºC. In South Africa, maternal costs of *P. guttatum* were fairly variable in air and water with 18 and 20 significant differences out of 36 possible temperature comparisons respectively. In Kenya, maternal costs showed very little significant variation along the experimental temperature range, with 2 and 0 significant differences out of 10 possible temperature comparisons in air and water respectively.

Uca urvillei maternal costs were affected by a significant interaction of the factors Air/water and Temperature and separately by the factor Region. Maternal costs differed between air and water at all experimental temperatures except 21ºC and 23ºC and generally maternal costs in air were greater than those in water. In air, there was moderate variability along the experimental temperature range with 15 significant differences out of 36 possible temperature comparisons while in water variability was high with 30 significant differences out of 36 possible temperature comparisons. Overall there was a significant difference in maternal costs between South Africa and Kenya.

2.4.13 Maternal costs summary

Overall, for *Perisesarma guttatum* there were limited differences in maternal costs in air between the two regions, but distinct differences throughout the temperature range in water. In South Africa, differences in maternal costs between air and water were noted at the lowest and higher experimental temperatures, while in Kenya differences were evident at the lower experimental temperatures. Variability across the temperature range was relatively high in South Africa for both air and water but almost non-existent in Kenya.

Overall, *Uca urvillei* maternal costs differed between regions and generally differed between air and water. There was more variability in maternal costs over the experimental temperature range in water than air.

Table 2.8: PERMANOVA tables comparing the maternal costs (μmol*g^{-1}*min^{-1}) of gravid *Perisesarma guttatum* and *Uca urvillei* between Kenya and South Africa.

	Maternal costs		
Source	d.f.	M.S.	Pseudo-*F*
Species = Sp	1	$2.69E^{-2}$	8.11**
Region = Re	1	0.94	282.72***
Air/Water	1	$2.40E^{-2}$	7.25**
Temperature = Temp	8	$7.22E^{-2}$	21.78***
Sp x Air/Water	1	$1.21E^{-1}$	36.52***
Sp x Temp	8	$8.89E^{-3}$	2.68**
Re x Air/Water	1	$8.37E^{-2}$	25.24***
Re x Temp	4	$2.08E^{-2}$	6.29***
Air/Water x Temp	8	$2.43E^{-2}$	7.33***
Sp x Re x Air/Water	1	$1.25E^{-1}$	37.59***
Re x Air/Water x Temp	4	$1.73E^{-2}$	5.22***
Residual	388	$3.32E^{-3}$	
Total	450		

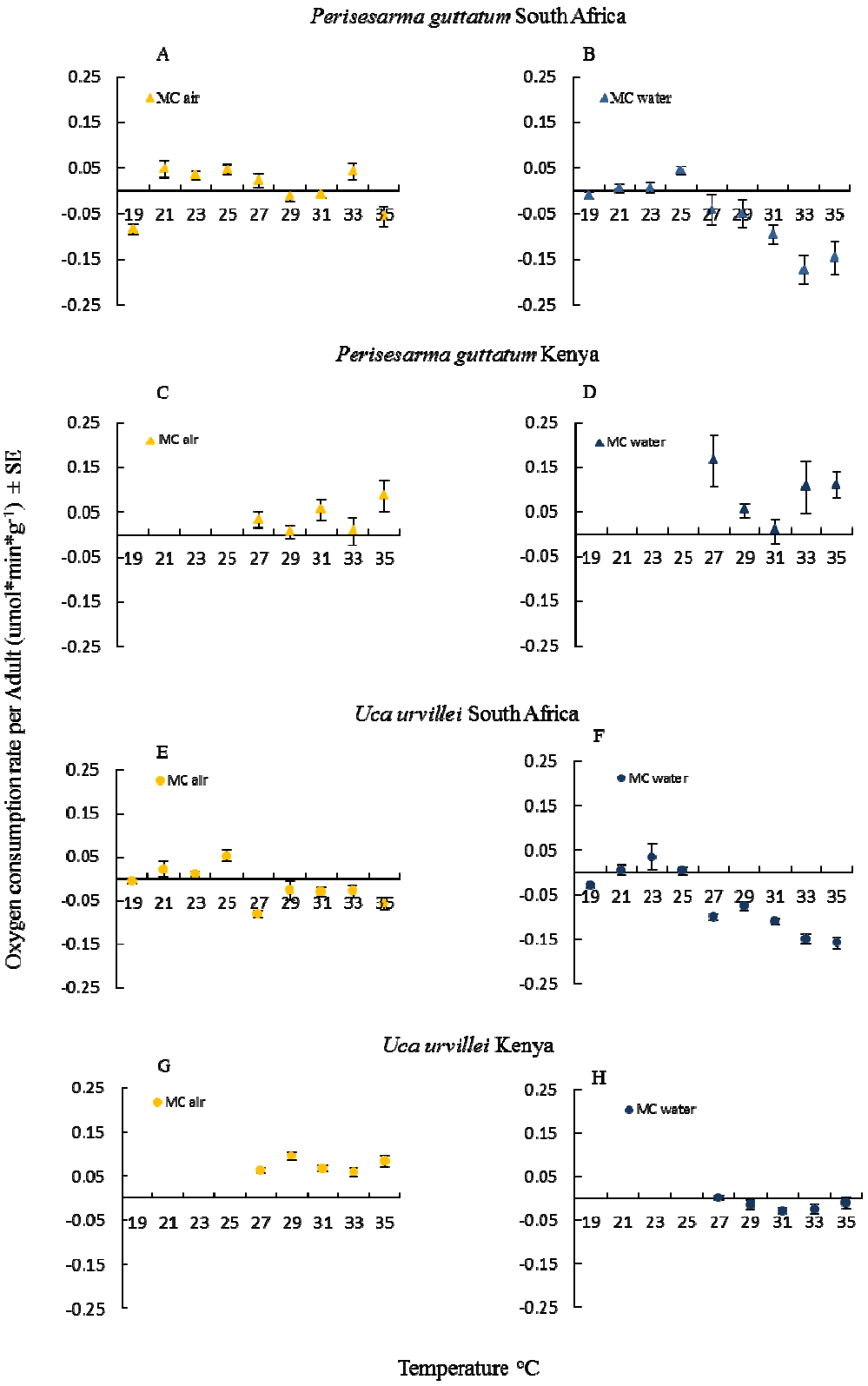

Figure 2.8: Average maternal costs (µmol*g^{-1}*min^{-1}) of *Perisesarma guttatum* in South Africa in (A) air, (B) water, and in Kenya in (C) air and (D), and of *Uca urvillei* in South Africa in (E) air, (F) water, and in Kenya in (G) air and (H) over a stepwise temperature ramp from 19ºC to 35ºC at 2ºC intervals. All error bars represent standard errors (n = 5 – 15). Note that no measurements were made between 19ºC and 25ºC in Kenya (C & D).

2.2.14 General results summary

In general, larval differences between regions were evident at higher temperatures in both species. In Kenya, there was no difference between species for larvae, while in South Africa differences occurred at higher temperatures. In Kenya, there was little variability in oxygen consumption rates with increasing temperature, while in South Africa there was generally more variability. Stage 2 embryos differed between regions in water, but not air for *Perisesarma guttatum*. *Uca urvillei* generally had greater rates in South Africa than in Kenya in air over all temperatures, while only at higher temperatures rates in water differed between South Africa and Kenya. In Kenya, rates for *P. guttatum* were greater in water than in air, while in South Africa this was true only for the higher experimental temperatures. Within Kenya, there was largely no difference between the two species in stage 2 embryo rates in air or water. Intraspecific differences of oxygen consumption for stage 2 embryos among temperature comparisons were scarcer in air compared with water for the two species in Kenya and the three species in South Africa. Stage 4 embryos of *P. guttatum* in air had greater oxygen consumption in South Africa than Kenya. In water, rates in Kenya were greater at cooler temperatures, but were lower at higher temperatures. In Kenya, oxygen consumption was generally greater in air compared with water for both species. In South Africa, rates were generally greater in water compared to air for *P. guttatum* and *U. urvillei*, but mostly similar between the two milieus for *Neosarmatium africanum*. In Kenya, differences between species in air were scarce at lower temperatures, while in water differences were lacking throughout. In South Africa, differences in oxygen consumption rates among all three species were more evident in water than in air. In air, *P. guttatum* had high variability among temperature comparisons in Kenya, but not South Africa, while in water there was more variability in South Africa than Kenya. *U. urvillei* had more variability among temperature comparisons in both milieus in South Africa than Kenya. For *N. africanum*, variability in oxygen consumption in air was less than in water.

Rates of oxygen consumption for non-gravid and gravid differed between South Africa and Kenya, in water for *Perisesarma guttatum*, but not in air. Within South Africa, differences were evident between non-gravid *P. guttatum* females in air and water at different spectra of the temperature range. In South Africa, non-gravid and gravid *P. guttatum* differed in oxygen consumption between air and water at higher temperatures, but in opposite directions. For *P. guttatum*, within Kenya differences in oxygen consumption rates between non-gravid and gravid females were rarely evident in air whereas in water differences were evident at higher temperatures. In Kenya, differences between air and water were evident at higher temperatures for non-gravid females but were scarcer for gravid females. Overall, for *P. guttatum*, there was more significant variability over the experimental temperature range in non-gravid females in both air and water compared to gravid females for both South Africa and Kenya.

Uca urvillei showed differences in oxygen consumption between South Africa and Kenya for rates in air, water and for gravid females, but not non-gravid females. Within South Africa and Kenya, rates of non-gravid and gravid females differed as did rates in air and water. Non-gravid *U. urvillei* rates did not differ between air and water, but did for gravid females. Non-gravid and gravid *U. urvillei* oxygen consumption rates differed in both air and water. Generally consumption rates differed between air and water over the experimental temperature range. There was less variability in oxygen consumption in air than water. Oxygen consumption rates of *U. urvillei* differed between non-gravid and gravid females at higher temperatures and rates of non-gravid and gravid females were fairly variable over the experimental temperature range.

In general maternal costs for *P. guttatum* between regions had differences in water, but limited differences in air. Maternal costs differed between air and water to varying degrees in both

regions and relatively high variability was observed across the temperature range in South Africa, but not Kenya. Generally, *Uca urvillei* had differences in maternal costs between regions and between air and water. More variability was observed in water than air.

2.5 Discussion:

Although the OCLTT may not have been not directly tested, the concept of OCLTT was supported across all life stages of the study species, including populations of *Persisesarma guttatum* and *Uca urvillei* in both South Africa and Kenya and *Neosarmatium africanum* in South Africa. High and low critical temperature values for these species was determined by means of lethal temperature (LT) experiments in a parallel study (Fusi *et al.* 2014) forming the baseline to which the temperature curves were fitted. According to this hypothesis, temperature increases oxygen consumption to fulfil cellular oxygen demand during warming through the response of the respiratory systems (Frederich and Pörtner 2000, Pörtner, 2001, 2002, 2010, Mark *et al.* 2002). Furthermore, my findings validate the hypothesis that bimodal breathing organisms can extend their thermal tolerance to varying degrees by shifting from aquatic to terrestrial respiration, taking advantage of the increased oxygen availability and diffusivity in air (Pörtner 2001, 2010, Verberk and Bilton 2013, Giomi *et al.* 2014, Fusi *et al.* 2014). Species have a tendency to respond strongly to increases in temperature above their acclimated temperature, initiating a strong stress response (Pörtner 2001, Baldanzi *et al.* 2015). Given the rates of consumption were generally higher in water encompassing all bimodal breathing ontogenetic life stages tested [stage 2 and stage 4 embryos, gravid and non-gravid females, at the centre (Kenya) and edge of latitudinal limits (South Africa) of their distributions], indicates that this method of extending thermal tolerance is as important during key reproductive phases as well as in during adulthood (this study and Fusi *et al.* 2014) of bimodal breathing species. It is not surprising that

elevated rates were observed in water as these crabs seldom spend more than a few hours submerged. Conversely, across all life stages study specimens had weak linear declines in response to decreasing temperatures. Addtionally, I found important differences between centre/edge populations, among ontogenetic stages and among species. The experiments were conducted over short term time periods and Pörtner (2002) notes that thermal tolerance is frequently investigated in this manner. Under these circumstances results are applicable to short term events of extreme temperature variation (Pörtner 2002) which are commonly associated with climate change (e.g. Vincent *et al*. 2011).

2.5.1 Effects of latitude:

The metabolism of ontogenetic stages in both study species at the centre and edge of their distributions were largely temperature dependent, as shown by the positive relationships for metabolic rates in both air and water. It must be noted that species in South Africa are naturally acclimated to cooler average temperatures. This implies that at the ambient experimental temperature (27ºC), they may have already been experiencing thermal stress, with the possible knock on effect of exhibiting greater stress than their Kenyan counter parts. As a general trend, both *Perisesarma guttatum* and *Uca urvillei*, early and late embryo stages exhibited metabolic stability in Kenya, with only slight increases in oxygen consumption over the experimental temperature range compared with South Africa. This tendency was particularly marked for embryos exposed to water, but clear in air too. In Kenya, larvae of both species had relatively stable oxygen consumption over the experimental temperature range with increases only at the upper end of the scale compared to larvae in South Africa, which were relatively stable at low temperatures, but exhibited drastic increases in oxygen consumption at higher experimental temperatures. These findings indicate that these species, at the central tropical latitudes, across the tested ontogenetic stages, are well adapted to warm temperatures, reflecting the thermal

stability of this region (Hoepffner *et al.* 2014, McClanahan 2014). Furthermore, as temperature changes at low latitudes are expected to be relatively small (Deutsch *et al.* 2008, Dillon *et al.* 2010), this should not negatively affect larvae or early and late stage embryos in this region.

Conversely, it must be noted that while embryos of species located at the centre of their distributional range generally exhibited greater metabolic stability over the tested temperatures, embryos in South Africa coped better with the lower temperatures in water, consuming less oxygen at these temperatures than their Kenyan conspecifics, though thereafter oxygen consumption increased considerably with increased experimental temperatures. Furthermore, larvae exhibited consistent and low metabolic responses to the lower experimental temperatures matching the present natural sea surface temperatures around South Africa (Smit *et al.* 2013, Hoepffner *et al.* 2014). Thereafter, the exponential increase in oxygen consumption at higher temperatures by *Perisesarma guttatum* and *Uca urvillei* suggests that these species do not often experience such warm temperatures at the observed South African coastline (Smit *et al.* 2013) and would therefore not be suitably adapted to these thermal conditions. In larvae of all three species in South Africa, oxygen consumption rates were similar at lower temperatures, with species-specific differences as temperatures increased, suggesting species-specific adaptations to warming in this region. The increase in oxygen consumption at higher temperatures by *P. guttatum* and *U. urvillei* larvae and embryos, suggests that these species do not often experience such warm temperatures at the observed South African coastline (Smit *et al.* 2013, Hoepffner *et al.* 2014) and in the case of sudden extreme temperatures would experience detrimental thermal stress.

Adult male *Perisesarma guttatum* have been shown to be adapted to a bimodal breathing lifestyle, but with a limited ability to extract oxygen from air (Fusi *et al.* 2014). Furthermore they are adapted to thermal regimes specific to different localities in their distributional range (Fusi *et al.* 2014), indicating an adaptation to local climatic regimes at different latitudes (sensu Angilletta 2009, Huey *et al.* 2012). In this study, *P. guttatum* only showed latitudinal differences in water. Extracting oxygen from air can alleviate thermal stress that would be otherwise constraining in water (Pörtner 2001, 2010, Verberk *et al.* 2011, Giomi *et al.* 2014) and this bimodal breathing strategy could possibly account for the lack of regional variability for *P. guttatum* in air, as aerial breathing supresses' thermal tolerance variability that is otherwise evident in water. Latitudinal differences of *Uca urvillei* were evident in air and water. These results differ to those of Fusi *et al.* (2014), who consider male *U. urvillei* a thermal generalist adapted to exploit the terrestrial environment and extract oxygen from air with the further ability to sustain activity at high temperatures. Furthermore, Fusi *et al.* (2014) found that male *U. urvillei* do not display differences between centre and edge populations in the aerial environment and experience extreme hypoxia in the aquatic environment in both regions. While results of this study do indicate differences between air and water, dramatic hypoxia as seen when adult males are submerged was not observed in females. This alludes to *U. urvillei* demonstrating a gender shift from aerial adaptation in males (Fusi *et al.* 2014) to a bimodal breathing adaptation in females.

2.5.2 Effects of species and ontogenetic stages:

Interspecific differences within regions reflected patterns of populations located at the centre and edge of their distributions. In Kenya, stage 2 and 4 embryos of both species generally showed a greater ability for extraction of oxygen from an aerial source than water, at all temperatures, while in South Africa embryos extracted oxygen equally efficiently from air and water at lower

temperatures, but at higher temperatures for both species oxygen extraction in water became less efficient. Stage 4 embryos of *Uca urvillei* showed similar oxygen consumption patterns in air and water, while those of *Perisesarma guttatum* showed slightly different patterns, with oxygen extraction at lower temperatures being less efficient in water than air. These results suggest that, in Kenya, both species have the ability to exploit the greater concentration and rates of diffusion of oxygen in air to maintain their aerobic scope (Fusi *et al.* 2014, Giomi *et al.* 2014), but at the same time are adapted to efficiently extract oxygen from both air and water under warming scenarios. At the edge of their distribution, these species seem to be well adapted to present temperatures and were able to extract oxygen efficiently from both air and water, but could face challenges in the event of warming.

Embryos at different stages of development are likely to have different metabolism, but general patterns were evident, with oxygen consumption in air being lower that in water and variability over the experimental temperature range being less variable in Kenya compared with South Africa. Early stage embryos, along with being at a lower level of cellular level differentiation, are often packaged with maternally invested cellular defences (innate defences) such as heat-shock proteins and antioxidant chemicals (Hamdoun and Epel 2007, Ericson *et al.* 2010). While innate defences come at the expense of the mothers energy reserves, they would not incur direct metabolic costs on embryos and thus embryos, during the early stages of development, would have lower metabolic rates than during the later developmental stages. Conversely, late stage embryos more heavily rely on self-induced defences or adaptive pathways to mitigate environmental stress (Hamdoun and Epel 2007, Ericson *et al.* 2010). These strategies would not only use more oxygen, but make these ontogenetic stages more sensitive to environmental change (Hamdoun and Epel 2007, Ericson *et al.* 2010). This is likely to have caused the observed steep increase in oxygen consumption rates at increased temperatures for the edge population.

The differences in cellular level differentiation are likely to give the observed patterns whereby early stage embryos show less structure in their responses to changing temperatures. Early stage embryos rely on innate defences provided by the mother. These are the product of the past history of their experience and generally results in protection against stressors previously encountered that might be encountered by the embryo (Hamdoun and Epel 2007). Later stage embryos, even though they rely less on innate defences, are able to produce defences that are more applicable to immediate stressors due to the accelerated progression through undifferentiated early stages and advances in cellular differentiation (Strathmann *et al.* 2002, Hamdoun and Epel 2007) later stage embryos show a more structured response to changing temperatures. A possible switch response in water was detected for stage 2 and stage 4 embryos of both species in South Africa whereby oxygen consumption suddenly increased between 25°C and 27°C. A response of this nature could likely be induced by an imposed stressor (temperature) causing a sudden increase in oxygen consumption. However after this respose oxygen consumption follows a linear increase to temperature. Larval rates are distinctly higher than those of late stage embryos, this is indicative of the high level of activity demonstrated by the larvae (pers. obs.) compared to late stage embryos where only heart beat and limited muscular movement is evident (pers. obs.).

Overall, stages 2 and 4 embryos of the Kenyan populations of *Uca Urvillei and Perisesarma guttatum* seem potentially well metabolically kitted to the predicted warming scenarios (IPCC 2014), with wide thermal tolerances. Additionally, embryos of both species in this region were able to take advantage of bimodal breathing habits provided by brooding females to extend their thermal tolerance by shifting from aquatic to aerial respiration and thus take advantage of the increased oxygen availability and diffusiveness in air (Pörtner 2001, 2010, Verberk and Bilton 2013, Giomi *et al.* 2014, Fusi *et al.* 2014). The aquatic larvae were similarly adapted to a wide

range of temperatures and again are not likely to be a weak link in persistence of these populations. Larvae and stages 2 and 4 embryos of *P. guttatum*, *U. urvillei* and *Neosarmatium africanum* are well adapted to present temperatures regimes in South Africa. Conversely, under increasing temperatures, thermal stress on early and late stage embryos becomes more evident especially in water. As embryos still require aquatic media for oxygen exchange and removal of metabolic waste (Cannicci *et al.* 2011, Simoni *et al.* 2011, Simoni *et al.* 2013), increasing metabolic rates during warming in water could have negative effects on survival. This could be a limiting factor for populations in this region causing population decrease or species disappearances in worst case scenarios (Fusi *et al.* 2014). The exponential increase in oxygen consumption rate of *P. guttatum* larvae and general increased in oxygen consumption of *U. urvillei* at higher temperatures in South Africa suggest that, at the edge of their distribution, this life stage could represent a risk for persistence of populations in South Africa. To cope with warming temperatures at current localities, tropical populations may shift to higher latitudes tracking optimal temperatures, while populations at current high latitude distributions (like South Africa in this study) may shift further south west (Silva *et al.* 2010b). The genetic connectivity of *P. guttatum* between centre and edge populations (Silva *et al.* 2010a) could, however, facilitate the flux of adapted genotypes toward higher latitudes given appropriate transport pathways. The flux of thermally tolerant genotypes to high latitudes would therefore facilitate the persistence of *P. guttatum* at the current edge of their distribution.

Previous findings have indicated that adult male *Uca urvillei* are adapted to exploit the terrestrial environment and extract oxygen from air with the further ability to sustain activity at high temperatures. *U. urvillei* has been described as a thermal generalist able to cope with a wide range of temperatures along its geographical distribution (Fusi *et al.* 2014). Contrastingly, adult male *Perisesarma guttatum* are more adapted to a bimodal breathing lifestyle with a limited

ability to extract oxygen from air and are adapted to thermal regimes specific to different localities in their distributional range (Angilletta 2009, Huey et al. 2012, Fusi *et al.* 2014). *P. guttatum* non-gravid females partially emulated these results, presenting a predominantly bimodal breathing adaptation spread over the species' distributional range, only showing differentiation between the centre and edge of their distribution in water. *U. urvillei*, however, demonstrated a shift from aerial adaptation in males to bimodal breathing adaptation in non-gravid females in South Africa, with extraction of oxygen typically not being significantly different between air and water. Non-gravid *U. urvillei* in Kenya maintained their efficiency in oxygen extraction from the aerial environment. Female *U. urvillei* also had the thermal generalist characteristics typical of males across latitudes (Fusi *et al.* 2014), with similar metabolic responses to temperature both at the centre and edge of its distribution in both air and water. The bimodal breathing adoption by females of both *U. urvillei* and *P. guttatum* in South Africa and Kenya presumably reflects the fundamental need of embryos as they require water for the removal of metabolic waste and facilitation of oxygen diffusion through the embryo membrane (Cannicci *et al.* 2011, Simoni *et al.* 2011, Simoni *et al.* 2013). Even though females show adaptation to aquatic submersion, this does not necessarily indicate that female and brood can stay submerged for prolonged periods of time and, as previously mentioned, embryos are still significantly less efficient in the extraction of oxygen from water compared to air.

Making use of high oxygen concentrations to alleviate thermal stress is not uncommon and has been noted for eurythermal crabs (Taylor and Wheatly 1979, Pörtner and Giomi 2013) and Antarctic eelpout (Mark *et al.* 2002). In this scenario, bimodal breathing animals make use of the higher oxygen concentrations and diffusiveness in air to reduce thermal stress (Pörtner 2001, 2010, Verberk *et al*. 2011, Giomi *et al.* 2014). The ability of bimodal breathing species to take advantage of air breathing is further aided by the special adaptations in the gill chambers, where

vascularised tissues help them perform as lungs, increasing the efficiency of oxygen extraction from air (Farrelly and Greenaway 1994, Morris 2002). It is therefore not unexpected that females and embryos also employ this strategy to reduce thermal stress.

2.5.3 Maternal costs:

Gravid females present complex responses to increasing temperatures possibly reflecting different maternal strategies employed by different species in different milieus at the centre and edge of their distribution. In Kenya, gravid *Perisesarma guttatum* had similar or higher oxygen consumption levels compared to non-gravid females in air and water. The same species in South Africa exhibited oxygen consumption rates well below those of their non-gravid counterparts in water, but similar rates in air. This suggests that maternal investment is greater in Kenya, with females expending additional energy to ensure successful reproduction, while in South Africa females do not invest energy in brood care to the same degree. In Kenya, gravid female *Uca urvillei* again showed greater rates of oxygen consumption than non-gravid females in air suggesting high maternal investment. However rates for gravid females in water were lower than non-gravid females. Given that *U. urvillei* is aerially adapted in this region, these females still invest considerable energy in maternal care in water. As with *P. guttatum*, *U. urvillei* in South Africa appears to take advantage of easy extraction of oxygen from air. Although at higher temperatures, gravid females have lower metabolic rates than their non-gravid counterparts. In water however, oxygen consumption by the clutch exceed that of the female itself, indicating negative oxygen consumption by gravid females.

Distinctly negative rates for gravid females seem to be a characteristic of *Uca urvillei* females exposed to water, additionally *Perisesarma guttatum* shows a decrease in oxygen consumption in water at higher temperatures in South Africa. From these data I propose that these are

approaching their upper thermal tolerance limits when in water, in line with the OCLTT curve (Frederich and Pörtner 2000, Pörtner, 2001, 2002, 2010, Mark *et al.* 2002, Pörtner and Farrell 2008), showing that their oxygen consumption is in a state of decline associated the onset of performance loss at the pejus temperature (sensu Pörtner and Farrell 2008). This occurs while egg clutch oxygen consumption rates continue to increase with increasing temperatures. Gravid females will have already invested considerable energy and resources in the production of gametes and in caring for the brood (Bauer 1989, Fernández *et al.* 2000, Ruiz-Tagle *et al.* 2002, Fernández and Brante 2003) depleting energy resources required to deal with thermal stress. When submerged at increased temperatures, they can no longer cope with the additional cost of extracting oxygen from water and care of the brood. In contrast to their non-gravid counterparts, this will have exhausted their energy reserves and increased their thermal stress, putting them on the downward slope on the OCLTT curve as temperature increases (Frederich and Pörtner 2000, Pörtner 2001, 2010, Pörtner and Farrell 2008, Wittmann *et al.* 2008). It has been suggested that in ectothermic vertebrates a wide range of stresses often converge at the challenge of dealing with mismatch of oxygen demand and coping with oxidative stress (Kassahn *et al.* 2009) and, as maternal care can be seen as a stress on females, it could possibly cause a mismatch between oxygen supply and demand.

Maternal costs illustrate the energy females invest in brood care more clearly as this value indicates the amount of oxygen used above or below that of a non-gravid female at the same temperature in the same milieu. *Perisesarma guttatum* in South Africa display marginal maternal care in water as shown by the negative maternal effort, although extraction of oxygen from the aerial environment sustains maternal care to some degree. While in Kenya, this species clearly invests energy in brood care in both air and water. *Uca urvillei* in South Africa showed minimal maternal care at lower temperatures and, above a threshold of 25ºC, completely abandoned

excess effort into maternal care in both air and water. In Kenya, *U. urvillei* again showed minimal maternal care in water, but in air, the increased concentration and rate of diffusion of oxygen allowed it to sustain maternal care. Negative maternal costs seem to be a characteristic for females of both species exposed to higher temperatures in water in South Africa. *U. urvillei* also experienced negative maternal effects when exposed to high temperatures in air in South Africa. This further supports the interpretation that these females reached an upper thermal tolerance limits beyond which gravid female oxygen consumption rates were suppressed, while embryo oxygen consumption rates continued to increase with temperatures, creating a negative maternal cost at higher temperatures. In cases where Maternal Costs (MCs) are marginally negative or marginally above zero, the female does not invest energy in maternal care. As a general trend, it seems maternal care was more effective in Kenya than in South Africa. Negative maternal costs suggest a break down in maternal care; essentially meaning embryos will have to fend for themselves and will not be able to rely on the mother. This could have serious implications as females will no longer ventilate (Woods 1999, Fernández *et al.* 2000, Fernández and Brante 2003) and clean (Bauer 1989, Fernández *et al.* 2000, Ruiz-Tagle *et al.* 2002, Fernández and Brante 2003) embryo masses as seen in non-stressed scenarios. Negative MCs may also prevent regular submersion in water to remove metabolic waste a adequately facilitate the diffusion of oxygen across the embryo membrane (Cannicci *et al.* 2011, Simoni *et al.* 2011, Simoni *et al.* 2013). Overall, the breakdown in maternal care is likely to drastically affect the survival of embryos, preventing the production of larvae and thus limiting the amount of new recruits entering systems and could have serious repercussions for populations in regions that show a break down in maternal care.

To verify that gravid females may in fact produce negative oxygen consumption rates in the adjustment for gravid females carrying eggs, there is evidence that clutches of brachyuran

embryos can consume as much oxygen as the brooding adult (Fernández and Brante 2003). Furthermore, the literature suggests that the rate of oxygen consumption by embryos is only affected below a critical concentration, above which it is not supressed (Naylor *et al.* 1999, Fernández *et al.* 2000, 2002, Baeza and Fernández 2002, Fernández and Brante 2003), although this may be species specific (Fernández *et al.* 2003). Additionally, there is evidence that, while oxygen concentrations may drop within the interior of the embryo mass, females attempt to ensure adequate oxygen supply by abdominal flapping, limiting the time embryos may spend below the critical concentration (Fernández *et al.* 2002). Also, measuring oxygen consumption of unstirred embryos produces results that are approximately half those of stirred embryos (Naylor *et al.* 1999) and that embryos in the interior of the egg mass may consume less oxygen than embryos at the periphery of the clutch (Fernández *et al.* 2003), but without measuring the exact differences involved, this is difficult to adjust for.

In conclusion, all bimodal breathing ontogenetic stages in this study were able to take advantage of the increased concentration and diffusiveness of oxygen in air to extend their thermal tolerances, allowing population persistence under climate change scenarios. Overall, embryos and larvae appeared to be more resistant to warming than adults which is not uncommon in juvenile ectothermic invertebrates (e.g. Peck *et al.* 2013). The ontogenetic stages of the two study species, *Perisesarma guttatum* and *Uca urvillei*, in Kenya were generally more robust to increasing temperatures than their South African counterparts, which in turn were better suited to present regional temperatures. Conspecific individuals at the centre and edge of their distributions in this study employed different strategies in maternal care that seem to be linked to thermal tolerance. Differing strategies in combination with thermal responses of individual life stages, is likely to affect the persistence of species under climate warming at the centre of their distributions. However, detrimental effects on species at their higher latitudinal limits due to

metabolic stress at higher temperatures and constraint of maternal care, could cause population shifts away from their current locations.

CHAPTER 3

SETTLEMENT PATTERNS OF BRACHYURAN CRABS AT MID AND HIGH LATITUDINAL LIMITS OF MANGAL DISTRIBUTIONS IN EAST AFRICA

3.1 Introduction:

Marine invertebrates generally produce pelagic larvae which spend varying amounts of time developing in the planktonic stage (Morgan and Christy 1995, Caley *et al.* 1996, Becker *et al.* 2007, Siegel *et al.* 2008, Cowen and Sponaugle 2009). Previously, it was assumed that during their pelagic phase, larvae were distributed over large distances resulting in extensively connected invertebrate populations (Scheltema and Williams 1983, Scheltema 1986, Levin 2006). Recent evidence suggests this is not always the case; technological advances coupled with recognition of new factors that influence the transport of pelagic larvae have caused a shift away from this theory (Swearer *et al.* 1999, Levin 2006, Almany *et al.* 2007, Cowen *et al.* 2007, Becker *et al.* 2007, Cowen and Sponaugle 2009). The drivers of larval dispersal are now thought to be more complex, involving behaviour, mortality, suitable settlement habitat and hydrodynamics (Metaxas 2001, Leis *et al.* 2003, Largier 2003, 2004, Becker *et al.* 2007).

The first contributing factor to dispersal is the generation of embryos. Along a latitudinal cline, this may vary significantly in both timing and intensity, as species exhibit different breeding cycles and strategies. The variation in these strategies depends on a trade-off between environmental factors and reproductive processes (Morgan and Christy 1995, Flores *et al.* 2002). Gonad maturation is largely mediated by temperature, but other prominent

factors include light, food availability, salinity, and tidal periodicity (Sastry 1983, Morgan and Christy 1995). Authors have shown that reproductive output, fecundity and embryo volume and weight in brachyurans vary with latitude (e.g. Lardies and Castilla 2001, Brante *et al.* 2003) and life history traits, such as the length of the incubation period and the number of broods per season vary with temperature, which is correlated to latitude (Dunn 2004, Tieleman 2009). Furthermore, the timing of the breeding season may shift along a latitudinal gradient. Species in temperate regions often breed seasonally due to periodic (seasonal) resource limitation (e.g. Emmerson 1994), while closely related species breed all year round in the near sub-tropics and tropics (Ituarte *et al.* 2004, Torres *et al.* 2009) and these patterns are consistent for many marine brachyuran species within Africa (e.g. Emmerson 1994, Gove and Mambonhe 2000, Flores *et al.* 2002, Litulo 2005a, b, c).

In cases where adult populations are in large estuaries, larvae may be retained avoiding transportation to offshore areas and the associated problems of returning to suitable habitats (Christy and Stancyk 1982, Stancyk and Feller 1986, Johnson 1985, McConaugha 1988, Paula *et al.* 2003). Behavioural mechanisms controlling diel vertical migration in the water column can be initiated by changes in light intensity, salinity and pressure and are used to prevent larvae being positioned in currents that would remove them from the estuary (Wheeler and Epifanio 1978, Cronin and Forward 1979, Lambert and Epifanio 1982, McConaugha 1988). Larval availability is the result of the reproductive output of the parental stocks and as such, the cause and effect relationship may be more evident in restricted systems like sheltered estuaries, where the number of new megalopae may directly reflect the reproductive output of parental stocks (Flores *et al.* 2002). Such direct links can have underlying effects on population dynamics (Cowen and Sponaugle 2009) and hence larval development and mortality due to environmental conditions can mask the effect of seasonal

or year-round breeding and affect the short term supply of new megalopae, influencing recruitment patterns, especially in restricted systems (Moloney *et al.* 1994, Flores *et al.* 2002, Cowen and Sponaugle 2009).

Synchronous larval release is common in many marine invertebrates (Morgan and Christy 1995, Skov *et al.* 2005) and can be exhibited in scenarios ranging from annual to lunar to tidal synchrony (Caspers 1984, Harrison *et al.* 1984, Skov *et al.* 2005). Tidal synchrony is common in brachyurans and is thought to be advantageous as it reduces predation risk (Morgan and Christy 1995) and mitigates against lethal salinity and temperature conditions (reviewed in Forward 1987). Most brachyuran larvae rapidly disperse seawards. The timing of larval release during nocturnal large amplitude ebb tides (Scheltema 1986, Morgan 1995, Morgan and Christy 1995), coupled with behavioural mechanisms that typically manoeuvre larvae into ebb-directional currents (e.g. Epifanio *et al.* 1984, Sulkin 1984, Zeng and Naylor 1996), aid in the rapid offshore transportation of larvae (Epifanio 1988, Dittel *et al.* 1991, Lago 1993a, Queiroga *et al.* 1994, Christy and Morgan 1998). Experimental evidence suggests that such strategic timing of larval release strongly reduces the risk of predation (Morgan and Christy 1994, 1995, 1996, Hovel and Morgan 1997). Several African mangrove crab species exhibit such tidal synchrony in their reproductive strategies at both the centre (tropical) and lower (temperate) limits of their distributions (e.g. Gove and Mambonhe 2000, Papadopoulos *et al.* 2002, Paula *et al.* 2004, Skov *et al.* 2005). Similar predation and physiologically driven selective pressures are thought to act on returning megalopae, selecting for nocturnal immigration to adult habitats (Acosta and Butler 1999, Papadopoulos *et al.* 2002, Ragionieri *et al.* 2015).

During the pelagic stage of the life cycle, the zoeae and megalopae of brachyurans demonstrate species- and stage-specific vertical distributions within the water column that are related to tidal currents, temperature, salinity, food concentration, hydrostatic pressure, light conditions, etc. Vertical distribution in turn affects the extent of their dispersal (Johnson 1985, McConaugha 1988, Zeng and Naylor 1996, Christy and Morgan 1998, Kingsford *et al.* 2002, Queiroga and Blanton 2005, Anger 2006). On return, chemical cues originating from the parental habitat and/or conspecifics are important in triggering and influencing larval moult cycles, larval development and eventually settlement (O'Connor 1993, Gebauer *et al.* 1998, 2003, 2005). Some species can independently shift through these life-history events following a genetic and hormonal programme while others rely heavily on environmental and chemical cues often linked to adult habitat or the presence of conspecifics (Gebauer *et al.* 2005).

Returning late stage zoeae or megalopae alter their behaviour and rely on stimuli to alter their positioning within the water column to maximise onshore transportation to suitable habitats (Christy and Morgan 1998, Kingsford *et al.* 2002, Queiroga and Blanton 2005, Anger 2006). Responses to external stimuli are usually species-specific and therefore the relative importance of physical processes transporting larvae back to parental habitat often differs among species (Christy and Morgan 1998, Kingsford *et al.* 2002, Shanks *et al.* 2003, Gardner *et al.* 2004, Anger 2006). Marine invertebrate larvae generally make use of the predictable nature of tides and currents and have frequently evolved convergent behaviours linked to the same transport mechanisms (Epifanio *et al.* 1984, Scheltema 1986, Epifanio 1988, Christy and Morgan 1998). Many species of marine invertebrates make use of high amplitude spring tides to aid in their transportation to suitable habitats (Christy and Morgan 1998, Pereira *et al.* 2000) and this has specifically been noted as a beneficial tactic in the recruitment of

brachyuran species to mangrove ecosystems (Paula *et al.* 2001, 2003, Flores *et al.* 2002, Ragionieri *et al.* 2015). Furthermore, prevailing weather conditions often affect larval supply. For example, in temperate regions, brachyuran megalopae rely on wind driven currents to aid in transportation to estuarine habitats (Morgan *et al.* 1996, Garvine *et al*. 1997, Botsford 2001, Flores *et al.* 2002, Olaguer-Feliú *et al.* 2010, Domingues *et al.* 2011), while tropical brachyuran species are thought to take advantage of wind driven currents in Maputo Bay, Mozambique, for transportation to suitable settlement habitats (Paula *et al.* 2001, 2003). These factors often act in conjunction with each other and account for the variability in larval supply in many regions (e.g. Paula *et al.* 2001, 2003, Olaguer-Feliú *et al.* 2010, Ragionieri *et al.* 2015).

Successful recruitment involves the transportation of larvae to suitable habitat, settlement and the survival of juveniles that persist into the adult population (Keough and Downes 1982). Marine invertebrates often experience a dramatic shift from a pelagic larval life stages to substratum based juvenile-adult phase that involve complex behavioural and developmental changes (Gebauer *et al.* 2005). In cases where megalopae are densely aggregated in structurally complex micro habitats removed from parental habitats, brachyurans will exhibit an ontogenetic habitat shift (Heck and Hambrook 1991, Spivak *et al.* 1994, Flores and Negreiros-Fransozo 1999), leading to migration from nursery to adult habitats. Once settlement has occurred, juvenile recruitment into a population is further influenced by numerous factors such as habitat complexity (McMillan *et al.* 1995, Stevens and Kittaka 1998, Loher and Armstrong 2000), predation (Dittel *et al.* 1996, Banks and Dinnel, 2000) and physiological constraints (Tolley *et al.* 2012, 2013). Understanding recruitment mechanisms is a step towards unravelling adaptive features in a species' reproductive strategy (Flores *et al.* 2002).

Mangals spanning the east coast of Africa cover tens of degrees of latitude and encompass the mid and higher latitudinal limits of floral and faunal components of this ecosystem (Fatoyinbo and Simard 2013). As it stands, the information on recruitment of brachyurans into mangrove ecosystems in east Africa is limited, with the majority of the studies concentrated in Mozambique (e.g. Paula *et al.* 2001, 2002, 2004, Flores *et al.* 2002, Litulo 2004, Litulo 2005a, b, c), although limited information from South Africa is available (e.g. Papadopoulos *et al.* 2002) and some literature deals with faunal recolonistaion of mangals in Kenya (e.g. Bosire *et al.* 2004) with further recent information on brachyuran settlement in Kenyan mangroves (Ragionieri *et al.* 2015). Returning megalopae will use similar pathways to those described above to locate and settle in suitable habitat such as high amplitude spring tides (e.g. Paula *et al.* 2001, 2003, 2004, Flores *et al.* 2002). Additionally, species compositions differ at the different latitudes of mangal distribution (Emmerson 1994, Kalk 1995, Dahdouh-Guebas *et al.* 2002, Emmerson *et al.* 2003, Gillikin and Schubart 2004, Cannicci *et al.* 2009, Morrisey *et al.* 2010) and will likely contribute to variations in settlement patterns due to megalopae following conspecific cues (O'Connor 1993, Gebauer *et al*. 1998, 2003, 2005, Anger 2006).

This study targeted settlement of brachyurans in mangrove systems, at mid and higher latitudinal limits of distribution. I hypothesise that settlement patterns between edge populations (South Africa) and centre populations (Kenya) will differ, with populations at the centre having higher settlement than at the edge. These settlement patterns will likely arise due to dynamic events such as meteorological conditions and hydrodynamics and regional specific traits in population biology (e.g. seasonal versus continuous breeding patterns at different latitudes, which would influence the availability of larvae for settlement.). Locally, in each region, I propose there will be temporal and spatial variation in settlement which will

again reflect the meteorological and hydrodynamic conditions. On the other hand, I hypothesise a synchronised preference for settlement during night spring high tides to avoid predators is expected across latitudes (e.g. Acosta and Butler 1999, Papadopoulos *et al.* 2002). Furthermore, I propose settlement during new moon spring tides is likely to be greater, again in accordance with the predator avoidance hypothesis (e.g. Acosta and Butler 1999, Pereira *et al.* 2000, Papadopoulos *et al.* 2002). I propose that species-specific preferences for different heights on the shore may alter settlement patterns within regions as brachyurans exhibit clear zonation patterns in each region (e.g. Emmerson 1994, Ruwa 1997, Dahdouh-Guebas *et al.* 2002).

3.2 Methods:

3.2.1 Field Methods and Materials:

Study sites were identified at the mid (Kenya) distributional range and higher latitudinal (South Africa) limits (referred to as centre and edge respectively) of mangrove ecosystems in eastern Africa. Sampling took place specifically at Gazi Bay (39^{o} 30' E, 4^{o} 22' S) and Shirazi Creek (4^{o} 31' S, 39^{o} 25' E) in Kenya and the Mngazana (29^{o} 25' E, 31^{o} 42' S) and Mntafufu (29^{o} 38' E, 31^{o} 33' S) estuaries in South Africa (Figure 3.1). These sites were chosen on the basis that the full complement of tree species for each region was present. These were: *Avicennia marina, Bruguiera gymnorrhiza, Ceriops tagal, Heritiera littoralis, Lumnitzera racemosa, Rhizophora mucronata, Sonneratia alba, Xylocarpus granatum* and *X. moluccensis* for Kenya and *A. marina, B. gymnorrhiza* and *R. mucronata* for South Africa.

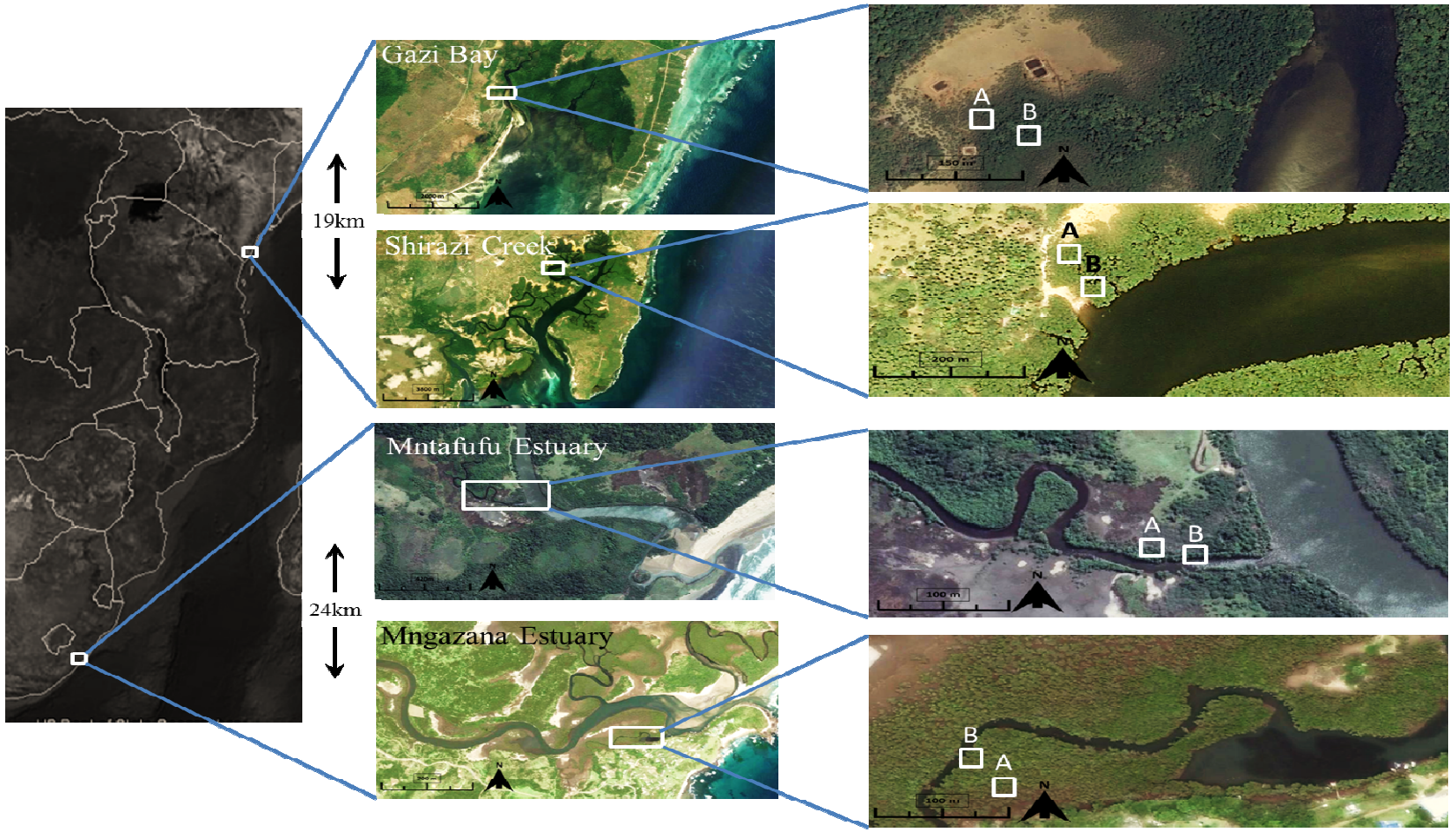

Figure 3.1: Map of East Africa indicating sampling sites in Kenya (Gazi Bay and Shirazi Creek) and South Africa (Mntafufu Estuary and Mngazana Estuary), boxes marked A indicate sampling sites located in zones dominated by *Avicennia marina* while boxes marked B indicate sampling sites in zones dominated by *Rhizophora mucronata*, all photos courtesy of Google Earth.

Sampling was conducted in Kenya between the 26th August 2010 and the 26th of September 2010 at both Gazi Bay and Shirazi Creek, and for a further four months, until the 11th of January 2011 at Gazi Bay. Limited data were collected in this region due to logistical constraints. These sampling dates corresponded to the northeast (NE) monsoon (McClanahan 1988, Wakibia *et al.* 2006). The SE monsoon is characterised by weak winds, high air and water temperatures, high solar radiation and low rainfall (McClanahan 1988). The NE monsoon was hypothesised to be the equatorial equivalent to the peak summer recruitment season in South Africa and likely to give the most information on recruitment dynamics. In South Africa, sampling took place at both sites from the 3rd of November 2010 until the 15th of October 2011. Sampling was conducted twice daily during spring tides, when the tidal amplitude exceeded 3.00m for more than one consecutive tide in Kenya and more than 1.65m for South Africa. This ensured that the megalopal collector mats in the upper *A. marina* zones were fully submersed at high tide.

Within each site, areas of monospecific zones of *Avicennia marina* and *Rhizophora mucronata* were identified. These zones were chosen as both were represented in the Kenyan and South African mangals, with *A. marina* forming the upper zonation limit of the mangrove forest, while *R. mucronata* is the preferred habitat for the targeted species of brachyurans. In the case of South African mangals, the *R. mucronata* and *Bruguiera gymnorrhiza* zones overlapped and areas where *R. mucronata* dominated were chosen. Megalopal collectors mimicked a complex settlement substratum. They were cut from air-conditioning filters and measured 33 cm by 33 cm by 1 cm thick. The technique of using artificial substrata to collect megalopae has been extensively used in estuaries in the Gulf of Mexico, the western Atlantic (e.g. van Montfrans *et al.* 1990, 1995, Olmi *et al.* 1990, Metcalf *et al.* 1995, Rabalais *et al.* 1995) and more recently in Mozambique and Kenyan mangals (Paula *et al.* 2003, Ragionieri

et al. 2015). I adapted the technique from floating collectors, as used by Paula *et al.* (2003) in the central channels, to collector mats placed flat on the sediment within specific zones of the mangal, as it has been shown that shape does not affect settlement on artificial substrata, provided the surface areas are comparable (Metcalf *et al.* 1995).

Six replicates were sampled in each monospecific mangrove zone. Each replicated consisted of a passive megalopal collection mat that was placed haphazardly among the trees in the two identified monospecific zones at each site. This was done approximately four hours before the first high tide in the spring tide cycle. The succeeding high tides amplitudes submerged all the mats (pers. obs.). The mats were pinned to the sediment with sticks to prevent movement during the ebb and flow tides. Mats were collected during the following low tide, after the ebb tide had receded enough to allow the traps to be fully exposed, minimising the escape of megalopae during collection. Each mat was then placed in a separate transparent pre-labelled Ziplock bag. The mats were immediately replaced with clean mats. The collector bags and mats were then transported back to the laboratory where the mats were removed from the bags and placed in plastic buckets. The bags were washed out thoroughly using freshwater sprayers to remove any megalopae trapped inside. The megalopal collection mats were then placed in plastic buckets and meticulously washed by submersing them in freshwater and using sprayers to dislodge any megalopae (van Montfrans *et al.* 1990). Megalopal specimens were collected and stored in 90% ethanol in labelled Eppendorfs to allow identification at a later stage. The date, state of the tide and zone in which the specimens were collected were recorded. This procedure was carried out at 12 hour intervals until the spring tide amplitude was no longer sufficient to submerge all the mats fully. During each spring tide, the mangals were sampled between 3 and 8 days in South Africa and 5 days in Kenya.

Representative adult specimens of *Epixanthus dentatus, Neosarmatium africanum, Neosarmatium smithii, Ocypode ceratophthalmus, Parasesarma catenata, Perisesarma guttatum, Potamonautes perlatus, Scylla serrata, Uca chlorophthalmus, Uca annulipes* and *Uca urvillei* were collected from Mngazana estuary during 2013 for DNA sequencing to help identify unknown megalopae.

3.2.2 Laboratory Methods and Materials:

Megalopae were identified to species level where possible using a dissecting microscope and the literature available on larval development of mangrove brachyurans (Lago 1987, 1989, 1993a, 1993b, Guerao *et al.* 2011). Species that could not be identified, due to the lack of literature describing mangrove species megalopae, were grouped by similar characteristics into different morphotypes and labelled as species 1, 2, 3 etc. A representative specimen from each identified and unidentified group was set aside for further DNA sequencing. This was done to either verify the identification based on the literature, or to attempt to match unidentified megalopae to known adult specimens collected from the Mngazana mangals or to sequences already present in the BOLD DNA Barcoding Database.

A randomly chosen voucher specimen from each group of identified and unidentified groups of megalopae was selected for DNA sequencing. Small tissue portions of each representative adult specimen and voucher specimen were removed and placed in separate wells in the sequencing plate in 30 mL of lysis buffer (http://www.ccdb.ca/docs/CCDB_DNA_ Extraction.pdf). The plate was then sealed and shipped to the Canadian Centre for DNA Barcoding (CCDB) for DNA sequencing and input into the BOLD DNA Barcoding Database. The standard PCR reaction protocol of the CCDB was used for amplifications

(http://www.dnabarcodes2011.org/conference/preconference/CCDB-Amplification-animals.pdf). Using the bold website, a BOLD taxon ID tree was constructed using the cytochrome *c* oxidase subunit – 5p (CO1-5p) marker and the Kimura 2 Parameter Distance Model in order to match sequenced voucher specimens to know adults. A further search for DNA sequence matches between sequenced voucher specimens and entries already present in the BOLD DNA Barcoding database was conducted using the BOLD Barcode Index Numbers (BINs) search engine which allows for comparisons of sequenced DNA to sequence clusters that closely approximate species.

3.2.3 Statistical Analysis:

The possible effects of several factors on numbers of brachyuran settlers between regions were analysed with the Permutational Multivariate Analysis of Variance (PERMANOVA) add-on in PRIMER 6. The Distance-based test for homogeneity of multivariate dispersions (PERMDISP) was used to check for homogeneity of the entire dataset, according to the full experimental design. All factors were considered to be fixed as they offered all available levels of the factors considered. Variances of response variables to "Site", "Zone" and "Day/Night" were homogenous for *P. guttatum*, while "Site" and "Day/Night" was homogenous for *P. catenata* and the total number of megalopae (PERMDISP, $P > 0.05$). Analyses were therefore conducted on square root transformed Euclidean dissimilarity matrices to reduce the effects of heterogeneous data. The heterogeneous nature of some of the data after transformations may induce type 1 errors within the analyses, forcing in precautious interpretation of results. The total numbers of megalopae collected were compared between regions (Kenya and South Africa). The factors, "Region" (2 levels), "Zone" (2 levels), "Moon" (2 levels) and "Day/Night" (2 levels) were fixed and orthogonal (Table 3.1).

Each region was then considered separately due to different amounts of data collected in each region and to find specific trends within each region. For South Africa, analyses were conducted on the total number of megalopae as well as those of the two most abundant species (*Perisesarma guttatum* and *Parasesarma catenata*) collected. These analyses were conducted separately to simplify otherwise highly complex statically interactions. Two analyses were carried out for the total number of megalopae and each of the two most abundant species. These analyses had to be separate as the levels in factor "Moon" were not present in each of the spring tides. The analyses were therefore designed to test for effects of spring tide in conjunction with the other factors and a separate analysis it was necessary to run to test for effects of new/full moon in conjunction with the other factors. The first analysis considered the effect of the factors "Spring Tide" (21 levels), "Zone" (2 levels) and "Day/Night" (2 levels) which were fixed and orthogonal while "Site" (2 levels) was random. Variances of response variables to "Site", "Zone" and "Day/Night" were homogeneous for *P. guttatum*, while variances of response variables to "Site" and "Day/Night" were homogenous for *P. catenata* and the total number of megalopae (PERMADISP, $P > 0.05$). Under square root transformations, variances of response variables to "Spring Tide" for *P. guttatum, P. catenata* and the total number of megalopae while the response variable to "Zone" was heterogeneous for *P. catenata* and the total number of megalopae (PERMDISP, $P < 0.05$) (Table 3.2). The effect of new or full moon was analysed separately as each spring tide involved either a new or a full moon only. In this case the factors "Moon" (2 levels), "Zone" (2 levels) and "Day/Night" (2 levels) were fixed and orthogonal, while "Site" (2 levels) was random. Variances of response variables to "Moon", "Site", "Zone" and "Day/Night" for *P. guttatum*, were homogeneous while variances of response variables to 'Site", "Moon" and "Day/Night" were homogenous for *P. catenata* and only variances of response variables to "Site" and "Day/Night" were homogenous for the total number of megalopae (PERMADISP,

P> 0.05). Under square root transformations, variances of response variables to "Zone" were heterogeneous for *P. catenata* and "Site" and "Zone" for the total number of megalopae (PERMDISP, *P*< 0.05) (Table 3.3).

For Kenya, analyses were likewise conducted on the total number of megalopae as well as the two most abundant megalopal species collected (*Perisesarma guttatum* and *Neosarmatium africanum*). Again, these analyses were conducted separately to reduce complexity. The data collected from the Kenyan sites were asymmetric, with 12 spring tides being sampled in Gazi Bay while four spring tides were sampled in Shirazi Creek. The factors "Spring Tide" (12 levels), "Zone" (2 levels) and "Day/Night" (2 levels) were fixed and orthogonal, while "Site" (2 levels) was random. Variances of response variables to "Site" and "Day/Night" were homogeneous for *P. guttatum* and the total number of megalopae (PERMADISP, *P*> 0.05). Under square root transformations, variances of response variables to "Spring Tide" and "Zone" were heterogeneous for the total number of megalopae and *P. guttatum* (PERMDISP, *P*< 0.05) (Table 3.4). Analyses comparing Gazi Bay and Shirazi Creek involved the factors "Spring Tide" (12 levels), "Zone" (2 levels), "Day/Night" (2 levels), were fixed and orthogonal, while "Site" (2 levels) was random, $n = 4$ (Table 3.4). Again, the effect of moon was considered separately. The factors "Moon" (2 levels), "Zone" (2 levels), "Day/Night" (2 levels) were fixed and orthogonal, while "Site" (2 levels) was random. Variances of response variables to "Site" and "Day/Night" were homogeneous for *P. guttatum*, *N. africanum*, and the total number of megalopae (PERMADISP, *P*> 0.05). Under square root transformations, variances of response variables to "Moon" and "Zone" were heterogeneous for *P. guttatum*, *N. africanum* and the total number of megalopae (PERMDISP, *P*< 0.05) (Table 3.5).

3.3 Results:

The Bold Taxon ID Tree that was used to confirm identifications made using keys in the literature as included in appendix 6.3. The tree was constructed using the Kimura 2 Parameter Distance model based on COI – 5P nucleotide markers (http:/www.boldsystems.org, Ratnasingham and Herbert 2006). This tree was used to successfully confirm 27 identifications by matching genetic samples from the recruits to genetic samples from adult specimens collected in the South African mangals.

During the 12 spring tides that occurred between 9 August 2010 and 24 January 2011, a total of 96 megalopal recruits were collected in the *Avicennia marina* and *Rhizophora mucronata* bands of the Gazi Bay and Shirazi Creek mangrove ecosystems (Figure 3.2). Both Shirazi Creek and Gazi Bay were sampled throughout the first four spring tides, during which Gazi bay yielded the highest number (16 megalopae; Figure 3.2). The peak in settlement occurred over the 8th spring tide. During this tide, megalopae settled in both zones at both sites but only in Gazi bay. The 3rd spring tide was the only one to receive megalopae settling in both zones at both sites (Figure 3.2).

Over the remaining eight spring tides between 21 October 2010 and 24 January 2011 only Gazi Bay was sampled, yielding 67 megalopae. The 8th spring tide had the highest peak settlement with a combined total of 32 megalopae settling in the *Avicennia marina* and *Rhizophora mucronata* zones (Figure 3.2) and the 9th and 12th spring tides also had settlement in both zones (Figure 3.2). Settlement occurred in one zone on the 5th (*R. mucronata*), 9th (*R. mucronata*), 10th (*R. mucronata*) and 11th (*A. marina* zone) spring tides, while no settlement was recorded on the 7th spring tide (Figure 3.2).

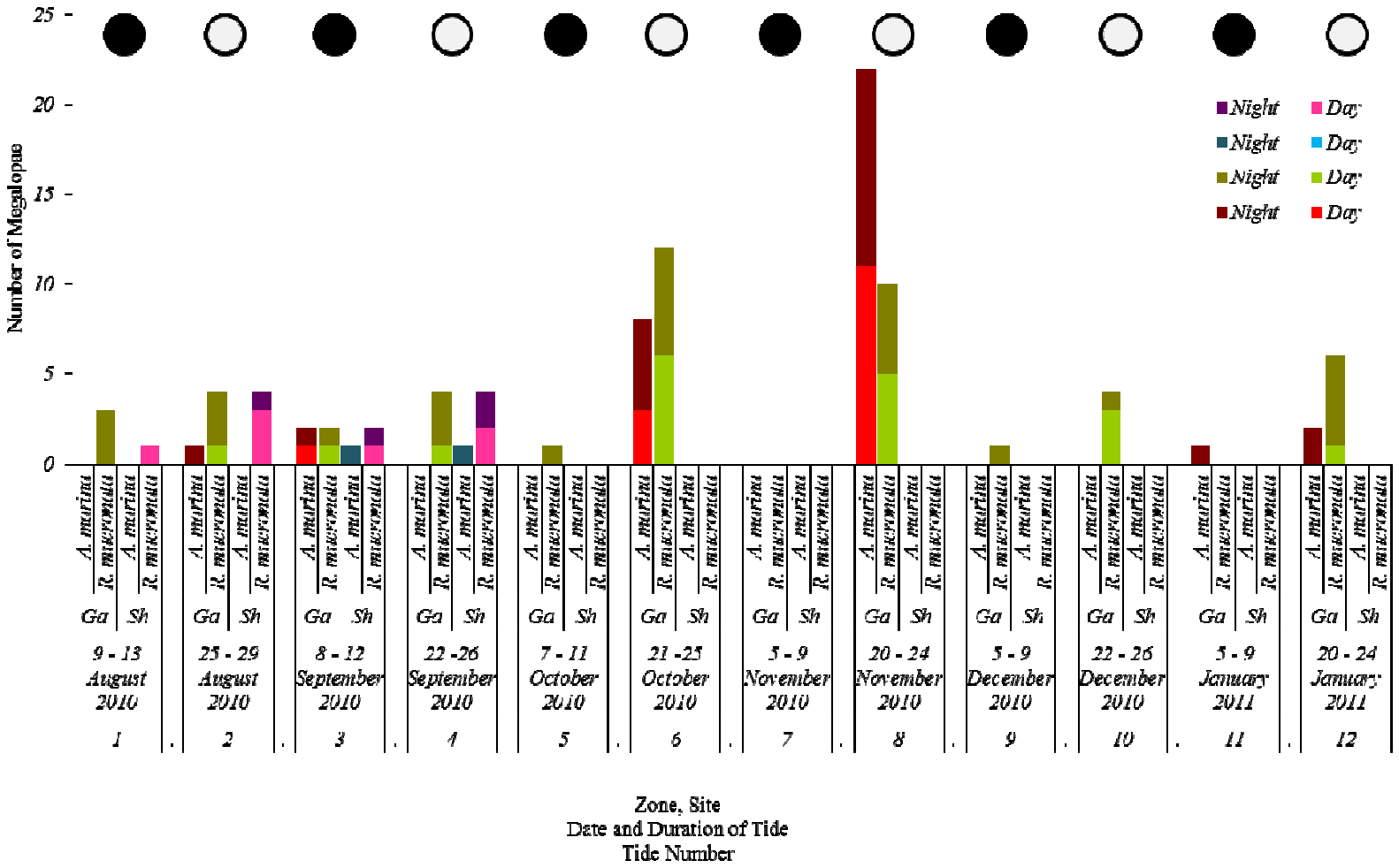

Figure 3.2: Total number of megalopae settling in *Avicenna marina* and *Rhizophora mucronata* zones at Gazi Bay (Ga) and Shirazi Creek (Sh) in Kenya during spring tides from August 2010 until January 2011 and August 2010 until September 2010 respectively. Light shades indicate megalopae settling during diurnal spring tides, dark shades indicate megalopae settling during nocturnal spring tides. Dark Circles indicate new moon spring tides, white circles indicate full moon spring tides. Note that no measurements were made for Shirazi after 7-11 October.

The *Avicennia marina* and *Rhizophora mucronata* zones in the Mngazana and Mntafufu estuaries, South Africa were sampled during 21 spring tides spanning 2010 and 2011, yielding a total of 579 megalopae. Megalopae settled in both zones at both sites over the 1st, 3rd, 4th, 8th, 9th, 10th, 19th and 20th spring tides (Figure 3.3). Megalopae settled only in the Mngazana estuary over the 12th spring tide, while only Mntafufu received megalopae on two occasions, over the 7th and 14th spring tides (Figure 3.3). Both sites received no settlers over the 15th, 16th and 17th spring tides (Figure 3.3). Overall, the *A. marina* zone at the Mngazana site recorded the highest number of recruits over the 21 spring tides sampled, with 345 megalopae, and the single greatest settlement event in this zone occurred over the 20th spring tide (230 megalopae). The *R. mucronata* zone at the Mngazana site received the fewest megalopae at 41 (Figure 3.3), while the *A. marina* and *R. mucronata* zones at the Mntafufu estuary each received 97 and 96 megalopae respectively.

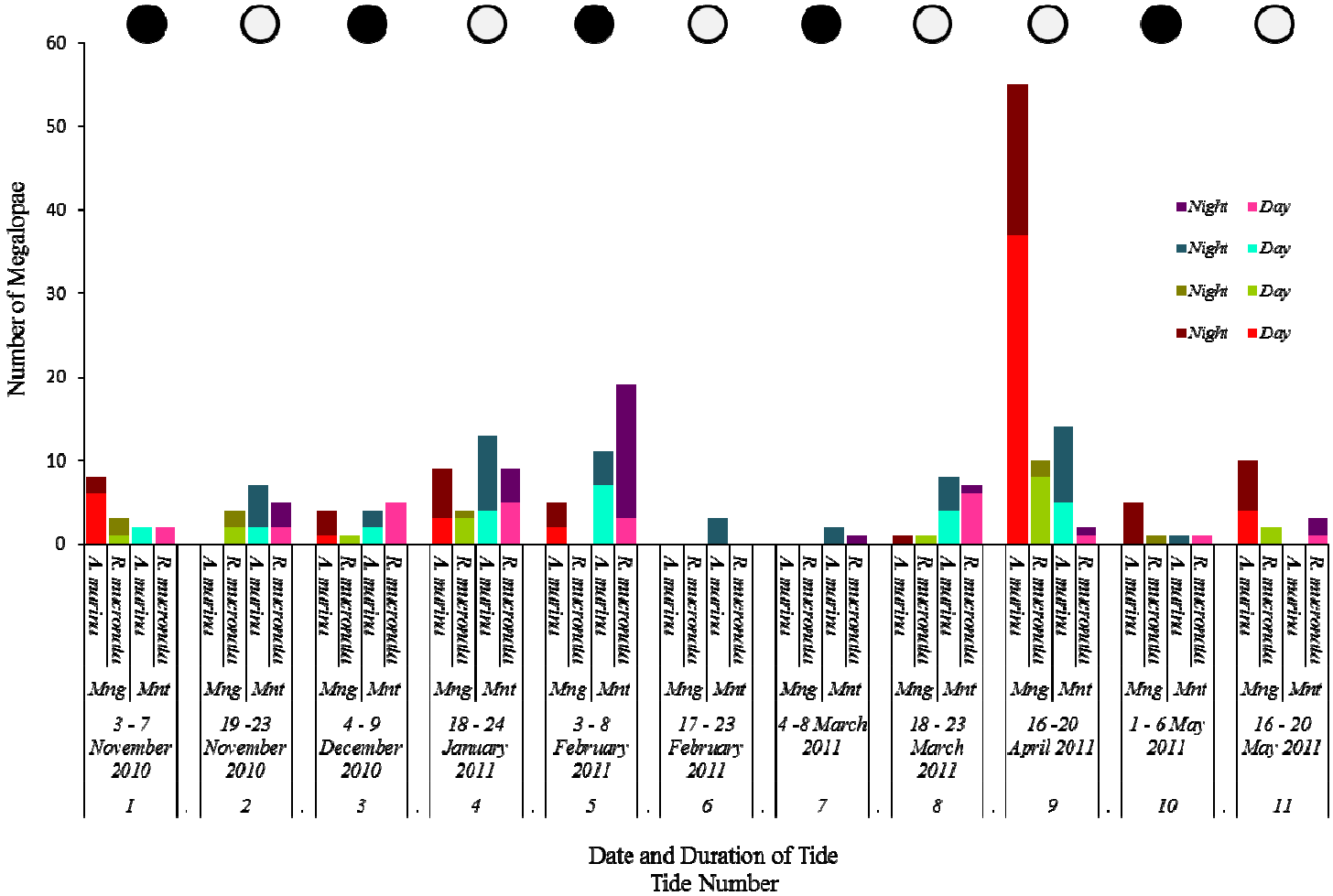

Figure 3.3: Total number of megalopae settling in *Avicennia marina* and *Rhizophora mucronata* zones at each of the two mangal sites Mngazana (*Mng*) and Mntafufu (*Mnt*) in the Transkei, South Africa during spring tides from November 2010 until October 2011. Light shades indicate megalopae settling during diurnal spring tides, dark shades indicate megalopae settling during nocturnal spring tides. Dark Circles indicate new moon spring tides, white circles indicate full moon spring tides.

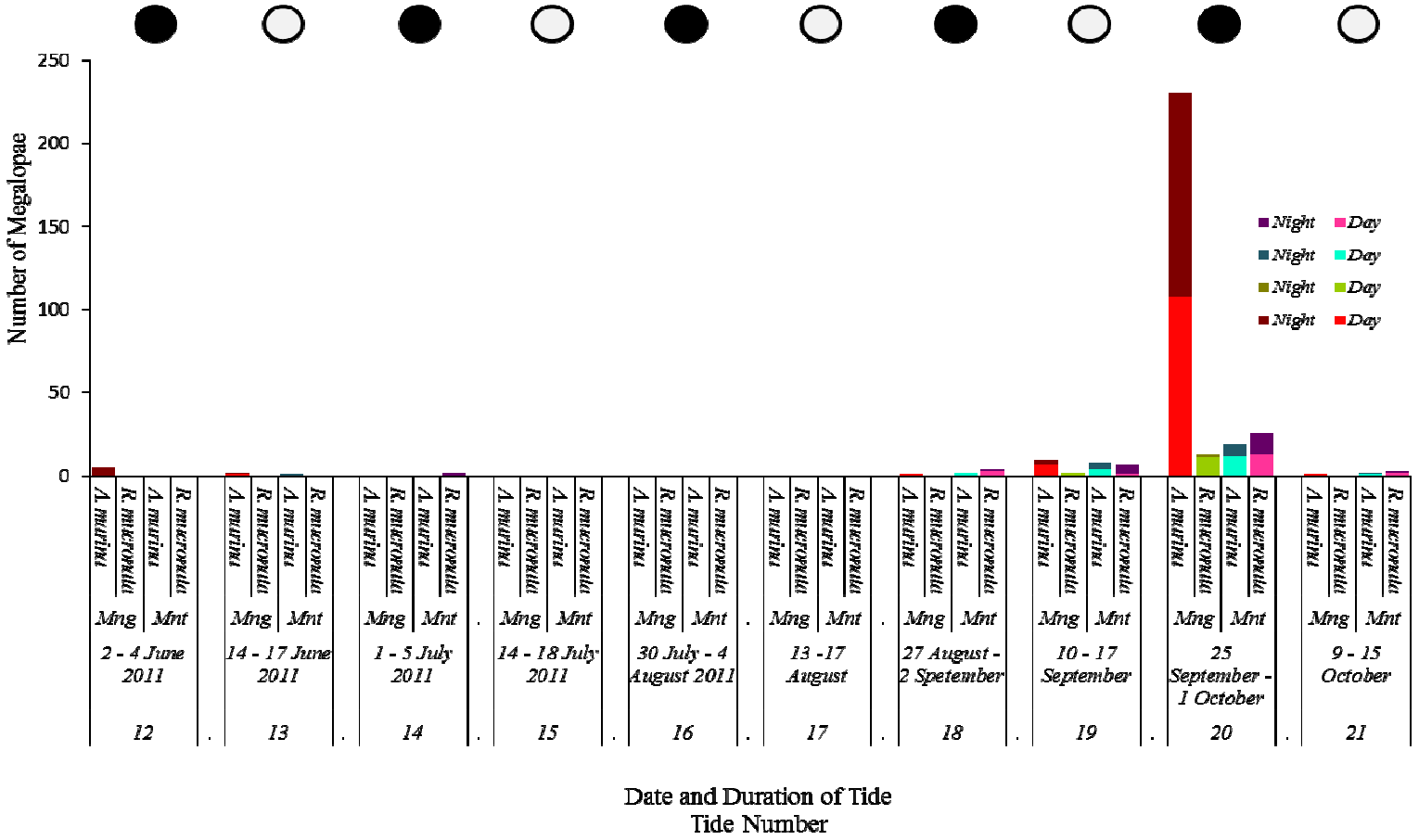

Figure 3.3 continued: Total number of megalopae settling in *Avicennia marina* and *Rhizophora mucronata* zones at each of the two mangal sites Mngazana (*Mng*) and Mntafufu (*Mnt*) in the Transkei, South Africa during spring tides from November 2010 until October 2011. Light shades indicate megalopae settling during diurnal spring tides, dark shades indicate megalopae settling during nocturnal spring tides. Dark Circles indicate new moon spring tides, white circles indicate full moon spring tides.

Overall, interactions of Region and Zone, and Region and Moon had significant effects on megalopal settlement between South Africa and Kenya. On a finer scale, within each region, highly complex interactions affected megalopal settlement. South Africa had the most variability, with settlement being affected by all factors tested, while settlement in Kenya was slightly less complex. In this and the following sections, probability levels refer to the result of Pairwise tests at an alpha level of 0.05 unless otherwise stated. Interactions among factors that did not have significant results across total megalopal, *Perisesarma guttatum* or *Parasesarma catenata* recruits were excluded from the statistical tables to reduce the length of tables.

Regional comparisons:

There were two significant 2-way interactions in the comparison of pooled megalopal taxa between regions: Region x Zone and Region x moon (Table 3.1). South Africa had significantly more megalopae than Kenya in the *Rhizophora mucronata* zone ($P < 0.01$), while there was no difference in the *Avicennia marina* zone. Within South Africa, there were significantly more megalopae in the *A. marina* than the *R. mucronata* zone, while in Kenya the opposite was true. Regarding the Region x Moon interaction, there were significant differences between South Africa and Kenya for both the new and full moon phases, but within Kenya numbers were higher during the full than the new moon ($P < 0.001$), with no such difference in South Africa. Individually, the main factors Region, Day/Night and Zone were not significant (Table 3.1).

Table 3.1: Regional analyses. PERMANOVA tables comparing the total number of megalopae between Kenya and South Africa. Levels of significance are indicated as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

		Total Megalopae	
Source	d.f.	M.S.	Pseudo-*F*
Region = Re	1	0.26	2.82
Zone = Z	1	29.1 E^{-2}	0.31
Moon	1	0.85	9.02**
Day/Night =D/N	1	5.93E^{-2}	0.63
Re x Z	1	1.11	11.891***
Re x M	1	1.74	18.64***
Residual	912	7.08E^{-2}	
Total	927		

South Africa, analyses for settlement among spring tides:

There was a significant 3-way interaction affecting settlement of pooled megalopal taxa and *Parasesarma catenata* megalopae as well as two 2-way interactions, while *Perisesarma guttatum* settlement was affected by multiple 3 and 2-way interactions.

Total megalopae:

There was a significant interaction among all three factors (Spring tide, Site and Zone; Table 3.2). Settlement of megalopae differed significantly in the *Avicennia marina* zone between Mngazana and Mntafufu over five spring tides and over two in the *Rhizophora mucronata* zone. At Mngazana, there were significant differences between zones over four spring tides, while at

Mntafufu, zones only differed over one spring tide. At Mngazana, spring tide had a significant effect on the total number of megalopae for 90 and 30 of the possible 210 spring tide comparisons for the *A. marina* and *R. mucronata* zones respectively. For Mntafufu, the values were 78 and 73 respectively, indicating more frequent zone effects at Mngazana. The three main factors were not significant (Table 3.2).

Perisesarma guttatum:

Settlement of *Perisesarma guttatum* was affected by all possible 3 and 2-way interactions (Table 3.2). As a result, the findings were complex, including some effects that were statistically significant, but not necessarily biologically meaningful. For example, sites may have differed in one zone during some spring tides, but not others. During night tides, significantly more megalopae settled in the *Avicennia marina* zone at Mngazana, while in the *Rhizophora mucronata* zone, significantly more settled at Mntafufu with no difference during the day. At Mngazana, the *A. marina* zone received significantly more settlers during the night, while in the *R. mucronata* zone, significantly more settled during the day. At Mntafufu there was no effect of day/night tides on settlement between the zones.

Over spring tides 9 and 20, there was significantly greater settlement in the *Avicennia marina* zone at Mngazana than Mntafufu. In contrast, settlement in the *Rhizophora mucronata* zone at Mntafufu was significantly greater than Mngazana, but only over spring tide 5 (Figure 3.3). At Mngazana, settlement was significantly greater in the *A. marina* zone over spring tide 9 compared with the *R. mucronata* zone. At Mngazana, significant effects of spring tide was noted for 33 and 0 of the 210 possible comparisons for the *A. marina* and *R. mucronata* zones respectively, while at Mntafufu, the values were 0 and 15 respectively.

Mngazana received significantly more settlers than Mntafufu during the night over spring tides 9 and 20, but there was no difference in settlement between sites during the day. At Mntafufu significantly more megalopae arrived over diurnal than nocturnal high tides during spring tide 5. At Mngazana, significant effects of spring tide were found for 16 and 30 of 210 possible comparisons for the diurnal and the nocturnal high tides respectively. At Mntafufu, the values were 0 and 16 respectively.

Parasesarma catenata:

There was a significant interaction among Spring tide, Site and Zone (Table 3.2). Settlement differed significantly between Mngazana and Mntafufu over six spring tides in the *Avicennia marina* zone and one spring tide in the *Rhizophora mucronata* zone. The *A. marina* zone received significantly more settlers than the *R. mucronata* zone over three spring tides at Mngazana and one tide at Mntafufu. At Mngazana, significant effects of spring tide was noted for 95 and 26 of 210 possible comparisons for the *A. marina* and the *R. mucronata* zones respectively ($P < 0.05$), while at Mntafufu, the values were 48 and 38 respectively. Individually the factors Site, Zone and Day/Night did not have any effect on the settlement patterns of *Parasesarma catenata* megalopae (Table 3.2).

Table 3.2: South Africa, Mngazana and Mntafufu analyses for Spring Tide. PERMANOVA tables comparing the settlement of (a) the total megalopae (all species), (b) *Perisesarma guttatum* megalopae and (c) *Parasesarma catenata* megalopae at Mngazana and Mntafufu estuaries, South Africa. Levels of significance are indicated as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

		(a) Total Megalopae		(b) *Perisesarma guttatum*		(c) *Parasesarma catenata*	
Source	d.f.	M.S.	Pseudo-*F*	M.S.	Pseudo-*F*	M.S.	Pseudo-*F*
Spring Tide = ST	20	1.29	3.98**	$6.99E^{-2}$	1.97	0.90	4.06***
Site = S	1	$2.57E^{-3}$	5.33	$1.18E^{-3}$	0.11	$5.79E^{-2}$	0.61
Zone = Z	1	1.41	1.20	$2.98E^{-2}$	0.32	0.60	0.58
Day/Night = D/N	1	$6.59E^{-4}$	$1.28E^{-2}$	$1.69E^{-4}$	$5.94\ E^{-3}$	$6.65E^{-3}$	$2.65E^{-2}$
ST x S	20	0.32	6.71***	$3.55E^{-2}$	3.23***	0.22	4.98***
S x Z	1	1.17	24.29***	$9.26E^{-2}$	8.41**	1.19	26.93***
ST x S x Z	20	0.26	5.32***	$2.19E^{-2}$	1.99**	0.24	5.60***
ST x S x D/N	20	$7.07\ E^{-2}$	1.46	$2.20E^{-2}$	2.00**	$5.56E^{-2}$	1.26
ST x Z x D/N	20	$5.61\ E^{-2}$	1.14	$3.66E^{-2}$	2.13*	$2.59E^{-2}$	0.79
S x Z x D/N	1	$2.00E^{-2}$	0.41	$4.56E^{-2}$	4.14*	$1.00E^{-2}$	0.23
Residual	504	$4.83\ E^{-2}$		$1.10E^{-2}$		$4.41E^{-2}$	
Total	671						

South Africa, analysis of Moon Phase:

There were significant 3-way and 2-way interactions affecting settlement of pooled megalopal taxa, while *Perisesarma guttatum* and *Parasesarma catenata* settlement was affected by a significant 2-way interaction (Table 3.3).

Total megalopae:

At Mngazana, significantly more megalopae settled during the new moon in the *Avicennia marina* zone, while significantly more megalopae settled in the *Rhizophora mucronata* zone during the full moon (Figure 3.3). During new moon tides significantly more megalopae settled in the *A. marina* zone at Mngazana compared to Mntafufu while the *R. mucronata* zone received significantly more settlers at Mntafufu (Figure 3.3).

Perisesarma guttatum and *Parasesarma catenata*:

Significantly more *Perisesarma guttatum* megalopae settled during the new moon compared with the full moon. *Parasesarma catenata* settlement was unaffected by moon phase. As discussed, there was a significant effect of the of Site x Zone interaction on the settlement of *P. guttatum* and *P. catenata* but individually, the main factors Site, Zone and Day/Night were not significant (Tables 3.2, 3.3).

Table 3.3: South Africa, Mngazana and Mntafufu analyses for Moon Phase. PERMANOVA tables comparing the settlement of (a) the total megalopae (all species), (b) *Perisesarma guttatum* megalopae and (c) *Parasesarma catenata* megalopae at Mngazana and Mntafufu estuaries, South Africa. Levels of significance are indicated as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

		(a) Total Megalopae		(b) *Perisesarma guttatum*		(c) *Parasesarma catenata*	
Source	d.f.	M.S.	Pseudo-*F*	M.S.	Pseudo-*F*	M.S.	Pseudo-*F*
Moon = M	1	0.16	2.57	$3.99E^{-4}$	295.43*	0.16	6.10
Site = S	1	$1.49E^{-3}$	$1.40E^{-2}$	$1.17E^{-3}$	$7.62E^{-2}$	$2.96E^{-2}$	0.34
Zone = Z	1	1.43	1.14	$2.78E^{-2}$	0.29	0.71	0.56
Day/Night = D/N	1	$7.68E^{-4}$	$1.93E^{-2}$	$1.96E^{-5}$	$6.57E^{-5}$	$2.83E^{-3}$	$4.21E^{-4}$
S x Z	1	1.25	11.63***	$9.49E^{-2}$	6.17*	1.26	14.76***
M x S x Z	1	0.50	4.71*	$7.52E^{-3}$	0.49	0.52	6.03
Residual	656	0.11		$1.54E^{-2}$		$8.55E^{-2}$	
Total	671						

Kenya, analyses for settlement among spring tides:

Pooled megalopae were affected by a significant 2-way interaction between Spring Tide and Zone, while *Perisesarma guttatum* was affected by a significant 3-way interaction (Table 3.4).

Total megalopae:

Significantly more megalopae settled in the *Rhizophora mucronata* zone than the *Avicennia marina* zone over spring tide 4. Spring Tide had a significant effect on the total number of megalopae settling in 48 and 14 of the 66 spring tide comparison combinations for the *A. marina* and *R. mucronata* zones respectively. The main factors Site, Zone and Day/Night had no effect on total settlement in Kenya (Table 3.4).

Perisesarma guttatum:

Perisesarma guttatum megalopae were affected by an interaction of the factors Site, Zone and Day/Night (Table 3.4). At Gazi bay during night high tides, there were significantly more megalopae settling in the *Rhizophora mucronata* zone than the *Avicennia marina* zone, while at Shirazi Creek, significantly more megalopae settled in the *R. mucronata* zone than the *A. marina* zone during day high tides. Spring Tide had a significant effect on the total number of megalopae settling in 44 of the 66 possible spring tide comparisons. The main factors Site and Day/Night had no effect on the number of *P. guttatum* megalopae settling in Kenya (Table 3.4).

Table 3.4: Kenya, Gazi Bay and Shirazi Creek analyses for Spring Tide. PERMANOVA tables comparing the settlement of (a) the total megalopae (all species) and (b) *Perisesarma guttatum* megalopae at Gazi Bay and Shirazi Creek, Kenya. Levels of significance are indicated as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

		(a) Total Megalopae		(a) *Perisesarma guttatum*	
Source	d.f.	M.S.	Pseudo-*F*	M.S.	Pseudo-*F*
Spring Tide = ST	11	0.46	32.92***	0.21	19.31*
Site = S	1	$3.80E^{-3}$	$9.16\ E^{-2}$	$2.41E^{-3}$	$7.21\ E^{-2}$
Zone = Z	1	0.10	40.51	0.37	412.04**
Day/Night =D/N	1	$1.84E^{-3}$	$2.88E^{-2}$	$6.20E^{-3}$	7.57
ST x Z	11	$5.99E^{-2}$	15.34*	$3.14E^{-2}$	2.73
S x Z x D/N	1	$8.93E^{-2}$	2.15	0.13	3.99*
Residual	192	$4.15E^{-2}$		$3.35E^{-2}$	
Total	255				

Kenya, Gazi Bay and Shirazi Creek analyses for Moon Phase:

There was a significant 2-way interaction and single factor affecting settlement of pooled megalopal taxa, while *Perisesarma guttatum* was affected by a 2-way significant interaction. *Neosarmatium africanum* showed no significant effects (Table 3.5).

Total megalopae:

There was a significant Moon x Site interaction for total megalopae (Table 3.5). During the full moon, significantly more megalopae settled in Gazi Bay than Shirazi Creek (Figure 3.2), but no significant differences between the two sites were observed during new moon tides. In Gazi Bay,

significantly more megalopae settled during full moon tides (Figure 3.2), while settlement in Shirazi Creek was unaffected. Overall, significantly more megalopae settled in the *Rhizophora mucronata* zone than the *Avicennia marina* zone (Table 3.5) (Figure 3.2).

Perisesarma guttatum:

Settlement of *Perisesarma guttatum* megalopae was affected by an interaction of Moon and Zone (Table 3.5). Pairwise tests could not determine the nature of this interaction. The main factors Site and Day/Night had no effect on settlement patterns of *P. guttatum* (Table 3.5).

Table 3.5: Kenya, Gazi Bay and Shirazi Creek analyses for Moon Phase. PERMANOVA tables comparing the settlement of (a) the total megalopae (all species), (b) *Perisesarma guttatum* megalopae and (c) *Neosarmatium africanum* megalopae at Gazi Bay and Shirazi Creek, Kenya. Levels of significance are indicated as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

		(a) Total Megalopae		(b) *Perisesarma guttatum*		(c) *Neosarmatium africanum*	
Source	d.f.	M.S.	Pseudo-*F*	M.S.	Pseudo-*F*	M.S.	Pseudo-*F*
Moon = M	1	0.82	3.60	0.51	9.79	$4.66E^{-2}$	1
Site = S	1	0.13	2.50	$1.24E^{-2}$	0.34	$6.16E^{-2}$	3.72
Zone = Z	1	0.33	5.55*	0.62	92.9	$4.66E^{-2}$	1
Day/Night =D/N	1	$2.59E^{-2}$	0.64	$6.18E^{-3}$	0.20	$9.12E^{-3}$	1
M x S	1	0.22	4.37*	$5.17E^{-2}$	1.43	$4.66E^{-2}$	2.82
M x Z	1	$9.02E^{-2}$	5.60	0.21	217.66*	$3.37E^{-2}$	1
Residual	240	$5.18E^{-2}$		$3.62E^{-2}$		$1.66E^{-2}$	
Total	255						

3.4 Discussion:

Settlement patterns of mangrove brachyuran megalopae differed between the centre and edge of their distribution. Analyses indicate that regional variability in settlement is likely to be driven by moon phase and/or zone, as separately, interactions of Region and Zone, and Region and Moon influenced megalopal settlement. Specifically, differences between regions were noted for

the *Rhizophora mucronata* zone, but not the *Avicennia marina* zone. Although Kenya and South Africa both host mangrove species common to the East African region, the mangals themselves are quite different in coastal location, appearance and species composition. South African mangals include fewer species and are limited to estuaries (Quisthoudt *et al.* 2013). Kenyan mangals, such as those found at Gazi bay and Shirazi Creek, are more extensive, species rich and are generally more exposed to open coastal dynamics though they are still influenced by estuarine factors (Kitheka and Mwashote 1997, Spalding *et al.* 1997, Dahdouh-Guebas *et al.* 2000, Cannicci *et al.* 2009). These differences may affect settlement patterns of megalopae, as South African megalopae are restricted to narrow bands of habitable space located within estuaries while Kenyan species can exploit large expanses of mangal in which to settle.

My data mostly supports the stratified patterns of megalopal settlement described by other authors for mangals along the east coast of Africa (Paula *et al.* 2003, Ragionieri *et al.* 2015). Vertical zonation within intertidal ecosystems is a common occurrence and extends from rocky shores (e.g. Moorjani 1982, Bustamante and Branch 1996) to estuaries. For example, grapsoid crabs exhibit vertical zonation within estuarine systems (Hartnoll 1975, Willason 1981, Frusher *et al.* 1994, Flores *et al.* 2002) and several authors have described brachyuran zonation in mangals (Emmerson 1994, Ruwa 1997, Dahdouh-Guebas *et al.* 2002). Zonation of brachyurans in mangals is thought to be linked to the zonation of mangal vegetation (Dahdouh-Guebas *et al.* 2002). Chemical cues play an important role in helping crabs locate suitable habitat; these cues often come in the form of chemical odours emitted from conspecifics or habitat forming species (Paula *et al.* 2001, Kingsford *et al.* 2002, Forward *et al.* 2003, Anger 2006, Diele and Simith 2007). Floral zonation within the mangal is the result of complex interactions of biotic and abiotic factors (Naidoo 1985, Smith 1992, Clarke and Myerscough 1993, Dahdouh- Guebas *et al*. 1998, Dahdouh-Guebas *et al.* 2002). Given that settling megalopae rely on conspecific and

habitat chemical cues for locating suitable nursery habitats (Forward *et al.* 2001, Paula *et al.* 2001, Kingsford *et al.* 2002, Anger 2006, Diele and Simith 2007), it is no surprise that zone generally had a significant effect on settlement patterns.

Species specific zone preferences emerged in both South Africa and Kenya. Although species were not considered, Ragionieri *et al.* (2015) also describe stratified settlement patterns in a Kenyan mangrove. In Kenya, the settlement of both dominant crab species collected during the study was influenced by zone, while a similar pattern emerged for *Parasesarma catenata* and the pooled taxa settling in South Africa. *Perisesarma guttatum* and *Neosarmatium africanum* show distinct zonation in Kenya (Skov 2001, Ólafsson *et al.* 2002, Gillikin and Schubart 2004), as does *P. catenata* in South Africa (Emmerson 1994). Previous studies have shown that conspecifics provide chemical cues for settlement in many decapod species (e.g. Forward *et al.* 2001, Paula *et al.* 2001, Kingsford *et al.* 2002, Forward *et al.* 2003, Anger 2006, Diele and Simith 2007). Conspecifics thus attract new settlers to suitable habitat, this is the likely case for *N. africanum* and *P. guttatum* in Kenya and *P. catenata* in South Africa. In the case of pooled megalopal settlement in Kenya, the lack of zonation indicates that pulses of megalopae reaching the mangals are species diverse and possibly exploit the two selected zones for settlement uniformly.

Settling megalopae may utilise alternate habitat adjacent to adult habitats as settlement/nursery areas before relocating to the preferred habitat (Spivak *et al.* 1994, Flores and Negreiros-Fransozo 1999, Diele 2000, Paula *et al.* 2001). In these cases, cues other than conspecific odours may induce settlement (Forward *et al.* 2003, Anger 2006, Diele and Simith 2007), although sediments adjacent to adult habitats may retain conspecific chemical cues due to their soluble

nature inducing megalopal settlement away from parental habitat (O'Connor 1991, O'Conner and Van 2006). Mobile decapods have the option to migrate at a later stage following settlement, making the initial selection of settlement habitat less critical than for sessile species (Moksnes *et al.* 2003, Moksnes 2004, Anger 2006). Studies in Mozambique suggest that megalopae settle in nursery areas and then migrate to suitable adult habitat after the first moult (Paula *et al.* 2001). *P. guttatum* megalopae in South Africa lacked a preference between zones when settling. This could be due to the compressed nature of the mangal. The ubiquitous distribution of conspecific odours may cause extensive settlement with migration to suitable nursery areas at a later stage or the ability of the megalopae to use both zones as nursery areas, with adults migrating to the lower *R. mucronata* zone for the completion of their life cycle (e.g. Paula *et al.* 2001).

Lunar phase (new moon/full moon) played an important role in the timing of settlement of megalopae in both regions, although its effects were not consistent in space or among species as also recently found by Ragionieri *et al.* (2015). Settlement of several brachyuran species has been shown to be influenced by the state of the tide (spring vs neap) or an interaction of tide and other factors in both temperate and tropical localities (e.g. Temperate: Mense *et al.* 1995, Pereira *et al.* 2000, Tropical: Moser and Macintosh 2001, Paula *et al.* 2001, Ragionieri *et al.* 2015). In most cases, recruitment is greater during tides associated with either new or full moon phases, but differences between new versus full moon spring tides is usually overlooked (e.g. Paula *et al.* 2001, 2003, 2004, Flores *et al.* 2002). Although, in some previous studies decapod settlement was greater during new moon than full moon spring tides (e.g. Acosta and Butler 1999, Pereira *et al.* 2000, Papadopoulos *et al.* 2002), this comparison has rarely been made (Skov *et al.* 2005). Settlement patterns associated with new/full moon were, however, recently described by Ragioneiri *et al.* (2015), indicating that specific sites in the mangal receive settlers during either new or full moon spring tides, but causal factors for these preferences were not addressed in

detail. Synchrony of settlement with new moon flood tides allows megalopae to avoid visual predators that rely on moonlight to locate food sources (e.g. Acosta and Butler 1999, Papadopoulos *et al.* 2002). These ideas apply to mangals in both South Africa and Kenya as they both experience high amplitude nocturnal flood tides during the new and full moon phases. Furthermore, the effect of lunar phase acts in conjunction with environmental factors such as wind, temperature, hydrodynamics and tidal amplitude which would all be unique to a specified study area, thus influencing settlement patterns and suggesting complex relationships between biological and physical processes over different temporal and spatial scales (e.g. Mense *et al.* 1995, Paula *et al.* 2003). Due to the scarcity of peaks in settlement a real effect of moon was hard to detect, as the outcome of the tests would be driven by when those peaks occurred in which region and site.

Spring tide significantly affected the settlement of megalopae in both regions. The significance of spring tide simply reflects temporal variability in settlement rates. Variability in time is, of course, expected with each spring tide being subjected to a unique set of conditions including weather conditions, hydrodynamics, wind stress, temperatures and salinities. Such variability has been documented in numerous studies in both temperate and tropical areas (e.g. Mense *et al.* 1995, Pereira *et al.* 2000, Moser and Macintosh 2001, Paula *et al.* 2001, 2003, 2004, Flores *et al.* 2002, Ragionieri *et al.* 2015). Only the megalopae of *Neosarmatium africanum* were significantly affected by an interaction involving spring tide and zone in Kenya. *N. africanum* exhibits clear zonation in mangals (Emmerson 1994, Skov 2001, Ólafsson *et al.* 2002) and settlement has been noted to occur in the upper *Avicennia marina* zone where adults burrow (Paula *et al.* 2003). Additionally, breeding periods are specific for this species and vary temporally between each region (Emmerson 1994, Skov 2001). These aspects of population

biology are likely to affect settlement patterns in such a way that both zone and spring tide are highly important.

Settlement in South Africa appears to be much more variable. Significant interactions between spring tide and site, and spring tide and zone were common for megalopae of *Perisesarma guttatum*, *Parasesarma catenata* and the pooled taxa. Furthermore, additional interactions were observed involving all factors in various combinations. During the migration from the pelagic environment back to the estuarine mangals, post larvae are likely to encounter many "complicating" and interacting factors. In Mozambican mangals, wind stress in conjunction with spring tides was found to have an important influence on settlement patterns of brachyuran megalopae (Paula *et al.* 2001, 2003) and the importance of wind stress on its own has previously been highlighted (e.g. Clancy and Cobb 1997, Eggleston *et al.* 1998, Xie and Eggleston 1999). Behaviour is also important in settlement as organisms respond to external stimuli (Kingsford *et al.* 2002) such as light (Moser and Macintosh 2001) and habitat/conspecific odours (Forward *et al.* 2001, Paula *et al.* 2001, Forward *et al.* 2003, Anger 2006, Diele and Simith 2007). The variability in delivery of post larvae/megalopae to estuaries is therefore likely to be high and dependent on the prevailing conditions and associated stimuli at the time. Heterogeneityof data may be due to poor capture rates (low numbers: more patchiness), short sampling duration in Kenya or an insufficient number of collectors per site, driving non-significance and significance (through possible type 1 error).

As a contrast to South Africa, the homogeneous nature of the Kenyan coastline with moderate, continuous mangal cover in this area (Spalding *et al.* 1997, Dahdouh-Guebas *et al.* 2000) could possibly make the delivery of megalopae relatively physically uniform among sites, reducing

site-specific effects in this region. On the other hand, settlement in South Africa seemed to be spatially highly variable, with many significant interactions between site and other factors. Spatial variation in settlement of marine organisms with pelagic larvae is a common occurrence (Navarrete *et al.* 2008). Transportation to suitable habitat generally relies on wind forcing and tides as larval swimming is insufficient to counteract tidal currents (Shanks 2006, Queiroga *et al.* 2007), although vertical migration is often used to control dispersal, particularly in estuarine systems (e.g. Provenzano *et al.* 1983). Spatial variation of brachyuran megalopae settlement has been detected in other temperate regions and is generally attributed to coastal hydrodynamics associated with wind stress (e.g. Flores *et al.* 2002) and wind stress itself has been noted to affect the temporal supply of megalopae to tropical mangal sites in Mozambique (Paula *et al.* 2001, 2003). In South Africa it has been suggested that delivery of pelagic larvae is a product of hydrodynamics interacting with near shore topography (McQuaid and Lawrie 2005, Porri *et al.* 2006), which would also influence the spatial supply of megalopae to the two study estuaries.

Although significant interactions of nocturnal and diurnal flood tide in combination with other factors affected settlement in both Kenya and South Africa, and the importance of nocturnal versus diurnal tides for the settlement of larvae has been highlighted in the literature (Christy and Morgan 1998, Christy 2003, Paula *et al.* 2004), nocturnal/diurnal tides were not shown to be important for settlement in South Africa or Kenya. Ragioieri *et al.* (2015) also indicate that there is a lack of nocturnal/diurnal preference in their study in a Kenyan mangal. When each of these systems was analysed separately, settlement patterns were not shaped by differences between nocturnal and diurnal flood tides. This is surprising given the amount of literature dedicated to the observation of these trends (e.g. Morgan and Christy 1994, 1996, 1997, Hovel and Morgan 1997, Paula *et al.* 2001, Christy 2003) and the sound theory behind the behavioural avoidance of transportation to settlement areas during diurnal flood tides due to predator avoidance (Morgan

and Christy 1994, 1996, 1997, Hovel and Morgan 1997, Christy 2003). Mangrove ecosystems are known to be important nursery areas for juvenile and young planktivorous fish that feed during daylight hours (Whitfield 1993) and predation has been shown to have significant effects on settlement of lobsters (Acosta and Butler 1999). Some authors have however shown a lack of relationship between settlement of megalopae and nocturnal/diurnal timing of the tide. *Uca* spp. abundances decrease during diurnal tides (Dittel and Epifanio 1990) and day light negatively affect their swimming behaviour, decreasing the likelihood of them being present in the water column (Tankersley *et al.* 1995, Moser and Macintosh 2001). Moser and Macintosh (2001) suggest that low light penetration into the water column can prevent exogenous light cues acting on ocypodid megalopae, controlling behavioural swimming activities and thus abundance in the water column during nocturnal/diurnal flood tides. Short developmental times and favourable predation pressure for one species over another can however also negate the need for settlement during nocturnal flood tides (van Montfrans *et al.* 1990). Others have found that megalopae are retained in estuarine environments due to not reaching full settlement competency by the time they reach suitable habitat (Paula *et al.* 2004), and consequently they may be delivered at times that do not coincide with typical settlement preferences. A lack of nocturnal patterns may again be a result of low capture numbers and insufficient collectors, influencing the significance of the results through type 1 errors.

This study indicates that regional variability is a result of either zonal preference and/or behavioural responses to lunar phase by settling megalopae. Species prevalent in the *Rhizophora mucronata* zone seemed to drive the zonal variations between regions. In relation to lunar phase, brachyuran species inhabiting temperate mangal distributions show a preference for settlement during new moon spring tides as opposed to full moon spring tide preference exhibited by species associated with tropical mangals. Temporal variability was common within both regions,

this is not unexpected as this is a general characteristic of brachyuran larval supply (e.g. Mense *et al.* 1995, Pereira *et al.* 2000, Moser and Macintosh 2001, Paula *et al.* 2001, 2003, Flores *et al.* 2002). Spatial variability in settlement was more evident in the temperate mangals than in tropical Kenya. Spatial variability in larval delivery has been well documented for the southern African coastline (e.g. McQuaid and Lawrie 2005, Porri *et al.* 2006), while this same aspect is relatively unstudied in tropical east Africa and in this study was somewhat unimportant. The effect of nocturnal vs diurnal settlement was minor in this study and rarely important in South Africa, while almost completely lacking in Kenya, a surprising finding given previous findings (e.g. Morgan 1995, Christy and Morgan 1998, Christy 2003, Paula *et al.* 2004) but falls in line with findings by Ragionieri *et al.* (2015). Although the mangals stretching across this latitudinal gradient host cosmopolitan botanical and brachyuran species, variability in settlement patterns are prolific and likely due to local stochastic events associated with weather, hydrodynamics, physical, chemical conditions and species specific behavioural responses to these events. Overall, within region (South Africa or Kenya), settlement seems to be the product of zonal preference, behavioural response to lunar phase and temporal variability in larval supply and in South Africa only, settlement is further influence by spatial variability in suitable habitat. On a larger scale, spanning degrees of latitude, lunar phase and zonal preference within the mangal seem to be the predominant factors influencing settlement.

CHAPTER 4

MODELLING AT THE CENTRE AND EDGE OF DISTRIBUTIONAL RANGES: INVESTIGATING REPRODUCTIVE OUTPUTS OF MANGROVE MACROBENTHOS

4.1 Introduction:

Anthropogenic climate forcing has been identified as a major threat to biodiversity and is predicted to cause mass extinction of vulnerable species globally (Thomas *et al*. 2004a, Pereira *et al*. 2010, Dawson *et al*. 2011, Bellard *et al*. 2012, Cahill *et al*. 2012). Biological responses to warming are mediated/initiated by an organism's physiological sensitivity to temperature change (Bernardo *et al.* 2007, Calosi *et al.* 2007, Deutsch *et al.* 2008). Species responses depend on the relationships between physical and chemical factors, organismal level processes and population dynamics (Somero 2002, Hofmann *et al*. 2005, Pörtner and Langenbuch 2005, Helmuth *et al.* 2006). These responses include proximate cascading effects, which include changes in morphology, behaviour and physiology of adults, propagules and larvae, changes in the population sizes of interacting species, interaction strengths, emergent effects such as micro-evolutionary changes, distributional shifts and changes in diversity (Harley *et al.* 2006, Helmuth *et al.* 2006).

Mangrove ecosystems are particularly vulnerable to environmental change as they inhabit the narrow transition area between the marine and terrestrial environments in low to high latitudinal coastal regions and are thus affected by the complex interactions of a multitude of chemical and physical stressors (Alongi 2008, Nagelkerken *et al.* 2008). Not only are these systems economically valuable in terms of the products (e.g. wood and fisheries) and services (e.g. storm protection, flood control) they provide (Wells *et al*. 2006, Gilman *et al.* 2008), but are highly diverse and contribute to the functioning of nearby systems, especially in their role as nursery habitats and in the maintenance of coastal water quality (Mumby *et al.* 2004, Nagelkerken *et al.* 2008). To survive in an environment that is affected by complex physio-chemical factors, the mangrove fauna has evolved specialised adaptations and strategies which have often resulted in impressive levels of diversity and biomass, for example, among mangrove crabs (Hartnoll *et al.* 2002, Fratini *et al.* 2005, Duke *et al.* 2007, Mukherjee *et al.* 2012, Vermeiren and Sheaves 2012). The role of these macrobenthic species has been recognised as crucial to the ecological functioning of mangrove forests, as they perform a host of ecosystem functions, including soil aeration, bioturbation, the enhancement of microbial activity and the control of plant recruitment (Cannicci *et al.* 2008).

A means of predicting and assessing the vulnerability of species under a changing climate regime has become critical. There is already an abundance of evidence highlighting and documenting the detrimental effects of climate change on species in a multitude of systems (e.g. Thomas *et al*. 2004a, Pereira *et al*. 2010, Dawson *et al*. 2011, Bellard *et al*. 2012, Cahill *et al.* 2012, Doney *et al*. 2012, IPCC 2014a, b, c, d). These effects are evident from local extinctions and contractions at the edges of species' ranges, which are most obvious at low latitudes and low elevations (Cahill *et al.* 2012). Proximate causes of these contractions and extinctions are not well identified within the literature that addresses climate change (Cahill *et al.* 2012) and, while

it is thought that physiological intolerance of increasing temperatures is the most obvious causation of local extinctions or loss of biodiversity (e.g. Deutsch *et al.* 2008, Somero 2010), especially for sessile organisms or organisms with limited thermoregulatory ability, there seems to be multiple contributing or alternate factors so that physiological tolerances cannot be solely held accountable (Cahill *et al.* 2012). Nevertheless, one of the most important factors controlling invertebrate growth, reproduction, development, and recruitment dynamics is undoubtedly temperature (O'Connor *et al*. 2007).

The standard metabolic rate (SMR) has been suggested as a good indicator of fitness for ectothermic and endothermic organisms responding to temperature, with the magnitude of change in metabolic rate over a temperature range being important (Crnokrak and Roff 2002, Nespolo *et al.* 2005, Nespolo and Franco 2007, Lardies *et al.* 2008). From SMR, the thermal sensitivity (Q_{10}) of a species or population can be determined (Nespolo *et al.* 2003). Thermal sensitivity (Q_{10}) is an individual trait that reflects the ability of an organism to change its metabolic rate over a range of temperatures and provides information on an organism's performance with implications for maintenance requirements and overall energy budgets (Ashby 1998, Nespolo *et al.* 2003, Lardies *et al.* 2008). Traditionally, Q_{10} values are calculated over a 10ºC temperature change (Schmidt-Nielsen 1995), however, studies in the literature support the calculation of Q_{10} values over narrower ranges and several authors utilise Q_{10} values for different sections of the temperature range in their studies (e.g. Thomas *et al.* 1999, Nespolo *et al.* 2003, MacMillan *et al.* 2013, Sinclair *et al.* 2013). Typical biological Q_{10} values are between 2.0 – 3.0 and values outside this are considered to be associated with some form of metabolic stress as either insufficient or excess oxygen is consumed for standard respiratory enzymatic reactions to occur (Withers 1992, Lloyd and Taylor 1994, Kirschbaum 2000, Atkin and Tjoelker 2003, Sinclair *et al.* 2013). The assessment of an organism's performance over a range of temperatures

can provide significant insights into its vulnerability or resilience in the face of climate change, particularly when the performance of individual life stages can be assessed to identify the weakest physiological bottlenecks in the life cycle.

Individual Based Models (IBMs) are simulation models that consider unique individuals interacting with each other and responding or adapting to their environment (Grimm and Railsback 2005). IBMs have thus proliferated as a useful tool for understanding ecological systems and forecasting the consequences of environmental change (see, e.g. DeAngelis and Gross 1992, Shugart *et al.* 1992, Grimm 1999, DeAngelis and Mooij 2005, Grimm and Railsback 2005), an objective which has been highlighted as being imperative by several authors (e.g. Harley *et al.* 2006, Cahill *et al.* 2012). The organisms described by the models have, as in nature, discrete characteristics such as age, weight or social rank that may vary during the course of an individual's lifetime (Huston *et al.* 1988). More recently, an exact definition of IBMs has been harder to settle on (DeAngelis and Mooij 2005, Grimm and Railsback 2005). In ecology, IBMs are used to simulate populations composed of individual organisms or groups of similar organisms with independent traits (DeAngelis and Mooij 2005). The processes described by IBMs account for individual variability and allow individual interactions or behaviours to influence responses to external inputs such as precipitation, flooding or temperature increase. IBMs operate differently to classical differential-equation and difference equation mathematical models by allowing local interactions as opposed to using differential equations averaged, according to the mean field theories (DeAngelis and Mooij 2005, Grimm *et al.* 2006). This allows researchers to study how the adaptive behaviour of individuals affects properties along the hierarchical steps within a system, or how these properties may affect individuals at each level, and use this information to address the hypotheses of the model (Railsback 2001, Strand *et al.* 2002, Grimm *et al.* 2006).

Many authors have recognised that, with rapid regional and global climate change, ecological forecasting is imperative (e.g. Clarke *et al.* 2001, Jeltsch *et al.* 2008, IPCC 2014a, b, c, d). As the use of IBMs is expanding and incorporating more facets of ecology, it will become integral in the forecasting of changes in ecosystems in response to anthropogenic climate change. IBMs dealing with plant dynamics, for example, constitute a large proportion of the existing literature and have been reviewed extensively (Ford and Sorrensen 1992, Shugart *et al.* 1992, Wyszomirski *et al.* 1999, Jeltsch *et al.* 2008). Plant population modelling dealing directly with climate change has expanded rapidly since the 1990s (Jeltsch *et al.* 2008), but models concerning fauna seem to be less abundant, with a large proportion focusing on fish shoaling and population dynamics which again have been comprehensively reviewed (DeAngelis *et al.* 1990, van Winkle *et al.* 1993, Tyler and Rose 1994). As things stand, a substantial proportion of IBMs incorporate climate change (e.g. Choi *et al.* 2004, Willis *et al.* 2006, Berger *et al.* 2008), but a limited number deal with mangrove ecosystems and these are mostly restricted to botanical aspects (e.g. Berger and Hildenbrandt 2000, Doyle *et al.* 2003, Berger *et al*. 2008). Few concern brachyurans (e.g. Bunnell and Miller 2005, Piou *et al.* 2007) and to my knowledge no IBMs deal with the population dynamics associated with the fauna found in mangrove ecosystems in relation to climate change. This is a serious lacuna given the importance of the mangrove ecosystem and the critical ecological role of crabs in these systems. Consequently, in the absence of a model dealing with these aspects in the face of climate change, I designed a model for assessing Changing Reproductive Dynamics (CReDy) of mangrove crabs in relation to climate change. The CReDy model seeks to use physiological thermal sensitivity (Q_{10}) to temperature change to predict the reproductive output of mangrove crabs. Using the CReDy model I aim to project the different reproductive output of populations from the centre and edge of their distributions exposed to different scenarios of increased temperature.

4.2 Methods:

The thermal tolerance of *Perisesarma guttatum* was investigated across several ontogenetic stages at the centre (Kenya) and edge (South Africa) of its distribution. Metabolic rates of female adult crabs, gravid female adult crabs, early (e2) and late (e4) stage eggs were measured along a thermal gradient (19ºC to 35ºC) in both air and water (full details in Chapter 3). Their thermal sensitivities (Q_{10} values) were then determined by using the equation $Q_{10} = (V2/V1)^{10/(T2 - T1)}$ in which V2 and V1 are the specific oxygen consumption rates at the respective temperatures T2 and T1 (Schmidt-Nielsen 1983, Hochachka and Somero 1984, Schmidt *et al.* 2009). This method was used for different thermal brackets (see the parameterisation section of the CReDy model documentation below) and used as proxies for fitness of the individual females and eggs respectively. Q_{10} values between 2 and 3 (not thermally stressed) were assumed to have no negative effects on brooding or egg development while values < 2 or > 3 (thermally stressed) (Kirschbaum 2000, Atkin and Tjoelker 2003, Sinclair *et al.* 2013) were assumed to adversely affect brooding and egg development (see design concepts section below).

The following section describes the CReDy model in relation to temperature change for the mangrove crab *P. guttatum.* I follow the standard protocol for describing Individual Based Models as proposed by Grimm *et al.* (2006, 2010), all programming (hence text below for the description of the model) was done using NetLogo programming language (Wilensky 1999)

4.2.1 Overview, Design concepts and Details (ODD):

1. Purpose:

The purpose of the model is to assess the effect of thermal sensitivity (Q_{10}) on specific ontogenetic life stages of the crab *Parasesarma guttatum* at localities at the centre and edge of its geographical distribution. Each ontogenetic state has a unique set of Q_{10} values governing decisions with respect to progression to the next stage according to a temperature and milieu profile measured for *P. guttatum* habitat in Kenya and South Africa respectively.

This model specifically focuses on the effect of increasing temperature and associated thermal sensitivity on:

I. The production of eggs (by female crabs).
II. Females carrying eggs to hatching.
III. The survival of eggs independently of the females.

The output of the model is the reproductive output (hatched larvae) per m^2 of mangrove forest for the species studied at each locality.

2. Entities, state variables, and scales:

The model considers 2 Breeds:

- Adult females
- Eggs

State variables:

Adult females are characterised by two state variables: [f-state] and [size]. [f-state] characterises two possible states, “f” meaning adult females without eggs or “fo” meaning adult females carrying eggs. [size] specifies the carapace width, normally distributed (mean – 20.5, standard deviation (sd) ± 1.83).

Eggs are characterised by a single state variable [e-state]. Two states are possible: “e2” indicates eggs in the first part of the developmental stage and “e4” indicates eggs in the last part of the developmental stage. The early developmental stages of the egg (e2) covers the first 10 days of a spawning cycle, while the late developmental stage of the egg (e4) covers the last 9 days of a spawning cycle, up until hatching (Skov 2001).

Environmental variables:

The environmental variables used within the model were temperature [°C] (applies to temperature in air or water, mean hourly values for a 19 day period) and milieu [Air or Water] (empirical measurements over a 19 day period).

Spatio-Temporal Scales:

Temperature changes in the landscape on an hourly basis.

The landscape goes through roughly two tidal cycles a day (two high and two low tides, with tidal heights inputted at hourly intervals for a 19 day period).

One time step is 1 hour, time interval at which the model updates itself.

One simulation is 19 days, equivalent to a spawning cycle for *P. guttatum* (Flores *et al.* 2002, Skov *et al.* 2005).

A simulation run stops after 1 spawning cycle (due to data availability).

The models thus uses two counters:

Hour (1…24) to define a day.

Days (1…19) to define a spawning cycle.

The model is spatially explicit.

Assumptions/limitations:

All females are sexually mature and have the ability to lay eggs. They do not grow during a simulation. The model scales up from a single agent to the density ascribed to each specific region according to region-specific density data (Flores *et al.* 2002, Hartnoll *et al.* 2002). Density can be freely chosen in the parameterization section. Typical values for the study sites are: 3.1 (SE ± 0.41) individuals*m^{-2} of *Rhizophora mucronata* in Kenya and 1.73 (SE ± 0.51) individuals*m^{-2} of *R. mucronata* in South Africa.

The landscape is inundated with water approximately every six hours, according to tidal cycles.

3. Process overview and scheduling:

Figure 4.1 shows the sub-models and their scheduling in logical order.

Initialise:

Produces females (f), according to the densities in their respective regions.

Females laying eggs (f):

Females without eggs assess the temperature and milieu on an hourly basis throughout a 19 day spawning cycle. If they encounter a temperature that is related to a favourable Q_{10} (>2 but <3) the probability of laying eggs remains at 100%. If they encounter a temperature that is related to an unfavourable Q_{10} (<2 or 3<) the probability of her laying eggs is decreased (probability principle). Q_{10} values vary depending on region (Table 2 & 3). At the end of the 19 day cycle they lay eggs with a certain probability (Generate eggs sub-model). Females (f) then either become gravid females (fo) or fail to produce eggs and revert back to f under the Revert to f sub-model.

Females carrying eggs (fo):

Females carry eggs according to the same probability principle previously mentioned, and are represented by Carry eggs sub-model. Q_{10} values vary depending on region (Table 4 & 5). If the probability of the females carrying eggs reaches 0% they abort the attempt and return to being non-gravid females (Revert to f sub-model) this can happen at any time during the 19 day cycle. The number of gravid females carrying the eggs to hatching is then counted and forms the first output of the model.

Early developmental stage eggs (e2):

Early developmental stage eggs assess the temperature and milieu on an hourly basis throughout the first 10 days of the 19 day spawning cycle (Skov 2001), and using the probability principle adjust probabilities accordingly, represented by the Grow e2 sub-model. Q_{10} values vary depending on region (Table 6). If the probability of the progression to e4 reaches 0% the eggs die (Die sub-model), this can happen at any time in the first 10 days.

Late developmental stage eggs (e4):

Late developmental stage eggs assess the temperature on an hourly basis throughout the last 9 days of the 19 day spawning cycle (Skov 2001) and adjust probabilities accordingly, represented by the Grow e4 sub-model. Q_{10} values vary depending on region (Table 7). If the probability of the progression to hatching reaches 0% the eggs die (Die sub-model), this can happen at any time in the last 9 days. At the end of the last 9 days, late stage developmental eggs with a probability greater than 0% then hatch under the Hatch sub-model. The number of e4 eggs hatching is then counted and forms the second output of the model. The total reproductive output of the model is therefore the cumulative result of Output 1 * Output 2. All sub-models and related parameterizations are outlined in detail in the Sub-models section of the ODD.

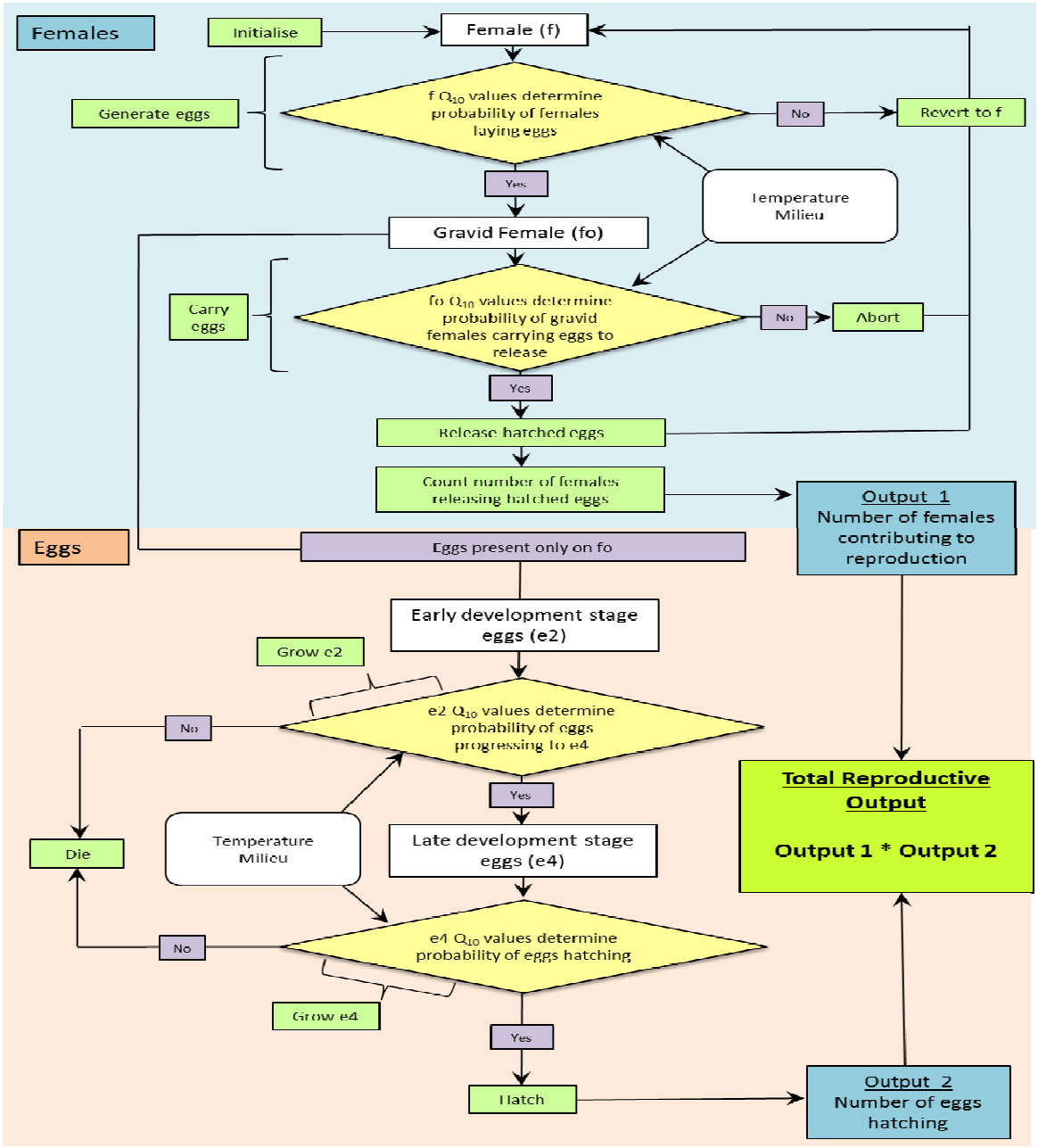

Figure 4.1: Simplified schematic overview of the processes incorporated in the Changing Reproductive Dynamics (CReDy) model in relation to temperature, white rectangles indicate life cycle stages considered in the model, yellow diamonds show parameterised values that determine the probability of progression from one life cycle stage to the next, light green rectangles indicate the processes (sub-models) undertaken by each life stage, rounded white rectangles represent the external environmental inputs that affect the probabilities of progressing from one life stage to another, purple rectangles show the general information and outcomes of progression probabilities pertaining to the model. Blue rectangles show the output of the model for both the females and eggs and the lime green rectangle indicates the total output of the model after a simulation.

4. Design concepts:

As a proxy for using metabolic rates to determine the scope for aerobic performance, the thermal sensitivity (Q_{10} values) of females, females carrying eggs and eggs at different developmental stages were calculated for different temperature ranges in different milieus (water/air). The Q_{10} values (thermal sensitivity of the animals) are temperature driven physiological responses that vary depending on milieu. Q_{10} values are calculated from empirical data and are specific to air or water and female condition and egg developmental stage (see Sub-models section of the ODD, Table 2 - Table 7). Each female state has a unique set of Q_{10} values determined for different temperatures and milieus (Table 3 - 6; Sub-model section) governing decisions with respect to laying or carrying eggs to release, as does each developmental stage of the embryos (Table 6 & 7; Sub-model section) for progressing to the next developmental stage. The model translates each of these Q_{10} values into a theoretical probability of laying eggs, carrying eggs until they hatch (for female) and progression of eggs from one stage to the next stage (for egg), according to an external file containing in-situ temperature and milieu profiles measured for *P. guttatum* habitat in Kenya and South Africa respectively.

The model inputs temperature and milieu (external input files) and selects the corresponding Q_{10} values (see Sub-models section of the ODD, Table 2 - Table 7). Q_{10} values invoked by temperature and milieu are then used to calculate the proportion of females that lay eggs or females with eggs that carry them to release (at any given time). This information, in combination with the data from eggs progressing from the early to late developmental stage and to hatching, will provide the total reproductive output of the system for the species.

Sensing

Females and eggs sense temperature within a given milieu and respond according to rules set out by Q_{10} values.

Stochasticity

The following functions are modelled assuming they are partly random, based on some stochasticity applied to empirical data from the current study and published literature (Table 4.1):

Agent density

Initial size distribution

Number of eggs produced

Proportion of females aborting / releasing eggs

Proportion of eggs progressing to e4 / hatching

Collectives

There are no collectives in this model.

Observation

The data collected from the model comprises of:

I. The number of females laying eggs.

II. The number of females carrying eggs to release.

III. The number of eggs progressing from early developmental stages to hatching.

The data is collected at the end of a spawning cycle allowing the calculation and comparison of the overall reproductive output between regions.

5. Initialization:

To start the simulations, set locality to Kenya or South Africa. Agents within the landscape are randomly distributed at their respective densities of 1.21 females*m^{-2} (SE ± 0.16) for Kenya and 0.68 females*m^{-2} (SE ± 0.20) for South Africa (MEAM 2001, PUMPSEA 2007). The size of the females is normally distributed (mean = 20.5, sd = ± 1.83; assumption). At initialisation females do not have eggs.

The model starts on the low tide of the first day of a spawning cycle during the reproductive season in either Kenya or South Africa.

```
to setup
  set locality
            [
               Kenya
               South Africa
             ]
end
ask agents [
        distribute randomly
        if locality = Kenya [set agent density 1.21 (SE ± 0.16) individuals*m-2 ]
        if locality = South Africa [set agent density 0.68 (SE ± 0.20) individuals*m-2 ]
        set size [set size according to a normal distribution between 15 and 26 mm ]
        set agents = f [all females start without eggs ]
            ]
end
```

Table 4.1: Details of input data and references for the established sub-model.

	Kenya	South Africa	Comments
Density	Mean = 1.21 (SE ± 0.16) individuals*m^{-2} of *R. mucronata*	Mean = 0.68 (SE ± 0.20) individuals*m^{-2} of *R. mucronata*	Densities obtained from MEAM (2001) and PUMPSEA (2007) projects
Sex ratio	Male:Female 1.56:1	Male:Female 1.56:1	Estimated from data presented by Flores *et al.* (2002), this sex ratio was then verified by comparing the M:F sex ratios for two closely related Sesarmids from South Africa; *S. catenata* 2.34:1 and *C. eulimene* 2.13:1 respectively
Size class	normal distribution mean = 20.5 sd = ± 1.83	normal distribution mean = 20.5 sd = ± 1.83	Females are sexually mature at approximately 15 mm carapace width and largest specimens found have a carapace width of 26mm (Flores *et al.* 2002). The size class distribution is assumed to be normal between these carapace widths with a mean of 20.5 mm and a standard deviation of 1.83mm as no data is available in this respect for *P. guttatum.* However, the size class distribution of a closely related Sesarmid from South Africa, *N. africanum*, was found to be normal (Emmerson 1992). Effects of size class distribution were tested using uncertainty analysis (Railsback and Grimm 2012).

6. Input data:

Temperature data (recorded empirical mean in-situ hourly values (ºC), over a 19 day period in the *R. mucronata* zone of the mangrove) for Kenya or South Africa.

Milieu data (water or air) over a 19 day period in the *R. mucronata* zone of the mangrove for Kenya or South Africa.

7. Sub-models:

to **generate eggs**

- Female (f) checks temperature and milieu every hour throughout a 19 day spawning cycle.
- If external input file indicates "air" use Q_{10} values for air (Table 4.2 & 4.3).
- If external input file indicates "water" use Q_{10} values for water (Table 4.2 & 4.3).
- If the temperature is unfavourable (f Q_{10} caused by temperature falls outside 2-3) the probability of laying eggs is decreased by a theoretical 0.001 in the next time step.
- If the temperature is favourable (f Q_{10} caused by temperature falls inside 2-3) the probability of laying eggs remains the same as it was in the previous time step.
- At the end of the 19 day spawning cycle the female sums the probability of laying eggs.
- If the probability is 0 she does not lay eggs and remains f.
- If the probability is >0 she lays eggs and becomes fo.
- If generate eggs = true (create agents (e2) according to regression for either Kenya or South Africa)

- Female generates eggs according to size, using y = 620.78x + 2505.7 for South Africa and y = 765.45x – 7972.2 for Kenya, where y is the number of eggs produced and x is the carapace width in millimetres (mm).
- end

The equations used for generating eggs according to female size is derived from a regression analysis whereby specimens were collected and the number of eggs was plotted against carapace width. Linear Regresion analyses are included in appendix 6.4. All Q_{10} values were calculated from experimental data (Chapter 3) using the equation $Q_{10} = (V2/V1)^{10/(T2 - T1)}$ and are as follows.

Table 4.2: South African Q_{10} values for non-gravid females (f) in air and water.

	Temperature 19 – 23ºC	Temperature 23 – 29ºC	Temperature 29 – 35ºC
South Africa f Q_{10} Air	6.73	0.91	2.35
South Africa f Q_{10} Water	9.86	4.53	2.45

Table 4.3: Kenyan Q_{10} values for non-gravid females (f) in air and water.

	Temperature 27 – 31ºC	Temperature 31 – 37ºC
Kenya f Q_{10} Air	0.65	0.94
Kenya f Q_{10} Water	11.11	1.91

to **carry eggs**

- Gravid female (fo) checks temperature and milieu every hour throughout a 19 day spawning cycle. If external input file indicates "air" use Q_{10} values for air (Table 4.4 and Table 4.5).
- If external input file indicates "water" use Q_{10} values for water (Table 4.4 and Table 4.5).
- If the temperature is unfavourable (fo Q_{10} caused by temperature falls outside 2-3) the probability of carrying eggs is decreased by a theoretical 0.001 in the next time step.
- If the temperature is favourable (fo Q_{10} caused by temperature falls inside 2-3) the probability of carrying eggs remains the same as it was in the previous time step.
- At the end of the 19 day spawning cycle the female sums the probability of carrying eggs.
- If the probability is 0 she aborts carrying the eggs and reverts back to f.
- If the probability is > 0 she releases hatched eggs and reverts back to f.
- end

Table 4.4: South African Q_{10} values for gravid females (fo) in air and water.

	Temperature 19 – 23ºC	Temperature 23 – 29ºC	Temperature 29 – 35ºC
South Africa fo Q_{10} Air	11.50	2.20	3.67
South Africa fo Q_{10} Water	4.86	4.15	2.12

Table 4.5: Kenyan Q_{10} values for gravid females (fo) in air and water.

	Temperature 27 – 31ºC	Temperature 31 – 37ºC
Kenya fo Q_{10} Air	2.55	0.85
Kenya fo Q_{10} Water	0.91	1.12

to **release eggs**

- count number of fo at the end of the spawning cycle (females carrying e4 eggs at day 19)
- record the number of fo at the end of the spawning cycle (Output 1)
- all fo at end of spawning cycle now become f
- end

to **grow e2**

- e2 eggs check temperature and milieu every hour throughout the first 10 days of the 19 day spawning cycle.
- If external input file indicates “air” use Q_{10} values for air (Table 4.6).
- If external input file indicates “water” use Q_{10} values for water (Table 4.6).
- If temperature is unfavourable (e2 Q_{10} caused by temperature falls outside 2-3) the probability of progressing to the late developmental egg stage (e4) is decreased by a theoretical 0.001 in the next time step.
- If the temperature is favourable (e2 Q_{10} caused by temperature falls inside 2-3) the probability of progressing to the late developmental egg stage (e4) remains the same as it was in the previous time step.
- At the end of the first 10 days of the spawning cycle the e2 sums the probability of progressing to the late developmental egg stage (e4).
- If the probability is 0 the e2 eggs dies.
- If the probability is > 0 the e2 eggs progress to e4 eggs.
- If the fo associated with e2 eggs becomes f, the e2 eggs die (abort)
- end

Table 4.6: Q_{10} values for eggs during the first stage of their development (e2) in air and water for both Kenya and South Africa.

	Temperature 19 – 23ºC	Temperature 23 – 29ºC	Temperature 29 – 35ºC
e2 Q_{10} South Africa Air	6.39	1.26	1.74
e2 Q_{10} South Africa Water	3.50	4.11	2.00
e2 Q_{10} Kenya Air	6.21	3.48	2.12
e2 Q_{10} Kenya Water	4.84	3.67	2.73

to **grow e4**

- e4 eggs check temperature and milieu every hour throughout the last 9 days of the 19 day spawning cycle.
- If external input file indicates “air” use Q_{10} values for air (Table 4.7).
- If external input file indicates “water” use Q_{10} values for water (Table 4.7).
- If the temperature is unfavourable (e4 Q_{10} caused by temperature falls outside 2-3) the probability of progressing to hatching is decreased by a theoretical 0.001 in the next time step.
- If the temperature is favourable (e4 Q_{10} caused by temperature falls inside 2-3) the probability of progressing to hatching remains the same as it was in the previous time step.
- At the end of the last 9 days of the spawning cycle the e4 sums the probability of progressing to the late developmental egg stage (e4).
- If the probability is 0 the e4 eggs dies.
- If the probability is > 0 the e4 eggs progress to hatching (hatch).

- If the fo associated with e4 eggs becomes f, the e4 eggs die (abort)
- end

Table 4.7: Q_{10} values for eggs during the second stage of their development (e4) in air and water for both Kenya and South Africa.

	Temperature 19 – 23ºC	Temperature 23 – 29ºC	Temperature 29 – 35ºC
e4 Q_{10} Kenya Air	10.45	2.71	4.20
e4 Q_{10} South Africa	0.84	1.02	2.96
e4 Q_{10} Kenya Water	6.59	1.08	2.20
e4 Q_{10} South Africa Water	2.78	0.67	4.74

to **hatch**

- count number of e4 eggs that hatch at the end of the spawning cycle (day 19 of the spawning cycle)
- end

For full CReDy model code as implemented in Netlogo 5.0.3 (Wilensky 1999) see Appendix 6.6

Model Procedure:

The simulations conducted in this chapter are run under a temperature increase of 6ºC for Africa as forecasted by RCP 8.5 (Moss *et al.* 2010, Riahi *et al.* 2011). This increase also covers scenarios outlined by RCP 2.6, RCP 4.5 and RCP 6 which forecast increases of <2ºC, 3-4ºC and

4-5ºC respectively (Wayne 2013, IPCC 2014a, c). RCP 8.5 is characterised by assumptions of high population growth with modest rates of technological change affecting emissions and energy intensity improvements in the absence of climate change policies (Moss *et al.* 2010, Riahi *et al.* 2011, IPCC 2014a, c). This RCP projects the highest greenhouse emissions and greatest temperature increase by 2100 (Moss *et al.* 2010, Riahi *et al.* 2011, IPCC 2014a, c). Experiments based on changes of 1ºC per hour have been extensively used to make inferences concerning long term effects of climate change on species (e.g. Lannig *et al.* 2004, Pörtner and Farrel 2008, Pörtner 2009, Fusi *et al.* 2014, Rummer *et al.* 2014). Simulations were run on empirical environmental data for South Africa and Kenya and then for the increasing temperature scenarios, at 1ºC intervals, from their in-situ temperature measurements to a 6ºC increase under RCP 8.5.

Simulations were conducted for over a 38 day period; during the first 19 days the model simulated females generating eggs, while over the second 19 day period the model simulated females carrying eggs, and eggs progressing from one stage to the next. This procedure was performed using specific temperature (in-situ) and tide profiles for each respective region in South Africa and Kenya and replicated 100 times (n = 100). To assess the potential for each variable parameter within the model to alter the final simulated output a local Sensitivity Analysis was then conducted on the CReDy model (Railsback and Grimm 2012). Parameters that affected the output of the model were identified and the model was firstly run with the reference parameters (P) as identified in the ODD protocol producing the final output of number of hatched eggs (C). Thereafter, the parameter was varied by d (+/-5%) giving dP and the model was run for positively and negatively varied parameters of ($P + dP$) and ($P - dP$) giving C^+ and C^- respectively. Sensitivity (S) was calculated as an approximation of the partial derivative of the

number of hatched eggs with respect to the parameter for sensitivity above and below (+/- 5%) (Railsback and Grimm 2012) the parameters reference value which in this case was:

$S^+ = (C^+ - C)/(dP/P)$ and $S^- = (C - C^-)/(dP/P)$

Results are presented in Table 4.8.

Subsequently, the temperature profile was changed by adding 1ºC to each temperature data point (in-situ + 1) and the simulations were repeated as above. The simulations were conducted over the following temperature profiles: in-situ, in-situ + 1, up to in-situ + 6ºC with an n = 100 for each respective region and at each respective temperature (Temperature profiles used in the model are included in appendix 6.5). This procedure was initially conducted on females with a normal size class distribution and subsequently the modelling procedure was repeated on females that had a uniform size class distribution for both regions at all projected temperatures. Comparisons between final model outputs (hatched eggs) of uniformly vs normally distributed females were analysed using an uncertainty analysis. Ultimately, a full analysis of all outputs of the model was conducted on the data produced by the model run on females with a normal size class distribution.

4.3 Statistical analysis:

4.3.1. Uncertainty Analysis:

In cases where a variable may have an effect on the outcome of the model, but the variable has not been quantified, I adjusted the variable within the model over a realistic range and analysed the subsequent results to check if model outcomes are affected (Uncertainty analysis; Railsback and Grimm 2012). Size class distributions in natural populations are variable and could therefore affect outcomes of the model. Two types of size class were chosen to check for effects on model

outcomes; uniform size class and normal size class distribution. The effects of size class distribution were tested using uncertainty analysis for each region, Kenya and South Africa respectively. Numbers of early developmental stage eggs (e2), late developmental stage eggs (e4) and hatched eggs are expected to vary with different size class distributions, while numbers of initial gravid females, final gravid females should not be affected. The effects of the factors "Normal Distribution" and "Uniform Distribution" on the outputs initial gravid females, final gravid females, early developmental stage eggs (e2), late developmental stage eggs (e4) and hatched eggs were analysed separately with the Permutational Analysis of Variance (PERMANOVA) add-on in PRIMER 6 for each region, South Africa and Kenya. Distance-based test for homogeneity of multivariate dispersions (PERMDISP) was used to check for homogeneity within each factor (Temperature, Distribution) in each region. Analyses were conducted on untransformed Euclidean dissimilarity matrices. The factors "Temperature" (7 levels) "Distribution" (2 levels) were fixed and orthogonal, $n = 100$. Unless otherwise stated, factors were fixed and orthogonal and variances were heterogeneous as there were no suitable transformations (PERMDISP, $P < 0.05$, untransformed data). Post hoc pairwise tests were performed when appropriate and all data are expressed as mean + standard error.

4.3.2 Model Simulation Analysis:

Under natural conditions, size class distributions tend to be normal as demonstrated by *Uca* sp. (Litulo 2004, 2005a) and *N. africanum* (Emmerson 1992), as such, analyses were conducted on model outputs produced using normally distributed females. The possible effects of the factors "Temperature" (7 levels) and "Region" (2 levels) on the outputs initial gravid females, final gravid females, early developmental stage eggs (e2), late developmental stage eggs (e4) and hatched larvae were analysed with the PERMANOVA add-on in PRIMER 6. The Distance-based test for homogeneity of multivariate dispersions (PERMDISP) was used to check for

homogeneity within each factor (Temperature and Region). Analyses were conducted on untransformed Euclidean dissimilarity matrices. The products of model simulations were compared between regions (Kenya and South Africa) and along the forecasted 6ºC increase under RCP 8.5. The factors "Temperature" (7 levels) and "Region" (2 levels) were fixed and orthogonal, $n = 100$.

4.4 Results:

In the following section, probability levels refer to the result of Pairwise tests at an alpha level of 0.05 unless otherwise stated. The number of simulations is a fixed at $n = 100$. This n-value influences the p-values of the statistical tests and is therefore only indicative of general trends emphasising the importance of not over interpreting the results.

4.4.1 Sensitivity Analysis:

Varying parameters by -5% generally had more effect on the sensitivity of the CReDy model than increasing parameters by 5%, with greater sensitivity indices being noted for all S^- parameters except the probability of generating eggs in Kenya, and the progression of e2 to e4 in both South Africa and Kenya (Table 4.8). Varying female attributes contributed much less to the sensitivity of the model with the exception of the size of females (S^+ and S^-) in Kenya than varying the probability parameters. Within the probability parameters there were exceptions which had relatively low sensitivity, such as the alteration of the probabilities of generating eggs and progression of e4 embryos to hatching in South Africa (S^+ and S^-), generating eggs in Kenya (S^-) and e2 progressing to e4 in South Africa (S^-) (Table 4.8).

Table 4.8: Local sensitivity analysis of the CReDy model

Process and Parameter	Reference Parameter (*P*)	Quality of Knowledge*	Sensitivity S^+	Sensitivity S^-
Female Attributes				
South Africa female density	0.68	5	131.22	-174.40
Kenya female density	1.21	5	-262.76	-1240.38
South Africa body size	20.5	3-4	-736.78	1804.30
Kenya body size	20.5	3-4	1934.08	4059.38
Female probabilities				
South Africa, generating eggs	0.001	1	361.54	392.66
South Africa, carrying eggs	0.001	1	-2370.36	-2524.18
Kenya, generating eggs	0.001	1	-2956.30	-124.94
Kenya, carrying eggs	0.001	1	-4957.88	-5388.82
Embryo development probabilities				
South Africa, e2 to e4	0.001	1	-1112.88	-446.04
South Africa, e4 hatching	0.001	1	-281.80	-695.80
Kenya, e2 to e4	0.001	1	2039.24	1642.30
Kenya, e4 hatching	0.001	1	-1380.30	10095.58

Note: Parameter values were increased/decreased by *dP* of 5%; Sensitivities (S+ and S-) were calculated as an approximation of the partial derivative of the number of hatched eggs with respect to the parameter (Railsback and Grimm 2012).

*Estimated quality of the empirical knowledge used to set the parameter value: 5 means highly certain knowledge, 1 means low certainty.

4.4.2 Uncertainty Analysis of effects of size class distribution:

The uncertainty analysis revealed that the factor Temperature produced significantly different numbers of females among all temperature combinations in South Africa (Table 4.9, Figure 4.2 A, B). In Kenya, there was no effect of either Temperature or Distribution on the number of initial gravid females produced. The number of initial eggs produced (e2) was significantly affected independently by the factors Temperature and Distribution in South Africa and Distribution in Kenya (Table 4.9; Figure 4.2 C, D). In South Africa, there were significantly different amounts of e2 embryos produced among 18 of 21 temperature comparison combinations and uniform distributions generally produced more e2 embryos. The number of final eggs (e4) was significantly affected independently by the factors Temperature and Distribution in both South Africa and Kenya (Table 4.9). Uniform distributions generally had more e4 embryos in both South Africa and Kenya (Figure 4.2 E, F); in South Africa there were significantly different amounts of e4 embryos produced at all experimental temperatures, while in Kenya there were significantly different amounts produced for 19 of 21 temperature comparison combinations. The factors Temperature and Distribution significantly affected the number of hatched eggs in South Africa while only the factor Temperature affected the number of hatched eggs in Kenya (Table 4.9). In South Africa, uniform distributions of females generally produced more hatched embryos than normal distribution females and differences in hatched embryos among temperatures was evident at all of the temperature comparison combinations (Figure 4.2 G, H). In Kenya, numbers of hatched embryos differed significantly for 19 of the 21 temperature comparison combinations.

Table 4.9: PERMANOVA tables comparing numbers of Initial gravid females, Initial e2, e4 embryos and hatched eggs produced by normal and uniform model simulations run over an increasing temperature range at one degree intervals in Kenya and South Africa using different size frequency distributions (Normal and Uniform). For this and following tables d.f. = degrees of freedom, M.S. = mean of squares and *F* = F-ratio. *P-value* = * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

		Number of Initial Gravid Females			
		South Africa		Kenya	
Source	d.f.	M.S.	Pseudo-*F*	M.S.	Pseudo-*F*
Temperature = T	6	4579.20	152.16***	40.91	1.33
Distribution = Di	1	41.54	1.38	6.97	0.23
Di x T	6	15.93	0.53	14.20	0.46
Residual	1386	30.10		30.82	
Total	1399				
		Number of Initial Eggs (e2)			
Temperature = T	6	$3.02E^{11}$	48.13***	$2.33E^{9}$	0.27
Distribution = Di	1	$1.65E^{11}$	26.29***	$2.59E^{11}$	29.62***
Di x T	6	$4.01E^{9}$	0.64	$1.12E^{9}$	0.13
Residual	1386	$6.27E^{9}$		$8.73E^{9}$	
Total	1399				
		Number of Final Eggs (e4)			
Temperature = T	6	$1.11E^{12}$	486.06***	$4.39E^{11}$	262.11***
Distribution = Di	1	$7.62E^{10}$	33.45***	$2.88E^{10}$	17.18***
Di x T	6	$3.75E^{9}$	1.65	$1.45E^{9}$	0.86
Residual	1386	$2.28E^{9}$		$1.68E^{9}$	
Total	1399				
		Number of Hatched Eggs			
Temperature = T	6	$1.34E^{11}$	1207.10***	$1.16E^{10}$	202.30***
Distribution = Di	1	$1.08E^{9}$	9.69**	$7.55E^{7}$	1.31
Di x T	6	$2.38E^{8}$	2.14	$7.37E^{7}$	1.28
Residual	1386	$1.11E^{8}$		$5.75E^{7}$	
Total	1399				

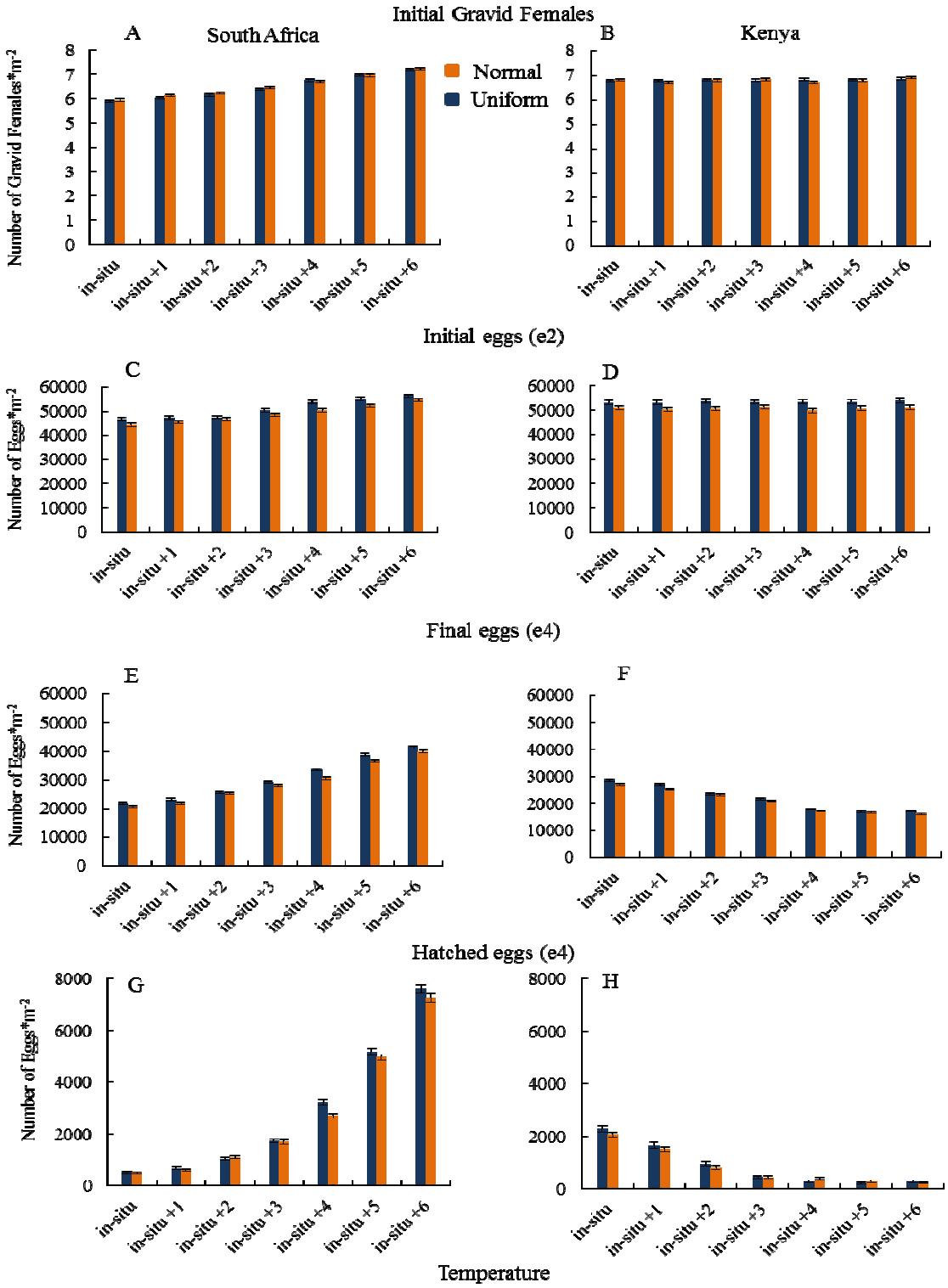

Figure 4.2: Model outputs for uniform and normally distributed females for numbers of Initial gravid females per m^{-2} in (A) South Africa and (B) Kenya, initial e2 per m^{-2} in (C) South Africa and (D) Kenya, e4 embryos per m^{-2} in (E) South Africa and (F) Kenya and hatched eggs per m^{-2} in (E) South Africa and (F) Kenya. All error bars represent standard errors (n = 100).

4.4.3 Effects of increasing temperature on simulated reproductive output of normally distributed females:

The PERMANOVA revealed a significant effect of the interaction between Region and Temperature on the initial number of gravid females (Gravid Females at day 1 of simulation) (Table 4.10). Significant differences between South Africa and Kenya were noted for all temperature simulations run except in-situ + 4ºC and in-situ + 5ºC. Simulations for Kenya produced more gravid females up to in-situ + 4ºC, but thereafter the numbers of gravid females were greater for South Africa than Kenya (Figure 4.3). Overall, the initial number of gravid females per m^{-2} increased from 5.94 (SE ± 0.06) to 7.22 (SE ± 0.05) with increasing temperature for *P. guttatum* populations in South Africa (Figure 4.3) and the differences between the number of gravid females was significantly different for 20 of the 21 comparisons among simulated temperatures. In Kenya, the initial number of gravid females per m^{-2} remained constant at approximately 6.8 for the entire forecasted temperature range (Figure 4.3), with only 2 of the 21 comparisons among numbers of females produced at different simulated temperatures being significantly different.

Table 4.10: PERMANOVA tables comparing number of initial gravid females (gravid females at day 1 of simulation) produced by model simulations run over an increasing temperature range at one degree intervals between Kenya and South Africa. For this and following tables d.f. = degrees of freedom, M.S. = mean of squares and *F* = F-ratio. *P-value* = * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Number of Initial Gravid Females			
Source	d.f.	M.S.	Pseudo-*F*
Region = R	1	2788.30	92.44***
Temperature = T	6	1219.5	40.43***
R x T	6	946.44	31.38***
Residual	1386	30.16	
Total	1399		

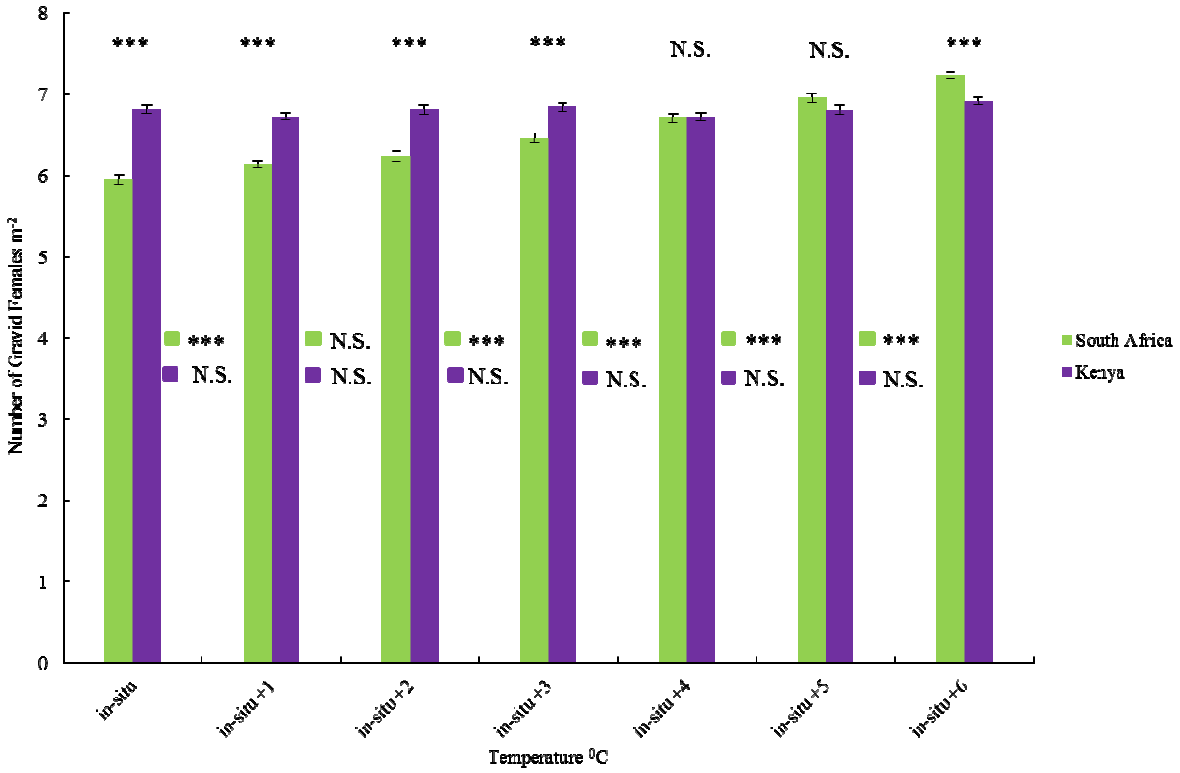

Figure 4.3: Average number of gravid females per m^{-2} (gravid females at day 1 of simulation) over increasing temperature range for *P. guttatum* in South Africa and Kenya. Levels of significance between regions are indicated above bars while levels of significance between temperatures within a region are indicated between bars, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ and N.S. = not significant. All error bars represent standard errors (n = 100).

There was a significant effect of the interaction between Region and Temperature on the final number of gravid females (Gravid Females at day 19 of simulation; Table 4.11). The final number of gravid females differed significantly between South Africa and Kenya for each temperature step simulation from the in-situ temperature data to the forecasted 6ºC increase. This number showed a positive increase from the in-situ temperature to the forecasted 6ºC simulations in South Africa, while for Kenyan simulations a decrease was observed (Figure 4.4). Within South Africa, all comparisons of simulations at different temperatures yielded significantly different numbers of final gravid females except for the comparisons between in-situ and in-situ

+ 1ºC. Within Kenya, all comparisons of simulations at different temperatures yielded significantly different numbers of initial gravid females except for the comparisons of simulations between in-situ + 4ºC and the in-situ + 6ºC, and in-situ + 5ºC and in-situ + 6ºC.

Table 4.11: PERMANOVA tables comparing number of final gravid females (Gravid Females at day 19 of simulation) produced by model simulations run over an increasing temperature range at one degree intervals between Kenya and South Africa. *P-value* = * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Number of Final Gravid Females		
Source	d.f.	M.S.	Pseudo-*F*
Region = R	1	13219	2666.70***
Temperature = T	6	1263.60	254.92***
R x T	6	2990.30	603.26***
Residual	1386	4.96	
Total	1399		

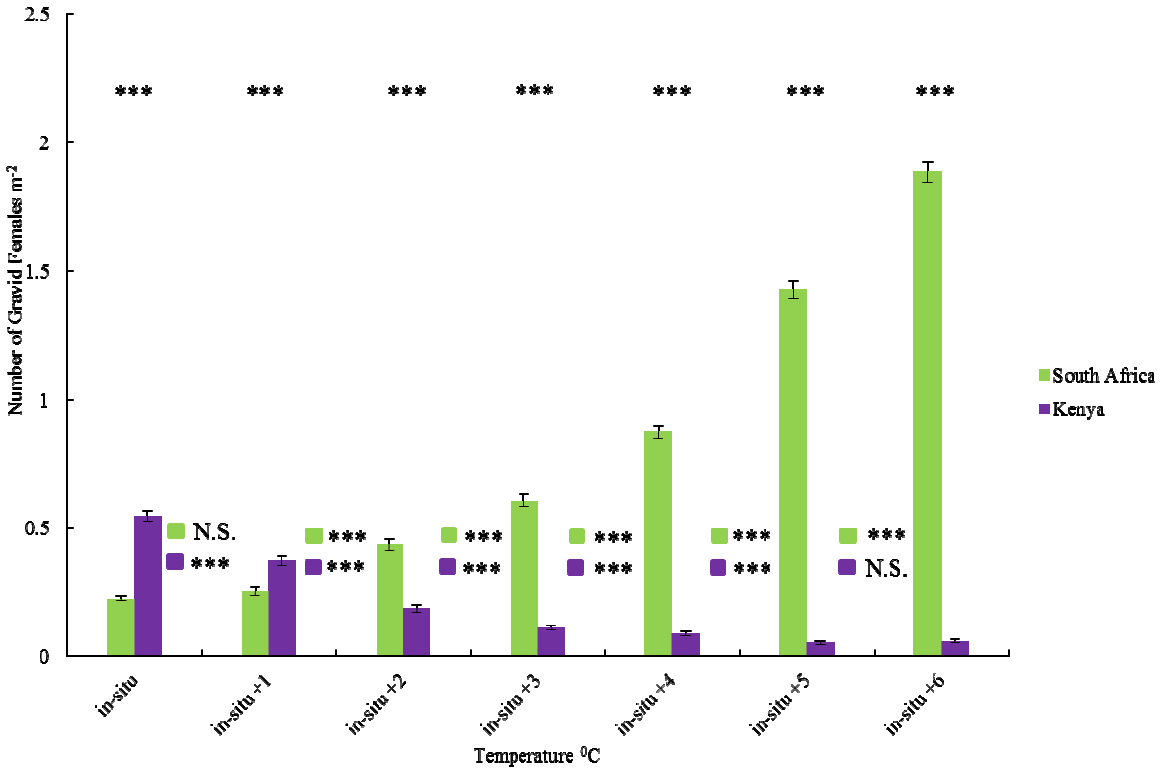

Figure 4.4: Average final number of gravid females per m^2 (Gravid Females at day 19 of simulation) over the simulated temperature range for *P. guttatum* in South Africa and Kenya. Levels of significance between regions are indicated above bars, while levels of significance between temperatures within a region are indicated between bars, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ and N.S. = not significant. All error bars represent standard errors (n = 100).

The initial number of eggs (e2) produced during simulations was significantly affected by an interaction between Temperature and Region (Table 4.12). Comparisons between Kenya and South Africa yielded significantly different numbers of eggs between in-situ and in-situ +3ºC and at the last simulated temperature, in-situ +6ºC, but not at in-situ +4ºC or in-situ +5ºC. Generally, the initial number of eggs (e2) produced in South Africa increased from the in-situ temperature data to the forecasted 6ºC increase (Figure 4.5) with only 5 of 21 comparisons among numbers of e2 eggs produced at different simulated temperatures yielding non-significant differences. In Kenya, however, the numbers of eggs produced remained relatively constant

(Figure 4.5) with no differences noted between numbers of eggs produced at different simulated temperatures.

Table 4.12: PERMANOVA tables comparing number of initial eggs (e2) produced by females in model simulations run over an increasing temperature range at one degree intervals between Kenya and South Africa. *P-value* = * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

		Number of Initial Eggs	
Source	d.f.	M.S.	Pseudo-*F*
Region = R	1	$1.06E^{11}$	15.04***
Temperature = T	6	$7.44E^{10}$	10.52***
R x T	6	$7.04E^{10}$	9.95***
Residual	1386	$7.07E^{9}$	
Total	1399		

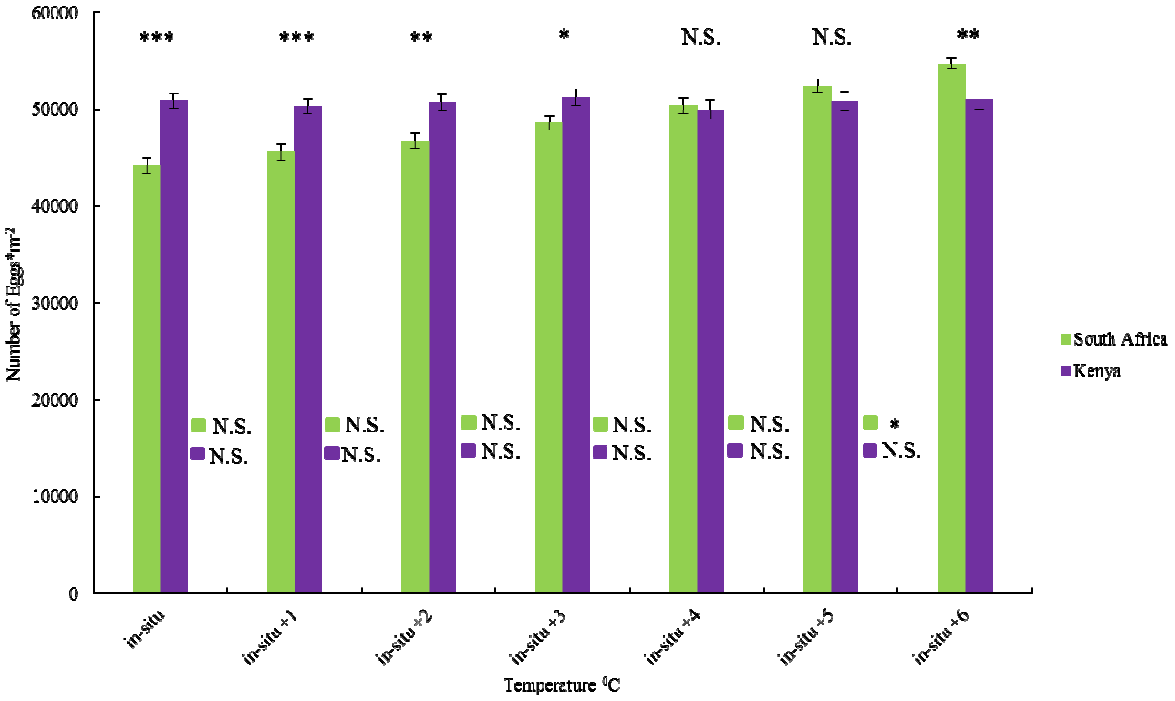

Figure 4.5: Average initial (day 1 of simulation) number of eggs produced by females at the beginning simulations (e2) over the simulated increasing temperature range for *P. guttatum* in South Africa and Kenya. Levels of significance between regions are indicated above bars while levels of significance between temperatures within a region are indicated between bars, * $P <$ 0.05; ** $P < 0.01$; *** $P< 0.001$ and N.S. = not significant. All error bars represent standard errors (n = 100).

The PERMANOVA revealed a significant effect of the interaction between the factors Region and Temperature on the average number of last developmental stage eggs (e4) produced at day 11 (Table 4.13). For all temperature simulations, there were significant differences in the number of last developmental stage eggs produced between South Africa and Kenya. Initially, up to in-situ +1ºC, simulations in Kenya yielded more eggs, but thereafter simulations in South Africa yielded more eggs (Figure 4.6). The average number of last developmental stage eggs (e4) increased steadily for simulations run in South Africa from the in-situ temperatures up to the forecasted 6ºC increase (Figure 4.6) with comparisons among all these simulations being

significantly different, while over the same forecasted temperature increase, the average number of last developmental stage eggs (e4) in Kenya decreased (Figure 4.6). In Kenya, all the comparisons between different simulated temperatures were significantly different except for in-situ +4ºC and in-situ +5ºC, in-situ +4ºC and in-situ +6ºC, and in-situ +5ºC and in-situ +6ºC.

Table 4.13: PERMANOVA tables comparing the number of late developmental stage (e4) eggs in model simulations run over an increasing temperature range at one degree intervals between Kenya and South Africa. *P-value* = * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

		Number of Late Eggs	
Source	d.f.	M.S.	Pseudo-*F*
Region = R	1	$2.41E^{12}$	1307.30***
Temperature = T	6	$5.46E^{10}$	29.66***
R x T	6	$6.67E^{11}$	362.21***
Residual	1386	$1.84E^{9}$	
Total	1399		

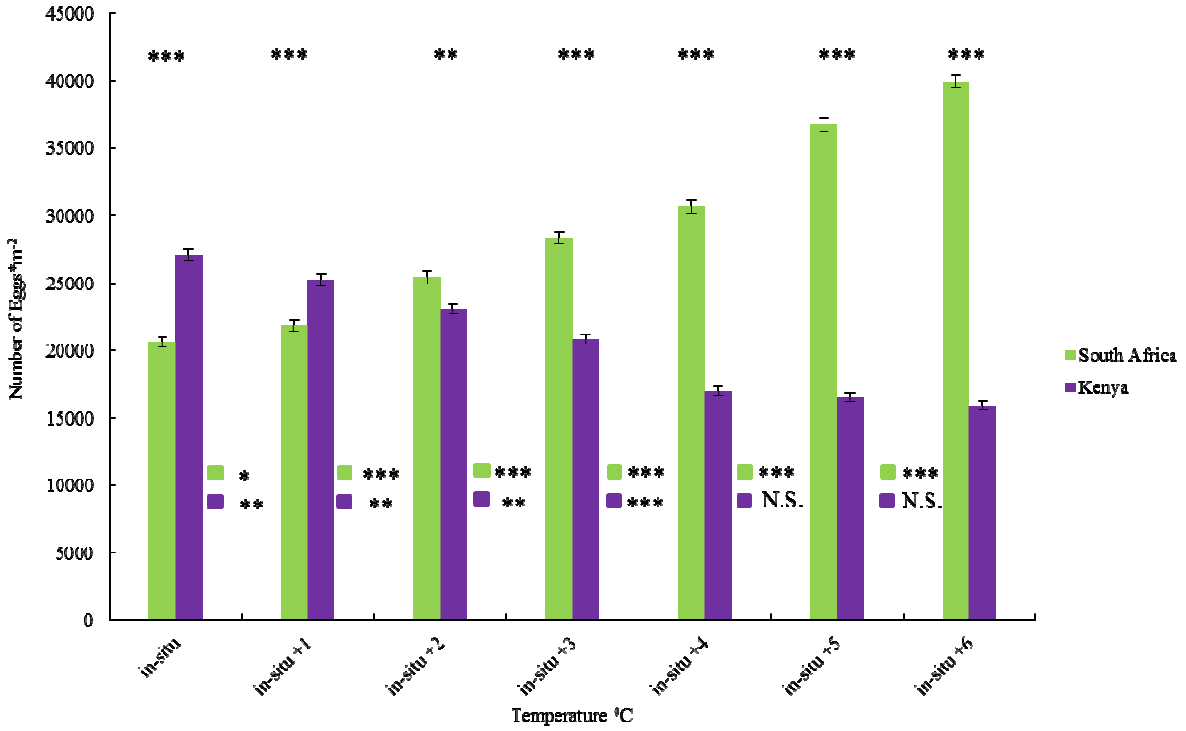

Figure 4.6: Average number of last developmental stage eggs (e4) at day 11 of simulation, over the simulated increasing temperature range for *P. guttatum* in South Africa and Kenya. Levels of significance between regions are indicated above bars while levels of significance between temperatures within a region are indicated between bars, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ and N.S. = not significant. All error bars represent standard errors (n = 100).

There was a significant effect of the interaction between Temperature and Region on the number of hatching eggs at the end of the model simulations (Table 4.14). Initially, using the in-situ and in-situ +1ºC temperature data simulations, Kenya produced over twice the number of hatched eggs compared to South Africa (Figure 4.7), but thereafter South Africa produced more hatched eggs than Kenya, with these differences among regions being significantly different at all simulated temperatures (Figure 4.7). Overall, for South Africa, the number of hatched eggs increased across all simulated temperatures (Figure 4.7) and all comparisons among numbers of hatched eggs at different simulated temperatures were significant (with the exception of in situ and in situ +1ºC). Simulations of increasing temperatures in Kenya produced a decrease in the

number of hatched eggs (Figure 4.7), differences among temperatures were significant in the case of lower temperatures and most high temperatures except in-situ +3ºC and in-situ +4ºC, in-situ +4ºC and in-situ +5ºC, and in-situ +5ºC and in-situ +6 ºC.

Table 4.14: PERMANOVA tables comparing the number of hatched eggs in model simulations run over an increasing temperature range at one degree intervals between Kenya and South Africa. *P-value* = * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

		Number of Hatched Eggs	
Source	d.f.	M.S.	Pseudo-*F*
Region = R	1	$1.23E^{11}$	1535.80***
Temperature = T	6	$2.09\ E^{10}$	261.93***
R x T	6	$4.69\ E^{10}$	586.42***
Residual	1386	$7.99\ E^{7}$	
Total	1399		

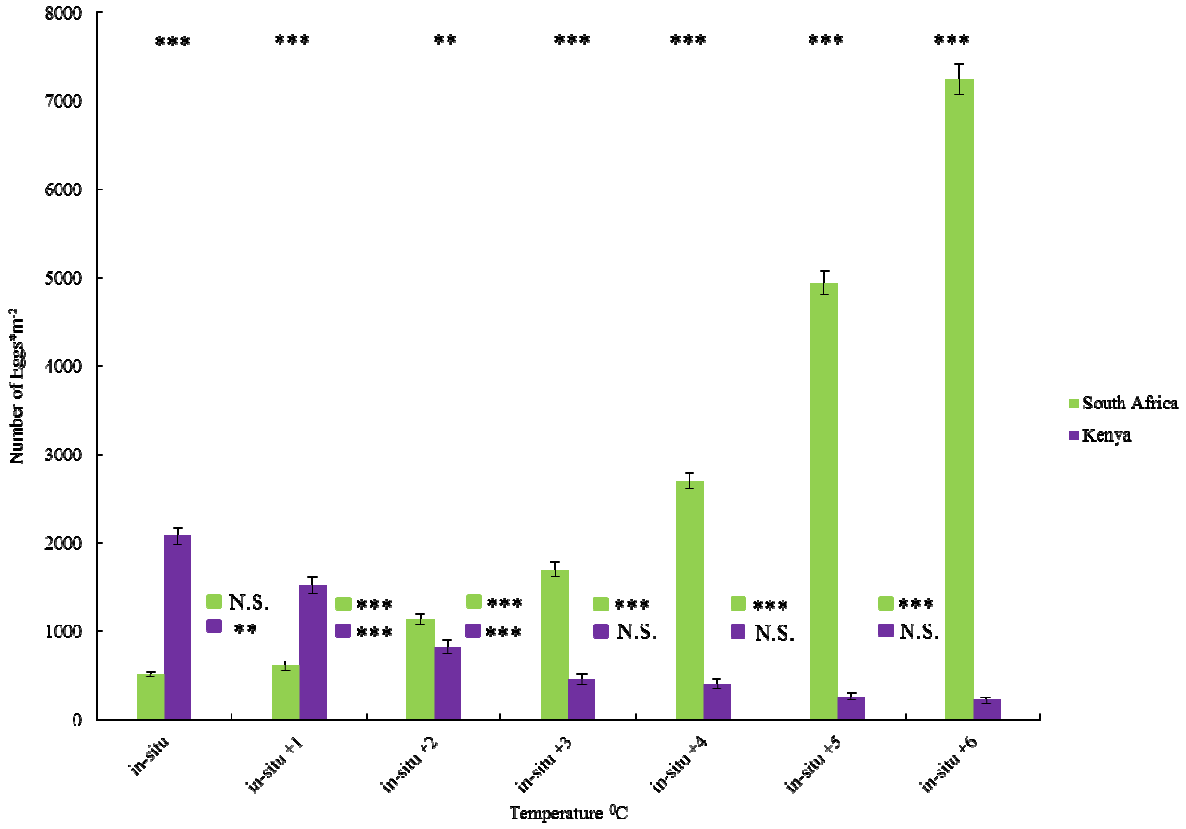

Figure 4.7: Average number of hatched eggs at the end of simulations (day 19 of simulation) over the increasing temperature range for *P. guttatum* in South Africa and Kenya. Levels of significance between regions are indicated above bars while levels of significance between temperatures within a region are indicated between bars, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ and N.S. = not significant. All error bars represent standard errors (n = 100).

4.5 Discussion:

The CReDy model facilitates the translation of metabolic thermal responses of specific life stages into reproductive success as each stage is likely to be affected by temperature to a different extent. Furthermore, it takes into account the complex changes in environmental conditions common to an intertidal ecosystem and, by using recent climate change forecasts (IPCC 2014a, c) in conjunction with experimental data, has the ability to simulate reproductive

output over different climate change scenarios. Additionally, parametrisation of vital model inputs (e.g. egg production according to female body size, Q_{10} values and environmental profile data) was done based on recent empirical data collected through the course of this study (Chapter 2). This strongly links the CReDy model to the natural systems that it simulates.

The existing literature indicates that terrestrial invertebrates living at low latitudes are close to their thermal optima (Krockenberger *et al.* 2004, Somero 2005, Deutsch *et al.* 2008, Huey and Tewksbury 2009, Dillon *et al.* 2010) and similar results have been found for some marine species (Nguyen *et al.* 2011, Faulkner *et al.* 2014, Rummer *et al.* 2014). On the other hand, species living at higher latitudes are exposed to temperatures below their thermal optima and consequently are performing below their thermal optimal levels (Deutsch *et al.* 2008, Dillion *et al.* 2010). Comparisons of CReDy model simulations for South Africa and Kenya using empirical in-situ environmental data (although over a 19 day period only) support these hypotheses. In all reproductive aspects considered, simulations on initial and final gravid females, early (e2) and late (e4) embryos and successfully hatched eggs, using in-situ environmental data, produced greater absolute numbers in Kenya compared with South Africa, based on metabolic responses to temperature. These results validate that indeed Kenyan populations are at or close to their thermal optima and are therefore out-performing South African populations, which are operating below their optimal levels.

Simulations on several scenarios of temperature increase in the CReDy model yielded contrasting intra-specific outputs for *P. guttatum* populations depending on their latitudinal location. In Kenya, reproductive processes either stagnated (e.g. initial numbers of gravid females and initial numbers of e2 embryos) or decreased (e.g. final numbers of gravid females,

initial numbers of e4 embryos and hatched embryos), while all reproductive processes in South Africa increased. Although at in-situ +1ºC, Kenyan populations still out performed South African populations in terms of absolute numbers of final gravid females, e4 eggs and hatched eggs and up to in-situ +3ºC for initial gravid females and e2 eggs, an overall decreasing trend in absolute numbers was observed in Kenya with further increasing temperatures. This implies detrimental consequences for this species at low latitudes under increasing temperature scenarios as has been forecasted for terrestrial invertebrates (Krockenberger *et al.* 2004, Somero 2005, Deutsch *et al.* 2008, Huey and Tewksbury 2009, Dillon *et al.* 2010), while populations at higher latitudes are expected to increase their fitness with increasing temperatures (Deutsch *et al.* 2008, Dillion *et al.* 2010) as seen for *P. guttatum* in South Africa. The decreased reproductive output in the CReDy model for Kenyan populations is likely to be due to reduced thermal flexibility evolved by species living in thermally stable, yet severe environments (Stevens 1989, Gaston *et al.* 2009, Rummer *et al.* 2014). Although these environments are thermally stable, they are in fact relatively extreme, and organisms within live close to their thermal limits. This tendency is known for Antarctic ectotherms which are expected to suffer reduced fitness with relatively small increases in seawater temperatures (Deutsch *et al.* 2008, Peck *et al.* 2009). Importantly, this implies that it is not 'species' in stable climates that have reduced flexibility, but 'populations'.

Historically, increasing temperatures have been suggested to induce pole-wards shifts in marine fauna (e.g. Fields *et al.* 1993) while recent studies have indicated that increasing temperatures will again induce distribution shifts pole-wards as organisms attempt to track optimal climates in line with their physiological thresholds (Parmesan and Yohe 2003, Rosenzweig *et al.* 2008, Hoegh-Guldberg and Bruno 2010). This process has been documented for marine vertebrates (Perry *et al.* 2005) as well as invertebrates (Zacherl *et al.* 2003, Precht and Aronson 2004) and is

due to an interaction of a multitude of factors. Populations accordingly disappear from their tropical distributions narrowing their range and shifting their distribution southwards where temperatures under climate change scenarios would reflect current tropical temperatures (Deutsch *et al.* 2008, IPCC 2014a, b, c, d). The CReDy model suggests that one of the driving factors behind these distribution shifts would be related to temperature affected metabolic stress associated with reproductive efforts, where the reproductive output of populations would not be sufficient enough to maintain populations at their current low latitudes.

Population growth has been highlighted as an aspect that is often negatively affected in the event of warming and indicates an overall decrease in species fitness (Deutsch *et al.* 2008, Dillon *et al.* 2010). The CReDy model indicates that, due to its physiological sensitivity, *P. guttatum* experiences in Kenya a decrease in fitness with increasing temperature with a resultant decrease in reproductive output and likely resultant decrease in recruitment and population size. Conversely, in South Africa the simulated increase in all reproductive aspects indicates that increasing temperatures are likely to invoke an increase in fitness at high latitudes resulting in population growth. In Mozambican mangrove systems, high recruitment of the mangrove crabs *Uca urvillei, Uca inversa* and *Uca annulipes* in winter has been linked to high reproductive output from the previous summer months which are generally warmer (Litulo 2005a, b, c) and main reproductive events during the hot months early in the year resulted in major recruitment events a few months later in two *Diogenes* hermit crabs (Teoh and Chong 2013). This temperature linked reproductive output-recruitment processes implies a degree of self-recruitment, highlighting the importance of reproductive output in population dynamics and further focus the importance of understanding contributing processes under climate change scenarios. Brachyuran species can exhibit variable breeding periods depending on their latitudinal distribution (Emmerson 1994, Gove and Mambonhe 2000, Flores *et al.* 2002, Ituarte

et al. 2004, Litulo 2005a, b, c) suggesting that this would need to be taken into account during longer simulations.

Different life stages are likely to show varying degrees of sensitivity to physical stressors (Hamdoun and Epel 2007, Byrne *et al.* 2009, 2010a, b). Ericson *et al.* (2010) show that fertilization and early cell development of the Antarctic nemertean worm, *Parborlasia corrugatus* and the sea urchin, *Sterechinus neumayeri* are relatively robust to pH changes, but later embryogenesis seems more sensitive to these same changes. Similar ontogenetic mediation of sensitivity to stressors has been found for other non–Antarctic marine invertebrates (e.g. Byrne *et al.* 2009, 2010a, b). Hamdoun and Epel (2007) indicated that eggs and early embryos are robust against physical stressors, including temperature, due to maternally invested cellular defences (e.g. heat shock proteins) that are also known as innate defences, while later developmental stages are more likely to respond due to induced defences or adaptive responses (Hamdoun and Epel 2007, Ericson *et al.* 2010). Adults are generally thought to be more robust to physical stressors than embryos (e.g. Dupont *et al.* 2010). In Kenya, the initial number of gravid females and the initial number of e2 eggs did not show much variability over the simulated temperature range, suggesting that these reproductive stages are fairly robust in terms of response to temperature change, while e4 embryos and hatched eggs showed more marked variations over the simulated increasing temperatures, highlighting their sensitivity as a possible weak link in the chain of overall reproductive success. In South Africa, increases were observed for all reproductive stages, although rates of increase for e4 embryos, hatched eggs and final number of gravid females showed a more marked increase between temperature steps than numbers of e2 embryos and initial numbers of gravid females, again indicating that early stage embryos (e2) seem to be more robust than later stages possibly due to innate defences to

physiological change passed from the mother to early stage embryos (Hamdoun and Epel 2007, Ericson *et al.* 2010).

It must be noted however, that these simulations were run for a single spring tide (19 day period) during peak reproductive seasons in their respective regions and are not representative of year-round breeding patterns. In South Africa, breeding cycles of *P. guttatum* are not fully understood, but the species is assumed to breed on a semi-lunar basis seasonally for approximately six to eight months during summer (pers. obs.) as is shown by the closely related species *Chiromantes eulimene, Neosarmatium meinerti* (now *Neosarmatium africanum*; Ragionieri *et al*, 2012) and *Parasesarma catenata* (Emmerson 1994, Flores *et al.* 2002). During the breeding period, all sexually mature females are assumed to have specific reproductive peaks (Emmerson 1994, Flores *et al.* 2002). Specific breeding peaks are not uncommon in temperate regions, as females' ustilise resources that are seasonally limited (Ituarte *et al.* 2004, Torres *et al.* 2009). On the other hand, species in tropical and subtropical regions can breed year round due to favourable environmental conditions and the continuous availability of resources (Skov 2001, Ituarte *et al.* 2004, Torres *et al.* 2009). Again, *P. guttatum* in Kenya, shows variation in breeding throughout the year (Skov 2001), but has less seasonality compared to populations in South Africa (pers. obs.). *P. guttatum* in South Africa (high latitudes) has a high reproductive output during peak breeding events, under increased temperature scenarios. While due to the constant breeding at lower latitudes, *P. guttatum* will possibly still have a higher overall annual reproductive output at low latitudes. Alternatively the increased temperatures at high latitudes may extend the breeding season, allowing comparable reproductive outputs between the centre and edge populations.

The uncertainty analysis, which looks at the effects of size class distribution of reproductive females, indicates that small changes in the parameterization of the model may significantly affect outputs, but may not necessarily change overall trends. Ultimately, a normal size class distribution was chosen for gravid females as other brachyuran species exhibit this characteristic, e.g. *Uca* sp. (Litulo 2005a). The initial number of *P. guttatum* females was kept fixed, based on density data for South Africa and Kenya (MEAM 2001, PUMPSEA 2007). The number of females was further split according to sex ratio data presented by Flores *et al.* (2002). No new recruitment or die off of female crabs was assumed as there is limited information on these processes (Flores *et al.* 2002). Evidence also suggests that latitude affects the structure of mangrove brachyuran populations, and that, within different localities, such structure is likely to vary depending on the zone within the mangrove (Hartnoll *et al.* 2002, Chapman and Tolhurst 2004). Furthermore, temporal differences are also evident due to seasonality present at mangroves at increased latitudes (Cannicci *et al.* 2009). Sex ratios of sesarmids, specifically *Parasesarma catenata* and *Chiromantes eulimene*, which are related to *P. guttatum*, have been shown to vary at times of the year and this might influence longer simulations (Emmerson 1994). Additionally, little is known about development rates once the new juveniles recruit into a system and age of sexual maturity with the only available data on this coming from Mozambique (Flores *et al.* 2002). This development is likely to be controlled by many different factors such as food availability, salinity and temperature (Flores *et al.* 2002) which will vary according to location and will affect females available for breeding.

While the CReDy model works and provides information on the reproductive output of crabs in mangrove ecosystems based on physiological data, this model still needs to be refined. The temperature parameters only go up to 37ºC for adults, 35ºC for eggs and down to 19ºC for both. Physiological data needs to be assessed for temperatures higher and lower than these ranges to

further simulate changing temperature scenarios. The simulations run are based on information of temperature increases included in the IPCC (2014a, c) report. However, the model does not take into account any extreme temperature events that may occur. The IPCC (2014b) report outlines that the frequency of extreme temperatures has increased (Seneviratne *et al*. 2012), with an increase in warm spells and heat waves. These events have not been factored into the model as of yet, but would be useful for extended simulations. The reaction of the crabs to these extreme events would firstly need to be observed and quantified before inclusion into the model as crabs may employ avoidance strategies such as retreating into cooler burrows to mitigate the effects of harsher temperatures (Emmerson 2001). As it stands, this model has not been compared to experimental or observational data on the actual reproductive output of *P. guttatum* in either South Africa or Kenya. It is important that models represent and simulate natural dynamics as closely as possible before predictive models can be implemented and trusted. This model needs further and rigorous testing against observed trends. Additionally, the sensitivity analysis identified parameters that cause considerably high variation in the final output of the model and that have little known information to estimate their values. Scaling metabolic stress experienced over the short term experiments (hours) used to parameterise the model may not equate to the true stress animals experience over long term time periods as simulated by the model (days, months, years). As Railsback and Grimm (2012) outline, these values require further attention to obtain an accurate calibration of the model and thus require further empirical research to reduce their uncertainty. This mainly pertained to probabilities governing progressions from one stage to the next in the case of embryos or affecting female capacities to generate or carry eggs. However, this can only be rectified by time intensive experimental procedures to ascertain realistic values to assign to these parameters, which at this stage were not feasible in the time frame of this thesis. Overall results from this chapter condradict the interpretations from Chapter 2. These simualations are based on very specific and limited

temperature data inputs into the model for this 19 day period and at no point is the model said to be representative of a year-long simulation. The model simply produced these results from a very specific and limited data set (temperature) and under these conditions these are the results produce by the simulations. By increasing the timeframe in which the model runs with annual temperature data very different patterns may emerge.

The CReDy model may have further application in determining the effect of other anthropogenic stresses exerted on brachyurans in mangrove ecosystems. One example would be assessing the effect of urban waste water on brachyuran reproductive output in mangrove ecosystems in conjunction with climate change. Waste water has been shown to increase the abundance of sesarmid and ocypodid crabs (Cannicci *et al.* 2009) and enhance reproductive outputs in some species. For example, studies on *Uca annulipes* indicate that waste water extends its reproductive season, increases fecundity, and improves embryo quality (Penha-Lopes *et al.* 2009).

While further improvements to the parameterization of the model have been outlined in this discussion, not all will prove to be significant in altering simulation outputs and any changes to the current parameters may have little effect. The majority of the defined parameters are robust within the context of the model as they have been thoroughly researched, implying that this is a reliable method of predicting reproductive output. Notably, the CReDy model produced two contrasting outputs for Kenya and South Africa, based solely on thermal sensitivity of *P. guttatum* females and eggs. The results support theories outlined in the literature, which suggest that populations living at low latitudes are close to their thermal optima, and with increasing temperatures decreasing fitness is expected, while at high latitudes populations are living below their thermal optima and therefore with increasing temperatures fitness is expected to increase

(e.g. Deutsch *et al.* 2008, Dillon *et al.* 2010 Nguyen *et al.* 2011, Faulkner *et al.* 2014, Rummer *et al.* 2014). These findings highlight interesting patterns of reproductive responses to temperature increase and provide insights into possible repercussions for population persistence or latitudinal shifts. The outputs of this model suggest a potential distribution shift, with population sizes in the tropics decreasing and possibly disappearing narrowing the distributional range. Edge populations will potentially increase in size as temperatures in this region will likely reflect those of the present tropical localities, enhancing reproductive outputs both over a temporal scale and within each breeding event, although population increase is likely to be constrained by limited habitat availability (Adams *et al.* 2004, Quisthoudt *et al.* 2013). With further development and testing, this novel model could further be implemented in many different scenarios involving reproductive outputs of not only invertebrates in mangrove ecosystems, but a wide variety of ecosystems worldwide.

CHAPTER 5

GENERAL DISCUSSION

With the acceleration of climate change, the dissection of patterns and mechanisms that influence species distributions and survival has never been more imperative. Climate change significantly alters the physical and chemical aspects of global ecosystems, affecting their functioning and structure with exacerbated predictions for the next 100 years (Walther *et al.* 2002, Deutsch *et al.* 2008, Hoegh-Guldberg and Bruno 2010, Doney *et al.* 2012, IPCC 2014a, b, c, d). Consequently, the interpretation of physiological strategies across latitudes has become increasingly important as a predictor of species distributions.

This study provides the opportunity of studying physiological aspects of cosmopolitan species inhabiting mangal habitats along the east coast of Africa, spanning many degrees of latitude. Regional inter- and intra-specific physiological comparisons of mangrove macrofauna were explored with the aim of assessing the effect of increasing temperatures in line with predictions for the next 100 years (IPCC 2014a, c) at centre- (Kenya) and edge- (South Africa) latitudinal distributions. Furthermore, a process key to the maintenance of populations, such as settlement was considered over the same scales, allowing for comparisons of dynamics affecting this facet on a latitudinal scale. Local variations of both physiological and settlement aspects were further assessed at each of these localities. An integrated interpretation of these results illuminates physiological strategies and constraints influencing sympatric species along a latitudinal cline and allows the synthesis of physiological and settlement factors influencing species at centre and edge localities at the present time and in the event of climate change.

5.1 Physiological patterns contributing to latitudinal patterns:

In Chapter 2 it was demonstrated that, across the latitudinal distribution considered, *Perisesarma guttatum* and *Uca urvillei* are able to utilize higher concentrations of oxygen in air compared to water to extend their thermal tolerances over all bimodal breathing life stages, as did *Neosarmatium africanum* in South Africa. Sensitivity to thermal stress in aquatic and terrestrial ectotherms can be explained by the theory of Oxygen and Capacity Limitation of Thermal Tolerance (OCLTT), which predicts that the ability of an organism to extract oxygen from its environment and deliver it efficiently to its tissues is one of the key determinants of its thermal tolerance (Frederich and Pörtner 2000, Pörtner 2001, 2002, 2010). Data on this concept are generally restricted to localised scenarios (e.g. Frederich and Pörtner 2000, Mark *et al.* 2002, Melzner *et al.* 2006, Wittmann *et al.* 2008), with limited studies dealing with OCLTT over latitudinal gradients and global scales (e.g. Solokova and Pörtner 2003, Fusi *et al.* 2014, Deutsch *et al.* 2015) and until recently neglects bimodal breathing organisms (e.g. Fusi *et al.* 2014, Giomi *et al.* 2014, in press). The benefit of a bimodal breathing lifestyle lies in the alleviation of oxidative stress during warming events by switching to a milieu where oxygen is more freely available (Fusi *et al.* 2014, Giomi *et al.* 2014, in press) and could provide oxidative stress release and enhance the survival of bimodal breathing organisms in the predicted climate change scenarios over the next 100 years (Walther *et al.* 2002, Deutsch *et al.* 2008, Hoegh-Guldberg and Bruno 2010, Doney *et al.* 2012).

Chapter 2 specifically highlights the benefit of bimodal breathing in conspecifics and species that are sympatric across a wide range of latitudes. This has so far only recently been studied over one ontogenetic stage in localised scenarios (e.g. Giomi *et al.* 2014, Giomi *et al.* in press) and over latitudinal gradients (e.g. Fusi *et al.* 2014). The findings from this chapter suggest that

bimodal breathing can extend thermal tolerance of an organism and it is therefore an important physiological adaptation available to bimodal breathing species across a wide range of latitudes that could possibly be applied to other ecosystems hosting bimodal breathing species. Furthermore, this builds on the idea that oxidative stress can be alleviated by utilising a medium with higher content and diffusibility of oxygen (e.g. Mark *et al.* 2002, Stevens *et al.* 2010, Pörtner and Giomi 2013), giving further insight into behavioural responses of species. For example, *Uca* species are known to plug their burrows during high tide preventing inundation (de la Iglesia 1994, Cannicci *et al*. unpublished data), while Sesarmids climb mangal trees to prevent submersion (Cannicci *et al.* 1999, Fratini *et al.* 2005). The drivers of these behavioural aspects could be two fold; reducing predation (Cannicci *et al.* 1999, Fratini *et al.* 2005) and alleviating physiological stress associated with extracting oxygen from water. Furthermore burrowing crabs may shelter in burrows to mitigate harsh temperatures (Emmerson 2001).

Although *Perisesarma guttatum* and *Uca urvillei* were able to employ similar mechanisms to alleviate oxidative stress, the ability to extract oxygen from the two different milieus was not identical across latitudes; regional differences were commonplace across all ontogenetic stages considered, but to varying degrees. This indicates different physiological adaptations or strategies are employed by conspecifics and different ontogenetic stages at the centre (Kenya) and edge (South Africa) of their latitudinal distribution. Typically in this study, populations of *P. guttatum* and *U. urvillei* at the centre of their distribution were able to extract oxygen from both milieus more efficiently than their South African conspecifics and differences were further enhanced at stressful temperatures, indicating a physiological advantage and greater thermal tolerance of species present at the centre of their distribution. South African individuals did, however, show adaptation to present temperatures experienced in this region, especially in water, suggesting that in this region they have specialised their oxygen extraction abilities for existing

conditions. Kenyan conspecifics are more generalist, allowing them to cope with a wider range of temperatures. Applying the OCLTT to these three species facilitated the description of thermal sensitivity across latitudes and among species and identified life stages that may be more vulnerable to warming events. Additionally, inter-specific differences in oxygen consumption within regions were further explored. *P. guttatum, U. urvillei* and *Neosarmatium africanum* are considered to be sympatric in South Africa and Kenya (Macnae 1968, Tomlinson 1986, Emmerson 1994, 1999) and yet display differences in their efficiencies in extracting oxygen in air and water across ontogenetic stages. This suggests that species and life stage specific adaptations play an important role in survival and reveals physiological adjustments to diverse lifestyles within the same habitat.

The OCLTT allowed the visualisation of thermal stress across a spectrum of temperatures and the effect of bimodal breathing across ontogenetic stages revealed insights into how these species can alleviate oxidative stress under increasing temperature scenarios. The most critical sign that these species may be under threat from climate change was the physiological response of their maternal costs to increasing temperatures. In the analysis of these data, it became evident that, with increasing temperatures, maternal care is abandoned especially in aquatic conditions, while the advantage of extraction of oxygen from the aerial environment was highlighted as this mode of breathing allowed continued maternal care even at stressful temperatures. Again, ontogenetic species-specific physiological responses to temperature had differences across milieus and regions, highlighting possible life history strategies at the centre and edge of their distributions. Ultimately, however, maternal care seems to be the weak link in the life history of these organisms as increasing temperatures may cause females to abandon maternal care, preventing existing populations from contributing to the larval pool from which new recruits repopulate the mangrove habitat.

These findings imply that there could be important consequences of global warming for the distributional ranges of these species. While populations at the centre of their range are seemingly robust to climate change, populations at the southern distribution are more at risk. Increased thermal stress in southern populations implies a loss of fitness, especially through effects on brooding females, and a decrease in population sizes with a worst case scenario of localised extinctions. This would cause a distributional shrink to lower latitudes contrary to many studies that project a poleward shift of species (e.g. Parmesan and Yohe 2003, Cheung *et al.* 2009, Bates *et al.* 2014). Generally the southern distribution limits of species is set by low temperatures (e.g. Sunday *et al.* 2011, Bates *et al.* 2014) whereas in this case higher temperatures appear to influence the distribution patterns of mangrove brachyurans. The extent of this shrinking of range could, however, be determined by possible differences among haplotypes of these species. *Perisesarma guttatum* is known to have two divergent phylogeographic clades; a southern Mozambique clade and a northern clade including northern Mozambique, Tanzania and Kenya (Silva *et al.* 2010a). This suggests that a shift of this species could affect mangals as far north as Mozambique. This does not, however, apply to the other two study species as Ragionieri *et al.* (2010, 2012) suggest that there is only one clade for *Neosarmatium africanum* along the east coast of Africa and there is no information on this aspect for *Uca urvillei.* Thus, without genetic clarification across the latitudinal distribution, predicting the extent of generalised distributional shifts across species would be difficult.

Ultimately, the decrease in population size or localised extinction of brachyuran species at the southern latitudinal limits of African mangals could have detrimental effects on the whole mangal ecosystem. Brachyurans have been implicated in ecosystem functioning as food sources

(Wilson 1989, Fry and Ewel 2003, Lugendo *et al.* 2006), ecosystem engineers altering physical and chemical sediment aspects (Smith *et al.* 1991, Mouton and Felder 1996, Botto and Iribarne 2000, Kristensen and Alongi 2006, Kristensen 2008), sequestering carbon in a number of ways (Micheli 1993, 1998, Skov and Hartnoll 2002, Hartnoll *et al.* 2002), facilitating oxygen supply to mangal roots (Gribsholt *et al.* 2003, Kristensen 2008, Cannicci *unpublished data*) and shaping mangal growth and regeneration due to propagule predation (Dahdouh-Guebas *et al.* 1998, Bosire *et al.* 2005). Thus, a loss of brachyurans may in fact cause a distributional reduction of the entire ecosystem.

5.2 Latitudinal variability in settlement:

In the assessment of settlement variability across latitudes (Chapter 3) lunar phase and zonal preference appeared to be the main drivers, while localised variability resulted from complex interactions of multiple factors in both Kenya and South Africa. Settlement and recruitment studies along the east coast of Africa are limited and primarily focused in Mozambique (e.g. Paula *et al.* 2001, 2003, 2004, Flores *et al.* 2002, Litulo 2005a, b, c), with a recent study on a Kenyan mangal (Ragionieri *et al.* 2015). Based on this literature, the influx and settlement of crab larvae within the mangrove seem mostly to be influenced by tidal state (neap vs spring) (Paula *et al.* 2001, 2003, 2004, Ragionieri *et al.* 2015), nocturnal vs diurnal flood tides (Paula *et al.* 2004), wind stress (Paula *et al.* 2001, 2003), lunar phase (Flores *et al.* 2002, Ragionieri *et al.* 2015) and season (Litulo 2005a, b, c). In Kenya, settlement patterns in neighbouring mangrove ecosystems suggest that there is high spatial and temporal variability, with seasonal effects (Nzali *et al.* 1998, Mangubhai *et al.* 2007, Kaunda-Arara *et al.* 2009) and moon phase (Kaunda-Arara *et al.* 2009) and effects of lunar phase and high temporal variability have recently been confirmed for mangrove macrofauna by Ragionieri *et al.* (2015). In South Africa, again larval

settlement studies in mangals are largely lacking, but influxes of larvae have been noted during nocturnal flood tides (Papadopoulos *et al.* 2002). It must be noted that due to the significant variation in the data for settlement rates, projections may have low levels of confidence associated with them.

Overall, dispersal from parental habitat to final localities in both terrestrial and marine environments greatly influences population distributions. Patterns of distribution are affected by complex interactions between multiple factors over multiple scales (Cowen *et al.* 2000, Michener *et al.* 2001, Nathan *et al.* 2005, Pineda *et al.* 2010). Marine invertebrates commonly produce larvae that spend a significant amount of time removed from the parental habitat in the pelagic environment (Morgan and Christy 1995, Caley *et al.* 1996, Becker *et al.* 2007, Siegel *et al.* 2008, Cowen and Sponaugle 2009). After pelagic development, larvae rely on behavioural tactics to guide them towards suitable habitat which are initiated by a multitude of factors once this phase of development is complete (Wheeler and Epifanio 1978, Cronin and Forward 1979, Lambert and Epifanio 1982, McConaugha 1988, Acosta and Butler 1999, Papadopoulos *et al.* 2002, Gebauer *et al*. 1998, 2003, 2005).

In highlighting zonal preference as an important factor affecting settlement (Chapter 3), the importance of conspecifics and chemical odours in settlement dynamics was illustrated in mangals spanning the east coast of Africa. Chemical cues have proved significant in affecting settlement dynamics in marine systems (e.g. Forward *et al.* 2001, Paula *et al.* 2001, Kingsford *et al.* 2002, Forward *et al.* 2003, Anger 2006, Diele and Simith 2007) and the results of Chapter 3 suggest that these are also applicable to mangal habitat. Furthermore, zonal differences between regions indicate that suitable available habitat is an important determinant of settlement patterns

across large scales and is primarily driven by the presence of conspecifics. Temporal and spatial variability were shown to be important factors influencing settlement for centre populations and other authors further indicate that settlement in tropical east African marine systems is a spatially and temporally variable process (Nzali *et al.* 1998, Mangubhai *et al.* 2007, Kaunda-Arara *et al.* 2009, Ragionieri *et al.* 2015). At the edge of the distributional range, settlement was shown to be highly spatially and temporally variable, time often acting in conjunction with several other factors. Overall, this indicates that settlement into mangal systems may be driven by synergistic interactions of physical and biological factors which results in variable settlement in time and space.

Perisesarma guttatum populations along the east coast of Africa are characterised by high haplotypic diversity (Lewontin 1974, Lavery *et al.* 1996, Silva *et al.* 2010a) with two distinct clades, the first being associated with populations in Kenya, Tanzania and northern Mozambique, while the second clade is present in southern Mozambique, (Inhaca Island and Maputo Bay) (Silva *et al.* 2010a). The clades are postulated to be a result of a fall in sea level in the Pleistocene which removed suitable shelf habitat. Such results are typical of other marine invertebrates spanning this distributional range (e.g. giant tiger prawn, *Penaeus monodon*; Benzie *et al.* 2002, Forbes *et al.* 1999; giant clam *Tridacna crocea*, Kochzius and Nuryanto 2008). Following the latest major sea level rise, populations are thought to have reinvaded from the north (Forbes *et al.* 1999). Overall, this indicates that for these species, there is little connectivity among these populations along the east coast of Africa, and with little gene flow among populations, advantageous physiological characteristics of centre populations are unlikely to be transferred to their edge of distribution counterparts. This, in conjunction with the high temporal and spatial variability and distinct seasonality in settlement at edge populations further isolates edge populations. Contrastingly, recent genetic analysis of *Neosarmatium africanum*

(formerly *Neosarmatium meinerti*, De Man 1887) and *Uca annulipes* had no genetic differentiation along the latitudinal cline (Silva *et al.* 2010a, Ragionieri *et al.* 2010, 2012). This suggests that these are open populations driven by large scale dispersal, where larvae are probably adapted to take advantage of the Agulhas Current, which is a prominent oceanographic feature in this region, to facilitate large scale dispersal (Lutjeharms 2006). Thus, edge populations of *N. africanum* (and maybe *Uca* spp.), although susceptible to physiological stress and sporadic recruitment events, may have a fairly high probability of persisting at edge localities, due to new recruits arriving from removed populations and, with them, the possibly added adaptations to physiological stress. As Palumbi (2004) describes, oceanographic currents can have varying effects of marine populations, either acting as gene-exchange corridors or constricting gene flow by acting as extrinsic and invisible physical barriers to dispersal. By using the genetic information presented in previous studies (e.g. Silva *et al.* 2010a, b. Ragionieri *et al.* 2010, 2012), possibly vulnerable species can be identified, while it has become apparent that species specific traits of dispersal may mitigate the effects of climate change by facilitating the expansion of advantageous physiological characteristics along the latitudinal distribution.

5.3 Predicting population persistence under climate change scenarios:

As it is imperative to forecast ecological changes due to rapid regional and global climate change (Clarke *et al.* 2001, Jeltsch *et al.* 2008), Individual based modelling (IBM), as used in Chapter 4, provides a useful tool for the prediction of population dynamics under scenarios of change. This form of modelling, using physiological data, has not been applied to brachyuran populations living in mangrove ecosystems. The outcomes of the Changing Reproductive Dynamics (CReDy) individual based model, based on the physiological reactions of *Perisesarma guttatum* to an empirical temperature and medium profile of the *Rhizophora mucronata* mangal zone,

suggest that, as temperature rises, this species reduces its reproductive output at the centre (Kenya) of its distribution compared to conspecifics at the edge (South Africa) of its distribution.

In contrast, Chapter 2 suggests that, due to the oxygen capacity limitation of thermal tolerance (OCLLT) of *Perisesarma guttatum* in both milieus, the centre populations are more adept at dealing with the temperature rises likely to occur over the next 100 years (Walther *et al.* 2002, Deutsch *et al.* 2008, Hoegh-Guldberg and Bruno 2010, Doney *et al.* 2012, IPCC 2014a, b, c). It must be noted that outcomes from the modelling study are based on one spring tide (19 days) out of an entire year and until it can be applied to temperature and tide data for an entire year, the model is only able to give a very limited temporal snapshot of the reproductive dynamics of populations in each region. Furthermore, behavioural aspects have yet to be considered in the model, while specific strategies may be key to either ensure the survival of the mother at the expense of the embryos or *vice versa.* The degradation of mangal ecosystems such as reducing tree cover (Semesi 1998, Ashton *et al.* 2003) would likely exacerbate any climate related stressors and should be considered in forecasting the impacts of climate change on these species. The contrasting views illustrated by these approaches highlight the importance of considering different temporal and spatial scales in assessing the effects of climate change (e.g. Ricklefs 1987, Brown and Maurer 1989, Cornell and Lawton 1992, Ricklefs and Schluter 1993, Gaston and Blackburn 2000, Gaston *et al.* 2009). Behavioural aspects and a greater temporal window are still to be included in the model. Once the relevant data become available, and with these modifications, reliable long term predictions will allow for comparisons to empirical physiological data, producing further insights into the drivers of population persistence at the centre and edge of distributions under climate change regimes.

5.4 Concluding Remarks:

Within this thesis, the principal of oxygen and capacity limitation of thermal tolerance (OCLTT), as applied to ectotherms across different localised ecosystems (Frederich and Pörtner 2000, Pörtner 2001, 2002, 2010, Mark *et al.* 2002, Melzner *et al.* 2006, Wittmann *et al.* 2008) has been successfully applied across latitudinal scales and ontogenetic stages, providing novel insights into ontogenetic and latitudinal inter- and intra-specific variability. This represents the first time that OCLTT has been applied across ontogenetic stages and follows on the work of Solokova and Pörtner (2003) and Fusi *et al.* (2014) in the application of this concept across large spatial scales. Within the context of OCLTT, I have shown that oxidative stress can be alleviated by switching milieus in bimodal breathing species, in line with work presented by Giomi *et al.* (2014, in press) and Fusi *et al.* (2014), and presented novel information on how bimodal breathing acts across ontogenetic stages and large scale inter- and intra-specific variability, bringing up the role of reproduction in the vulnerability of populations to temperature. Empirical data from the physiological studies and environmental loggers were applied to the CReDy individual based model in the first attempt to forecast reproductive output of mangrove crabs across latitudes, based on their physiological responses to milieu and temperature at the centre (Kenya) and edge (South Africa) of their distribution. The physiological and modelling studies highlight the importance of maternal input in the production and care of viable embryos from a physiological point of view and suggest that this is an important facet in controlling population persistence at the centre and edge of distribution. Settlement dynamics at the centre and edge of mangal distribution along the east coast of Africa further provided insights into vulnerability of population over regional and local scales especially in conjunction with genetic information from previous studies (Ragionieri *et al.* 2010, Silva *et al.* 2010a, b). Overall, this thesis provides valuable perceptions of physiological aspects affecting population dynamics over large scales and lays the foundations for predicting population dynamics based on physiological sensitivity to

climate change in bimodal breathing species. Furthermore, the importance of large scale spatial and temporal studies is highlighted for determining patterns and processes, while the importance of localised studies in determining finer scale variability is maintained. In this study populations at the edge of their distribution appear to be the most vulnerable to climate change with maternal care being highlighted as a critical process in determining the persistence of populations. As a result, at the edge of distribution, with increasing temperatures, the contribution of gravid females to offshore larval pools from which new recruits are drawn is likely to decrease in size. In conjunction with settlement dynamics associated with this region, this decreasing contribution will ultimately affect population sizes and persistence and consequently have knock on effects within the mangrove ecosystem possibly causing a contraction of the entire ecosystem.

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APPENDIX

6.1 PERMANOVA tables comparing gravid and non gravid species

Table 7: PERMANOVA tables comparing the oxygen consumption rates of gravid and non-gravid *Perisesarma guttatum* and *Uca urvillei* between Kenya and South Africa.

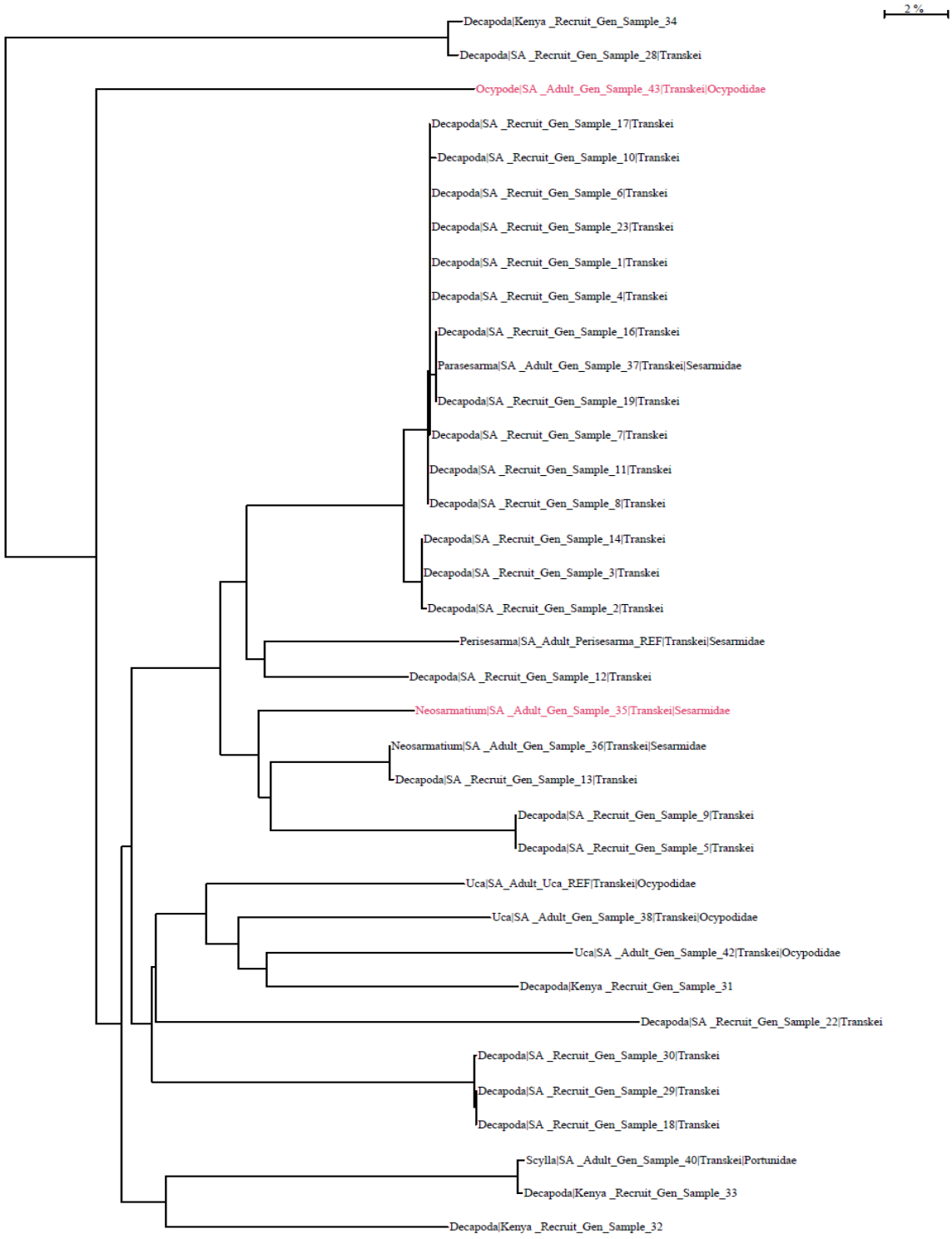
		Oxygen consumption Rate	
Source	d.f.	M.S.	*F*
Species = Sp	1	$2.22E^{-2}$	7.94**
Region = Re	1	0.43	153.7***
Air/Water	1	$1.10E^{-3}$	0.39
Condition (Gravid/Non-gravid) = Co	1	$9.50E^{-2}$	33.94***
Temperature = Temp	8	$5.43E^{-2}$	19.39***
Sp x Co	1	$1.44E^{-2}$	5.15*
Sp x Air/Water	1	0.10	37.09***
Sp x Temp	8	$1.75E^{-2}$	6.27***
Re x Co	1	0.48	169.84***
Re x Air/Water	1	$5.19E^{-2}$	18.562***
Co x Air/Water	1	$1.33E^{-2}$	4.74*
Co x Temp	8	$3.52E^{-2}$	12.57***
Sp x Co x Air/Water	1	$6.23E^{-2}$	22.25***
Re x Co x Air/Water	1	$4.19E^{-2}$	14.97***
Re x Co x Temp	4	$1.05E^{-2}$	3.77**
Co x Air/Water x Temp	8	$1.18E^{-2}$	4.21***
Sp x Re x Co x Air/Water	1	$6.40E^{-2}$	22.89***
Re x Co x Air/Water x Temp	4	$8.60E^{-3}$	3.07*
Residual	785	$2.80E^{-3}$	
Total	899		

6.2 PERMANOVA tables comparing maternal costs among species

Table 8: PERMANOVA tables comparing the maternal effect of gravid *Perisesarma guttatum* and *Uca urvillei* between Kenya and South Africa.

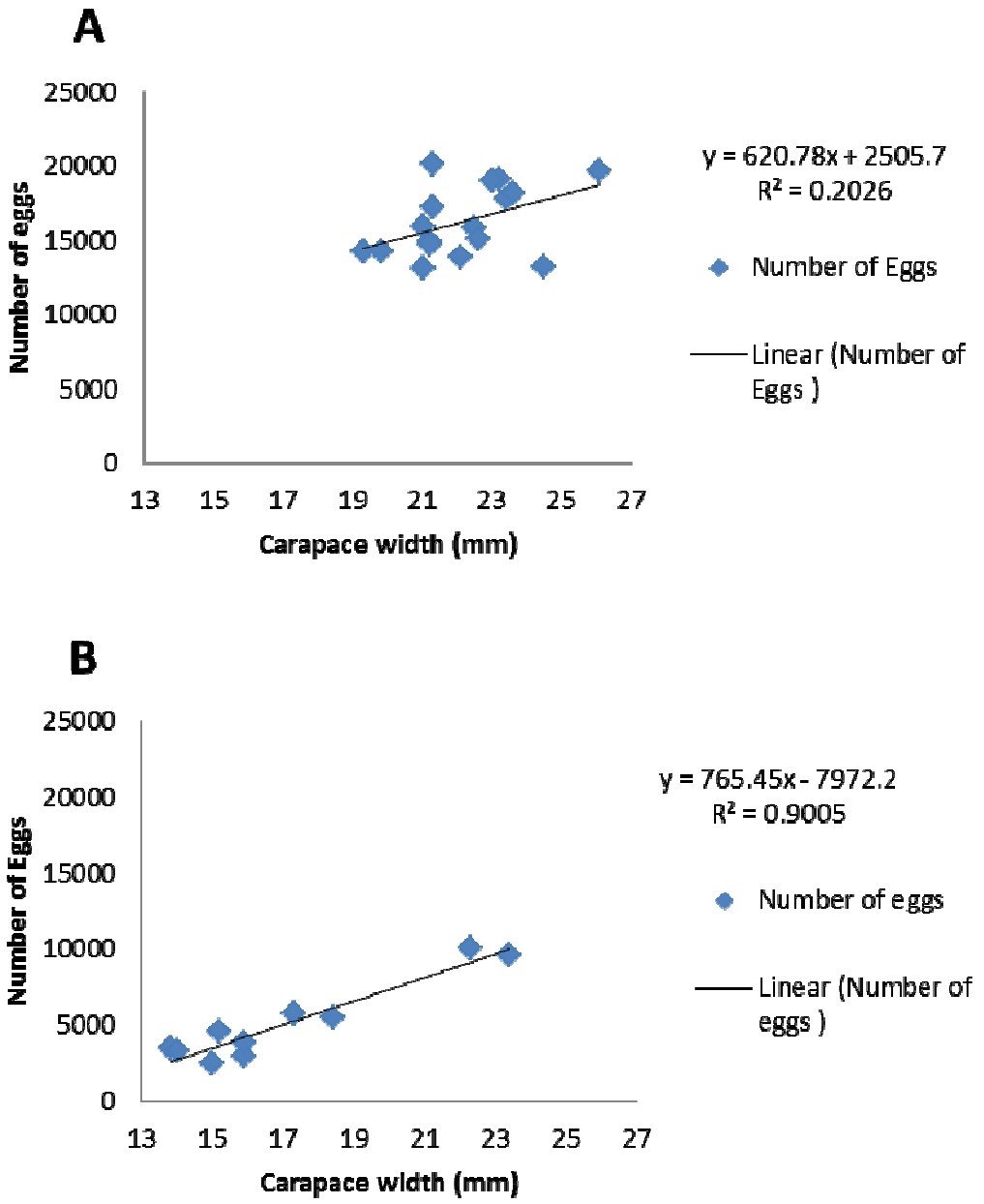
		Oxygen consumption Rate	
Source	d.f.	M.S.	*F*
Species = Sp	1	$2.69E^{-2}$	8.11**
Region = Re	1	0.94	282.72***
Air/Water	1	$2.40E^{-2}$	7.25**
Temperature = Temp	8	$7.22E^{-2}$	21.78***
Sp x Air/Water	1	$1.21E^{-1}$	36.52***
Sp x Temp	8	$8.89E^{-3}$	2.68**
Re x Air/Water	1	$8.37E^{-2}$	25.24***
Re x Temp	4	$2.08E^{-2}$	6.29***
Air/Water x Temp	8	$2.43E^{-2}$	7.33***
Sp x Re x Air/Water	1	$1.25E^{-1}$	37.59***
Re x Air/Water x Temp	4	$1.73E^{-2}$	5.22***
Residual	388	$3.32E^{-3}$	
Total	450		

6.3 Bold Taxon ID Tree



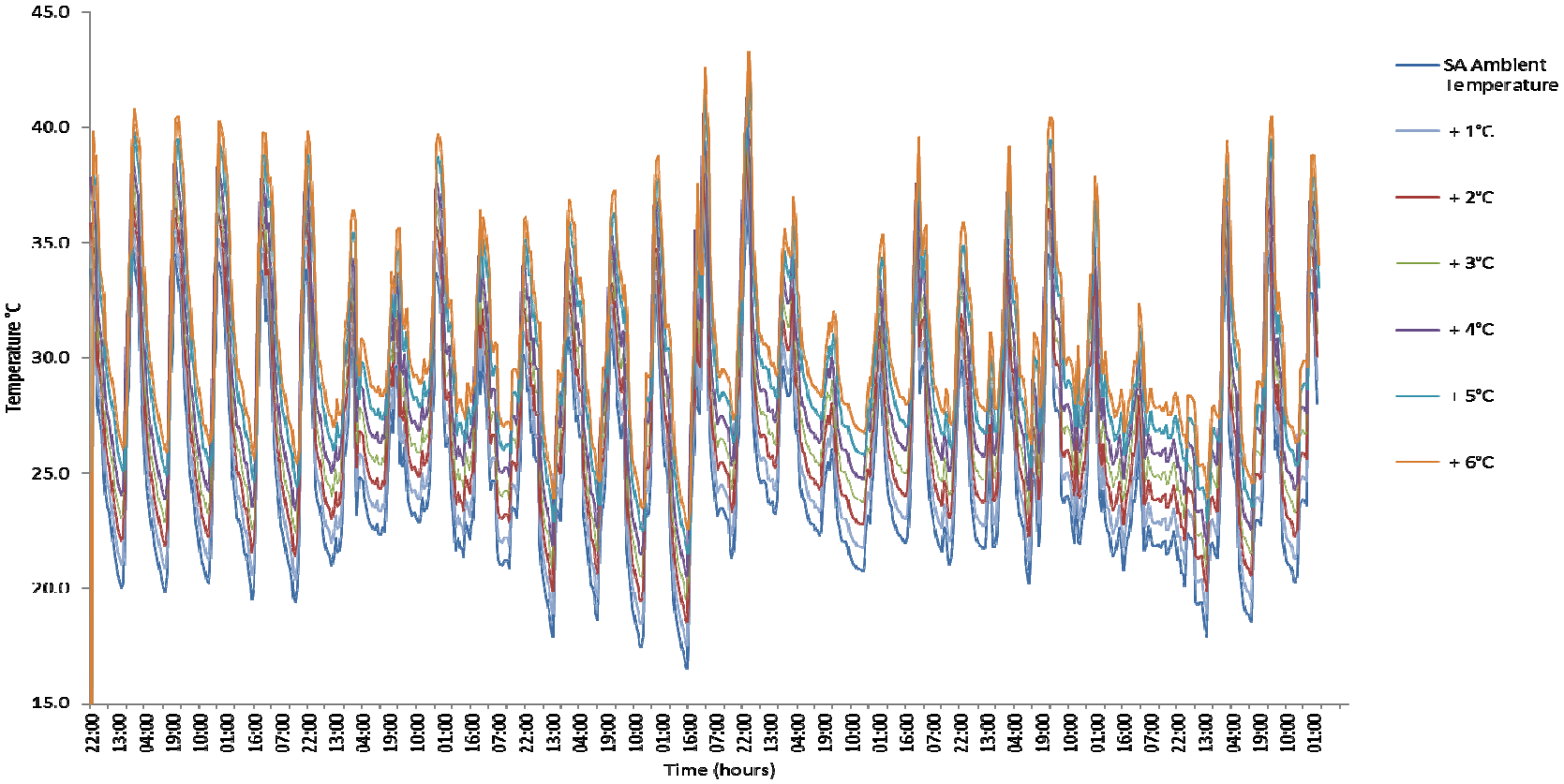
Appendix 6.3: Bold taxon ID tree showing groupings of megalopal recruits in relation to known specimen DNA.

6.4 Linear regressionof Carapace with to number of eggs

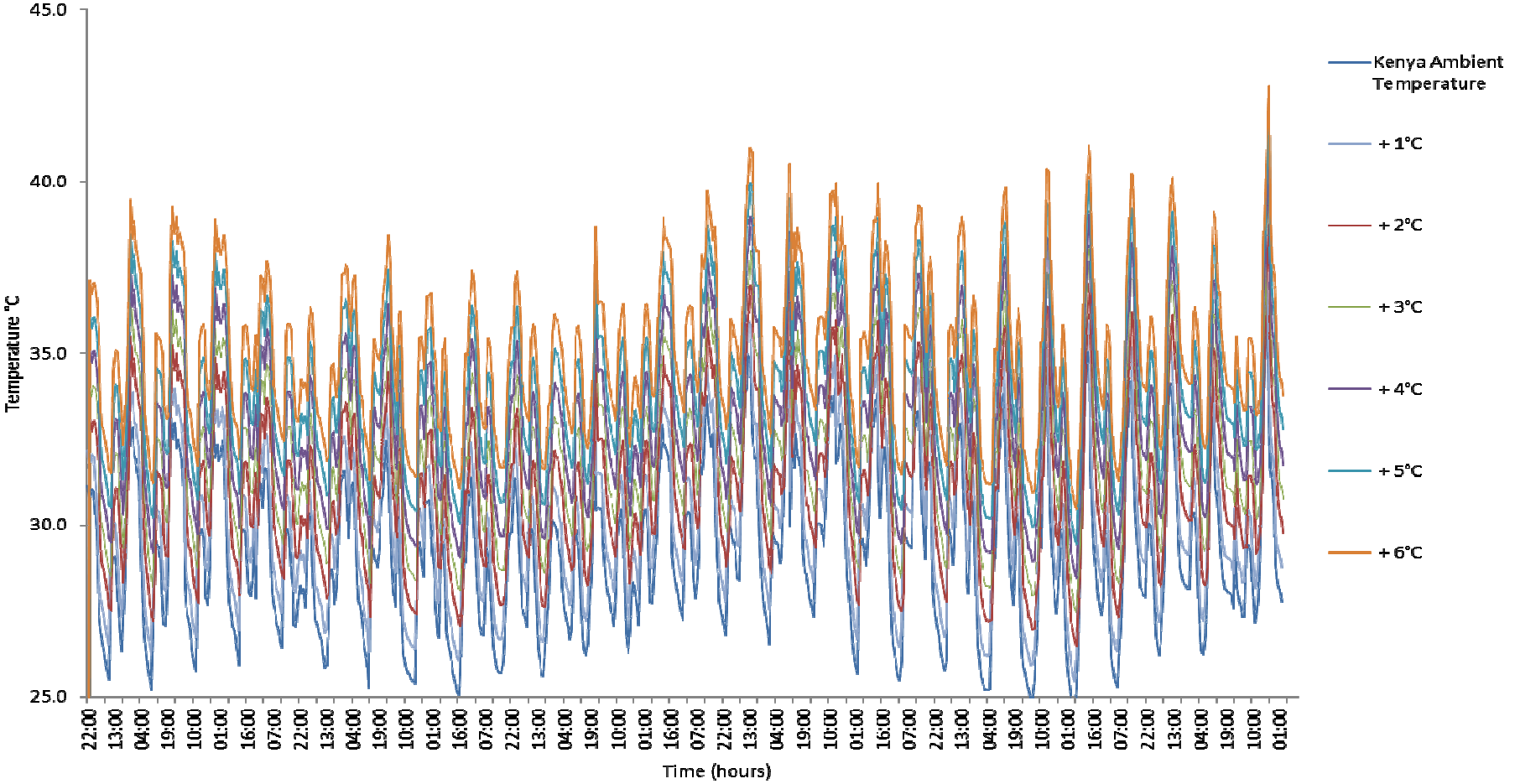


Appendix 6.4, Figure 1: Linear regressions of carapace width of gravid female *Perisesarma guttatum* to the number of eggs present on gravid females in (A) South Africa and (B) Kenya.

6.5 Temperature profiles used in model simulations



Appendix 6.5, Figure1: Temperature profile used in CReDy simulations indicationg the increasing temperatures from ambient temperatures in South Africa (recorded in situ) to 6 °C above ambient.



Appendix 6.5, Figure2: Temperature profile used in CReDy simulations indicationg the increasing temperatures from ambient temperatures in Kenya (recorded in situ) to 6 °C above ambient.

6.6 CReDy Model Code:

[As implemented in Netlogo 5.0.3 (Wilensky 1999)]

```
breed [adults adult]

adults-own
[
state
bodySize
E2
E4
]

globals
 [
  milieu
  hour
  tide
  day
  month
  temperature
  tempWater
  tempAir
  probGenEggs
  probCarryEggs
  probE4
  probHatch
```

```
  hatchedEggs
 ]

to setup

 file-close
 ca
 reset-ticks
 set hour 0
 set day 1
 set month 1

 if location = "SA" [set file "SA.txt"]
 if location = "Kenya" [set file "Kenya.txt"]

 random-seed seed

  ask patches[
   if location = "Kenya" [sprout-adults round (random-normal 1.21 0.16)]
   if location = "SA"    [sprout-adults round (random-normal 0.68 0.20)]
  ]

  ask adults[
   set bodySize random-normal 20.5 1.83
   set size 1 + (Bodysize - 20.5) * 0.1
   set state "genEggs"
   set color white
  ]
```

```
  resetProbGenEggs

  file-open file

  repeat 19 * 24[
    set temperature file-read
    set milieu file-read
    decreaseProbs
  ]

  resetProbs

  file-close
  file-open file

end

to resetProbs
      set probCarryEggs 1
      set probE4 1
      set probHatch 1
end

to resetProbGenEggs
  set probGenEggs 1
end

to go
```

```
tick
set hour hour + 1

if hour = 25[
  carryEggs
  set hour 1
  set day day + 1
  if day = 11[
    growE2
  ]
  if day = 20[
    growE4
    releaseEggs
    set day 1
    set month month + 1
  ]
]

if file-at-end? = TRUE [stop]
set temperature file-read
set milieu file-read

decreaseProbs

if day = 1 and hour = 1 [resetProbs
  generateEggs
  resetProbGenEggs
]
```

```
end

to decreaseProbs

  if location = "SA" [
    if milieu = "water" [

      if temperature < 31 [
        set probGenEggs probGenEggs - redGenEggs
        set probCarryEggs probCarryEggs - redCarryEggs
      ]
      if temperature < 29 [
        set probE4 probE4 - redE4
        set probHatch probHatch - redHatch
      ]
    ]

    if milieu = "air" [

      if temperature < 31 [
        set probGenEggs probGenEggs - redGenEggs
      ]
      if temperature < 25 [
        set probCarryEggs probCarryEggs - redCarryEggs
      ]
      set probE4 probE4 - redE4
      set probHatch probHatch - redHatch
    ]
  ]
```

```
if location = "Kenya" [
  if milieu = "water" [
    set probGenEggs probGenEggs - redGenEggs
    set probCarryEggs probCarryEggs - redCarryEggs
    if temperature < 29 [
      set probE4 probE4 - redE4
      set probHatch probHatch - redHatch
    ]
  ]

  if milieu = "air" [

    set probGenEggs probGenEggs - redGenEggs
    if temperature > 31 [
      set probCarryEggs probCarryEggs - redCarryEggs
    ]
    if temperature < 29 [
      set probE4 probE4 - redE4
      set probHatch probHatch - redHatch
    ]
  ]
]

if probGenEggs < 0 [set probGenEggs 0]
if probCarryEggs < 0 [set probCarryEggs 0]
if probE4 < 0 [set probE4 0]
if probHatch < 0 [set probHatch 0]
```

```
end

to generateEggs

  ask adults with [state = "genEggs"][
    if random-float 1 <= probGenEggs [
      set state "carryEggs"
      set color red
      set E2 round (765.45 * bodySize - 7972.2)
    ]
  ]

end

to carryEggs

  ask adults with [state = "carryEggs"][
    if random-float 1 >= probCarryEggs[
      set E2 0 set E4 0
      set state "genEggs"
      set color white
    ]
  ]

end


to releaseEggs
```

```
  print "number of fo at the end of spawning cycle: " print count adults with [state = "carryEggs"]
  ask adults with [state = "carryEggs"][
    set state ["genEggs"]
  ]

end

to growE2

  ask adults with [state = "carryEggs"][
    set E4 rbinom E2 probE4
    set E2 0
  ]

end

to growE4

  ask adults with [state = "carryEggs"][
    set hatchedEggs hatchedEggs + rbinom E4 probHatch
    set E4 0
  ]

end

to-report rbinom [n p]
     report sum n-values n [ifelse-value (p > random-float 1) [1] [0]]
end
```