The role of microhabitats within mangroves: an invertebrate and fish larval perspective

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By

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Abstract

Microhabitats provided through structural complexity are central for the diversity, productivity, connectivity and niche differentiation within and among ecosystems. Mangrove forests afford juvenile fish and invertebrates with nursery and recruitment habitats, facilitated by the fine scale configuration of their specialised root systems. Although the importance of mangroves for resident and transient juveniles is well recognised, the roles that mangrove microhabitats play for larvae is not yet comprehensively understood. This study aimed to determine how microhabitats with varying degrees of complexity influence the composition, abundance and distribution of larval communities that inhabit mangrove forests and the physiological responses of larvae to acute temperature variations in relation to ontogenetic stage and microenvironment exposure. Two relatively pristine study sites were selected to represent a warm temperate and subtropical mangrove system in the Eastern Cape and KwaZulu-Natal on the east coast of South Africa, respectively.

The differences in complexity among the root systems of *Rhizophora mucronata, Avicennia marina* and *Bruguiera gymnorhiza* were assessed using 3D scanning and the computed 3D models were then analysed using four complexity metrics. Results indicated that *A. marina* is the most complex in terms of surface-volume ratio, *R. mucronata* has the most interstitial space among its roots and *B. gymnorhiza* and *R. mucronata* differ in their fractal dimensions. Larvae collected in each microhabitat at each site using light traps showed that, despite temperature and salinity homogeneity across microenvironments, spatio-temporal differences occurred in both fish and invertebrate assemblages. This trend suggests that microhabitat structural complexity exerts an influence on larval community composition by acting as a microscape of available habitat, which ensures ecological linkages within and among the mangrove forest and

adjacent ecosystems. In addition, the oxygen consumption rates of mangrove-associated brachyuran larvae varied according to mangrove microhabitat, whereby larvae collected at less complex environments had the highest metabolic rates at increased temperatures. Moreover, ontogenetic shifts in physiology were prevalent as older brachyuran larvae were more eurythermal than earlier stages, suggesting that thermally stressful events will have a greater impact on recently spawned larvae.

Overall, the interstitial spaces within individual root systems are the most important complexity measure, as utilisation of these mangrove microhabitats is scale-dependent, and larvae will most likely occupy spaces inaccessible to large predators. Likewise, microscale variation in the environmental conditions and ontogenetic stage of brachyuran larvae within the mangrove microscape, can amplify the physiological responses to rapid temperature variations. Results suggest that early stage larvae are the most vulnerable to mass-mortality, and if thermally stressful events increase in frequency, duration and magnitude, the larval supply for the successful recruitment into adult populations could be under threat. Through linking how mangrove microhabitat complexity influences larvae in terms of community metrics and physiology, this study paves the way for further advancement of our understanding of how microscale processes emerge into meso- and macroscale patterns and influence the stability and functioning of highly productive ecosystems.

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Dedication

"As we let our own light shine, we unconsciously give other people permission to do the same."

– Nelson Rolihlahla Mandela.

This thesis is dedicated to my grandparents, Frederick and Joyce Vorsatz, who are still around, and the late Cynthia and Dennis Williams. I know you are no longer here but I am sure you would have been immensely proud of me for completing this thesis and being a first-generation doctoral candidate. This thesis is also for those from similar circumstances like myself with the drive to succeed and allow their lights to shine brightly.

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Chapter 1: General introduction

Complexity in systems that are either biological or computational is a function of the numerous different parts and the irregularity in their arrangement (McShea 1991). The complexity of a system exists in the presence of emergence and its extent depends on the amount of information needed to describe a given level of organisation (Standish 2008).

Complexity in natural systems arises from the interactions among its biotic and abiotic components (Érdi 2008, Cilliers et al. 2013). In ecology, complex systems essentially encompass five intrinsically linked features; emergence, non-linearity, evolutionary dynamics, self-organisation and scale-dependence (Bar-Yam 2002, Wu 2008, Newman et al. 2019). Emergence ensues when the properties of the entire system transpire through the interactions among individual lower level entities that are not qualitatively similar to each other (Fig. 1.1) (Harre 1972). Many phenomena in ecology result as a consequence of emergence, where small-scale interactive mechanisms result in macro-scale processes e.g. community-level structure and function, patch dynamics and disturbance regimes (Breckling et al. 2005, Ponge 2005, Newman et al. 2019). Non-linearity suggests that the behaviour of a complex system cannot be easily predicted, as small changes in the primary conditions can lead to different spatio-temporal dynamics, depending on the state of the system at a given time (Cilliers 1998). This is well described in the variability of the physical defense provided by coastal ecosystems, where the extent of the protection varies non-linearly due to plant density, location, species, tidal regime, seasonality and latitude (Koch et al. 2009).

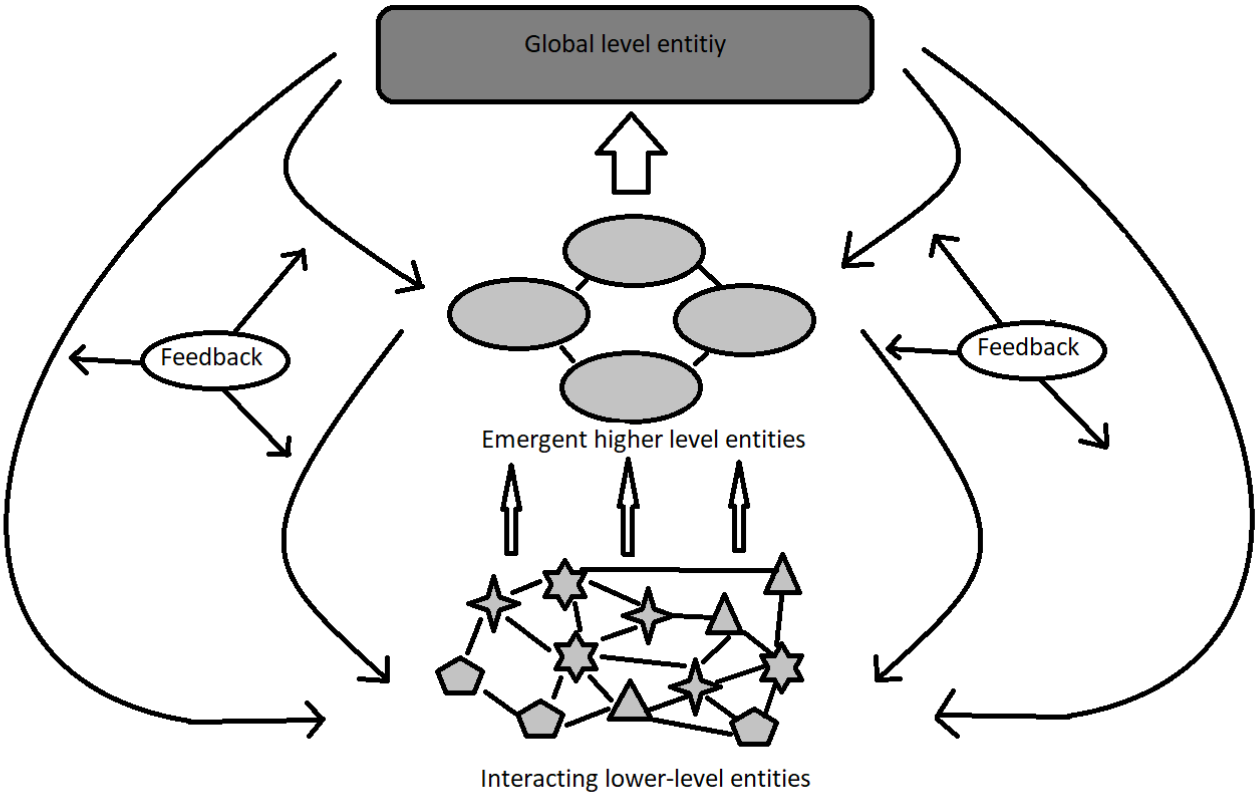

Fig. 1.1 Conceptual diagram of a complex ecological system, where interactions among lower level entities give rise to emergent patterns, processes and configurations. These emergent aggregates may rise at many scales. Adapted from Parrott (2002).

Evolutionary dynamics within complexity indicate that a system is never at rest, the variations experienced and the ability to adapt to non-linearity select those components that are fit for the changed conditions, akin to natural selection (Yaeger 2009). The influence of climate change and species invasions demonstrate this principle well, whereby invasives have the ability to exploit conditions better than natives and can establish themselves due to changes in the dynamics of a particular system (Stachowicz et al. 2002, MacDougall and Turkington 2005, Anger 2006, Hellmann et al. 2008, Demopoulos and Smith 2010, Pyšek and Richardson 2010).

When a system becomes sufficiently complex, order will spontaneously arise due to self-organisation. Self-organisation is a bottom-up process that appears at multiple levels due to the interactions commencing among lower-level components and stepping up to higher/global levels (Fig. 1.1). This progressive escalation gives precedence to non-linear outcomes at the macro-scale, e.g. population development and community composition result from microscale interactions similar to emergence (Levin 2005). Self-organisation ensures that ecosystems do not descend into randomness with a bearing on how well they function through maintaining productivity, stability and species diversity (Malina and Kauffman 1996, Rietkerk and van de Koppel 2008, Zhao et al. 2019). Ultimately, the scale at which we describe complexity is fundamental to improve the precision and relevance of observations (Bar-Yam 2004). In ecology, the scale at which observations are interpreted has a profound influence on the inferences made in understanding how complex systems operate (Morris 1987, Newman et al. 2019). The patterns and variability range from millimetres to hundreds of kilometres across ecosystems, while patterns that emerge at a certain scale, can be noise at another. Understanding the scales at which certain processes operate is therefore central to untangling multi-scale processes inducing functioning at the ecosystem level (Hewitt et al. 2017).

To fully understand a system, it is necessary to understand all of its complexities (Cilliers et al. 2013). This includes the interactions with its environment, which in itself is complex, rendering observational work humanly impossible for multi-scale processes, and the knowledge of how complex systems operate to be inferred only through models and frameworks (Cilliers 1998, Cilliers et al. 2013). Thus, frameworks to describe the dynamic relationships among ecological patterns, and processes from micro- to global scales have been designed (Newman et al. 2019). The most important framework currently adopted in ecology is Hierarchical Patch Dynamics (Wu and Loucks 1995). The Hierarchical Patch Dynamics (HPD) framework is qualitatively

applied to discrete spatial quantities to resolve problems of scale and non-equilibrium. Furthermore, HPD entails that ecosystems operate as nested discontinuous hierarchies of patch mosaics, where patches are nested functional units, implicating that larger patches contain smaller ones (e.g. patches of different species of mangrove trees are nested in the forest). Given this framework, processes that occur at the microhabitat level theoretically reverberate up the ecological hierarchy.

Other frameworks such as macroecology and lacunarity operate under the assumption that quantitative scaling laws are near continuous in large ecosystems (Newman et al. 2019). Theoretically, macroecology works to find empirical patterns which hinge on universal scaling laws that transcend several levels of organisation and orders of magnitude (Gaston and Blackburn 2007). Furthermore, it seeks to describe the mechanistic processes of individual components within a system that contribute to emergence (Brown 1999, Kerr et al. 2007). Thus, macroecology mainly focuses on modelling predictable patterns of biodiversity, species distribution ranges and shifts, as well as allometric scaling relationships at the individual, population or species level (Ruggiero and Hawkins 2006, Smith et al. 2008, Connolly et al. 2017). The macroecology framework, however, falls short in predicting patterns involved in fine scale processes due to statistically aggregating metrics at the highest levels only (Beck et al. 2012). On the other hand, lacunarity is a metric based framework that characterises configurations of objects spatially e.g. habitats patches (Plotnick et al. 1993, 1996). Lacunarity is a static property of patterns and is specifically used to estimate the irregularity or "gappiness" of a pattern as a fractal dimension, but is generally applicable to estimate the properties of self-similar fractal like patterns (Karperien et al. 2013). While, lacunarity has mainly been used in remote sensing and landscape metrics to configure forest gaps and spatial patterns, its effective

use in 3D space still needs to be verified (Plotnick et al. 1993, 1996, With and King 1999, McIntyre and Wiens 2000).

Traditionally, the elements that define complexity have been largely described qualitatively (Tokeshi and Arakaki 2012). Particularly for aquatic habitats, these elements of complexity have been referred to as easily recognisable ordinal features such as rocks, stones, sediment composition, submerged macrophytes or geomorphological structures (Tokeshi and Arakaki 2012, Carter 2013). Quantitative metrics have subsequently been used to describe the complexity of habitats that include surface-area to volume ratios (Reichert et al. 2017), shape index (Moser et al. 2002), surface rugosity (Risk 1972), slope (Friedman et al. 2012), vertical relief (Luckhurst and Luckhurst 1978), number of holes (Gratwicke and Speight 2005), curvature (Fukunaga et al. 2019) and volume of interstitial space within and among structures (Warfe et al. 2008, Sadchatheeswaran et al. 2019). While useful, these indices are scale dependent and thus not applicable across multiple scales (Tokeshi and Arakaki 2012). Fractal dimension analyses have thus found applications in ecology as a unitless metric to measure scale-independent changes in complexity (Mandelbrot 1967). Fractal dimension is described as the extent of self-similarity an object or habitat possesses, i.e. the multi-scale repetitiveness of patterns observed in an object or habitat (Mandelbrot 1983). Fractal dimension analysis has been successfully applied to quantify the complexity of rivers, coral reefs, mussel beds and subtidal macrophyte habitats (Jeffries 1993, Vasconcelos et al. 2011, Kovalenko et al. 2012, Tokeshi and Arakaki 2012, Young et al. 2017).

Structural complexity is an emergent property of components that display morphological organisation (Nicolis et al. 1990). It is hence a subset within ecosystem complexity and is

defined as the arrangement of physical structures within a habitat (Lassau and Hochuli 2004) or as several different interacting "elements" that form a distinct habitat (Kovalenko et al. 2012). Numerous methods have been employed to capture structural complexity of terrestrial and aquatic habitats to infer the importance of heterogeneity to biotic and abiotic processes. Terrestrially, methods such as LiDAR terrestrial laser scanning, remote sensing, right angle densitometers and spherical crown densitometers have been used to quantify the complexity observed within vegetative ecosystems (Dubayah and Drake 2000, Fiala et al. 2006, Ashcroft et al. 2014, Eichhorn et al. 2017). While, in aquatic environments, sonar, satellite, LiDAR, photogrammetry and several manual methods such as the chain-and-tape method for surface rugosity, are used to measure complexity (Risk 1972, Moravec and Elfes 1985, Wedding et al. 2008, Young et al. 2017). These methods have only been conducted in 2 and 2.5 dimensions, only up until recently, when computed tomography was applied to measure the extent of 3-dimensional complexity in coral surfaces, soil porosity and root systems limited to in-laboratory purposes (McCormick 1994, Perret et al. 2003, Lontoc-Roy et al. 2006, Naumann et al. 2009). With the rapid advancement of technology, the 3D scanning of habitats has become readily available to generate accurate 3D models in order to measure fine scale changes in complexity among habitats in the field, at a fraction of the scale and cost of using terrestrial LiDAR scanners (Kamal et al. 2014).

Habitat complexity exerts an integral control in structuring communities, affecting the species abundance and richness, productivity and overall ecosystem functioning (Kovalenko et al. 2012, Tokeshi and Arakaki 2012). The overarching themes in accounting for the observed biotic structuring derived from habitat complexity encompasses; increased productivity, niche differentiation and predator mediation (Kovalenko et al. 2012). The competitive exclusion principle among species requires that organisms are able to exploit different niches effectively

or be competitively excluded (Hardin 1960). This concept has been extended to include not only habitat shapes and ranges, but also the volumetric dimensions in which organisms can fit for survival (Holling 1992). The textural discontinuity hypothesis (TDH) suggests that the discontinuous structure of a particular habitat will dictate the size of the organisms that are able to exploit it efficiently (Holling 1992). This hypothesis links closely to predator-prey dynamics and the ability of complex habitats to increase available protected living space, subsequently reducing niche overlap. Small organisms might move into areas that their predators are too large to access. Thus, the availability of refugia likely decreases the over-exploitation of prey items through spatial uncoupling (Scheffer and De Boer 1995, Scheffer 1997). Moreover, habitat complexity alters the physico-chemical characteristics of the aquatic environment (Kamal et al. 2017). The presence of complex structures rescales turbulence which enriches nutrient cycling, as observed in various habitats such as mussel beds, coral reefs and littoral macrophytes (Tokeshi and Arakaki 2012). Habitat complexity is also critical for the survival of early life stages of many aquatic species e.g. red drum *Sciaenops ocellatus* (Perciformes: Sciaenidae) (Rooker et al. 1998), red king crab *Paralithoides camtschaticus* (Decapoda: Lithodidae) (Pirtle and Stoner 2010) and green frog *Rana clamitan* (Anura: Ranidae) (Tarr and Babbitt 2002).The preference for complex habitat structures is hence biologically linked to mediating predator-prey interactions, increased food availability, favourable physico-chemical conditions and improved survival of early ontogeny (Rooker et al. 1998).

The degree to which habitat complexity alters the environmental conditions at small spatial scales proliferates the establishment of microhabitats. Microhabitats are defined as distinguishable units encompassing the minimum area, in which an organism performs all of its biological functions (Morris 1987). Furthermore, a microhabitat is quantified by its physical and chemical variables that influence the time and energy allocated by an individual within its

home range (Morris 1987). In terrestrial and aquatic ecosystems, microhabitat adaptive selection is hypothesised to be driven by natural selection to increase an organism's fitness (Martin 1998). The effects of physiological buffering in microhabitats through the provision of shelter and food availability is one of the main drivers of microhabitat selection of terrestrial organisms (MacArthur and MacArthur 1961, Martin 1998, Stratford and Stouffer 2015). Amphibious toads select microhabitats seasonally that are suitable for diurnal shelter to avoid dehydration (Seebacher and Alford 2002); while the thermal properties that allow lizards to thermoregulate are the driving factor behind microhabitat selection (Trillmich and Trillmich 1986, Middendorf and Simon 1988, Smith and Ballinger 1994, Ramírez-Bautista and Benabib 2001, Smith and Ballinger 2001, Buckley et al. 2015, de Souza Terra et al. 2018). Additionally, selection of microhabitats by insectivorous birds is driven by responses to nest predation and prey abundance in vegetation fragments (Martin 1998, Barlow et al. 2006, Stratford and Stouffer 2015). Even polar microbial communities take advantage of the variation in physical substrate in order to gain protection from attenuated UV radiation flux (Cockell et al. 2003).

In aquatic environments, the complexity of structures and substrates provides microhabitats for organisms that are able to exploit them (Taniguchi and Tokeshi 2004). Water has greater viscosity and density than air, therefore, structures in an aquatic system exert an increased drag on individuals, rendering it crucial for the protection of organisms in high-flow environments (Defeo and McLachlan 2005, Mann and Lazier 2005, Steneck and Johnson 2014). In rocky intertidal areas, distinct microhabitats are provided through abiotic and biogenic sources which encompass crevices, tidal pools, cobbles, algal canopies, macrophytes, mussel and barnacle beds and oyster reefs (Flores and Paula 2001, Taniguchi and Tokeshi 2004, Kovalenko et al. 2012, Tokeshi and Arakaki 2012). These microhabitats can enhance the abundance and diversity of organisms by increasing the surface area for intertidal colonisation as well as

protection from predators, desiccation and thermal regulation for micro and macrofauna (Flores and Paula 2001, Kelaher et al. 2001, Castillo and Helmuth 2005, Denny et al. 2011, Miller et al. 2015, Monaco et al. 2015). Similar patterns are observed for increases in size-specific biodiversity and abundance in seagrass (Heck and Wetstone 1977, Attrill et al. 2000, Boström et al. 2006, Moore and Hovel 2010, Camp et al. 2013, Lefcheck et al. 2019), coral reef (Eggleston 1995, Nagelkerken et al. 2000b, Kovalenko et al. 2012, Kimirei et al. 2013a, Fukunaga et al. 2019, Lefcheck et al. 2019) and mangrove microhabitats (Nagelkerken et al. 2000a, Laegdsgaard and Johnson 2001, Jennerjahn and Ittekkot 2002, Procheş et al. 2010, Xavier et al. 2012, Kimirei et al. 2013b, Lee et al. 2014).

Mangroves are characterised by assemblages of tropical and subtropical trees and shrubs that have the ability to grow within the intertidal zone (Tomlinson 1986, Kathiresan and Bingham 2001). Mangroves require highly specialised adaptations to persist within these harsh environments (Alongi 2002, 2008). These include coping with exposure to natural stressors such as tidal inundation, flow, and high salinity in the sediment (Lugo 1980, Kathiresan and Bingham 2001, Alongi 2002, Kitaya et al. 2002, Polidoro et al. 2014). Mangroves have developed specialised lateral root systems, which include, the stilt roots of the genus *Rhizophora*, the knee roots of the genus *Bruguiera* and the pneumatophores of the genus *Avicennia*, to persist in these harsh conditions (Fig. 1.2) (Duke et al. 1998, Kathiresan and Bingham 2001).

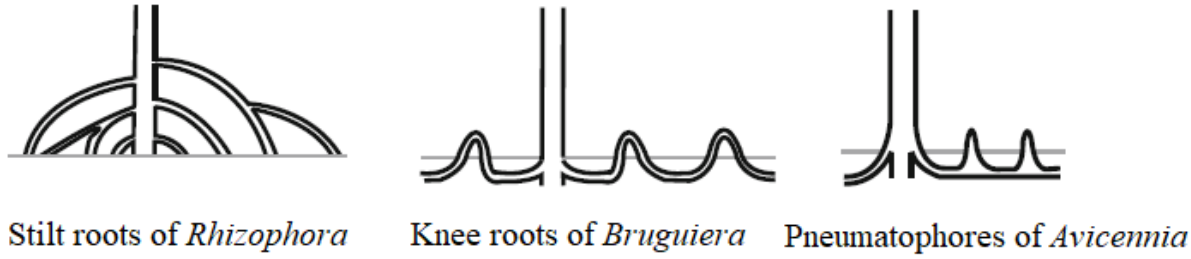

Fig. 1.2. Schematic diagram of the morphology of mangrove root types. Adapted from Ohira et al. (2013).

As a consequence of their adaptation, these specialised root systems decrease the impact of wave action and retain the elevation of shorelines (Scoffin 1970, Mazda et al. 1997, Hashim et al. 2010). Furthermore, they also provide a suitable 3-dimensional habitat to many species including estuarine and marine animals, fungi and bacteria (Kathiresan and Bingham 2001, Lee 2008, Nagelkerken 2009, Igulu et al. 2014). Microhabitats created by mangrove root systems, burrowing taxa, seagrass beds and tidal creeks all appear to play a critical role in the young life history stages of fish and invertebrates (Moser and Macintosh 2001, Paula et al. 2001, 2004a, Ikejima et al. 2003, Igulu et al. 2014, Muzaki et al. 2017). Studies on the finer scale roles of microhabitats within mangrove systems on the functional physiology of invertebrate and fish larvae, as well as their distribution and recruitment into these systems are, however underestimated. Moreover, attempts to quantify the generic differences in complexity of specialised mangrove root systems in 3D have been limited.

1.1 Objectives

The objective of this thesis is to apply a multi-disciplinary approach to provide insights into the influence mangrove microhabitats have in terms of structuring larval communities. Herein, microhabitat complexity was linked to the abundance and distribution of both fish and

invertebrate larval communities inhabiting two mangrove forests, in two different biogeographic regions. The physiological responses to microhabitat exposure, ontogenetic stage and acute temperature changes was also assessed in commonly occurring mangrove-associated brachyuran larvae. This thesis focuses on three questions centred around the regulatory role that microhabitats and their coupled degrees of complexity exert on larvae to promote the successful development and recruitment into adult populations either offshore or within the mangrove forest.

1.2 Outline of the thesis

This thesis has been assembled according to the Rhodes University policy guidelines on preparing a PhD thesis as a series of unpublished or published papers. With the exception of chapters 1 and 5, each of the chapters contained within this thesis is written as standalone studies carried out at the same sites and therefore some overlap occurs in the description and available microhabitats at each site.

Chapter 1 provides the general introduction that delivers the framework of complexity theory and highlights how structural complexity influences the structuring of biotic communities. Chapter 2 assesses the differences in structural complexity of three mangrove tree species' root systems: *Rhizophora mucronata, Avicennia marina* and *Bruguiera gymnorhiza*. Realistically scaled models of microhabitat were generated using a novel, low-cost 3D scanning technique developed by Kamal et al. (2014). Fractal dimensions and traditional complexity measures were used to provide a holistic estimation of shape, irregularity pattern, self-similarity and overall structural complexity of the mangrove root systems. These complexity indices were

then used to infer possible abiotic effects and subsequent larval use as refugia for occurring or recruiting species. Chapter 3 examines the composition, abundance and distribution of invertebrate and fish larval assemblages, within microhabitats. The objective of this chapter was to relate the larval assemblages to the environmental characteristics of the microhabitats and to determine the extent of mangrove microhabitat use for invertebrate and fish larvae. Chapter 4 assesses the effects of acute temperature changes within the thermal range experienced during austral summer on the physiological performance of stage-specific (zoeal and megalopal) mangrove-associated brachyuran larvae collected at different microhabitats. Lastly, Chapter 5 provides a general synthesis of the results of the study providing an adaptation of the conceptual model of the complex ecological systems within the context of microhabitat and larval assemblages.

Chapter 2: Structural complexity of mangrove tree root systems: possible biotic and abiotic implications

Abstract

Complex structures within habitats have been widely recognised to increase productivity, biodiversity and ecosystem functioning through the provision of microhabitats. In mangroves, structural complexity provided by the morphologically characteristic root adaptations have allowed mangroves to persist in the intertidal zone. To date, the literature discerning the ecological implications that these microhabitats provide over fine scales is limiting. Here, the general differences in structural complexity among the root systems of three mangrove tree species; *Rhizophora mucronata, Avicennia marina* and *Bruguiera gymnorhiza* at two mangrove forests in South Africa, was assessed using 3D scanning techniques to infer their abiotic and biotic implications and how they might favour the occurrence of marine larval communities within the system. Complexity was assessed using four metrics from 3D models; fractal dimensions, surface-volume (S/V) ratio, Blender interstitial volume and sphericity. Results indicated that *A. marina* is the most complex is terms of surface-volume ratio, *R. mucronata* has the most interstitial space among its roots and *B. gymnorhiza* and *R. mucronata* differ in their fractal dimensions. Parameters (S/V ratio, fractal dimensions) involving the actual structures of the root systems might be the best suited to infer how these structures affect the physico-chemical processes. The interstitial spacing within the individual root systems, however, seemed the most important measure to determine how larvae may interact with microhabitats. The structural complexity provided by the specialised roots, particularly in terms of available interstitial space could therefore be a major factor influencing how marine larval communities utilise these root systems.

2.1 Introduction

Complexity can be defined as a combination of both order and randomness which arises through interactions between all the components within a system (Cilliers 1998, Cilliers et al. 2013). The theory of complexity provides a framework that allows for a better understanding of systems which scale from the lowest e.g. atomic, to the highest e.g. galactic, levels of organisation (Zimmerman et al. 2009). In biology, these levels exist from molecules to ecosystems and human societies (Mazzocchi 2008).

The ecological complexity of available habitat generally influences the biological community structure by promoting species coexistence through reducing niche overlap (Levins 1979, Chesson 1994, 2000, Kremer and Klausmeier 2013), mediating predation by providing refuge for smaller organisms and altering the physical environment (Crowder and Cooper 1982, Rönnbäck et al. 1999, Granek and Frasier 2007, Nagelkerken 2009). These effects have been observed in both terrestrial (e.g. Tews et al. 2004; Finke and Denno 2006) and aquatic systems (Robertson and Duke 1987, Jenkins et al. 1997, Hindell and Jenkins 2004).

Ecosystems display non-linear dynamics in space and time (Parrott 2010). Spatially, habitats, which interact with various biological and physical processes to form an ecosystem, can be characterised as configurations of a particular structure in space, at a particular moment in time (Parrott 2010, Kovalenko et al. 2012, Smith et al. 2014). The complexity of self-organising aquatic habitats has been estimated using a variety of tools over varying spatial extents (Gratwicke and Speight 2005, Kovalenko et al. 2012). The indices and methods used to compare complexity of habitats vary from rugosity and surface area of mussel beds (Aronson

and Precht 1995, Parravicini et al. 2006, Burlakova et al. 2012), vertical relief of corals (Luckhurst and Luckhurst 1978, McCormick 1994, Ferrari et al. 2016), the chain-and-tape techniques for rocky habitats (Beck 1998, Kostylev et al. 2005), the interstitial distances provided by mangrove root systems (Nagelkerken et al. 2010) and the fractal dimensions of various natural objects and habitats in 2 and 2.5D space (e,g. Gee and Warwick, 1994; Meager, Schlacher and Green, 2011; Kamal *et al.*, 2017; Reichert *et al.*, 2017). The stride in technological advancement in recent years has enabled the fractal dimensions of objects to be used in 3D space via tomography (e.g. Perret et al. 2003), photogrammetry (e.g. Márquez and Averbuj 2017, Fukunaga et al. 2019) and 3D scanning (e.g. Kamal et al. 2017; Reichert et al. 2017). These 3D models have been used to address issues of ecological importance such as quantifying coral habitat complexity, sediment accretion in mangroves and implications of artificial structures in fish assemblages using mathematical equations to calculate fractal dimensions of objects to quantify non-integer complexity (Kamal et al. 2017, Reichert et al. 2017, Porter et al. 2018).

The complexity provided by mangrove root systems is thought to provide critical nursery habitat for numerous species of ecological and commercial importance (Primavera 1997, Rönnbäck et al. 1999, Nagelkerken 2009, Demopoulos and Smith 2010), as well as play a pivotal role in protecting coastal communities from storm surges (Blankespoor et al. 2017). Only one study (Kamal et al. 2017) however has made use of realistic quantitative measures to explore the complexity-service dynamics, whilst simple mimics and artificial units of the actual habitat have otherwise been used to assess the role of root attributes in attracting juvenile fish species (Nagelkerken et al. 2010). Despite the numerous literature on the ecosystem services that mangrove habitat complexity facilitates, no study has been conducted to explore the generic differences in habitat complexity among root systems in 3D space of different

mangrove tree species and how these differences may explain biotic structuring of larval communities.

This study therefore aimed to assess the differences in structural complexity of three mangrove tree species' root systems; *Rhizophora mucronata, Avicennia marina* and *Bruguiera gymnorhiza* at a microhabitat volumetric level of 1 m^3. This was done using a novel, low-cost 3D scanning technique developed by Kamal et al. (2014) to produce realistic models of microhabitat complexity. In addition to using this 3D technique, fractal dimensions and traditional complexity measures were determined to compare the complexity of resulting 3D models and give a holistic estimation of shape, irregularity pattern, self-similarity and overall structural complexity of the mangrove root systems. These complexity indices were then used to infer possible enhancing effects for favourable physico-chemical conditions and subsequent larval usage for occurring or recruiting species within these mangrove microhabitats.

2.2 Materials and methods

2.2.1 Study area

Two mangrove forests, situated in the subtropical and warm temperate bioregions on the east coast of South Africa, were sampled during October 2018 to determine the structural determinants of the mangrove tree species' root complexity (Fig. 2.1). The Mlalazi Estuary (28°57'15" S, 31°46'33" E) is situated in the subtropical region of the northern Kwazulu-Natal province, ~120 km north of Durban. The mangrove area is composed of a large number of stands of *B. gymnorhiza* and *A. marina*, whilst *R. mucronata* forms a small stand on the banks along the creeks within the forest. The Mngazana mangrove forest (31°42"S, 29°25" E) is situated in a warm temperate region in the north of the Eastern Cape province, ~250 km south-

west of Durban and is one of the most southerly mangrove forests in the world (Quisthoudt et al. 2013). This mangrove forest has the largest stand of *R. mucronata* in the country and is dominated by *A. marina* in terms of percentage coverage followed by *B. gymnorhiza* (Rajkaran et al. 2004, Peer et al. 2018).

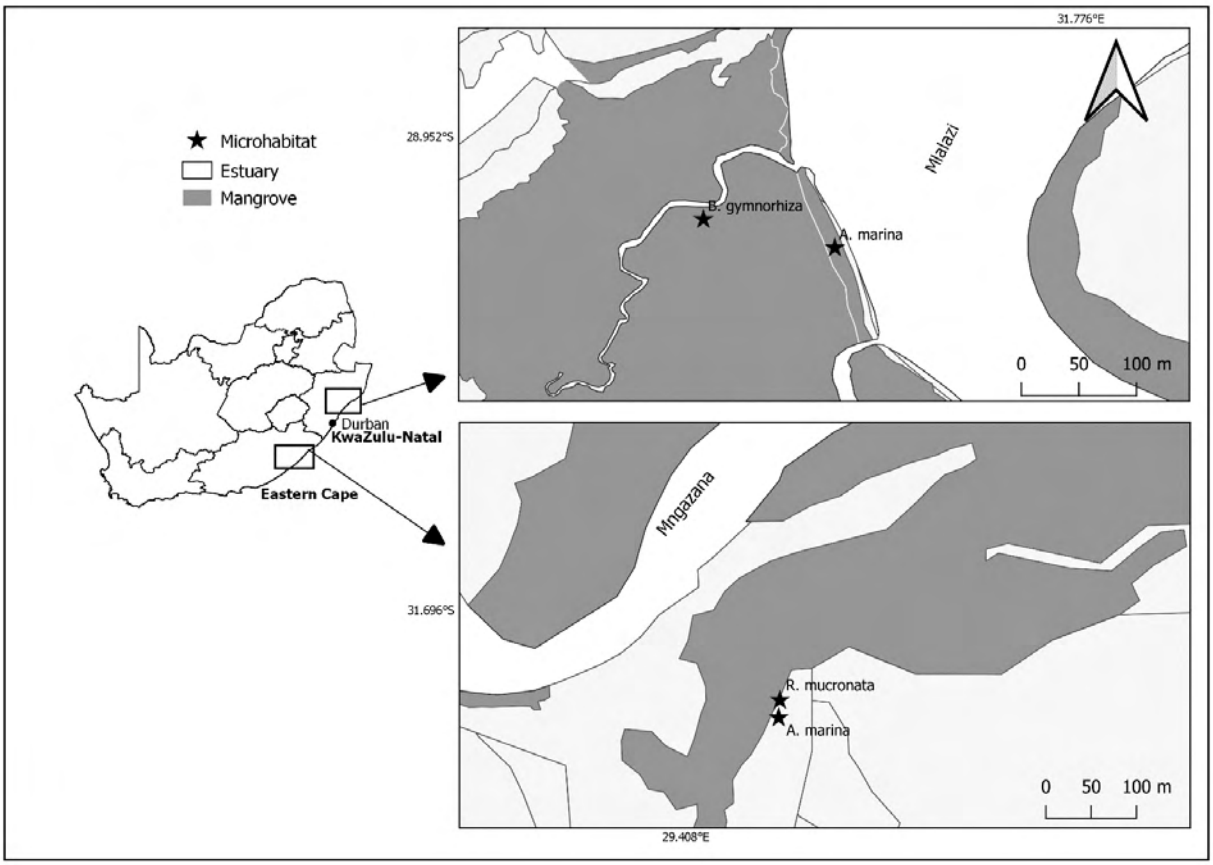

Fig. 2.1. Map of study area indicating the habitats where samples were scanned for resultant 3D models in Mlalazi (top) and Mngazana (bottom).

2.2.2 3D scanning

Three haphazard 1x1 m^2 patches of *A. marina and B. gymnorhiza* at Mlalazi and *A. marina* and *R. mucronata* at Mngazana were identified and scanned using the technique developed by Kamal et al. (2014). This technique involves using an Xbox Kinect V2 for windows sensor,

connected to a HP 450 G4 probook, powered by an inverter and 12V battery for use in the field. The Kinect sensor was carefully moved in a sine shape above the root system whilst changing the pitch and rolling angle to capture the full 360° around the root system of interest. Due to hardware limitations, the scanning parameters were set at 256^3 voxel m^{-3} resolution where each voxel is equivalent to 4 mm and saved as a Wavefront file (.obj). As suggested by Kamal et al. (2014), scans were usually conducted at low tide during dusk to minimise interference (holes in the resulting 3D mesh) due to temperature differences, moisture or sunlight exposure effects. The advantage of using this method is that it is low-cost, simple and produces rapid real-time images in order to assess the completeness of the resulting 3D model.

Raw 3D models (.obj files) (Fig. 2.2A-C) for each patch were imported and visualised in Blender v2.8 (an open source 3D program; www.blender.org/features/). Errors in the original 3D models were assessed with minor holes (<15 mm) closed and duplicate surfaces, non-manifold edges and unwanted objects mistakenly recorded in the mesh deleted to produce a 'clean, watertight' mesh of the 3D models (Fig. 2.2D-F). The models were then positioned so that the substrate captured in the scan was aligned to the x-axis of the box frame. The resulting 3D models were then exported as Wavefront .obj files for subsequent analysis.

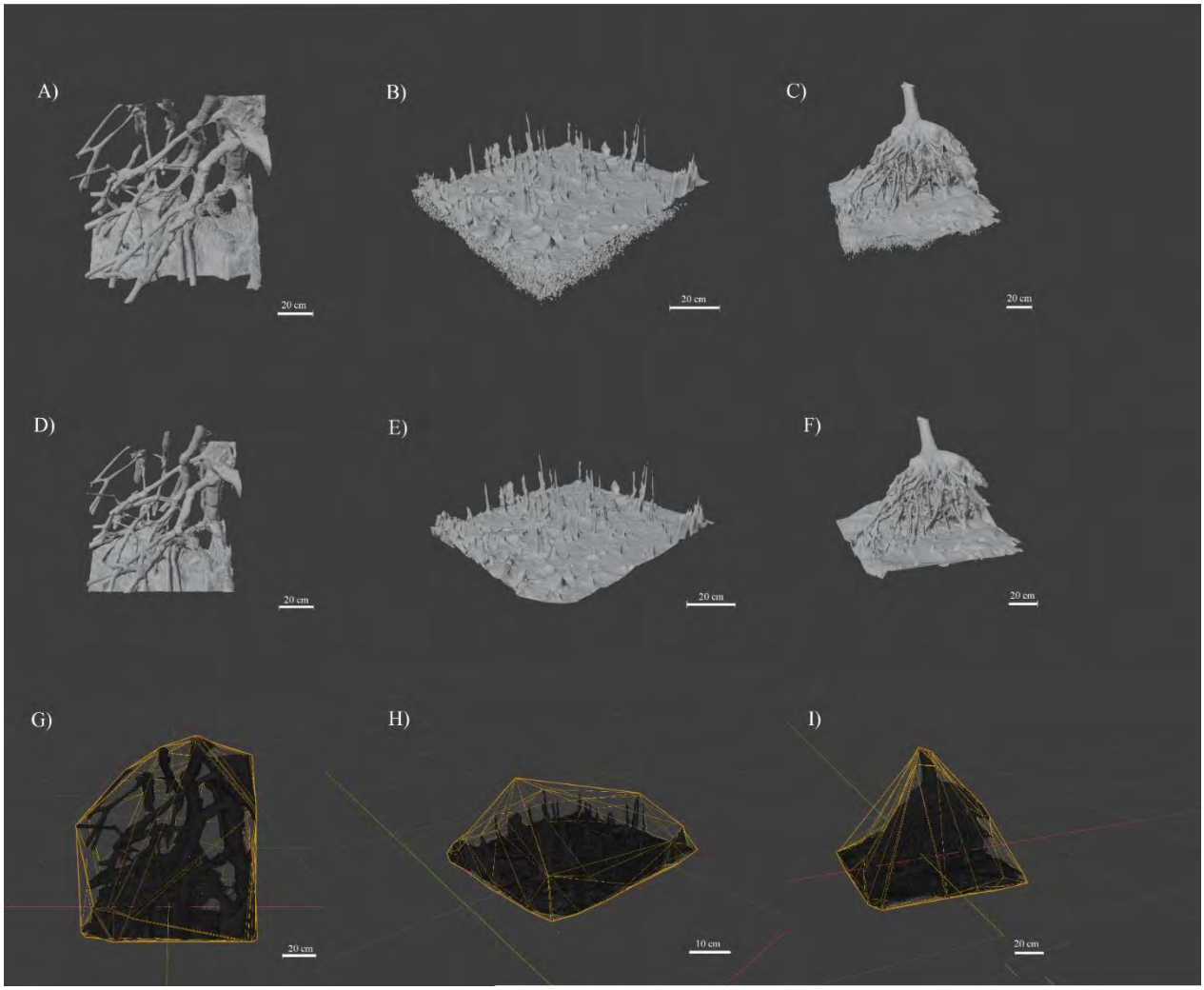

Fig. 2.2. Examples of the raw 3D models of mangrove tree species' root systems (A-C), cleaned meshes (D-F) and the 'shrinkwrap tool' (G-I) used in order to estimate the Blender interstitial volume for *R. mucronata* (left), *A. marina* (middle) and *B. gymnorhiza* (right).

The fractal dimension *D* of the 3D models was calculated from the Wavefront .obj files based on the Bouligand-Minkowski method, using the freely available Bouligand-Minkowski 3D-Toolbox (https://www.facom.ufu.br/~backes/mink3d.html) (Backes et al. 2010). The Bouligand-Minkowski method is based on the influence volume of an object computed from its dilation (Fig. 2.3), where the fractal dimension can be estimated as:

$$D = 3 - lim_{r \to 0} \frac{\log(V(r))}{\log(r)} \quad (1)$$

Where $V(r)$ is the influence volume of the object after the dilation process and r is the dilation radius used in the model and corresponds to an absolute value of 1 which is equal to the resolution of the mesh in the 3D model (4 mm for this study) (Florindo et al. 2015). The fractal dimension D was then calculated for each model with a dilation radii of 3 – 20 ($r = \{i \in \mathbb{Z} \mid 3 \leq i \leq 20\}$). The Bouligand-Minkowski method is considered the most accurate method for calculating fractal dimensions of objects due to its rotational invariance and sensitivity to fine scale structural changes in models (Tricot 1995, Backes et al. 2009, 2010, Reichert et al. 2017).

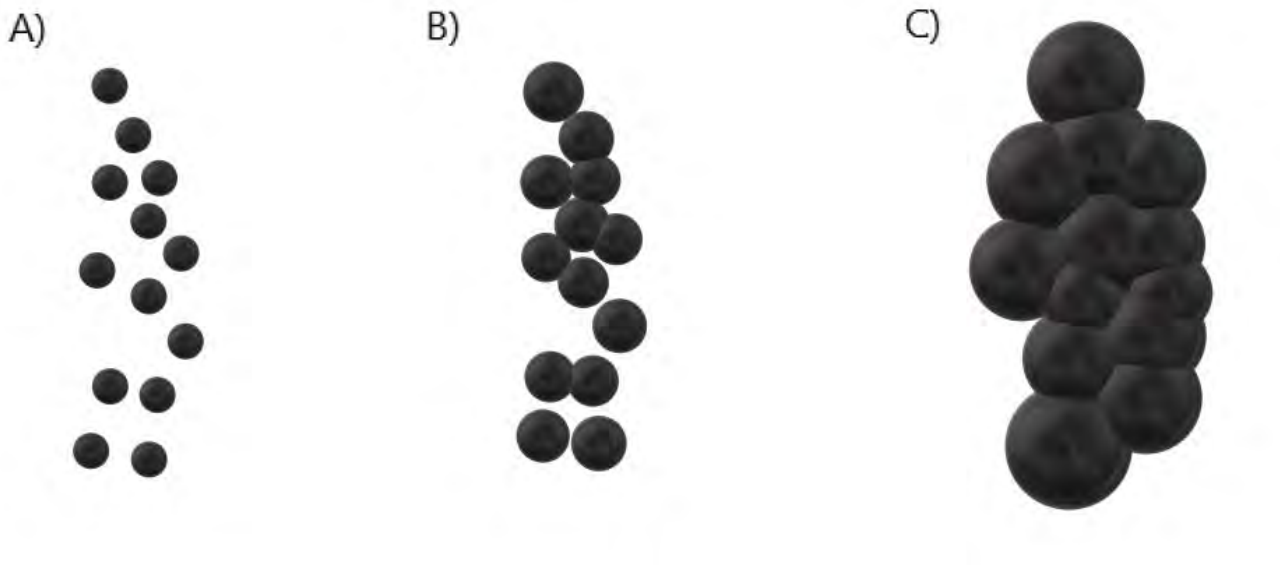

Fig. 2.3. The principle of the Bouligand-Minkowski method. The influence volume $V(r)$ generated as the radius dilation (r) values increase from A-C. With an increase in dilation radius, there are more interactions among the spheres, producing an influence volume characteristic of the 3D mesh. Adapted from Reichert et al. (2017).

Three additional traditional complexity measures were estimated for each 3D model for comparison with fractal dimension D analysis. The surface area-volume ratio (S/V ratio) links the surface area covered by the model in relation to the volume of the model to its maximum extent within its box frame. The S/V ratio was computed from each 3D model using the 'Print 3D toolbox' add-on in Blender v2.8, which readily computes the values of surface area and

volume of the model. The spherical index provides an indication of how close an object is to a perfect sphere and is defined as the ratio of surface area of a sphere that has the same volume as the object to the surface area of the object itself (Wadell 1935). The spherical index (SI) of an object can be estimated using:

$$Spherical\ Index = \frac{\left(36\pi V^3\right)^{1/3}}{A^2} \quad (2)$$

Where V is the volume of the model in cm^3 and A is the area of the model in cm^2. The third traditional complexity measure used for comparison with fractal dimension D was the Blender interstitial volume. The Blender interstitial volume is defined as the total amount of volumetric space of interstitial gaps of an object and was calculated on each 3D model using the 'shrinkwrap' modifier tool in Blender v2.8 as outlined in detail in Sadchatheeswaran et al. (2019) (Figs. 2.2H-I). The model is 'wrapped' using the 'shrinkwrap' modifier tool, whereby the volume of the 'shrink-wrapped' model is computed. The difference in the volume of the solid model as calculated using the 'Print 3D toolbox' and the volume of the 'shrink-wrapped' model is calculated to obtain the 'Blender interstitial volume'.

2.2.3 Statistical analysis

All measures of complexity were tested for the assumptions of normality and homogeneity using Shapiro-Wilk and Levene's test respectively. To compare the fractal dimensions among individual 3D models, an ANCOVA, using the log-radius (log (r)) as a covariate and individual model as a fixed factor. Whereafter, Benjamini-Hochberg adjusted pairwise t-tests were used (Benjamini and Hochberg 1995). Interspecific differences among species in relation to the complexity measures were analysed with separate 1-way ANOVAs and, significant differences among species were further carried out using pairwise t-tests. The relationship among the complexity measures were explored using Pearson's correlations. All statistical tests were

carried out in the R environment for computing statistics (R v3.3.1) (R Development Core Team, 2018) using the *Vegan* (Oksanen et al. 2018) and *Car* (Fox et al. 2018) packages.

2.3 Results

All 3D models were scanned successfully with minor holes in some scans due to moisture of the soil that compromised the ability of the RGB-D (Red, Green, Blue-Depth) sensor to effectively close holes at the base of the roots considered. At the 256^3 voxel^{-3} resolution, the tips of the *A. marina* pneumatophores were systematically slightly truncated and, in cases where the pneumatophores were tightly spaced together, they appeared fused at the base. The diameter of the pneumatophores also appeared increased in the scans due to the epiphytic algae that colonised the surface of these roots. There were significant differences among the log-log slopes between dilation radii and influence volume (ANCOVA, $F_{(11, 3912)} = 1965.5$, $p < 0.001$; Fig. 2.4). Furthermore, pairwise tests indicated significant differences ($p < 0.05$) among all models except between models 1 and 3 of *A. marina* from Mngazana ($p = 0.93$) and models 1

and 3 for Mlalazi (p = 0.123). Models 1 and 2 (p = 0.14), and 2 and 3 (p = 0.06) of *B. gymnorhiza* also did not differ in their slope (Fig. 2.4).

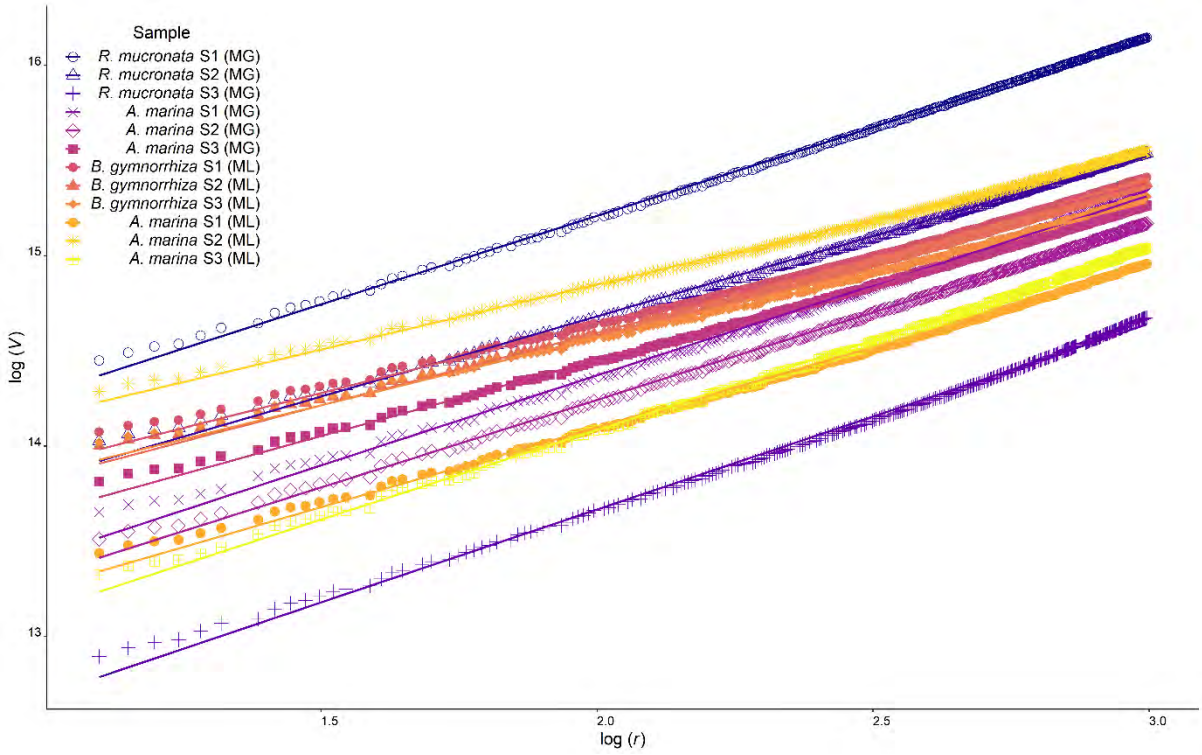

Fig. 2.4. Log-log plot of influence volume as a function of dilation radii as calculated from the Bouligand-Minkowski method to estimate the fractal dimension D of each 3D model of the root systems of *R. mucronata, A. marina* and *B. gymnorhiza.* Brackets indicate the site at which the models were scanned, (ML) Mlalazi and (MG) Mngazana.

In order to provide a comprehensive measure of shape and complexity of mangrove root systems, four complexity measures were compared (Fig. 2.5 A-D). Overall, S/V ratio ranged from 0.72 to 2.66, with *A. marina* from Mlalazi exhibiting the largest (2.3 ± 0.39) and *B. gymnorhiza* the smallest (0.93 ± 0.08) S/V ratio. The spherical index varied between 0.0023 and 0.0057, with *R. mucronata* having the smallest (0.003 ± 0.001) mean value and *A. marina* (Mngazana) having the largest (0.004 ± 0.001) value. Blender interstitial volume lay between 41.31 to 502 cm^3, *R. mucronata* (424.46 ± 103.75 cm^3) and *A. marina* from Mlalazi (155.40 ±

98.83 cm^3) had the highest and lowest mean values, respectively. Fractal dimension *D* ranged from 2.02 to 2.31, with the most complex root system on average being that of *B. gymnorhiza* (2.26 ± 0.02) and the least complex being *R. mucronata* (2.08 ± 0.06).

Values for S/V ratio, SI, Blender interstitial volume and fractal dimension *D* were normally distributed and homoscedastic. There were significant differences among mangrove root systems that derived from different species in S/V ratio (ANOVA, $F_{(3,9)} = 1.103$, $p < 0.001$; Fig. 2.5A) and Blender interstitial volume (ANOVA, $F_{(3,9)} = 7.113$, $p = 0.002$; Fig. 2.5B). Pairwise t-tests indicated that for the S/V ratio all species were significantly different ($p < 0.05$) from each other except between *B. gymnorhiza* and *R. mucronata* ($p = 0.264$). Post-hoc tests for the Blender interstitial volume indicated *R. mucronata* had significantly higher values when compared to *A. marina* from both Mngazana ($p = 0.007$), Mlalazi ($p = 0.003$) and *B. gymnorhiza* ($p = 0.023$).

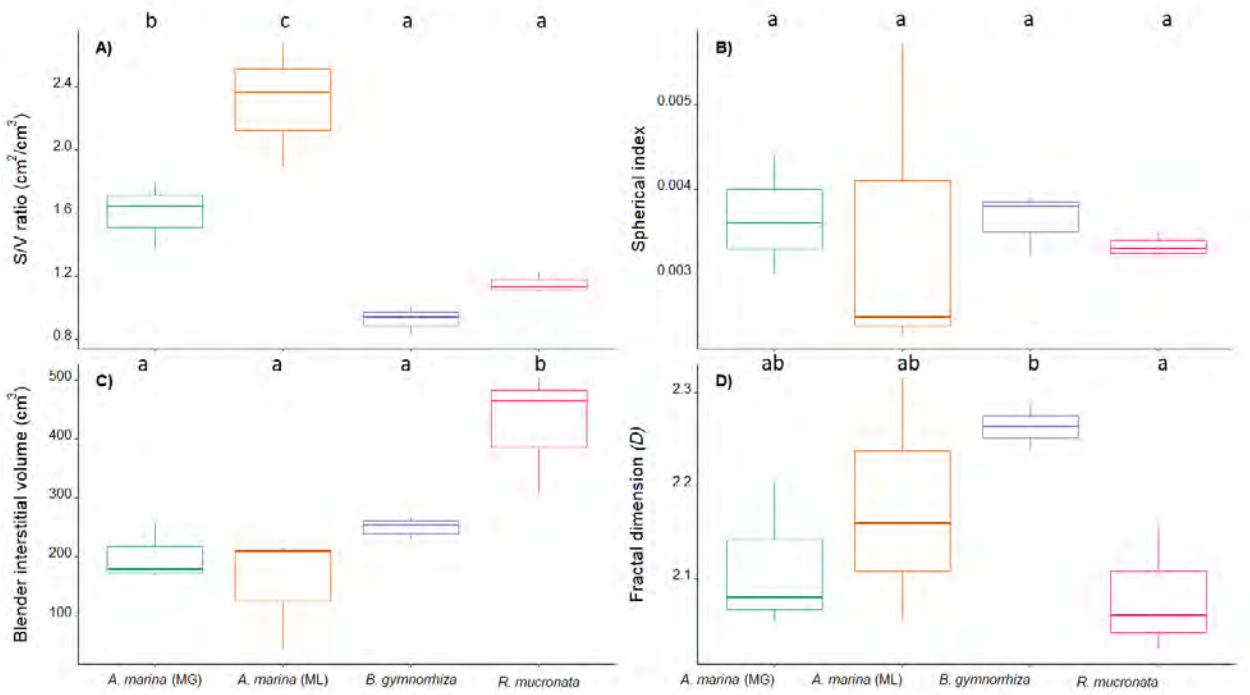

Fig. 2.5. Box-plots of species-specific measures of complexity A) S/V ratio, B) spherical index, C) Blender interstitial volume and D) fractal dimension *D*. The lower and upper limits of each box represent the 25 and 75% percentiles; the horizontal line indicates the median, the vertical lines of each box indicate 1.5x above and below the interquartile range. Letters above each plot indicate homogenous groups derived from multiple pairwise t-tests ($p < 0.05$).

No differences were observed in the spherical index (ANOVA, $F_{(3,9)} = 0.064$, $p = 0.977$; Fig. 2.5C) and fractal dimension *D* (ANOVA, $F_{(3,9)} = 2.716$, $p = 0.115$; Fig. 2.5D). The power of the similarity between *A. marina* and *R. mucronata* could have possibly masked any significant difference among the species' root systems. When a t-test between *B. gymnorhiza* and *R. mucronata* was computed, they differed significantly ($t = -2.64$, $p = 0.029$). Only S/V ratio was significantly correlated with interstitial volume (Fig 2.6).

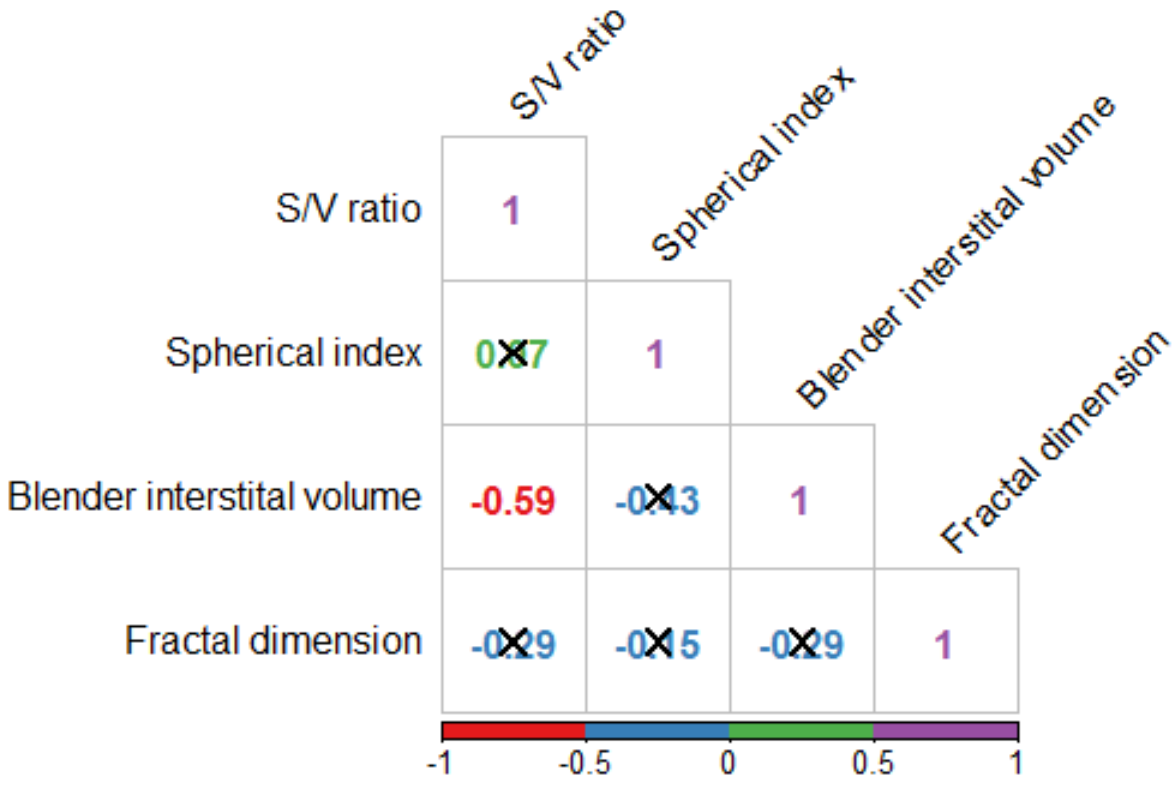

Fig. 2.6. Correlation matrix between complexity measures. Non-significant relationships ($p > 0.05$) between measures are denoted with an X.

2.5 Discussion

In this study, the difference in complexity of the root systems according to mangrove tree species was based on individual models and resulted in inter- and intraspecific (species) differences in the log-log slope of dilation radius to influence volume. Intraspecific variability in complexity using photogrammetry techniques has previously been highlighted among quadrats of pneumatophores of *A. marina*, but not between sites (Beck 1998). Such differences could be result of the natural variability in the root system of individual trees. Individual variability associated to the root systems of the three species of mangroves trees considered,

depends largely on the number of roots, distribution and density of pneumatophores, the height and number of branching roots from the stem of *R. mucronata* and the number of aerial roots extruding from the base of the stem of *B. gymnorhiza* (Kathiresan and Bingham 2001).

Three of the four measures (S/V ratio, Blender interstitial volume and fractal dimension *D*) indicated differences in the complexity of the root systems of three species of mangrove trees. The S/V ratio indicated that the pneumatophores of *A. marina* are statistically more complex than *R. mucronata* and *B. gymnorhiza*, and *R. mucronata* is slightly more complex than *B. gymnorhiza*, but not significantly so. The measures on the Blender interstitial volumes indicated that there is more space within the root system of *R. mucronata* than the other two mangrove tree species. While there was a significant difference between *B. gymnorhiza* and *R. mucronata*, there was no difference in fractal dimension *D* between the visibly distinct root morphology of *A. marina* and *R. mucronata,* which is similar to the observations reported by Kamal et al. (2014). Some of these findings are however contradictory to those of Kamal et al. (2014) who observed *R. mucronata* to have a larger S/V ratio than *A. marina*. Conversely, the interstitial space within the root systems of *R. mucronata* is larger than *A. marina*.

The pneumatophores of *A. marina* can be characterised as thin, pencil-like roots that extend from the soil to a maximum length of 50 cm (Tomlinson 1986, Ish-Shalom-Gordon and Dubinsky 1992, Dahdouh-Guebas et al. 2007). The *R. mucronata* are characterised by branching roots that derive directly from the trunk of the tree and grow down towards the soil (Gill and Tomlinson 1971, Tomlinson 1986). Moreover, *B. gymnorhiza* commonly develops knee roots that can radiate up to 10 meters from the trunk, this species also develops short aerial roots which do not reach the soil but are tightly arranged at the base of the stem (Tomlinson 1986, Kathiresan and Bingham 2001). The results of the S/V ratio follow the general

assumption that smaller organisms/objects have a larger surface area to volume ratio, as observed for *A. marina* and *R. mucronata* (Vogel 1988). The architecture of branching roots also allows for more space within the stilt roots of *R. mucronata* than the pneumatophores and aerial roots of *B. gymnorhiza* due to the latter ones being generally densely distributed and filling up vertical 3D space effectively (Kamal et al. 2014, Srikanth et al. 2016). Differences in the arrangement, compactness and extent to which roots grow above the soil can therefore account for the difference in S/V ratio as well the Blender interstitial volumes within the root systems of the tree species examined. The seemingly geometrically dissimilar pneumatophores and stilt roots did not differ in terms of fractal dimension and this could be because the fractal dimension analyses the irregularity pattern of the model and is quantified in terms of space-occupation and self-similarity (Tricot 1995, Smith et al. 1996). Fractal dimension analysis has been subject to methodological problems, in that objects with distinct morphologies as seen in this study, can have similar fractal dimensions and the fractals in 3D of natural objects vary over very narrow ranges (Halley et al. 2004). The spherical index could not discriminate among species and can be seen as less informative for complexity than the other indices measured in this study. The spherical index estimates how close an object resembles a sphere (Wadell 1935), mangrove root systems are too irregular in shape for the spherical index to deliver meaningful values of shape characterisation. Hence, the spherical index is better suited to disentangling subtle differences in objects that resemble round and platonic shapes such as pollen grains, eggs, sediment particles and habitat forming rhodoliths (Riegl 1995, Encabo et al. 2002, Lirman and Manzello 2009, Sciberras et al. 2009). Here, the measure that performed best is intrinsically linked to the research question at hand. The Blender interstitial volume worked best to infer how organisms may benefit from the complexity of the habitat structure, while the S/V ratio best performed if the underlying question was to determine how these structures might benefit sedimentation, wave dissipation and the colonisation of their surfaces.

Habitat complexity in nature is generally seen as a means whereby the physical structure of the environment influences the composition of biotic communities increasing both abundance and diversity, through the provision of niches (Smith et al. 2014, Bracewell et al. 2018). In mangroves, the root complexity aids in the promotion of diversity, abundance and assemblage structure of species (González-Megías et al. 2007, Jaxion-Harm 2010, Sheaves et al. 2014). In general, mangrove habitats, which are considered to present increased complexity, attract higher numbers of juvenile fish and shrimp than less complex habitats such as mudflats and tidal channels (Rönnbäck et al. 1999, Laegdsgaard and Johnson 2001, Cocheret De La Morinière et al. 2004).

The increased volume of interstitial spaces within the roots of *R. mucronata* may be more advantageous for sheltering organisms that are of a particular, yet considerable size and who are able to navigate through the narrow gaps to avoid larger predators (Morton 1990; Rönnbäck et al. 1999; Granek and Frasier 2007; Nagelkerken et al. 2000; Nagelkerken 2009). The scales at which these complex habitats operate hence become important depending on the size of the organisms that are able to exploit them. The enhanced complexity, in terms of the large volume of interstitial spaces within the roots of *R. mucronata*, may therefore not necessarily benefit small larvae or juveniles of certain organisms more than that of the densely compacted pneumatophores of *A. marina.* The increment of open spaces will allow larger organisms such as planktivorous fish to navigate and feed whilst they are within the microhabitat, therefore larvae will be more protected in areas where they are able to fit and move freely, that are inaccessible for sizeable organisms that feed on them (Porter et al. 2018). The enlarged S/V ratio of particular root systems of tree species may allow for colonisation of epiphytic biota and thus amplify the amount of food available to primary consumers which is recognised as an

attractant for organisms that utilise microhabitats (Verweij et al. 2006). The utilisation and interpretation of complexity and its relation to habitat use is therefore dependent on the scale at which the organism of interest experiences its environment as well as species-specific characteristics such as shape, size and feeding habits (Cocheret De La Morinière et al. 2004).

The complexity of the mangrove roots also alters the physical environment with which it interacts (Krauss et al. 2003, Kathiresan 2014, Kamal et al. 2017). Mangrove root systems with greater complexity have been reported to influence the change in pressure and the flow characteristics of water interacting tidally with the root structures (Kamal et al. 2017). Densely packed roots influence the dissipation of the energy of the flow as water that encounters obstacles increases the drag coefficient and forces the stream around the roots (Husrin et al. 2012). The height of the root system and water depth further determine the level of wave energy absorption (Mazda et al. 1997, Vo-Luong and Massel 2008, Vanegas et al. 2019). In this specific context, pneumatophores of *A. marina* are more complex than *R. mucronata,* but their ability to dissipate and absorb wave energy will further depend on the above-ground height and biomass of the roots and the depth of the water that flows through these structures (Srikanth et al. 2016). It is thus expected, that at low water levels of ebbing or flooding tides, *A. marina* might be more effective at changing the pressure and flow characteristics of water, while during storm surges and highest water levels, *R. mucronata* might offer protection against high water velocities. This further reiterates that the functions of complex structures and habitat heterogeneity in aquatic environments, such as intertidal rocky and boulder shores and subtidal kelp forests and seagrass beds, are determinant at the scales at which they operate and are interpreted (Williams and Heck 2001, Londoño-Cruz and Tokeshi 2007, Kurimoto and Tokeshi 2010). The reduction of tidal flow by complexity of root structures also influences sedimentation within mangrove forests (Furukawa and Wolanski 1996, Furukawa et al. 1997)

An altered tidal flow in highly complex structures with large AVR indices like pneumatophores change boundary layer dynamics, create eddies and regions of stagnation more efficiently and hence organic particle aggregation and the deposition and change of sediment composition (Kamal et al. 2017). These areas of particle aggregation driven by changes in boundary layer dynamics may benefit larval retention in areas of reduced flow and sedentary suspension-feeding organisms by facilitating increased ingestion of suspended particles (Lim et al. 2020). Such retentive mechanisms would generally be considered positive, however, complex habitat may also disproportionately aggregate microplastics over their surfaces, acting as sinks of contaminants and hence increasing the risk of ingestion of anthropogenic waste for filter feeding individuals occurring within these habitats (Lim et al. 2020). While not directly related to the complexity of the root structures, the dense above ground foliage of mangrove tree canopies also provide shade, which moderates temperature and indirectly controls algal abundance (Granek and Frasier 2007). Moreover, shade has been reported to be a driving factor for juveniles of the bluestriped grunt *Haemulon sciurus* (Perciformes: Haemulidae), who recruit into shaded areas in order to hide from visual predators whilst not being hindered by structures when they need to escape (Cocheret De La Morinière et al. 2004). Ultraviolet radiation in open areas also have an effect on crab zoeae and delay moulting from stage I to stage II (Hovel and Morgan 1999, Hernández Moresino et al. 2011). Exposure to ultraviolet radiation also increases swimming activity of crab larvae, thus, negatively affecting their energy budgets and moulting capacities (Hernández Moresino et al. 2011).

The inclusion of using the fractal dimensions as an additional parameter coupled with three traditional complexity measures provides a holistic measure of shape, complexity and irregularity of the root systems (Reichert et al. 2017). Fractal dimensions are more user friendly and less error-prone in comparison with other complexity measures due to their insensitivity to

the orientation of the model in question (Tricot 1995). The use of fractal dimensions to address complexity provides a different description of shape and irregularity as it combines information across scales and is related to shape irregularity, the space occupied by the model and its level of self-similarity (Tricot 1995, Smith et al. 1996, Kamal et al. 2014, 2017, Reichert et al. 2017). Additionally, fractal dimension analyses also allow for cross study comparisons because it is expressed as an absolute value.

Mangroves are one of the most productive ecosystems that contribute to both human and environmental well-being, but are declining at a rate of 1-3% per year (Friess et al. 2019). Efforts for mangrove rehabilitation have largely focused on planting of monospecific stands of *Rhizophora* spp. with a relatively low success rate in the reestablishment of the forest, fauna and functionality (Primavera and Esteban 2008, Cormier-Salem and Panfili 2016, Lewis et al. 2019). The structural diversity of mangrove tree species' root systems shown here likely supports diverse early stage communities as a consequence of larval body size relative to the volume of interstitial space offered within a specific microhabitat (Holling 1992). In such context, the protection of natural mangrove forests should be prioritised over rehabilitation due to the nuances in fine scale processes of assorted habitat provided by root diversity that have an impact on the overall functioning of the ecosystem.

The accuracy and results of traditional complexity and fractal analyses are only as good as the underlying 3D models used. The 3D models generated are comprised of polygonal meshes made up of a collection of points in 3D space and could thus be limited in their accuracy if the hardware used (3D scanners and laptops) does not meet the technical specifications to get the desired model. Thus, scanning objects of interest at a higher resolution becomes important in

order to get a full model devoid of holes in the resultant mesh. Environmental conditions may also be limiting in producing quality 3D models as differences in surface temperature and moisture effects may create holes in the mesh, therefore *in situ* scans of habitats should be carried out in low light conditions at low tide in dry conditions in mangrove forests (Kamal et al. 2014). Here, due to logistical constraints three replicates of each species' root system at each site were used to test for generic differences in their structural complexity, in the future, the sample size should be increased to develop a more robust dataset, as to further discriminate the structural complexity among species. In the present study, I provide a baseline of complexity measures that can be incorporated in conservation management decisions for prioritisation of implementing further protectionary measures.

Overall, the present study showed that there are indeed differences in complexity of three species of mangrove roots systems. Three of the four measures (S/V ratio, Blender interstitial volume and fractal dimension *D*) indicated these differences. The interstitial spaces within root systems might be the most important measurable parameter to discern how larvae interact with microhabitats provided by the roots, while the actual structures might be more useful to infer how these structures affect physico-chemical processes. When used in unison, these metrics can provide a holistic measure and subsequent interpretation of ecological implications and should therefore be considered when exploring complexity-service dynamics of mangrove root systems in a context of conservation management.

Chapter 3: Ecological scaling in mangroves: the role of microscapes for the distribution of larval assemblages

Abstract

Mangroves are regarded as important spawning grounds as well as nurseries for larvae and juvenile fishes and invertebrates due to the sheltered nature of these ecosystems. The present study examined the spatial and temporal distribution of fish and invertebrate larvae simultaneously among microhabitats within two South African mangrove forests using light traps. Results indicate that despite temperature and salinity homogeneity across microhabitats, spatio-temporal differences occurred in both fish and invertebrate larval assemblages. The offshore expulsion of invertebrate larvae that utilise an export life history strategy was passively delayed by the structurally complex root system of mangrove trees and subtidal seagrass beds. Invertebrate taxa that utilise a retention strategy exploited the tidal forcing within the creeks and the microhabitat structures to actively avoid discharge from the mangrove. Larvae of marine fish which are estuarine dependent inhabitat mangrove habitats, suggesting they use structural mangrove patchiness as corridors or temporary nurseries before settling *in situ*, into their juvenile habitat. This study steers that the proposed nursery function or early stage role that mangroves play is driven by the structural uniqueness of mangrove microscapes thus ensuring ecological linkages and functionality of these critical coastal environments.

3.1 Introduction

Mangroves have been identified as nursery areas for juvenile fishes and settling grounds for invertebrates (Rönnbäck et al. 1999, Nagelkerken et al. 2000, Sheridan and Hays 2003, Jones et al. 2010, Sheaves et al. 2012, Gajdzik et al. 2014, Rousseau et al. 2017). Habitats only serve as nurseries if they supply a greater proportion of individuals to the adult populations, than the

average contribution by all habitats used by juveniles regardless of area coverage (Dahlgren et al. 2006). Recently, authors have highlighted the need to view coastal nurseries as interconnecting heterogeneous habitats coupled with the influence of abiotic and human impacts as "seascape nurseries", to identify underlying processes that underpin their nursery value (Nagelkerken et al. 2015, Litvin et al. 2018, Lefcheck et al. 2019).

Numerous studies suggest that the complexity offered by mangrove roots provides a valuable habitat for resident and transient juvenile and larval fish, shrimp and crabs that utilise or inhabit these ecosystems (Morton 1990, Primavera 1997, Nagelkerken and Van Der Velde 2002). The root structures increase the surface area for colonisation by epiphytic organisms that are important nekton food resources (Layman 2007, Demopoulos and Smith 2010) and provide refuge from predation by larger fish or crabs (Vance et al. 1996, Primavera 1997, Rönnbäck et al. 1999). The structural complexity created in microhabitats alters flow, food availability and larval retention rates (Granek and Frasier 2007). Additionally, provision of complex microhabitats are known to result in higher biological diversity (e.g. Green et al. 2012, Sheaves et al. 2014, Gajdzik et al. 2014, Ferrari et al. 2016).

Globally, studies have focused on faunal assemblages within mangrove habitats, but have mainly been conducted on juvenile fish species (e.g. McIvor and Odum 1988, Nagelkerken et al. 2000, Weerts and Cyrus 2002, Jaxion-Harm 2010, Kramer et al. 2015). These studies, however, lacked the ability for inter-habitat comparison due to the different methodologies used, reflecting sampling bias (Beck et al. 2001). Furthermore, most studies relating to larval fish and invertebrate communities have sampled the water bodies adjacent to mangrove stands and not directly within the forest itself. This is mainly because sampling gear such as enclosure traps, block nets, fyke nets, plankton nets, gill nets, seine nets and trawls are ineffective directly

within most types of mangrove vegetation (Sheridan and Hays 2003b). Some authors (Beck et al. 2001, Sheridan and Hays 2003a) speculate that this could provide misinformation regarding the communities that inhabit mangroves. Furthermore, all studies related to invertebrate larval assemblages were performed to investigate the temporal patterns of larval flux mainly within the inlet of a mangrove lined embayment or at the mouth of mangrove lined estuaries (Dittel and Epifanio 1990, Papadopoulos et al. 2002, Paula et al. 2004a). Globally, no previous study to the best of my knowledge has targeted fish and invertebrate larval communities at multiple mangrove microhabitats simultaneously using one single and reliable sampling technique.

The present study aimed to investigate the composition, abundance and distribution of invertebrate and fish, larval assemblages, within microhabitats of two South African mangrove systems: Mlalazi and Mngazana. The objective was to relate the larval assemblages to the environmental characteristics of the microhabitats and to determine the extent of mangrove microhabitat use for invertebrate and fish larvae. We tested whether mangrove areas with greater complexity host different fish and invertebrate larval assemblages from less structurally complex, open habitats (e.g. tidal creeks) (Granek and Frasier 2007).

3.2 Methods and materials

3.2.1 Study sites

Two mangrove forests on the east coast of South Africa were selected, which included the subtropical Mlalazi and warm temperate Mngazana mangrove forests' (Fig. 3.1). The Mlalazi Estuary (28°57'15" S, 31°46'33" E) is in a relatively pristine condition and supports a mangrove forest estimated to be 40ha, dominated by *Bruguiera gymnorhiza* and *Avicennia marina*, and a

small population of *Rhizophora mucronata* which has started to establish along the creeks within the mangrove forest (Peer et al. 2018).

The Mngazana Estuary (31°42”S, 29°25” E) is situated close to the southern-most global distributional limit of mangrove forests (Rajkaran et al. 2004, Morrisey et al. 2010, Hoppe-Speer et al. 2015), and holds the third largest mangrove area (118ha), and largest stand of *R. mucronata* in South Africa (Adams and Rajkaran, 2015; Peer *et al.*, 2018). *Avicennia marina* dominates the percentage species composition of the Mngazana Estuary followed by *B. gymnorhiza* and *R. mucronata* (Peer et al. 2018).

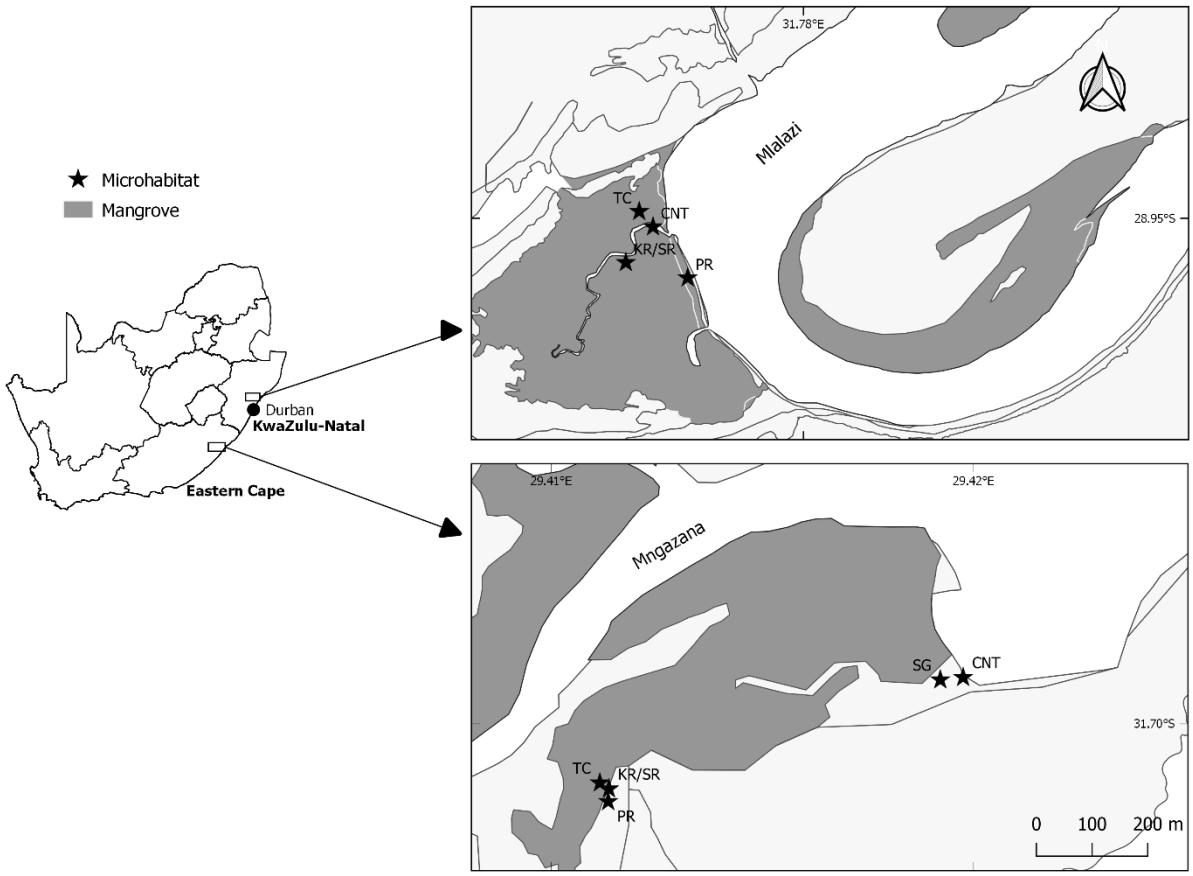

Fig. 3.1. Map of study areas (top; Mlalazi and bottom; Mngazana) on the east coast of South Africa. Microhabitats sampled are the knee/stilt roots (KR/SR), pneumatophores (PR), tidal creek (TC) and control site (CNT) at each mangrove forest including the seagrass beds (SG) at Mngazana are indicated with a star symbol (★)

3.2.2 Field sampling

For both the Mlalazi and Mngazana estuaries, while mangrove zonation is apparent, different tree species also co-occur in patches within the same elevation (Macnae, 1963). Herein, microhabitats are defined as localised, fine-scale environments encompassing the habitable unit (<2m) of different structural spaces (complexity of root systems, seagrass, tidal creeks and open water) pertaining to life history-stage (Morris 1987, Smith and Hindell 2005). Microhabitats within these co-occurring patches were identified and ranked intuitively from most to least qualitatively complex according to their structural arrangement as: 1) knee roots/stilt roots of *B. gymnorhiza* and *R. mucronata* (KR/SR) that dominated the study area of Mlalazi and Mngazana, respectively, 2) a bed of *Zostera capensis* seagrass only present at Mngazana 3) pneumatophores of *A. marina* (PR), 4) constantly inundated soft-bottom tributary tidal creeks (< 1 km in length, < 2 m in width) that flow through the mangrove forest (TC) and 5) a control area (CNT) in open water situated at the mouth of the estuary in Mngazana and the main inlet into the mangrove forest from the Mlalazi Estuary.

Small (30 cm in height and 15 cm in diameter) light traps (Chan et al. 2016) with a spatial resolution of up to 1.5 m (based on a 0 lx light intensity measurement at distances greater than 1.5 m from the light source in air), were used to collect larvae (Fig.3.2). The use of light traps with a spatial resolution of 1.5 m ensures that larvae collected are actively moving in or passing through the microhabitats sampled.Traps were deployed for 2 nights prior and after the new moon (to maximise the efficiency of the light traps) spring tides, bimonthly from September 2017 and monthly in 2018 from January to March. Two areas were identified for each microhabitat type: e.g., knee roots one (KR/SR1), knee roots two (KR/SR2), etc (Fig. 3.3). Two traps were placed at least 5m apart to avoid sample overlap within each area of microhabitat

type on each sampling night. Light traps were deployed at sunset and retrieved and emptied the following day at sunrise. This routine was repeated over two consecutive days. The collected sample was transferred from the light trap into 5 L buckets, ensuring no spillage and then sifted onto a 65 µm mesh sieve. The collected samples were preserved in 99% ethanol for identification and further analysis.

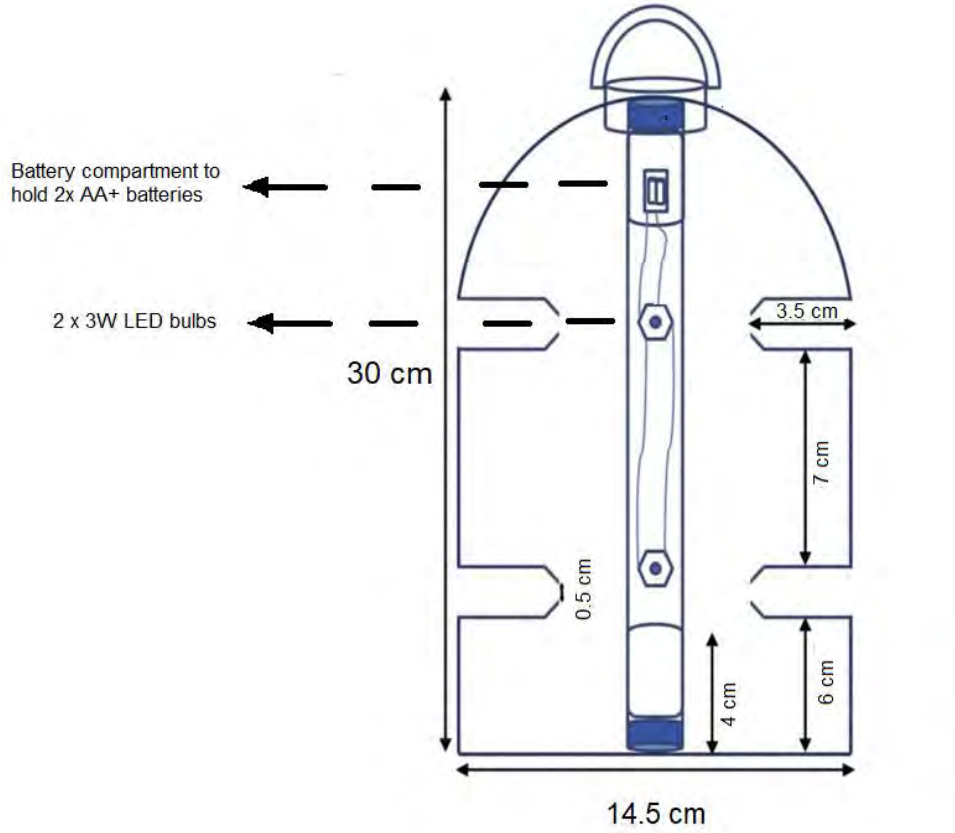

Fig. 3.2. Illustration of the design and structure of the light trap used to collect larvae (Adapted from Chan et al. 2016).

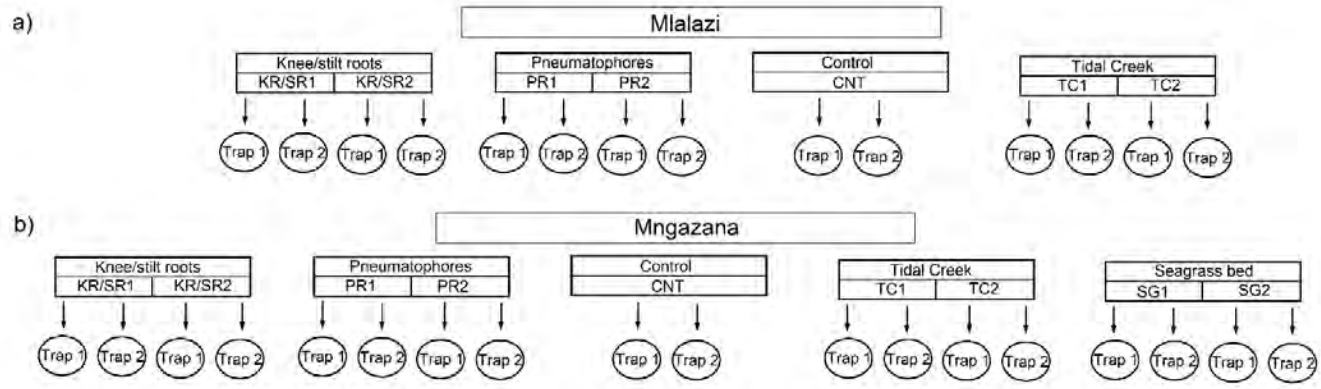

Fig. 3.3. Schematic diagram of the sampling design among microhabitats for a) Mlalazi and b) Mngazana. Sampling was repeated over two consecutive nights for five separate occasions (September, November 2017, January, February and March 2018).

In the laboratory, larvae were sorted, counted and identified to their lowest possible taxonomic level using a dissecting microscope and published descriptive species keys (Chaudhari and Jalihal 1993, Neira et al. 1998, Leis and Carson-Ewart 2000, Smith and Heemstra 2012, Bento and Paula 2018). When samples were too dense to be counted as a whole, after removal and identification of any large, rare organisms, they were sub-sampled using a Motodo plankton splitter (Motoda 1959), until approximately 300 individuals of the most dominant taxa were counted (Partridge and DeVries 1999, Mack et al. 2012).

3.2.3 Environmental variables

Temperature was recorded at each microhabitat over the sampling period using temperature iButton data loggers (Maxim Integrated Products, ColdChain Thermodynamics). Temperature iButton loggers were placed within 30 cm of each light trap to characterise the environment over the time of the trap deployment. Salinity was measured *in situ* using a handheld sea water

refractometer (RedSea) upon the retrieval of each light trap. Predicted tide data was sourced from the South African Navy.

3.2.4 Statistical analyses

All statistical analyses were conducted in the R environment for computing statistics (R v3.3.1) (R Development Core Team 2018). Hourly average temperature and salinity were compared among microhabitats and months, per site. Shapiro-Wilk and Levene's test were used to test for normality and homogeneity of variance, respectively. These tests showed a violation of the assumptions of normality and homoscedasticity for temperature and salinity at both sites. A Kruskal-Wallis test was conducted to test for differences in temperature and salinity among microhabitats within each month. An Aligned Rank Transformation was hence applied on the data to conduct nonparametric factorial analyses of variance among months and microhabitats using the *ARTool* package (Wobbrock et al. 2011). Pairwise comparisons were conducted using Tukey post-hoc tests with a Benjamini-Hochberg correction for multiple testing on significant effects (Benjamini and Hochberg 1995).

Separate statistical analyses were conducted for fish and invertebrates for each site owing to the relative orders of magnitude between these two broad taxonomic categories. Each microhabitat was considered separately in the same way as the traps were deployed: knee/stilt roots one (KR/SR1), knee/stilt roots two (KR/SR2), tidal creek one (TC1), etc. This was to ensure that the subsequent dataset used for statistical analyses was appropriately replicated and balanced. A model-based multivariate generalised linear model (*ManyGLM*), using a negative binomial distribution to analyse the effects of microhabitat and month as categorical factors and temperature, salinity and maximal tidal height as continuous predictors on community

composition (Wang et al. 2012). Multiple pairwise comparisons, via a free stepdown resampling procedure and univariate tests, were run in the *ManyGLM* to discern which microhabitats carried different community compositions, and which species were driving the differences among communities based on the species contribution to the *Sum-of-LR* (Wang et al. 2012, Warton et al. 2012). Univariate tests of individual species abundance among microhabitats were run in the *MASS* package with the *glm.nb* and *multcomp* function to resolve if certain species driving shifts in the larval assemblages among microhabitats were more abundant in one or more particular microhabitats (Venables and Ripley 2002).

Non-metric multidimensional scaling (nMDS) was used as a means to visualise community composition. Data were log (x+1) transformed and Wisconsin double-standardised prior to the calculation of the Bray-Curtis similarity matrix. Distance-based approaches such as the Bray-Curtis similarity matrix implicitly assumes a mean-variance relationship of the data, whereas ecological count data rarely satisfies this assumption (Warton et al. 2012). Non-metric dimensional scaling is less tolerant to the presence of many zeroes within in a dataset, therefore nMDS was used only as means to visualise community composition among microhabitats for each site independently.

3.3 Results

At Mlalazi, tidal height over the sampling period ranged from 0.16 - 2.28 m, while the range at Mnagazana was 0.20 - 1.90 m (Fig. 3.4). Overall, salinity ranged from 15 - 35 with a mean of 21 for Mlalazi (Fig. 3.5a) and 20 - 38 with a mean of 30 for Mngazana (Fig. 3.5b). Water temperature across all habitats had a mean of 24.70 °C and ranged from 16.93 - 34.46 °C for

Mlalazi (Fig. 3.6a), while the mean for Mngazana was 21.26 °C, with a range of 12.20 - 30.30 °C (Fig. 3.6b). There were no differences in salinity or temperature among microhabitats within each month for Mlalazi or Mngazana. There were, however, significant differences in temperature and salinities among months at Mlalazi ($F_{3,43} = 14.48$, $p < 0.001$) and Mngazana ($F_{4,63} = 34.01$, $p < 0.001$).

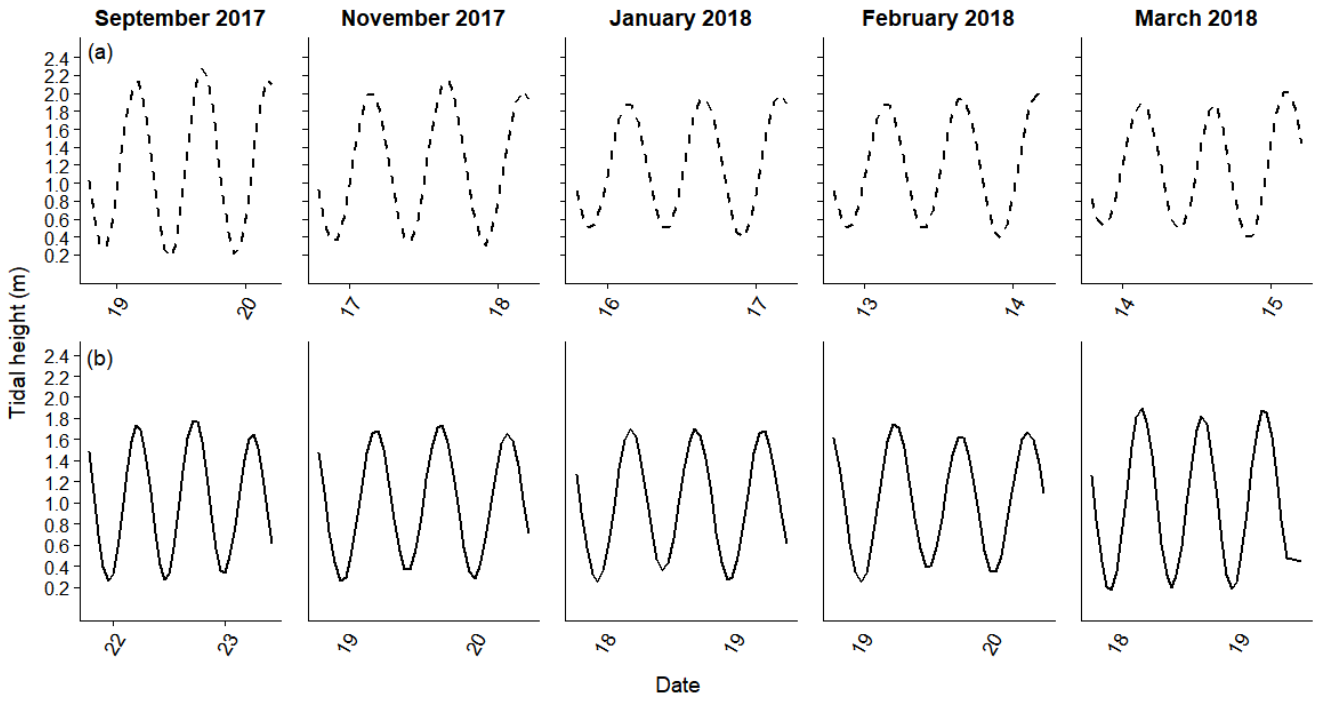

Fig. 3.4. Tidal amplitude based on predicted tides over the sampling period September 2017-March 2018 for A) Mlalazi and B) Mngazana.

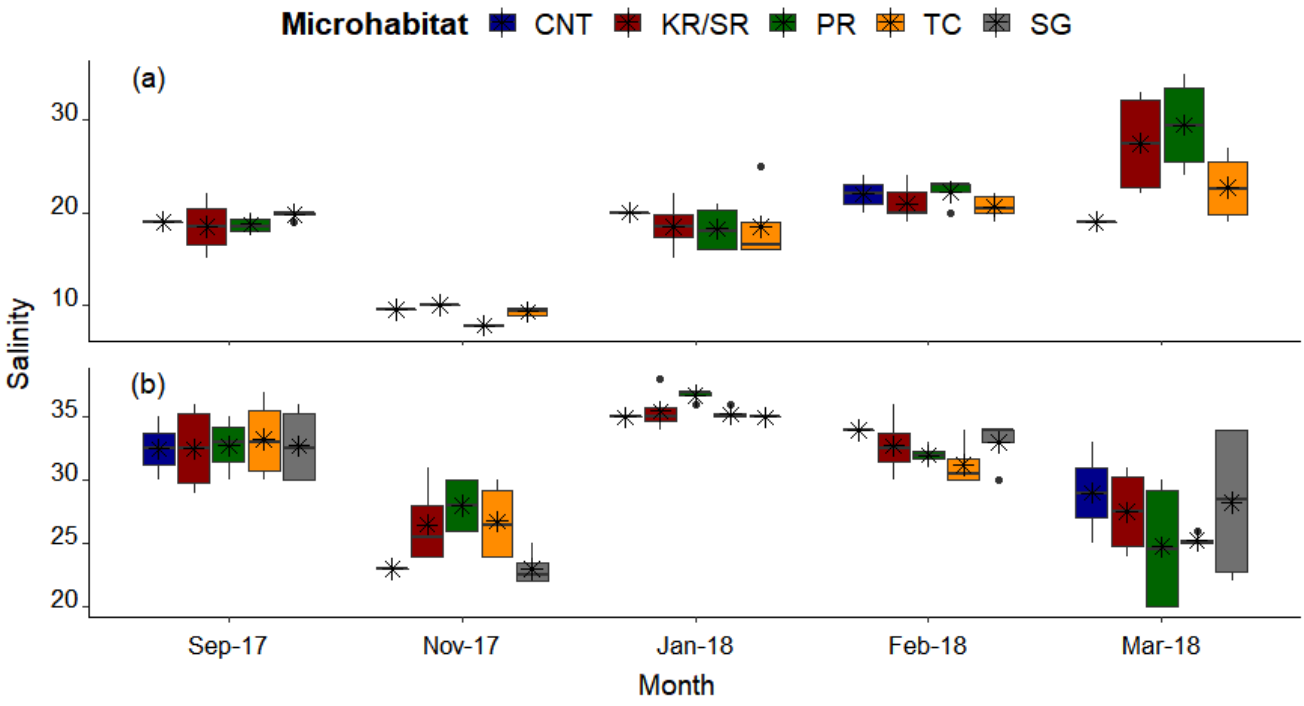

Fig. 3.5. Box plots of salinity at (a) Mlalazi and (b) Mngazana at each microhabitat sampled per month at Mlalazi. The 25 and 75% percentiles are represented by the lower and upper limits of each box; the horizontal line indicates the median, the vertical lines of each box indicate 1.5x above and below the interquartile range, the asterisk (*) indicate the mean and the dark circles (●) show outliers. There were no significant difference in salinity among habitats within each month for both Mlalazi and Mngazana. CNT: control, KR/SR: knee/stilt roots, PR: pneumatophores, TC: tidal creek, SG: seagrass bed

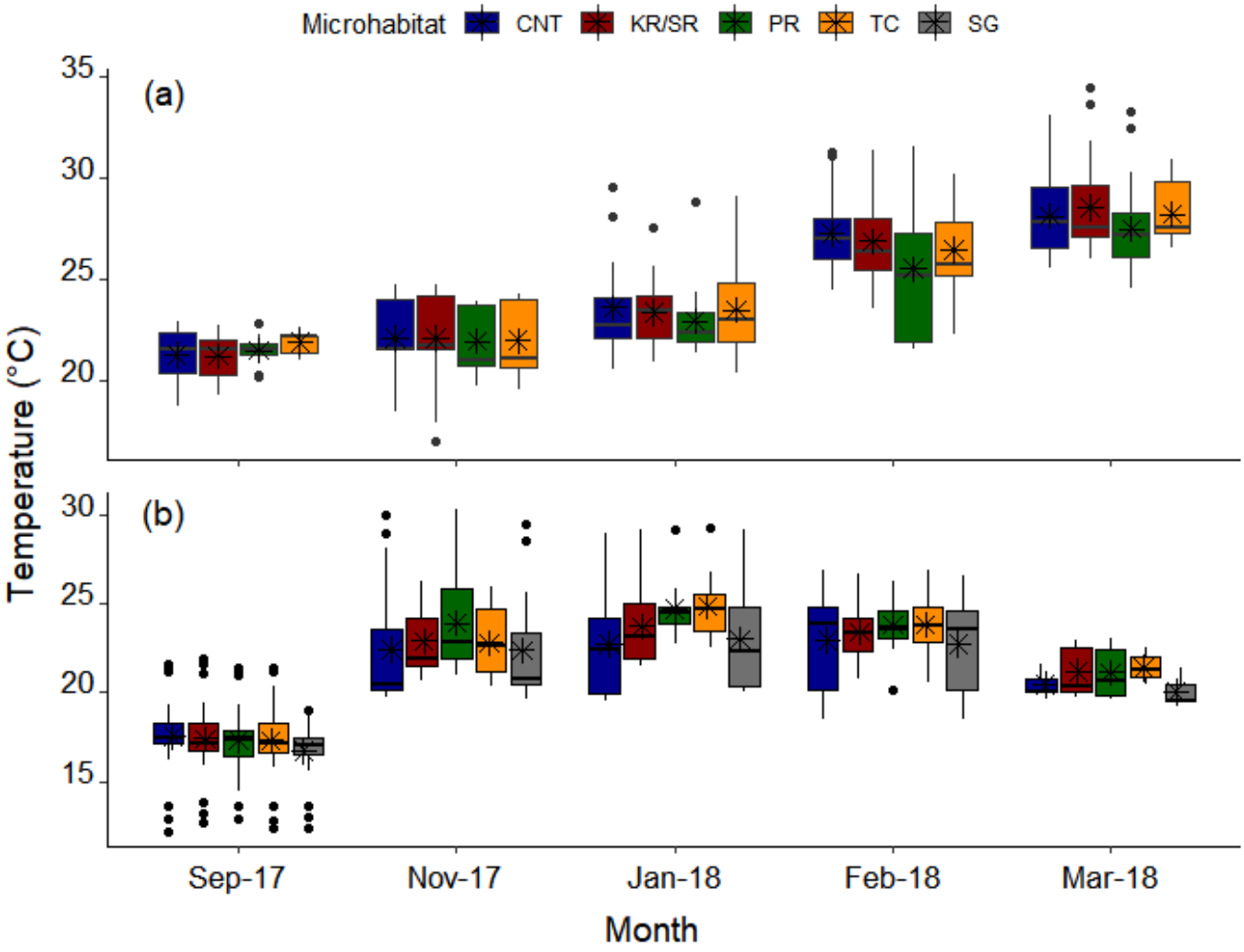

Fig. 3.6. Box plot of temperature at (a) Mlalazi and (b) Mngazana of each microhabitat sampled per month. The 25 and 75% percentiles are represented by the lower and upper limits of each box; the horizontal line indicates the median, the vertical lines of each box indicate 1.5x above and below the interquartile range, the asterisk (*) indicates the mean and the dark circles (●) show outliers. There were no significant difference in temperature among habitats within each month for both Mlalazi and Mngazana. CNT: control, KR/SR: knee/stilt roots, PR: pneumatophores, TC: tidal creek, SG: seagrass bed

At Mlalazi, a total of 11 328 invertebrate larvae were collected, comprising 19 taxa (Table 3.1) of which the zoeae of *Pinnotheres* sp. was the most abundant, making up ~37% of the total invertebrates sampled, followed by *Parasesarma catenatum* megalopa (~17%) and sesarmid zoea (~15%) (Fig. 3.7a). Due to the inability to accurately taxonomically distinguish co-

occurring stage one zoeal larvae of commonly occurring sesarmid species, they were grouped into "sesarmid zoea" throughout, unless specified otherwise. Additionally, 1018 fish larvae, consisting of 19 taxa (Table 3.2, Fig. 3.8a), dominated by *Redigobius dewaali* (~52%) and *Elops machnata* (~19%) were also sampled by the light traps. At Mngazana, ~729 312 invertebrate larvae were sampled, which comprised 19 taxa (Table 3.1, Fig. 3.7b). The most common were the zoeae of sesarmid (65%), *Pinnixa* sp. (~15%) and *Upogebia africana* (~15%). For the fish larvae, only 229 individuals from 11 taxa were identified (Table 3.2, Fig. 3.8b), and were dominated by *R. dewaali* (~55%) and *Caffrogobius gilchristi* (~26%).

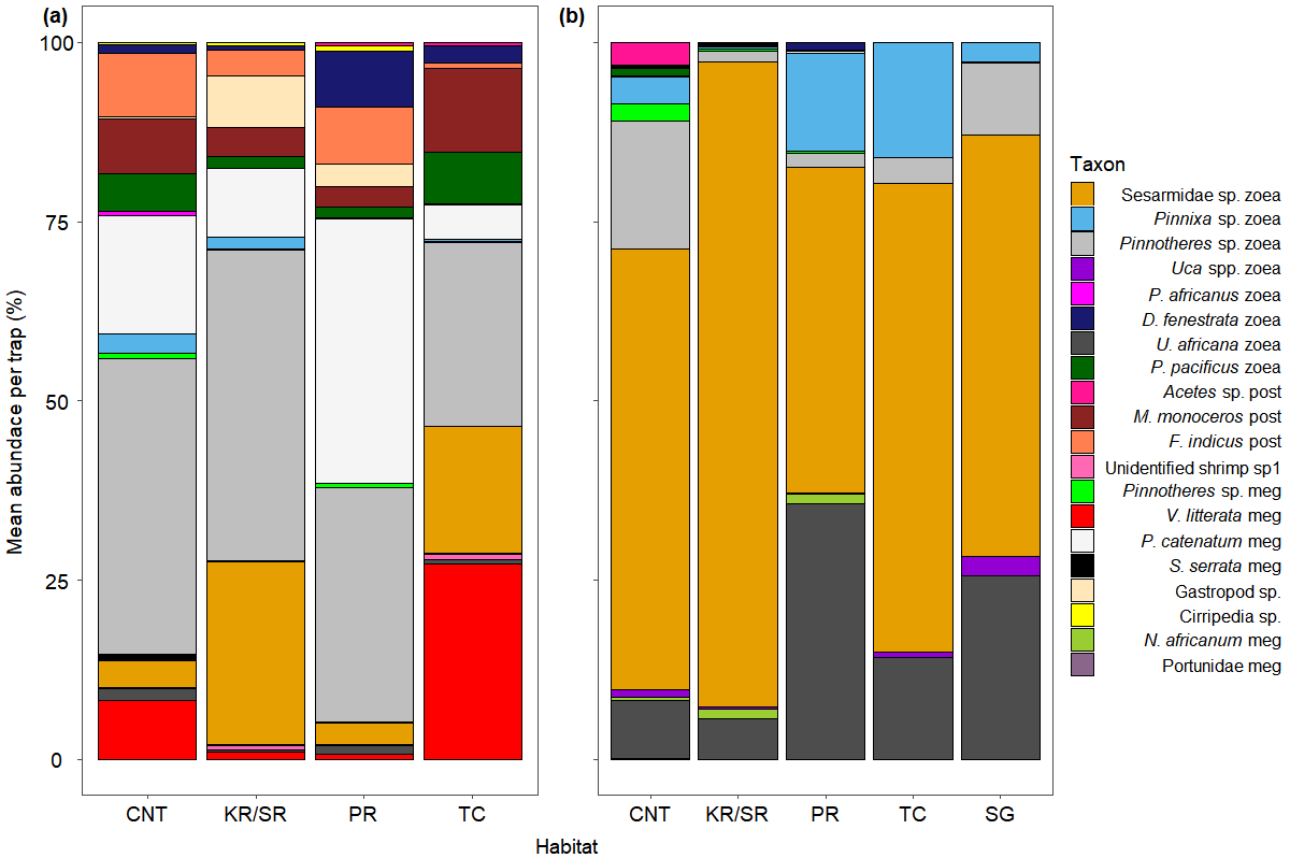

Fig. 3.7. Mean abundance of species per trap (%) among microhabitats in invertebrate larval communities at Mlalazi (a) and Mngazana (b). CNT: control, KR/SR: knee/stilt roots, PR: pneumatophores, TC: tidal creek, SG: seagrass bed.

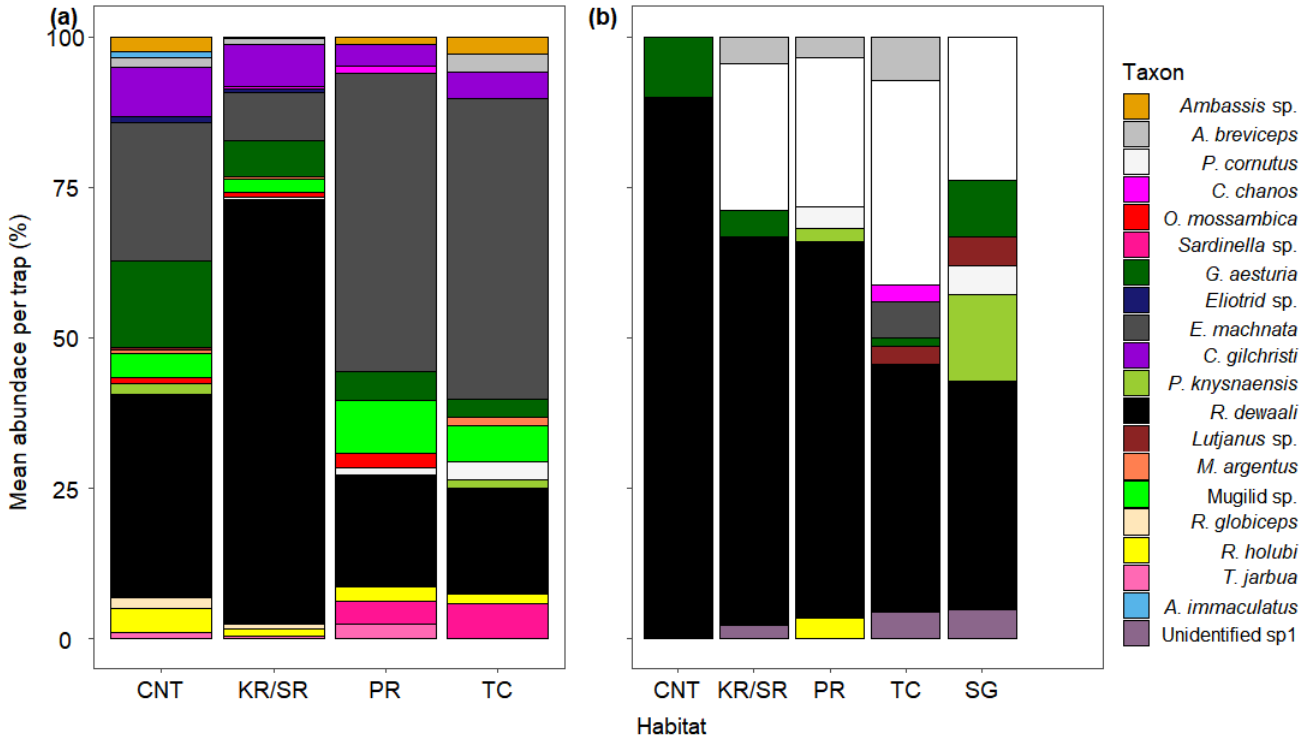

Fig. 3.8. Mean abundance of species per trap (%) among microhabitats in fish larval communities at Mlalazi (a) and Mngazana (b). CNT: control, KR/SR: knee/stilt roots, PR: pneumatophores, TC: tidal creek, SG: seagrass bed.

The results of the multivariate generalised linear models indicate significant differences in invertebrate and fish larval community composition among microhabitats and months for Mlalazi (Table 3.3, Figs 3.9a and b) and Mngazana (Table 3.3, Figs 3.10a and b,). The interaction between microhabitat and month was significant at both sites, indicating the composition of larval assemblages within different microhabitats depended on month. Environmental variables (average, maximum and minimum temperature, salinity and maximum tidal height) were significant predictors of community composition for invertebrates at Mlalazi (Table 3.3). For invertebrate larvae, pairwise comparisons at Mlalazi indicated a significant difference between species composition among microhabitat communities; KR/SR (1 & 2), PR (1 & 2) and CNT were significantly different to TC2, while KR/SR1 was significantly different to PR1 (Table 3.4). All months differed from each other for invertebrate communities, highlighting the temporal variability of species abundance over the sampling period (Table 3.5). Based on the deviance as a proportion to the *sum-of-LR*, the species commonly driving differences in the invertebrate community among microhabitats and months as well as the interaction between microhabitats and month at Mlalazi were *V. litterata* megalopa, *Fenneropenaus indicus* post larvae *, P. catenatum* megalopa, *,* sesarmid zoea and *D. fenestrata* zoea (Table 3.3).

Table 3.1. Invertebrate larval composition and abundance by number (N) per microhabitat sampled as a percentage of the total catch at Mlalazi and Mngazana. CNT = control, . KR/SR1 = knee/stilt root 1, KR/SR2 = knee/stilt root 2, PR1 = pneumatophore 1, PR2 = pneumatophore 2, TC1 = tidal creek 1, TC2 = tidal creek 2, SG1 = seagrass bed 1, SG2 = seagrass bed 2.

Developmental stage	Taxon	N	CNT	KR/SR1	KR/SR2	PR1	PR2	TC1	TC2	SG1	SG2	Total %
					Mlalazi							
Zoea	Sesarmid	1670	4.1	34.9	37.6	3.8	1.8	13.7	4.1	NA	NA	14.8
	Pinnixa sp.	131	37.4	1.5	55	0	0.8	0.8	4.6	NA	NA	1.2
	Pinnotheres sp.	4244	17.8	20.8	28.2	6.8	17	7.5	2.7	NA	NA	37.5
	Uca spp.	9	0	77.8	0	0	0	0	22.2	NA	NA	8
	Panopeus africanus	18	55.6	5.6	5.6	0	16.7	11.1	5.6	NA	NA	0.2
	Dotilla fenestrata	328	6.7	6.7	0.6	11	62.8	8.8	3.4	NA	NA	2.9
	Upogebia africana	88	35.2	3.4	6.8	42.1	2.3	4.6	5.7	NA	NA	0.8
	Palaemon pacificus	337	28.5	1.8	20.5	4.8	9.2	27	8.3	NA	NA	3
Megalopa	*Pinnotheres* sp.	39	38.5	18	5.1	10.3	38.5	0	2.6	NA	NA	0.3
	Varuna litterata	672	22.2	4.2	3.3	0.3	1.8	5.1	63.2	NA	NA	6
	Parasesarma catenatum	1971	15.3	12.1	10.9	19.6	38.1	3.3	0.8	NA	NA	17.4
	Scylla serrata	26	65.4	7.7	19.2	0	7.7	0	0	NA	NA	0.2
Veliger	Gastropod	445	1.1	32.6	44.3	16.4	5.4	0	0.2	NA	NA	3.9
Cyprid	Cirrpedia	51	9.8	37.3	13.7	35.3	3.9	0	0	NA	NA	0.5

Post-larval prawn	*Metapenaeus monoceros*	624	22.8	12.8	18.4	3	11.2	12.7	19.1	NA	NA	5.5
	Unidentified shrimp sp1	49	4.1	0	59.2	0	8.2	14.3	14.3	NA	NA	0.4
	Acetes sp.	25	0	0	0	36	32	8	24	NA	NA	0.2
	Fenneropenaeus indicus	586	27.7	17.9	10.9	20.5	21	1.5	0.5	NA	NA	5.2
	No. of taxa	19	17	17	16	14	18	13	16			
					Mngazana							
Zoea	Sesarmid	474028	0.2	0.2	0.4	0.2	7	39.9	54.9	0.3	3.9	65
	Pinnixa sp.	111686	6	1	0	8	0.2	36.9	61.9	0.5	0.3	15.3
	Pinnotheres sp.	28457	1.1	4	0.1	9	8	2.1	84.5	3.2	8.8	3.9
	Uca spp.	6725	0.3	3	0.1	1	4	70.4	16.1	0.6	12.4	0.9
	Panopeus africanus	5	0	20	0	20	0	0	0	60	0	0
	Dotilla fenestrata	101	3	1	4	14.9	10.9	65.4	1	0	0	1
	Upogebia africana	107296	0.1	0.1	7	0.3	0.5	35.3	55.5	4.4	3.7	14.7
	Palaemon pacificus	169	11.2	0.6	1.2	1.2	0	84	1.2	0.6	0	2
Megalopa	*Pinnotheres* sp.	90	45.6	5.6	4.4	4.4	4.4	1.1	4.4	24.4	5.6	1
	N. africanum	121	5	11.6	26.5	14.1	13.2	21.5	2.5	5	0.8	2
	Parasesarma catenatum	13	7.7	15.4	7.7	7.7	38.5	0	23.1	0	0	0
	Scylla serrata	12	50	0	0	0	0	0	0	16.7	33.3	0

	Portunidae	2	0	0	0	0	0	0	0	100	0	0
	Varuna litterata	5	20.0	0	0	20	0	20.0	0.0	0	40	0
Cyprid	Cirrpedia	510	0.8	0	0	0	0	0	0	49	50.2	7
Post-larvae	*Metapenaeus monoceros*	12	25	25	0	25	0.0	8.3	8.3	8.3	0	0
	Unidentified shrimp sp1	5	0	0	20	0	0	0	80.0	0	0	0
	Acetes sp.	69	76.8	7.3	1.5	0.0	0	4.4	0	10.1	0	1
	Fenneropenaeus inidicus	4	25	0	0	0	0	50	0	0	25	0
	No. of taxa	19	16	13	12	13	9	13	12	14	11	

Table 3.2 Fish larval composition and abundance, overall contribution of each species and microhabitat to the total catch (%) and developmental stage sampled at Mlalazi and Mngazana. CNT = control. . KR/SR1 = knee/stilt root 1, KR/SR2 = knee/stilt root 2, TC1 = tidal creek 1, TC2 = tidal creek 2, PR1 = pneumatophore 1, PR2 = pneumatophore 2, SG1 = seagrass bed 1, SG2 = seagrass bed 2. Ys = yolk sac, Pr = preflexion, F = flexion, Po = postflexion, Ej = early juvenile, Ad = Adult. Dominant developmental stages given in bold

Family	Species	N	KR/SR1	KR/SR2	TC1	TC2	PR1	PR2	CNT	SG1	SG2	Total catch %	Mean SL (Range) (mm)	Developmental stage
							Mlalazi							
Ambassidae	*Ambassis* sp.	12	0	2	5.9	0	0	1.8	2.5	NA	NA	1.2	6.9 (5.5-9.7)	Po
Atherinidae	*Atherina breviceps*	11	1	0.8	2.9	2.9	0	0	1.4	NA	NA	1.1	10.8 (6-13.9)	Pr**. Po**
Blennidae	*Parablennius cornutus*	5	0	2	0	2.9	5.9	0	0	NA	NA	0.5	3.3 (2.9-3.7)	Pr
Chanidae	*Chanos chanos*	3	0.2	1	0	0	0	1.8	0	NA	NA	0.3	12.6 (11-13.5)	Po
Cichlidae	*Oreochromis mossambica*	10	0.4	2.9	0	0	5.9	0	1.1	NA	NA	1	8.1 (7.2-8.6)	Po
Clupeidae	*Sardinella* sp.	7	0	0	14.7	0	0	3.5	0	NA	NA	0.7	12.1 (11-13)	Po
	Gilchristella aestuaria	81	6.1	4.9	0	5.9	2.9	7	14.3	NA	NA	8	13.6 (3.6-25)	Pr. F. Po. **Ej**
Eliotridae	Eliotrid sp.	7	0	3.9	0	0	0	0	1.1	NA	NA	1.1	11 (10.5-12.2)	Po
Elopidae	*Elops machnata*	195	3.1	30.4	32.4	67.6	58.8	54.4	22.9	NA	NA	19.2	28.7 (10.5-37)	**Po**. F
Gobiidae	*Caffrogobius gilchristi*	70	5.6	13.7	8.8	0	5.9	1.8	8.2	NA	NA	6.9	3.8 (1.5-15)	**Pr**. F. Po. Ej
	Psammogobius knysnaensis	6	0	0	0	2.9	0	0	1.8	NA	NA	0.6	6.5 (1.5-12.9)	Pr. **Po**. Ej
	Redigobius dewaali	528	81.2	21.6	32.4	2.9	8.8	15.8	33.7	NA	NA	51.9	6.8 (1.7-19)	**Pr**. F. Po. Ej
Lutjuanidae	*Lutjanus* sp.	1	0	0	0	0	0	0	0.4	NA	NA	0.1	14	Po
Monodactylidae	*Monodactylus argentus*	5	0.4	0	0	2.9	0	0	0.7	NA	NA	0.5	6.58 (6.4-6.8)	Po
Mugilidae	Mugilid spp.	35	0.6	9.8	2.9	8.8	5.9	8.8	3.9	NA	NA	3.4	13 (9.5-16.1)	Po

Sparidae	*Rhabdosargus globiceps*	11	0.6	2	0	0	0	1.8	1.8	NA	NA	1.1	9.2 (5.2-12.9)	Po
	Rhabdosargus holubi	21	0.4	4.9	0	2.9	2.9	1.8	3.9	NA	NA	2.1	9 (5.7 -11.1)	Po
Terapontidae	*Terapon jarbua*	7	0.2	1	0	0	2.9	1.8	1.1	NA	NA	0.7	11 (10.1-12)	Po
Tetraodontidae	*Arothron immaculatus*	3	0	0	0	0	0	0	1.1	NA	NA	0.3	8.5 (8.1-8.8)	Po
No. of taxa		19	12	14	8	9	10	9	16	NA	NA			
							Mngazana							
Atherinidae	*Atherina breviceps*	10	10.5	0	15	4.2	4.9	2.3	0	0	0	4.4	11.5 (4.1-24)	**Pr**. Po. Ej
Blennidae	*Parablennius cornutus*	4	0	0	0	0	4.9	2.3	0	7.7	0	1.7	3.3 (3-3.5)	Pr
Chanidae	*Chanos chanos*	2	0	0	5	2.1	0	0	0	0	0	0.9	10.1 (6.5-13.7)	Po
Clupeidae	*Gilchrestella aestuaria*	6	0	7.7	0	2.1	0	0	10	15.4	0	2.6	15.7 (8.4-28)	**Po**. Ej
Elopidae	*Elops machnata*	4	0	0	0	8.3	0	0	0	0	0	1.7	24.7 (22-27)	Po
Gobiidae	*Caffrogobius gilchristi*	60	47.4	7.7	25	37.5	43.9	6.8	0	30.8	12.5	26.2	5 (1.5-21)	Ys. **Pr**. Po. Ej
	Psammobobius knysnaensis	5	0	0	0	0	2.4	2.3	0	15.4	12.5	2.2	7.3 (2.4-15)	Pr. **Po**
	Redigobius dewaali	127	42.1	80.8	35	43.8	36.6	86.4	90	30.8	50	55.5	5.6 (0.4-37)	Ys. **Pr**. F. Po. **Ej**. Ad
Lutjidae	*Lutjanus* sp.	3	0	0	5	2.1	0	0	0	0	12.5	1.3	15	Po
Sparidae	*Rhabdosargus holubi*	3	0	0	0	0	7.3	0	0	0	0	1.3	10.5 (9.9-11.3)	Po
Unknown	Unidentified sp1	5	0	3.8	15		0	0	0	0	12.5	2.2	10.7 (10-12)	Po
No. of taxa		11	3	4	5	8	6	5	2	5	5			

Table 3.3. Summary results of the generalised linear model (*ManyGLM*) indicating the change in community composition with microhabitat and month as categorical variables and average, minimum and maximum temperature, salinity and maximum tidal height as continuous predictor variables. LRT = Deviance, Coefficients (C) are given to indicate the direction of change in abundance for taxa significantly affected by continuous predictor variables, NS = not significant; $p > 0.05$.

	Invertebrate larvae			**Fish larvae**		
Parameter	**LRT**	***p*-value**	**Drivers of difference in community composition related to predictor variables (% deviance explained, C = Coefficient)**	**LRT**	***p*-value**	**Drivers of difference in community composition related to predictor variables (% deviance explained, C= Coefficient)**
			Mlalazi			
Microhabitat	269.2	**0.001**	***V. litterata* megalopa (11.9), *P. catenatum* megalopa (9.7), sesarmid zoea (8), *D. fenestrata* zoea (7.2)**	95.41	**0.001**	***R. dewaali* (11.7)**
Month	461.2	**0.001**	***F. indicus* postlarvae (16.8), *P. catenatum* megalopa (15.6), *Pinnotheres* sp. zoea (8.9), *V. litterata* megalopa (4.9)**	157.5	**0.001**	***E. machnata* (11.3%), *G. aestuaria* (10.2), *R. dewaali* (10.1%)**
Average temperature	49.5	**0.001**	***V. litterata* megalopa (25.5, C = -0.78), *D. fenestrata* zoea (18.9, C = -0.33)**	57.2	**0.001**	**Mugilid sp. (24.4, C = 2.83), *R. globiceps* (16.3, C = -12.41), Eliotrid sp. (15.9, C = -7.47)**

Maximum temperature	34.8	**0.012**	**Sesarmid zoea (28.9, C = 0.22)**	30	**0.026**	***G. aestuaria* (44.6, C = -2.65)**
Minimum Temperature	32.3	**0.029**	**NS**	28	**0.039**	***C. gilchristi* (35.1, C = 6.14)**
Salinity	55.5	**0.001**	**Unidentified shrimp sp1 (31.8, C = 0.15), *P. africanus* (22.83, C = -3.57)**	15.6	0.33	**NS**
Maximum tidal height	42.5	**0.004**	***Acetes* sp. (34.7, C =-9.55)**	20.9	0.097	**NS**
Microhabitat: Month	507.3	**0.001**	***D. fenestrata* zoea (14.5), *Pinnotheres* sp. zoea (13.3), *M. Monoceros* post larvae (12.3) *V. litterata* megalopa (8.2)**	159.96	**0.001**	***E. machnata* (22.4), *R. dewaali* (13.4), *T. jarbua* (12.4)**
			Mngazana			
Microhabitat	632	**0.001**	**sesarmid zoea (19.3), *U. africana* zoea (17.1), *Pinnotheres* sp. zoea (16.1), *Pinnixa* sp. zoea (11.6)**	107.8	**0.001**	***C. gilchristi* (19.4)**
Month	292	**0.001**	***Pinnixa* sp. zoea (25.2), sesarmid zoea (12.5), *U. africana* zoea (10.6), *Pinnotheres* sp. zoea (6.3)**	101.6	**0.001**	***C. gilchrsti* (11.2)**

Average temperature	35	0.52	**NS**	2.9	0.673	**NS**
Maximum temperature	2145	**0.001**	***Pinnotheres* sp. zoea (95, C = 0.11), sesarmid zoea (4.1, C = 2.99)**	0.3	0.958	**NS**
Minimum Temperature	133	**0.001**	***Pinnixa* sp. zoea (71.8, C = 0.02), sesarmid zoea (9.7, C = 1.13)**	8.4	0.058	**NS**
Salinity	1211	**0.001**	***Pinnotheres* sp. zoea (91.3, C = - 0.04)**	15.7	0.325	**NS**
Maximum tidal height	8410	**0.001**	**Sesarmid zoea (76.2, C = 5.15), *Pinnixa* sp. zoea (23.1, C = 1.25)**	20.9	**0.004**	***C. gilchristi* (45.1, C = 41.27)**
Microhabitat: Month	2947	**0.001**	**sesarmid zoea (85.3), *U. africana* zoea (3.6), *Pinnixa* sp. zoea (2.3),**	145	**0.001**	***R. dewaali* (56.2), *C. gilchristi* (43.6%)**

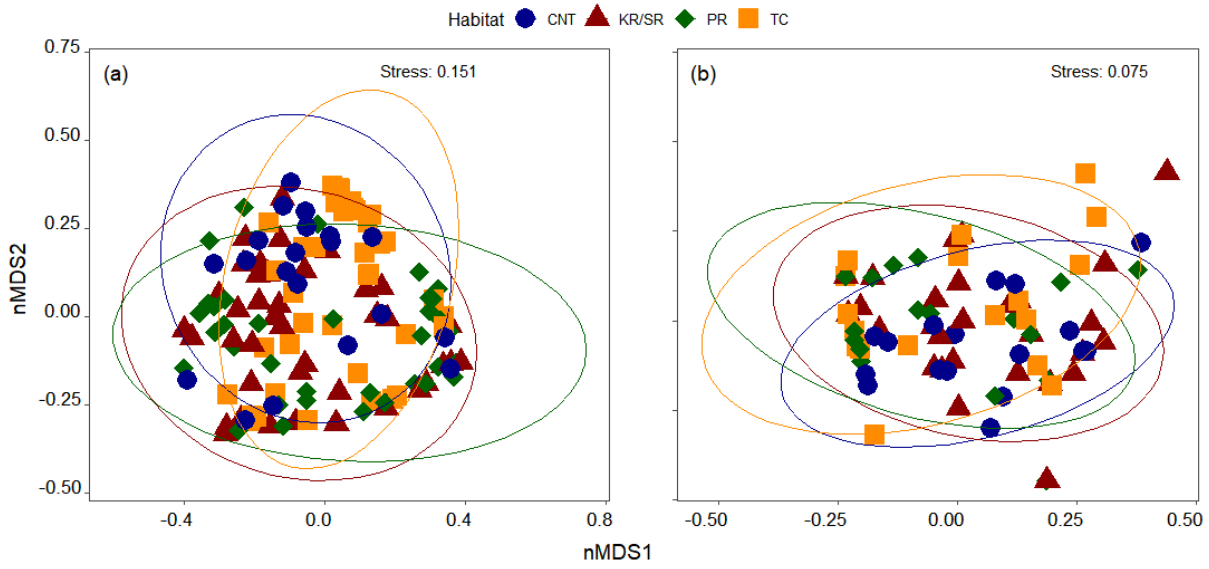

Fig. 3.9. Non-metric multi-dimensional scaling plot of invertebrate (a) and fish (b) larval communities among microhabitats at Mlalazi. CNT: control, KR/SR: knee/stilt roots, PR: pneumatophores, TC: tidal creek.

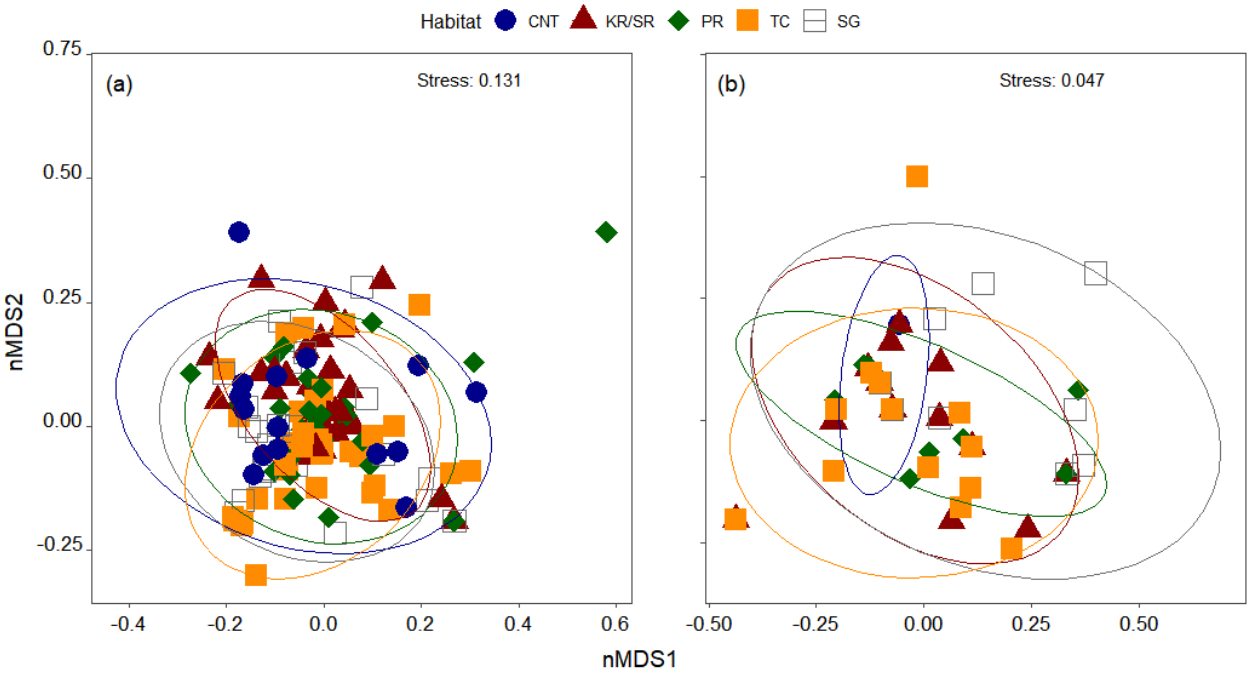

Fig. 3.10. Non-metric multi-dimensional scaling plot of invertebrate (a) and fish (b) larval communities among microhabitats at Mngazana. CNT: control, KR/SR: knee/stilt roots, PR: pneumatophores, TC: tidal creek, SG: seagrass bed.

Table 3.4. Significant pairwise comparisons among microhabitats for both invertebrate and fish larval assemblages at Mlalazi.

	Invertebrates		Fish	
Post-Hoc microhabitat pairwise comparisons	Observed Statistic	*p*-value	Observed Statistic	*p*-value
KR/SR2 vs TC2	83.49	**0.002**	39	0.123
PR1 vs TC2	76.15	**0.007**	14.81	0.877
KR/SR1 vs TC2	75.12	**0.007**	22.07	0.836
PR2 vs TC2	63.62	**0.021**	14.79	0.877
CNT vs TC2	59.80	**0.035**	55.31	**0.008**
KR/SR2 vs PR1	58.91	**0.037**	30.57	0.478
CNT vs TC1	55.03	0.059	58.21	**0.003**
CNT vs PR1	41.05	0.249	50.29	**0.014**
CNT vs PR2	27.70	0.686	50.98	**0.012**

Table 3.5. Significant pairwise comparisons among months for both invertebrate and fish larval assemblages at Mlalazi and Mngazana. Significant results are given in bold.

	Invertebrates		Fish	
Post-Hoc pairwise comparisons of month	Observed Statistic	*p*-value	Observed Statistic	*p*-value
Mlalazi				
November vs September	203.39	**0.001**	122.89	**0.001**
January vs November	893.83	**0.001**	80.05	**0.001**
February vs November	114.84	**0.001**	78.12	**0.001**
March vs November	228.11	**0.001**	74.4	**0.001**
March vs September	120.82	**0.001**	67.49	**0.001**
January vs September	106.76	**0.001**	65.65	**0.001**
February vs September	159.35	**0.001**	60.31	**0.001**
February vs March	100.83	**0.001**	46.12	**0.001**
January vs March	103.5	**0.001**	43.9	**0.001**
February vs January	105.93	**0.001**	18.24	0.087
Mngazana				
November vs September	75.94	**0.002**	13.14	0.066
January vs November	34.78	**0.021**	24.52	**0.004**
February vs November	187.53	**0.001**	16.16	**0.025**

March vs November	73.86	**0.003**	38.74	**0.001**
March vs September	65	**0.005**	27.83	**0.002**
January vs September	69.99	**0.003**	17.44	**0.025**
February vs September	213.47	**0.001**	18.35	**0.025**
February vs March	239.47	**0.001**	27.7	**0.002**
January vs March	85.04	**0.001**	25.58	**0.004**
February vs January	191.99	**0.001**	2.83	0.504

At Mngazana, the overall invertebrate community composition significantly differed among microhabitats. Furthermore, maximum and minimum temperatures in addition to salinity and maximum tidal height were significant predictors of invertebrate community dynamics (Table 3.3). Pairwise comparisons, however, could not resolve the difference between microhabitats and the interaction between microhabitat and month. Community composition among and between months were significantly different (Table 3.3 & 3.5). Based on the *sum-of-LR* sesarmid, *U. africanum*, *Pinnotheres* sp., and *Pinnixa* sp. zoea were driving the differences in the overall community structure among microhabitats, months and the interaction between microhabitat and month (Table 3.3).

At Mlalazi, sesarmid zoea mostly occurred in the knee root microhabitat, *D. fenestrata* zoea in the pneumatophore microhabitat, *V. litterata* in the tidal creek microhabitat, whereas*P. catenatum* megalopae and *F. indicus* post larvae occurred in significantly less numbers in the tidal creeks when compared to all other microhabitats sampled (Fig. 3.11a). Temporally, *F. indicus* post larvae and *P. catenatum* megalopa were most abundant in September (Fig. 3.11b). Additionally, *Pinnotheres* sp. zoea abundance peaked in November, while, *V. litterata* megalopa were more abundant in September as compared to January and March (Fig. 3.11b). Univariate tests of individual species at Mngazana, showed that the mean abundances of *U. africana, Pinnotheres* sp., *Pinnixa* sp. and *Uca* spp. zoea were significantly higher in tidal creeks and seagrass beds when compared to other microhabitats (Fig.3.11c). The species

driving the temporal variation among months were *Pinnixa* sp., sesarmid, *U. africana* and *Pinnotheres* sp. zoeae which all occurred more abundantly in February than any other month accounting for > 95% of the individuals collected over the sampling period (Fig. 3.11d).

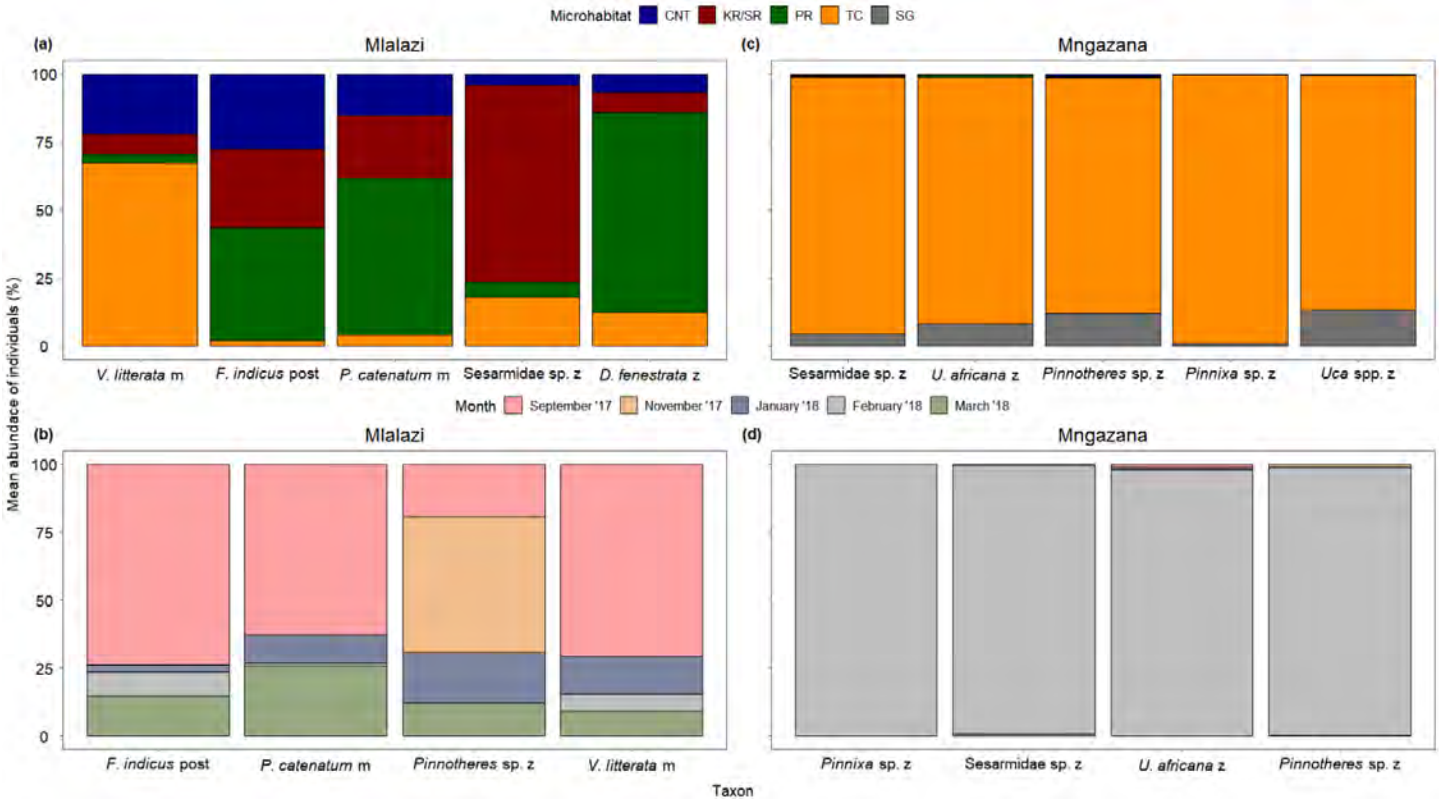

Fig. 3.11. Mean abundance of individuals (%) of selected taxa driving significant differences among microhabitats (a, c) and months (b, d) in invertebrate larval communities at Mlalazi (a, b) and Mngazana (c, d). CNT = control. KR/SR = knee/stilt root, PR = pneumatophore, TC = tidal creek, SG = seagrass bed.

The variance in the larval fish community composition among microhabitats was driven by, *R. dewaali* in Mlalazi and *C. gilchristi* and *R. dewaali* in Mngazana (Table 3.3). At Mlalazi, pairwise comparisons of larval assemblages indicated that the CNT was significantly different to TC (1 & 2) and PR (1 & 2). Univariate tests showed that the abundance of *R. dewaali* at Mlalazi was significantly lower in pneumatophores and tidal creeks than the control and knee root microhabitats (Fig. 3.12a). Pairwise comparisons indicated that fish larval assemblages

from SG were different to that from TC at Mngazana. *Caffrogobius gilchristi* occurred more in TC than in SG, while *R. dewaali* was more abundant in PR than SG (Fig. 3.12c). There were however temporal differences between September and November with March at Mlalazi. Temporally, all months differed in fish larval assemblages except February and January. The abundance of *Elops machnata* was significantly lower in March, although, *Gilchristella aestuaria* and *R. dewaali* were commonly more abundant in November (Fig. 3.12b). Additionally, there were temporal differences in all months except between November and September, and between February and January at Mngazana (Table 3.5). These temporal differences were driven by *C. gilchristi* and occurred more abundantly in January, September and March as compared to November (Fig. 3.12d).

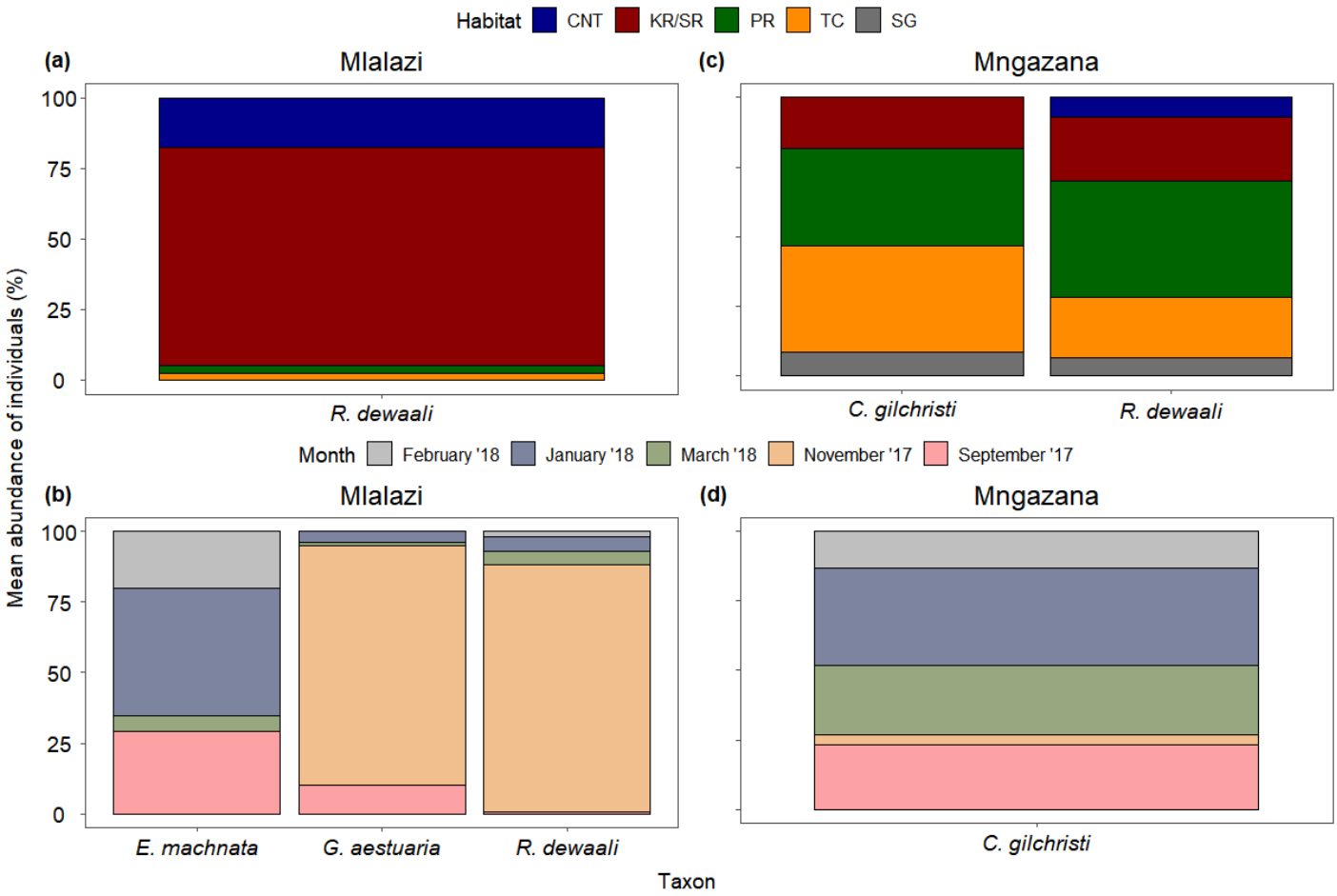

Fig. 3.12. Mean abundance of individuals (%) of selected taxa driving significant differences among microhabitats (a, c) and months (b, d) in fish larval communities at Mlalazi (a, b) and Mngazana (c, d). CNT = control. KR/SR = knee/stilt root, PR = pneumatophore, TC = tidal creek, SG = seagrass bed.

3.4 Discussion

The abundance and composition of invertebrate and fish, larval communities, differed at the microhabitat level both spatially and temporally. Tidal creeks, which run through the mangrove stands and seagrass beds, supported the highest mean abundance of almost all species at Mngazana. Whereas the highest abundance of various species at different life history stages occurred in different microhabitats at Mlalazi. It has to be acknowledged that the larval community is likely to be more speciose due to the selectivity in only sampling positively phototactic invertebrate and fish larvae. Distinctive larval community composition and abundance at varying microhabitats at two independent sites nevertheless indicates the generality of use of such microhabitats and relative importance for dominant taxa.

At Mlalazi, *Dotilla fenestrata* zoea was significantly more abundant in the pneumatophores than any other habitat. Sesarmid zoea occurred in higher numbers in the knee roots when compared to the control and pneumatophores. The increased localised abundance of *D. fenestrata* and sesarmid zoea could most likely be due to passive transport from hatching areas to the more complex root habitat when larvae are being exported by the ebbing tide. It would however be remiss not to acknowledge the fact that in this study "sesarmid zoea" encompasses several species, some of them dwelling the root systems as adults and could possibly reflect populations spawning within these microhabitats (Hartnoll et al. 2002). The larval abundance of invertebrates in tidal creeks and seagrass beds was higher than that of the control, two days after maximal new moon spring tide at Mngazana. This spatial pattern was driven by individual species abundances of the zoea of *U. africana, Pinnotheres* sp*., Pinnixa* sp., sesarmid and *Uca* spp. that occurred in significantly higher abundance in tidal creeks and seagrass beds when compared to other microhabitats, including the control. This trend suggests a lag in the rapid

export of larvae to the sea, considering the control is situated at the mouth of the estuary for Mngazana and would therefore measure the full extent of larval export. While larvae could have been exported to sea at a later stage, it did not occur in the period of maximal tidal height for the months sampled, which is generally the expected period for maximum export (Dittel and Epifanio 1990, Papadopoulos et al. 2002, Paula et al. 2004a).

Maximum abundances of newly hatched larvae have been recorded previously at the mouth of the Mlalazi Estuary, 2-3 days after the maximum tidal height (Papadopoulos et al. 2002), while larval transport can be delayed by a few hours in bays (Dittel and Epifanio 1990, Paula et al. 2004a). The presence of complex microhabitat patches that zoeae passively encounter during export could delay the speed of transport and aid in short term retention of larvae within mangroves and seagrass before being exported to sea. The complex structures associated to the mangrove roots and elongated leaves of seagrass beds may create a comb-like physical barrier delaying larval export passively. Alternatively, microhabitats like tidal creeks, which are not as structurally complex, may favour active retention whereby larvae take advantage of bottom currents influenced by the reduced tidal forcing within the creeks and only get exported once they are competent to respond to favourable exogenous cues (Queiroga et al. 2002). This active retention could also be a result of the reduced energetic costs of vertical movement within the water column due to a lower flow rate of water within tidal creeks than within the main channel of the estuary hence delaying the mass export (Epifanio and Cohen 2016).

Parasesarma catenatum megalopa were more abundant within complex microhabitats and the control as when compared to the tidal creeks at Mlalazi. Crab megolopal development consists of two phases: a competent and a non-competent (Paula et al. 2004a). When megalopae reach

competence, they actively respond to exogenous cues to facilitate selective transport to settlement areas for further development and ecdysis (Epifanio et al. 1988, Papadopoulos et al. 2002, Saigusa et al. 2003, Paula et al. 2004a, Forward et al. 2017). The presence of *P. catenatum* megalopa at the control possibly reflects their returning on the night time flood tide to settle into the mangrove vicinity, a trend previously observed in sesarmids recruiting into mangroves (Dittel and Epifanio 1990, Paula et al. 2004a). Contrarily, *V. litterata* megalopa were more abundant in the tidal creeks than any other habitat. The inhabiting of tidal creeks in this study could be a response to predation pressure in deeper waters (Connell and Robertson 1986, Ryan and Choy 1990, Mos et al. 2017) as their well-developed legs during their competent megalopal stage facilitate moving onto land adjacent to the creeks and effective predator escape (Ryan and Choy 1990, Mos et al. 2017). The different use of microhabitats of late stage larvae approaching settlement could be in response to chemical cues that facilitate navigation to settlement habitat and metamorphosis (Forward et al. 2017) which could be crucial in supplying individuals to the adult population through the availability of microscapes, to make use of areas with complexity gradients that aid development.

Temperature and salinity did not differ among microhabitats within a given month, indicating homogeneity of the environment at both Mlalazi and Mngazana, while significant differences of these environmental parameters resulted among months. Temperature and salinity were significantly correlated with larval assemblages in Mlalazi, while temperature and maximum tidal height were positively correlated with late stage invertebrate larval assemblages in Mngazana. These observations match those of other temperate and subtropical estuarine systems (Dittel and Epifanio 1990, Fusté and Gili 1991, González-Gordillo and Rodríguez 2003). Early and late stage decapod larvae rely on these environmental cues (temperature, salinity and maximal tidal phase) in order to facilitate larval release and selective tidal stream

transport for transport back into the vicinity of settlement habitats (Little and Epifanio 1991, Gonçalves et al. 2003).

The occurrence of all larval developmental stages of *R. dewaali., C. gilchristi, Psammogobius knysnaensis, Gichristella aestuaria* and *Atherina breviceps* in the study indicate that all these species use these mangroves as both spawning and nursery habitats (Ooi and Chong 2011). The presence of all ontogenetic stages of these species of gobiid, clupeid and atherinid larvae are also somewhat expected, as these species are classified either as "estuarine and marine", "estuarine and freshwater" or "solely estuarine species" (Potter et al. 2015). There were significant differences in larval fish community composition between microhabitats at both estuaries, although, these differences were driven by two common occurring gobiid species (*R. dewaali* at Mlalazi and *C. gilchristi* at Mngazana). The association of *R. dewaali* to roots and its vicinity to an open channel could be due to the larvae moving between the estuary and the mangrove root system to feed, while occupying the interstitial spaces created by the structurally complex knee roots of *B. gymnorhiza* to seek refuge from predators (Sheridan and Hays 2003b, Ellis and Bell 2004), a trend often reported for temporary juvenile fish migration (Vance et al. 1996, Rönnbäck et al. 1999, Laegdsgaard and Johnson 2001, Cocheret De La Morinière et al. 2004, Verweij et al. 2006).

The presence of postflexion larvae of "marine estuarine-dependent species" (*Elops machnata*, *Rhabdosargus holubi*, *Terapon jarbua*) suggests that the mangrove system acts as a potential corridor to adjacent habitats (e.g. shallow banks of the estuary) at low tide, and a functional nursery area to a certain degree at high tide in Mlalazi and, to some extent, Mngazana. The co-presence of flexion and postflexion larvae across several microhabitats within a single system

postulates that the mosaic of microscapes allows for stepwise shifts of larvae to settlement habitats on very small spatio-temporal scales (Cocheret De La Morinière et al. 2002, Grol et al. 2011, Nagelkerken et al. 2015).

Furthermore, fish enter estuaries and mangroves at the juvenile, postflexion and even flexion stage and utilise them as habitats. This is evidenced by the size ranges (10-37 mm) of postflexion *E. machnata, T. jarbua* (10.1-12 mm) and *R. holubi* (5.7-11.9 mm) observed from the mangrove microhabitats. This finding is novel and expands on the general assumption that only juveniles make efficient use of shallow water ecosystems as "nurseries" (Sheaves et al. 2006).

Temporally, invertebrate and fish larval communities differed among months sampled likely reflecting the environmental conditions that occurred across months. Temperature and salinity did not differ among microhabitats within a given month, indicating spatial homogeneity of the water masses at both sites, Mlalazi and Mngazana, while expected significant differences of these environmental parameters resulted among months. Temperature, salinity and maximum tidal height were significant predictors of invertebrate larval community composition and abundance at both estuaries. These trends match those of other temperate and subtropical estuarine systems (Dittel and Epifanio 1990, Fusté and Gili 1991, González-Gordillo and Rodríguez 2003). Early and late stage decapod larvae rely on environmental cues such as temperature, salinity and maximal tidal phase in order to facilitate larval release and selective tidal stream for transport back into the vicinity of settlement habitats (Little and Epifanio 1991, Gonçalves et al. 2003).

Temperature and maximum tidal height were the environmental features that structured larval fish communities. This observation agrees with previous studies in South Africa and elsewhere (Harris and Cyrus 2000, Pattrick and Strydom 2008, Ooi and Chong 2011). Environmentally driven temporal variations of fish and invertebrate larval communities potentially impact the ecological functioning within mangroves, as food web dynamics are affected. The larvae sampled in this study are common or preferred food sources for planktivirous fishes that occur in mangroves and estuaries (Morgan 1990, de Medeiros et al. 2017). The increased abundance and availability of zooplankton within peak spawning months (November, January and February) could support the broad nutritional needs of economically and ecologically important fish entering mangroves and adjacent seagrass microhabitats in attempts to forage efficiently while simultaneously avoiding sizeable predators (Granek and Frasier, 2007; Nagelkerken *et al.*, 2008).

Habitat heterogeneity, through the provisioning of microhabitats of varying complexity, allows biodiversity to persist (González-Megías et al. 2007, Jaxion-Harm 2010, Sheaves et al. 2014). Mangrove microhabitats seem to play this role by mechanistically delaying seaward export of larvae or through the reduced tidal forcing within the creeks, enhancing continued retention of invertebrate larvae spawned within the system. A delay in export could advance the ontogenetic development of early stages before exportation in response to exogenous cues for their continued development in neritic water masses. For fish, this study postulates that marine estuarine-dependent larvae recruit into mangroves as postlarvae, much earlier than previously claimed (Whitfield 1999, Kisten et al. 2015), and utilise these microscapes as corridors and temporary nurseries before settling into a suitable habitat as juveniles. The need to review coastal ecosystems like mangroves from “seascape nurseries” (Nagelkerken et al. 2015) to “microscape nurseries” is thus fully justified, where single systems are interconnected by

heterogeneous patches of microhabitats that serve its own function at local scales and operate as corridors to the adjacent coastal environment for the successful development of fish and invertebrate larvae utilising these habitats.

Chapter 4: Mangrove microhabitats and larval ontogeny shapes the thermal physiology of early stage brachyurans (Crustacea: Decapoda)

Abstract

Mangrove microhabitats are thought to moderate stress through increased productivity, greater protection from predation and the shading effects of the dense overhead canopies of trees. Brachyurans have complex life-history strategies, usually comprising a zoeal and megalopal stage, which need to be completed before successful recruitment into adult habitats. The present study aimed to investigate the effects of acute temperatures on the physiology of stage-specific mangrove-associated larvae collected at different microhabitats at two mangrove forests in South Africa. Results indicate that microhabitats from which larvae originated can influence their physiology to short-term acute temperature exposures. Larvae (zoeae and megalopa) from exposed, less complex environments (control areas) had higher metabolic rates at increased temperatures than within the more complex root habitat. Furthermore, the larval thermal optimum shifted ontogenetically to become increasingly eurythermic as individuals developed from stage I zoea through to megalopa. Mangrove crab larvae in their early zoeal stages are hence increasingly vulnerable to acute temperature exposures, which could be particularly harmful to the populations if thermally stressful events increase in magnitude and frequency.

4.1 Introduction

Temperature affects all levels of biological organisation and its effects are suggested to shape the biogeographical distributions of organisms (Fangue et al. 2009, Sunday et al. 2012, Donelson et al. 2019, Harada and Burton 2019). Moreover, the physiology of ectotherms is closely influenced by temperature (Angilletta 2009). An organisms' ability to adapt to rapid temperature variations could therefore play a bigger role than its ability to adapt to average rising thermal stress in climate change scenarios (Clusella-Trullas et al. 2011, Harada and

Burton 2019, Scheffler et al. 2019). These adaptive responses to variation in temperatures rely on phenotypic plasticity expressed by organisms in novel or changing environments (Ghalambor et al. 2007). The plasticity of an organism can operate at different life-stages resulting in irreversible phenotypic alterations which are influenced by changes in its developmental environment and possibly increase performance and/or fitness (Hoffman and Parsons 1991, Mathur and Schmidt 2017). In organisms occupying aquatic systems, especially ectotherms, thermal effects, including the diurnal warming and cooling of water, are inescapable (Leiva et al. 2018). Assessing how different aquatic ectotherms metabolically respond to short- and long-term variations in temperature is therefore imperative to understand the community and ecosystem dynamics at both local and global scales (Walther et al. 2002, Harley et al. 2006).

Brachyurans have complex life-history strategies usually comprising of zoeal and megalopal stages, of which both need to be completed successfully for recruitment into adult populations (Byrne 2012). The persistence of mangrove brachyuran (the true crabs) populations hence relies on such a supply of planktonic larvae (Roughgarden et al. 1988). Approximately 99% of this larval pool however, does not make it pass the dispersal stage due to biological stressors such as competition for space, predation as well as pressure from the environment (Thorston 1950; Pechenik 1999). These life history traits and subsequent population dynamics of brachyuran crabs are hence directly expressed through physiological processes and can therefore be linked to the environment experienced (Young et al. 2006, Small et al. 2015). Understanding the physiological responses to acute temperatures changes, throughout larval ontogeny of crustaceans can inform on the vulnerability of each life stage and ultimately communities to environmental changes due to climate change (Tagliarolo et al. 2018).

The metabolic responses of organisms correlate with the thermal range they experience (Spicer and Gaston 2009). Thus, variations in the physiological traits can be credited directly to the environment an individual experiences, even transiently. It has also been observed that more diverse environmental circumstances will likely result in greater physiological dissimilarity (Spicer and Gaston 2009). The avoidance of extreme environmental conditions through the provision of microhabitats in aquatic environments is used to minimise different levels of physiological stress, particularly in shallow-coastal waters (Gordon et al. 1985, Heath et al. 1993, Levin 2003, Curtis and McGaw 2012, Monaco et al. 2015). If organisms have the ability to exploit these microhabitats, but their availability is limiting, it is expected that some individuals will be excluded as they will not be able to access refugia to avoid lethal or sublethal heat stress (Beck 1997, Mota et al. 2015, Lima et al. 2016).

Despite a critical need to understand how larvae in particular respond to the environment, the literature mostly emphasises the relationships between physical changes and major life history events such as; growth, development and survival and less so on stage-specific metabolic responses (Paschke et al. 2010, Schiffer et al. 2014, Alter et al. 2015, Small et al. 2015, Leiva et al. 2018). Regarding the physiology of mangrove crabs, studies have been conducted on adults, investigating their responses to heavy metal and waste water accumulation (Harris and Santos 2000, Pinheiro et al. 2012, de Almeida Duarte et al. 2017, Ortega et al. 2017), salinity (Gillikin et al. 2004) and temperature stress (e.g. Vernberg and John, 1966; Macintosh, 1978; Eshky, Atkinson and Taylor, 1995; Fusi *et al.*, 2015), with less literature available on the responses to thermal stress by early stage invertebrates (Simoni et al. 2013, Srijaya et al. 2014, Mostert 2015, Rebolledo and Collin 2018).

Studies on the larval responses to environmental change of sesarmid and other mangrove-associated crabs include respirometric research conducted on the embryos of several mangrove crab species which utilise different life history strategies as adults (Simoni et al. 2013). Numerous authors have also focused on the physiological responses of larvae to salinity stress and their stage-specific osmoregulatory capabilities (Anger and Charmantier 2000, Charmantier et al. 2002, Diele and Simith 2006, Simith et al. 2014). Moreover,studies that have investigated the metabolic responses to variation in temperature are limited to the combined effects of salinity and temperature on larval development (Paula et al. 2004b) and the ontogenetic thermal sensitivity of mangrove crabs at the centre and edge of their distributional ranges (Mostert 2015). No studies to the best of my knowledge has investigated the response of mangrove crab larvae to acute and possibly transient temperature variations which is thought to be crucial in maintaining mangrove crab populations (Clusella-Trullas et al. 2011, Harada and Burton 2019, Scheffler et al. 2019).

The present study aimed to investigate the effects of acute temperature changes within the thermal range experienced during austral summer reproductive seasons of brachyurans in the region (Papadopoulos et al. 2002) on the physiological performance of stage-specific (zoeal and megalopal) mangrove-associated brachyuran larvae collected at different microhabitats, across two biogeographical regions. I firstly hypothesised that the type of microhabitat would have no effect on the metabolic performance of larvae as aquatic environments are generally considered to be thermally uniform. Secondly, larvae should not show signs of declining metabolic performance even at the maximum experimental temperature, as the temperatures tested are within the range naturally experienced. Lastly, metabolic rates and activation energy,

which is the energy needed for biochemical reactions to occur, should differ according to ontogenetic stage, because the earliest life stages of brachyuran larvae have less energetic demands when compared to more developmentally advanced stages (Gimenez and Anger 2005).

4.2 Materials and methods

4.2.1 Sampling areas and environmental conditions

Two mangrove forests on the east coast of South Africa were selected for larval collection that included the subtropical Mlalazi and warm temperate Mngazana mangals (Fig. 4.1). The Mlalazi mangrove forest is estimated to be ~40ha, dominated by *Bruguiera gymnorhiza*, *Avicennia marina*, and a small population of *Rhizophora mucronata* (Peer et al. 2018). The estuary is considered permanently open, largely natural, in good condition and located within a protected area managed by Ezemvelo KZN Wildlife (Ortega-Cisneros and Scharler 2014). The Mngazana mangrove forest is dominated by *A. marina*, followed by *B. gymnorhiza* and the largest stand of *R. mucronata* in South Africa. This site is also one of the southernmost in global mangrove distribution (Morrisey et al. 2010, Quisthoudt et al. 2013, Hoppe-Speer et al. 2015).

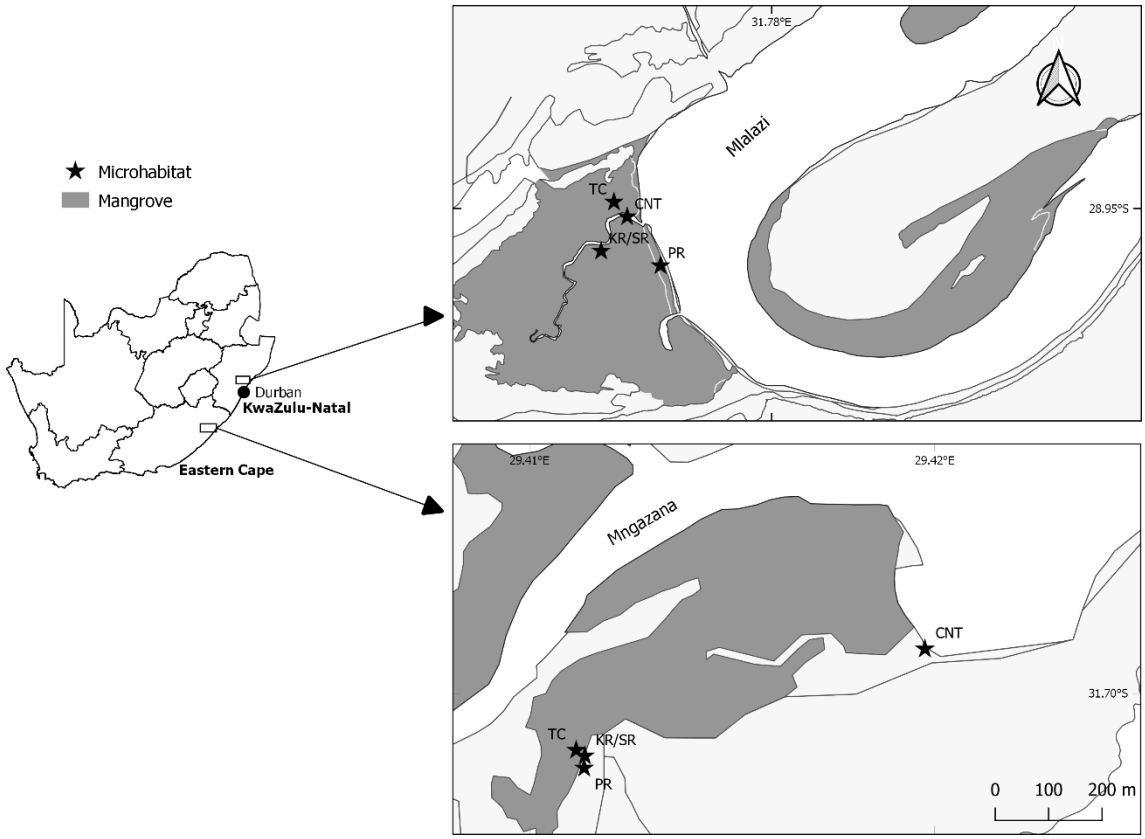

Fig. 4.1. Map of study areas (top; Mlalazi and bottom; Mngazana) on the east coast of South Africa. Microhabitats sampled are the knee/stilt roots (KR/SR), pneumatophores (PR), tidal creek (TC) and control site (CNT) at each mangrove forest and are indicated with a star symbol (★).

Both mangrove forests have mixed stands where patches of tree species co-occur within a 250 m radius (Macnae 1963). Microhabitats identified from both mangrove forests include the knee roots or stilt roots of *B. gymnorhiza* and *R. mucronata* (KR/SR) at Mlalazi and Mngazana, respectively, pneumatophores of *A. marina* (PR) and the tributary tidal creeks (<1 km in length) that flow through the mangrove forest (TC). Control (CNT) habitats, situated at the mouth of the estuary in Mngazana and the main inlet into the mangrove forest from the Mlalazi Estuary respectively, were also chosen. At Mngazana, due to their low abundance in the mixed stands,

the knee roots of *B. gymnorhiza* were replaced with the stilt roots of *R. mucronata*. For the purpose of this study, *B. gymnorhiza* and *R. mucronata* were pooled together for consistency and ease of comparison to knee roots/stilt roots (KR/SR) at either sites.

To assess the variability of the main environmental parameters among microhabitats, temperature and salinity were monitored *in situ* over two days bimonthly, from September 2017 and monthly from January to March 2018 (five trips were carried out within this period) in each experimental plot around new moon spring tide using temperature iButton loggers (Maxim Integrated Products, ColdChain Thermodynamics) and a handheld seawater refractometer (RedSea), respectively. A separate 24-hours monitoring for water temperature was conducted in the tidal creeks in February 2018 to gather data for the average and maximum experimental temperature range experienced at the peak of the sampled brachyuran reproductive season (February) (Papadopoulos et al. 2002).

4.2.2 Animal collection

Larvae were collected at each study site using small modified light traps (as Chan et al. 2016) that were deployed at each microhabitat for approximately 12 hours from sunset and retrieved the following day at dawn, around new moon spring tides in February, March and October 2018. The collected samples were transported to an on-site laboratory < 5 minutes from the sampling areas. On arrival at the on-site laboratory, each sample was sifted through a 65 µm mesh sieve before being placed into separate 500 ml beakers filled with filtered seawater and acclimated in a water bath for at least one hour at the temperature they were collected. After the acclimation at the collection temperatures, larval samples were coarsely sorted into zoea or megalopa before being placed back into the water bath. The temperature was then ramped up

or down by 1°C every 15 minutes (Kelley et al. 2011) until the desired experimental temperature (see details below) was reached. Larvae were then acclimated at the experimental temperature for at least an additional hour.

4.2.3 Experimental setup

Three experimental temperatures were selected based on the monitoring period detailed above. With an additional 24-hour *in situ* monitoring period in February 2018, encompassing the nominal low, average and high temperatures for each study site were 20°C, 28°C and 33°C for Mlalazi and 19°C, 24°C and 30°C for Mngazana (Fig. 4.2). The temperatures selected were typically experienced by larvae during the brachyuran reproductive season (summer).

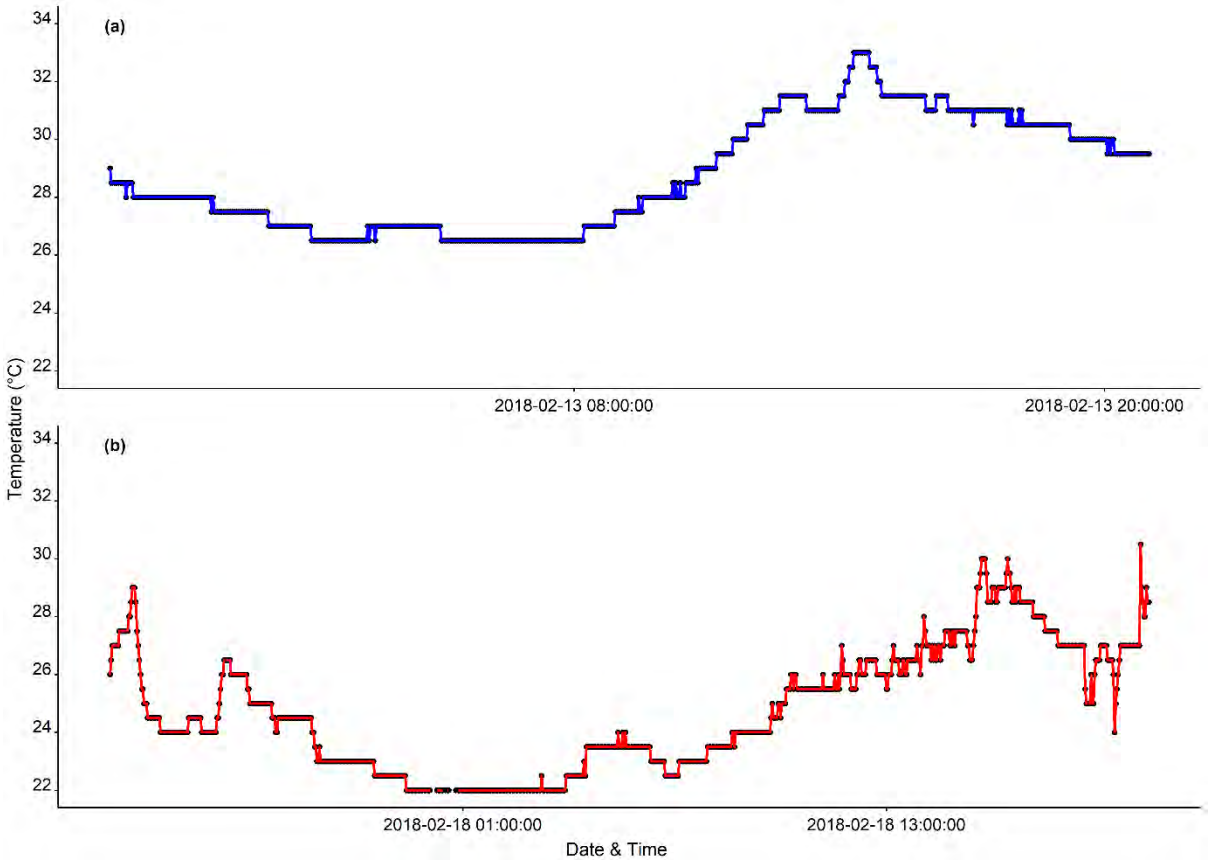

Fig. 4.2. Line graphs of 24-hour temperature monitoring in the tidal creek of A) Mlalazi (blue) and B) Mngazana (red).

The oxygen consumption (MO_2) rates of brachyuran larvae were measured using an optical fluorescence-based oxygen meter (Sensor dish reader SDR2, PreSens, Germany). A closed respirometry system was utilised where up to three larvae, depending on their size and life stage, were placed in individually sealed 80 µl (zoea) or 200 µl (megalopa) wells within a Loligo Systems (Denmark) 24-well glass microplate. Larvae were unfed and kept in the dark during the respirometry trials approximating the results to resting metabolic rate (Clarke 2004). Additionally, up to four wells on each plate during each trial were filled with filtered estuarine water to control for background respiration. Measurements of oxygen consumption were taken every minute throughout the experimental run, for approximately 60 minutes, and recorded using the SDR version 4.0.0 software (PreSens, Germany). Oxygen consumption was recorded as the linear change of oxygen content over time per individual well and only the first 30% pO_2 linear decrease in air saturation was used to calculate the oxygen consumption rate. Lastly, MO_2 was corrected for background respiration and expressed as nmol O_2 min^{-1} ind^{-1}.

At the end of each experimental trial, larvae were preserved separately for photographs to be taken, identification to the lowest possible taxonomic unit and further measurements using a high-powered stereo microscope (Olympus SZX2-ILLB). Dominant taxa identified at both Mlalazi and Mngazana sites included the sesarmid, *Pinnotheres* sp., *Pinnixa* sp. and *Panopeus africanus* zoea and *Neosarmatium africanum*, *Parasesarma catenatum*, *Pinnotheres* sp. and *Metopograpsus thukuhar* megalopa. The biovolumes of individuals were estimated using geometric shapes to correct for the volume of each experimental well to calculate individual oxygen consumption. The biovolume of zoeae were estimated from the formula for a sphere, ($V = \frac{4}{3}\pi r^3$), where V represents volume and r represents the radius. The biovolume of megalopae was estimated from the formula for a rectangular prism, ($V = l*w*h$), where V represents the volume, l represents the maximum length, w represents the maximum width and

h represents the maximum height (Smit et al. 1993, Hillebrand et al. 1999). Carapace lengths of larvae were then measured and converted to dry weight (µg) using published equations as in (Espinoza & Bertand 2008). The dry weight of each larvae was used to calculate the mass corrected MO_2 and expressed as nmol O_2 min^{-1} μg^{-1}.

4.2.4 Statistical analysis

Temperature and salinity values were tested for normality and homogeneity of variances using Shapiro-Wilk and Levene's test, respectively. These tests showed a violation of the assumptions of normality and homoscedasticity for temperature and salinity at both sites. Average hourly temperature and salinity were therefore compared among microhabitats within each month sampled using a Kruskal-Wallis test (Ashcroft and Pereira 2003).

The main statistical trends of temperature-dependent respiration rates were not affected when expressed as nmol O_2 min^{-1} μg^{-1} or nmol O_2 min^{-1} ind^{-1}. Metabolic rate is therefore given as nmol O_2 min^{-1} μg^{-1} to highlight the variation in mass-specific respiration rates as calculated from biovolume estimates of individual zoeae and megalopa. This serves to avoid reporting possibly misleading results of rates expressed as nmol O_2 min^{-1} ind^{-1} which is bounded to the specific stage (I, II, II, etc.) of the individual larvae and therefore limits inferences of inter-individual comparisons as these are not laboratory-reared specimens hatched synchronously (Storch et al. 2009). The relationship between the log-transformed metabolic rate and dry mass was predicted using linear regressions (Fig. 4.3). Preliminary analyses, using generalised linear models (GLM), were carried out on zoeae and megalopae separately to determine if log-transformed (base 10) mass-specific metabolic rates varied between sites and among temperature and species. Results of the preliminary analyses indicated that there were weak,

but significant relationships between log-transformed metabolic rate and dry mass. The scattering of the data-points signify the weak relationship of log-transformed metabolic rate with dry mass could be due to the narrow size ranges within the ontogenetic stages targeted here. Additionally, the interactions between log-transformed dry mass with temperature, site and species did not have an effect on log-transformed mass-specific metabolic rates for megalopae, although, the interaction between log-transformed dry mass and species was significant for zoeae (Fig. 4.3, Table 4.1).

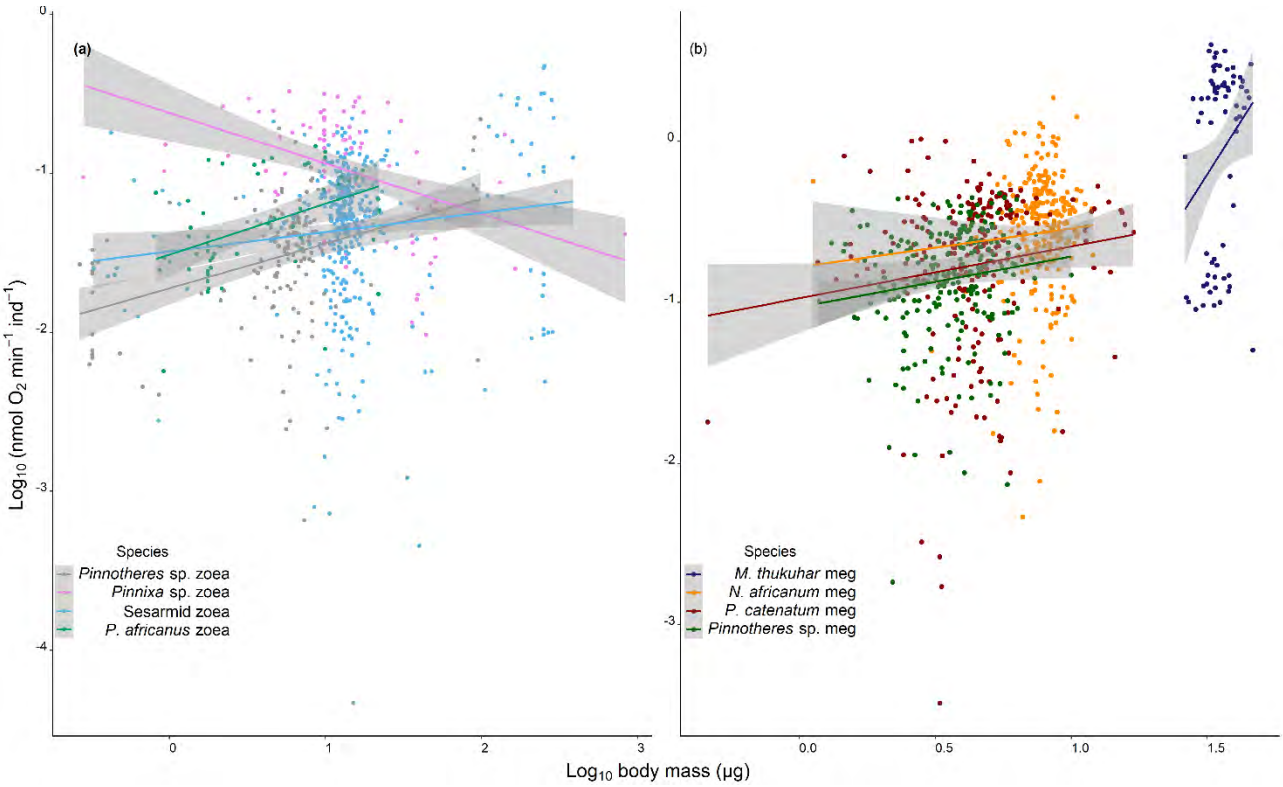

Fig. 4.3. Linear regressions of the log_{10}-transformed data of MO_2 and body mass for a) zoeae and b) megalopae.

Table 4.1. Metabolic scaling exponents calculated from the generalised linear model as a function of log-body mass. (R^2) adjusted R-squared, (F) Fisher statistics, (b) logarithm of the taxon specific normalisation constant, (c) metabolic-scaling exponent, (±SE) standard error (p) significance value is indicated for each linear model.

Life stage	Taxon	R^2	F	b	c	±SE	p
Zoea	*Pinnotheres* sp., sesarmid, *P. africanus*	0.05	(1, 595) = 32.45	-1.58	0.189	0.03	**<0.001**
	Pinnixa sp.	0.176	(1,83) = 18.94	- 0.62	- 0.317	0.07	**<0.001**
Megalopa	*Pinnotheres* sp., *N. africanum*, *P. catenatum*, *M. thukuhar*	0.198	(1,788) = 195.8	-1.193	0.677	0.04	**<0.001**

One metabolic scaling coefficient was thus calculated for megalopae while post-hoc tests revealed that sesarmid, *Pinnotheres* sp. and *P. africanus* zoea were not significantly different to each other and one scaling coefficient was calculated for the three taxa (Tables 4.1; 4.2). Furthermore, *Pinnixa* sp. zoea were significantly different to the sesarmids, *Pinnotheres* sp. and *P. africanus* zoea. Thus, metabolic scaling coefficients were calculated separately for *Pinnixa* sp. zoea using the general theory of Gillooly et al. (2001). The metabolic scaling coefficients were then fitted using the power function:

$$R = M^b \quad (1)$$

Where R is the log-transformed respiration rate (nmol O_2 min^{-1} ind^{-1}), M is the log-transformed body mass (µg) and b is the metabolic scaling coefficient. Linear regressions were then calculated from an Arrhenius plot on the mass-corrected respiration rates using the equation (Arrhenius 1889):

$$\ln R = \ln a - \frac{E}{k} * \frac{1}{T} \quad (2)$$

Where R is the mass-corrected respiration rate, a is taxon specific the normalisation constant, E is the activation energy (calculated using: $a = -E/k$), k is Boltzmann's constant and T is water temperature in Kelvin.

Table 4.2. Outcome of the linear models indicating the effect of different sources of variation on metabolic rate (LogMO_2) of different taxa used in this study. (d.f) Degrees of freedom, (*SS*) Sum of squares, (*F*) Fisher statistics, (AIC) Akaike's Information Criterion, (R^2) adjusted R-squared, (*p*) significance value and (Post-hoc) outcome of post-hoc tests are indicated for the linear model calculated for each life-stage

Taxa	Response variable	Source of variation	d.f	*SS*	*F*	*p*	AIC	R^2	Post-hoc
Zoea	LogMO_2	LogMass	1	4.419	28.41	<**0.001**	703.22	0.235	
		Species	4	13.73	25.602	<**0.001**			
		Temperature	4	4.571	7.34	<**0.001**			
		Site	1	9.14	58.782	<**0.001**			
		LogMass x Species	3	3.088	6.61	<**0.001**			*Pinnotheres* sp.[a], sesarmid[a], *P. africanus*[a], *Pinnixa* sp.[b]
		LogMass x Site	1	0.174	1.11	0.29			
		LogMass x Temperature	4	1.35	2.17	0.19			
Megalopa	LogMO_2	LogMass	1	36.464	223.265	<**0.001**	842.79	0.296	
		Species	3	8.942	10.73	< **0.001**			
		Temperature	5	8.942	13.687	<**0.001**			
		Site	1	0.001	1.455	0.228			
		LogMass x Species	3	1.203	2.194	0.08			
		LogMass x Site	1	0.238	1.455	0.228			
		LogMass x Temperature	4	1.737	2.658	0.06			

Due to variable numbers of each taxon per microhabitat and temperature (Appendix 4.1), separate GLM's were conducted per site to test for differences among microhabitats at each temperature, per taxon. Assumptions of normality and homogeneity of residuals were tested using Shapiro-Wilk and Levene's test, respectively. Where residuals did not meet these assumptions, generalized linear models (gamma distribution with a log-link function) were used. If there were no differences among microhabitats at a given temperature for each taxon, the data from each microhabitat at that temperature were pooled to test for differences in MO_2 among temperature and taxa using GLM's (Appendix 4.2; 4.3). If there were statistical differences in MO_2 among microhabitats, the microhabitat/s with the highest MO_2 were used for comparison among temperatures. This decision was taken as to represent the optimum metabolic rate for a given temperature. An ANCOVA was used to test for differences in the activation energy (aE) among taxa, where the taxon was a fixed variable and the inverse of absolute temperature (Kt) was the covariate. All tests had a significance criterion of $p < 0.05$ and where results were significant, they were followed by Tukey post-hoc tests using a Benjamini-Hochberg correction (Benjamini and Hochberg 1995). All statistical analyses were conducted in the R environment for computing statistics (R v3.3.1) (R Development Core Team, 2018).

4.3 Results

Overall, water temperature and salinity were homogenous among microhabitats within months for both Mlalazi and Mngazana (Figs 4.3 & 4.4). Water temperature ranged between 16.93 - 34.46 °C, with a mean of 24.70 °C for Mlalazi, while the mean for Mngazana was 21.26 °C, with a range of 12.20 - 30.30 °C. Point salinity measurements ranged from 15 - 35, with a mean of 21 for Mlalazi and 20 - 38 with a mean of 30 for Mngazana.

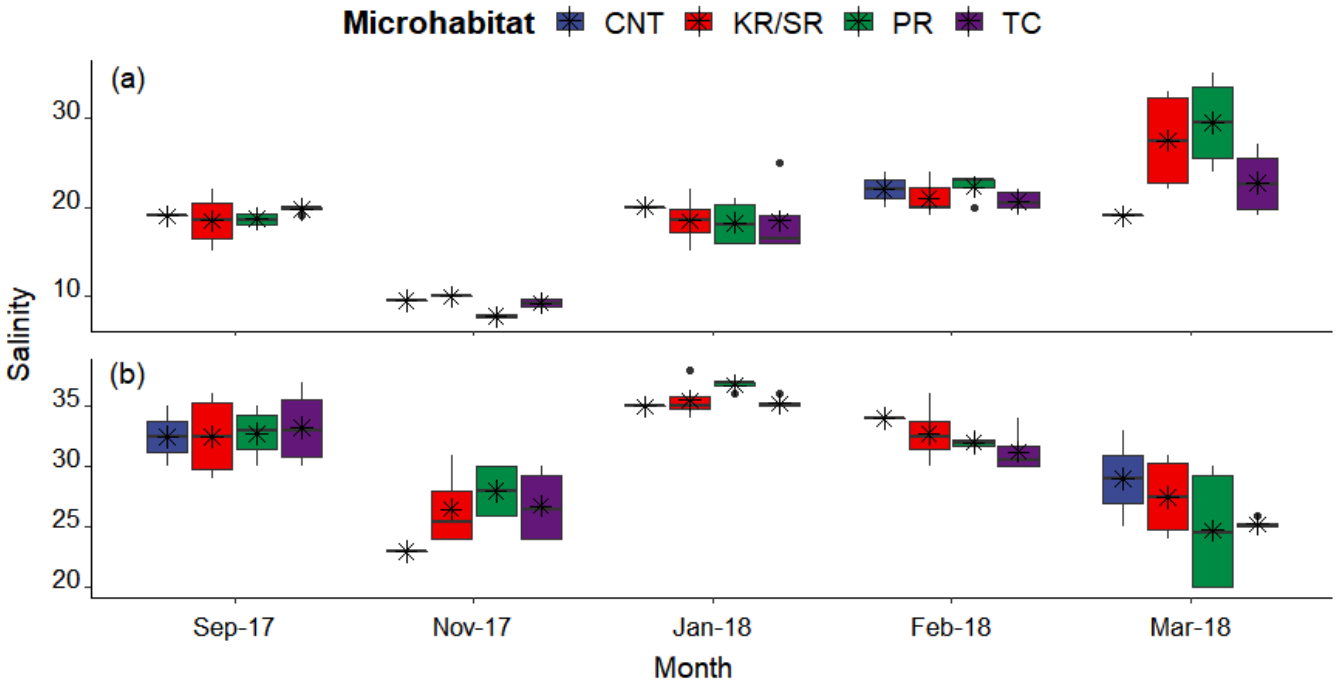

Fig. 4.3. Box plots of salinity at (a) Mlalazi and (b) Mngazana at each microhabitat sampled per month at Mlalazi. The 25 and 75% percentiles are represented by the lower and upper limits of each box; the horizontal line indicates the median, the vertical lines of each box indicate 1.5x above and below the interquartile range, the asterisk (*) indicate the mean and the dark circles (●) show outliers. There were no significant difference in salinity among habitats within each month for both Mlalazi and Mngazana

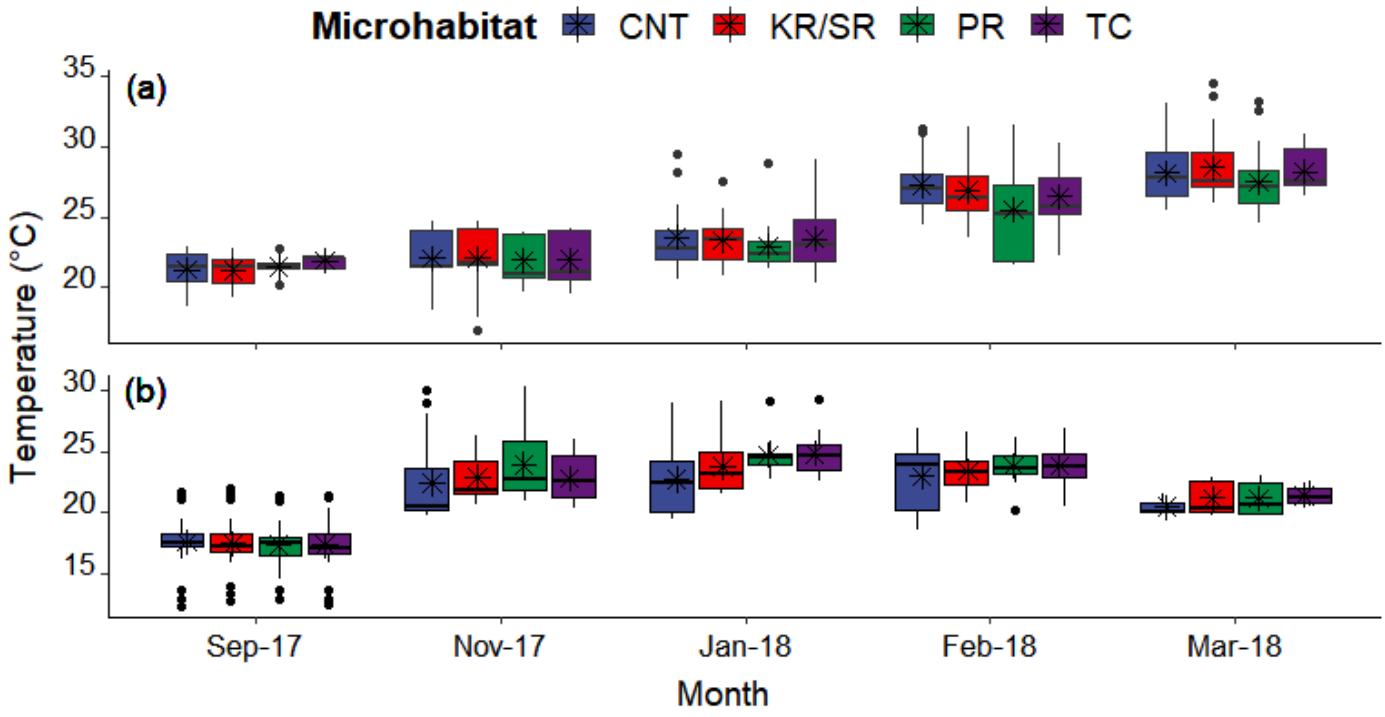

Fig. 4.4. Box plot of temperature at (a) Mlalazi and (b) Mngazana of each microhabitat sampled per month. The 25 and 75% percentiles are represented by the lower and upper limits of each box; the horizontal line indicates the median, the vertical lines of each box indicate 1.5x above and below the interquartile range, the asterisk (*) indicates the mean and the dark circles (●) show outliers. There were no significant difference in temperature among habitats within each month for both Mlalazi and Mngazana

Metabolic scaling coefficients were unaffected by the interaction between log dry mass and species for megalopae, but were significant for zoeae (Table 4.2). There were significant relationships between log-transformed metabolic rates with log-body mass and these scaled allometrically for all taxa and life stages tested (Table 4.1). Megalopae had the highest metabolic scaling coefficient (0.677), while *Pinnixa* sp. zoea was negatively scaled (-0.317).

Overall, significant differences in MO_2 within species among microhabitats became apparent only at increased temperatures (Figs 4.5 & 4.6). No significant differences in MO_2 were exhibited among microhabitats for the majority of species at Mlalazi tested at 20°C (Table 4.3). *Parasesarma catenatum* megalopa were the exception (GLM; $X^2_{(3)} = 8.532$, $p = 0.036$), with MO_2 significantly higher in specimens collected from the CNT, PR and KR/SR microhabitats than TC ($p < 0.001$) (Fig. 4.5A). At 28°C, significant differences in MO_2 among microhabitats were observed for *Pinnotheres* sp. zoea (GLM; $X^2_{(2)} = 11.074$, $p = 0.003$), *N. africanum* (GLM; $X^2_{(2)} = 46.074$, $p < 0.001$) and *Pinnotheres* sp. megalopa (GLM; $X^2_{(1)} = 6.436$, $p = 0.013$). MO_2 for individuals collected from the control were significantly higher than those from the PR microhabitat for *N. africanum* ($p < 0.001$) and *Pinnotheres* sp. megalopa ($p < 0.001$; Fig. 4.5B). At 33°C, no differences among microhabitats were observed for sesarmid (GLM; $X^2_{(3)} = 1.183$, $p = 0.757$) and *Pinnixa* sp. zoea (GLM; $X^2_{(1)} = 0.069$, $p = 0.791$), there were however differences in MO_2 among microhabitats for *N. africanum* (GLM; $X^2_{(3)} = 46.074$, $p < 0.001$), *P. catenatum* (GLM; $X^2_{(3)} = 42.711$, $p < 0.001$) and *Pinnotheres* sp. megalopa (GLM; $X^2_{(1)} = 6.091$, $p = 0.013$). The MO_2 of specimens from the CNT were again significantly higher than specimens from other microhabitats ($p < 0.05$; Fig. 4.5C).

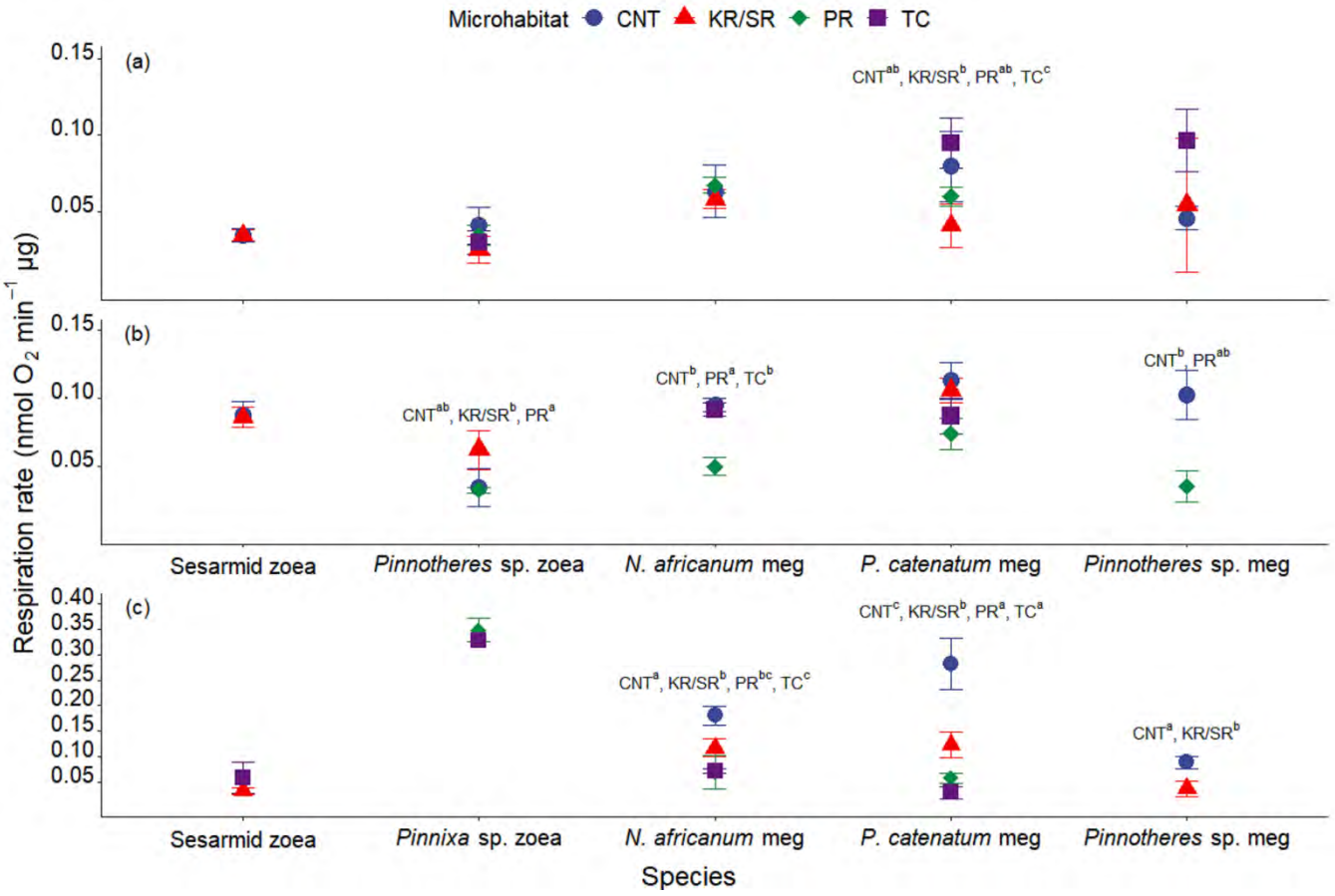

Fig. 4.5. Mass-corrected oxygen consumption rates expressed as mean ± SE of dominant brachyuran larvae (zoea; megalopa, meg) collected at the control (CNT; green circles), knee/stilt roots (KR/SR; red triangles), pneumatophores (PR; green diamonds) and tidal creeks (TC; purple squares) within the Mlalazi mangrove forest tested at the experimental temperatures of (a) 20°C, (b) 28°C and (c) 33°C. Where MO_2 significantly differed among habitats within species, post-hoc tests indicating homogenous groups (letters) are given.

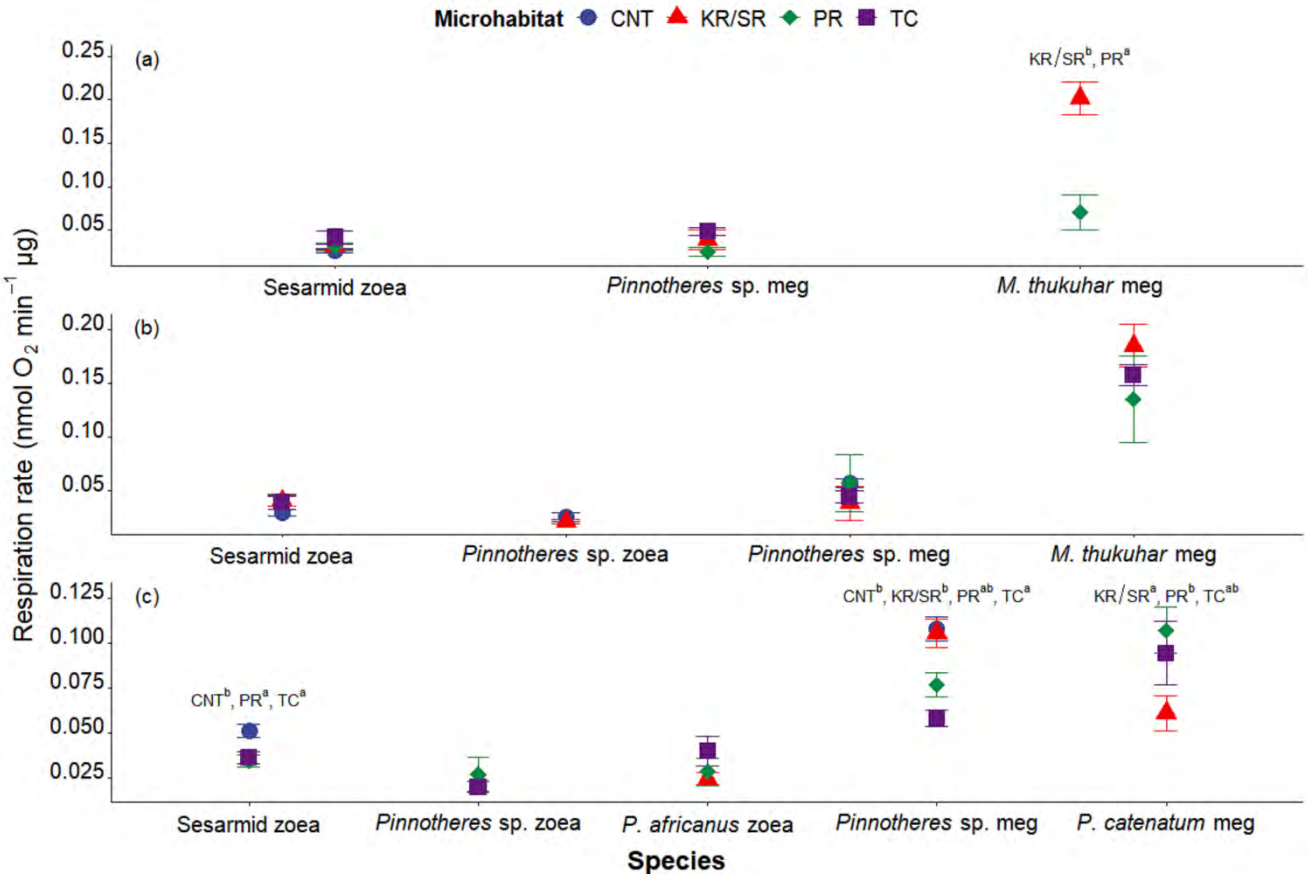

Fig. 4.6. Mass-corrected oxygen consumption rates expressed as mean ± SE of dominant brachyuran larvae collected at the control (CNT; blue circles), knee roots (KR/SR; red triangles), pneumatophores (PR; green diamonds) and tidal creeks (TC; purple squares) within the Mngazana mangrove forest tested at the experimental temperatures of a) 19°C, b) 24°C and c) 30°C. Where MO_2 significantly differed among habitats within species, post-hoc tests indicating homogenous groups (letters) are given.

Table 4.3. Outcome of the generalised linear models testing for differences in MO_2 among microhabitats (fixed effect) for each taxon and temperature, at each study site. (χ^2) chi-squared test statistics, (d.f) Degrees of freedom, (*p*) statistical significance and Post-hoc test results are indicated for each linear model.

Taxon	Temperature (°C)	χ^2	d.f	*p*
Mlalazi				
Sesarmid zoea	20	0.005	1	0.940
	28	0.026	1	0.871
	33	1.195	1	0.274
Pinnotheres sp. zoea	20	1.159	3	0.763
	28	11.583	2	**0.003**
Pinnixa sp. zoea	33	0.069	1	0.791
	20	1.0176	2	0.601
N. africanum megalopa	28	16.763	2	**<0.001**
	33	46.074	3	**<0.001**
	20	8.532	3	0.036
P. catenatum megalopa	28	6.131	3	0.105
	33	42.711	3	**<0.001**
Pinnotheres sp. megalopa	20	5.406	2	0.066
	28	6.436	1	**0.011**
	33	6.091	1	**0.013**
Mngazana				
Sesarmid zoea	19	5.045	3	0.168
	24	4.684	3	0.196
	30	15.815	2	**<0.001**
Pinnotheres sp. zoea	24	1.217	1	0.269
	30	0.821	1	0.364
P. africanus zoea	30	2.093	2	0.351
P. catenatum megalopa	30	7.795	2	**0.021**
Pinnotheres sp. megalopa	19	5.278	2	0.071
	24	3.031	3	0.386
	30	17.995	3	**<0.001**
M. thukuhar megalopa	19	16.041	1	**<0.001**
	24	1.665	2	0.434

At Mngazana, no differences in MO_2 were observed within sesarmid zoea (GLM; $X^2_{(3)}$, = 4.934, p = 0.176) and *Pinnotheres* sp. megalopa (GLM; $X^2_{(2)}$, = 5.278, p = 0.071) at 19°C, the MO_2 of *M. thukuhar* however differed among microhabitats (GLM; $X^2_{(1)}$, = 16.041, $p < 0.001$), where rates at KR/SR were significantly higher than at PR ($p < 0.001$; Fig. 4.6A). No significant differences in MO_2 were found among microhabitats within each species at 24°C (Table 4.3; Fig. 4.6B). At 30°C, differences in MO_2 were found within sesarmid zoea (GLM; $X^2_{(2)}$, = 15.455, $p < 0.001$), *Pinnotheres* sp. (GLM; $X^2_{(3)}$, = 17.995, $p < 0.001$) and *P. catenatum* megalopa (GLM; $X^2_{(3)}$, = 7.795, p = 0.021). For the sesarmid zoea, the MO_2 of specimens collected from the control were significantly higher than those from the PR and TC microhabitats ($p < 0.05$; Fig. 4.6C). The MO_2 of *Pinnotheres* sp. megalopa MO_2 were significantly higher in specimens collected from the CNT and KR/SR microhabitats ($p < 0.05$) than the ones from the TC. Additionally, the MO_2 of *P. catenatum* megalopa from PR were higher than those collected from the KR/SR ($p < 0.05$; Fig. 4.6C).

At Mlalazi, there was a significant difference in MO_2 within species among the three experimental temperatures for sesarmid (GLM; $X^2_{(2)}$, = 42.499, $p < 0.001$) and *Pinnotheres* sp. zoea (GLM; $X^2_{(2)}$, = 115.52, $p < 0.001$) as well as *N. africanum* (GLM; $X^2_{(2)}$, = 93.05, $p < 0.001$) and *P. catenatum* megalopa (GLM; $X^2_{(2)}$, = 85.989, $p < 0.001$) (Fig. 4.7A). Sesarmid and *Pinnotheres* sp. zoea exhibited no difference in MO_2 between 20°C and 33°C ($p > 0.05$), while MO_2 was significantly higher at 28°C ($p < 0.05$) than at the other two experimental temperatures. The MO_2 of all megalopae tested was always highest at 33°C except for *Pinnotheres* sp. megalopa, where MO_2 was highest at 28°C but not significantly different among temperatures (Fig. 4.7A; Table 4.4).

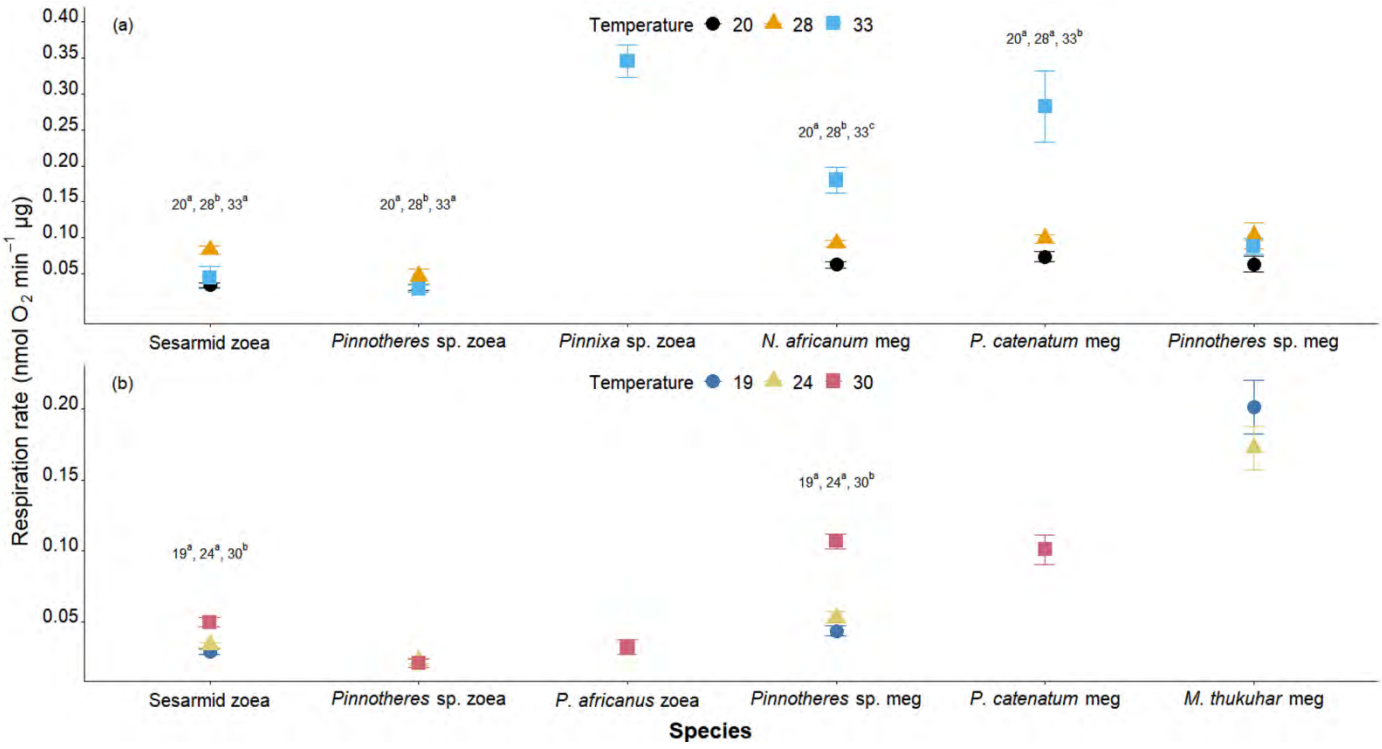

Fig. 4.7. Mass-corrected oxygen consumption rates expressed as mean ± SE of dominant brachyuran larvae at a) Mlalazi at temperature treatments of 20°C (black circles), 28°C (gold triangles) and 33°C (blue squares) and b) Mngazana at temperature treatments of 19°C (blue circles), 24°C (yellow triangles) and 30°C (red squares). Where MO_2 was significant among temperatures within species, post-hoc tests indicating homogenous groups (letters) are given.

Table 4.4. Results from the generalised linear models testing for differences among temperatures for each taxon, at each study site. (χ^2) chi-squared test statistic, (d.f) degrees of freedom, and (*p*) statistical significance is indicated for each linear model. Significant results are given in bold.

Taxa	χ^2	d.f	*p*
	Mlalazi		
Sesarmid zoea	42.499	2	**<0.001**
Pinnotheres sp. zoea	115.520	2	**<0.001**
N. africanum megalopa	93.051	2	**<0.001**
P. catenatum megalopa	85.989	2	**<0.001**
Pinnotheres sp. megalopa	2.160	2	0.339
	Mngazana		
Sesarmid zoea	14.437	2	**<0.001**
Pinnotheres sp. zoea	0.231	1	0.63
Pinnotheres sp. megalopa	101.620	2	**<0.001**
M. thukuhar megalopa	1.388	1	0.238

The only significant difference in MO_2 among the experimental temperatures within each taxon at Mngazana was exhibited by sesarmid zoea (GLM; $X^2_{(2)}$, = 14.437, $p < 0.001$) and *Pinnotheres* sp. megalopa (GLM; $X^2_{(2)}$, = 101.62, $p < 0.001$), where MO_2 were higher at 30°C when compared to 19°C and 24°C. Furthermore, there was no significant difference between 19°C and 24°C for both sesarmid zoea and *Pinnotheres* sp. megalopa (Fig. 4.7B; Table 4.4). The natural log of the mass corrected respiration rate of *M. thukuhar* megalopa and *Pinnotheres* sp. zoea decreased with increasing absolute temperature and thus was not compatible with the Arrhenius equation (Fig. 4.8; Table 4.5). Activation energy (eA) extracted from the linearised slopes for the rest of the taxa ranged between 0.45 – 0.64 eV. There was a difference in significant eA among species (ANCOVA, $F_{(7,797)} = 48.07$, $p < 0.0001$). Megalopae had higher eAs than sesarmid zoeae. The eA of *N. africanum* and *Pinnotheres* sp. did not differ from *P. catenatum* megalopa, but differed from each other (Table 4.6).

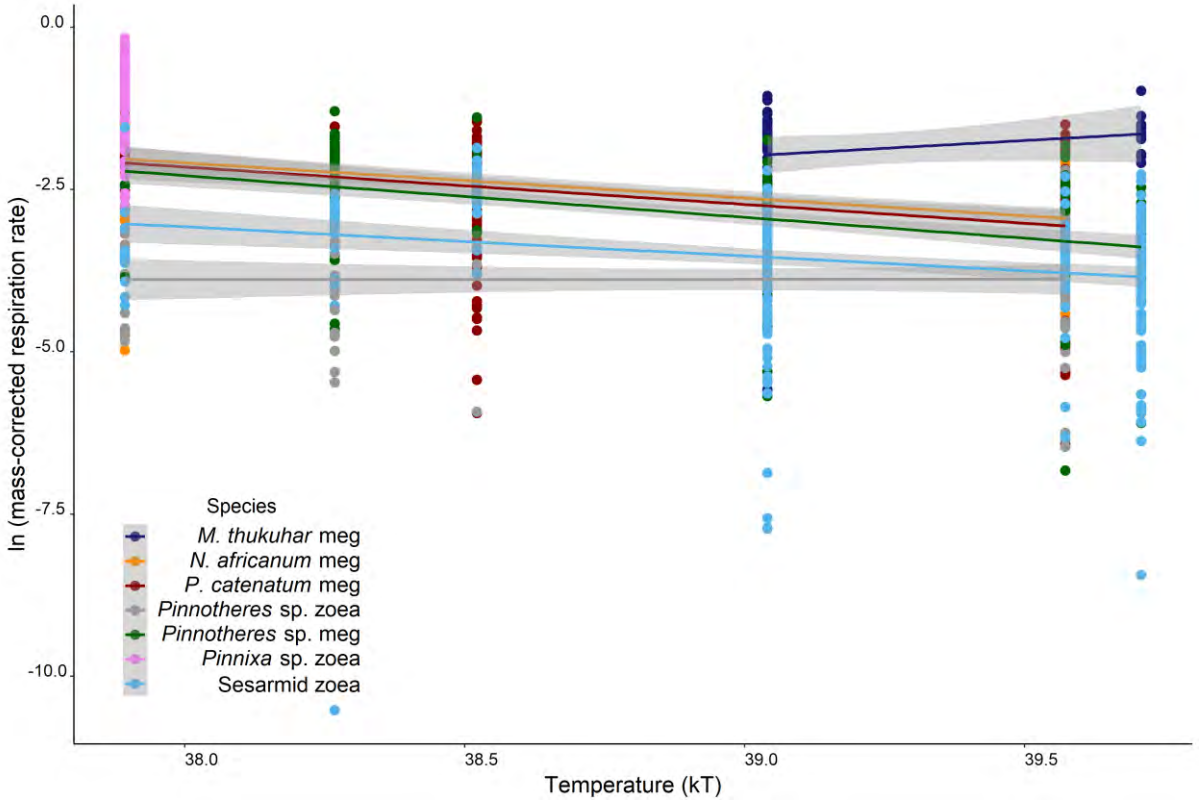

Fig. 4.8. The relationship between temperature and mass corrected respiration rates for each taxon plotted in Arrhenius form. Separate regression lines were fitted for each taxon as the natural logarithm of the mass-corrected metabolic rate as a function of inverse absolute temperature (K) multiplied by the Boltzmann constant (0.0000862 eV K-1). Grey bands indicate the 95% confidence interval of each regression.

Table 4.5. Parameters of the linear regressions calculated from the inverse of absolute temperature multiplied by Boltzmann's constant as a function of the natural logarithm of the mass-corrected respiration rate of each taxon. (R^2) adjusted R-squared, (E) activation energy, (b) natural logarithm of the taxon-specific normalisation constant and (p) significance value are indicated for each linear model.

Taxon	R^2	E	b	p
Sesarmid zoea	0.05	0.45	14.01	**<0.001**
Pinnotheres sp. zoea	-0.01	0.00	-3.95	0.987
N. africanum megalopa	0.25	0.54	18.50	**<0.001**
P. catenatum megalopa	0.11	0.58	19.76	**<0.001**
Pinnotheres sp. megalopa	0.20	0.64	22.15	**<0.001**
M. thukuhar megalopa	0.01	-0.48	-20.65	0.227

Table 4.6. Pairwise comparisons of significant activation energies (eAs) between taxa. Significant results are given in bold.

Post-hoc pairwise comparisons	estimate	*SE*	d.f	*t*-value	*p*
N. africanum meg vs *P. catenatum* meg	0.0961	0.1042	797	0.92	0.793
N. africanum meg vs *Pinnotheres* sp. meg	0.2906	0.0992	797	2.93	**0.018**
N. africanum meg vs sesarmid zoea	0.8974	0.0941	797	9.54	**<0.001**
P.catenatum meg - *Pinnotheres* sp. meg	0.1946	0.0947	797	2.05	0.169
P.catenatum meg - sesarmid zoea	0.8013	0.0893	797	8.96	**<0.001**
Pinnotheres sp. meg vs sesarmid zoea	0.6067	0.0834	797	7.27	**<0.001**

4.4 Discussion

Overall, an increase in temperature resulted in stage-specific responses of brachyuran larvae in MO_2. Metabolic scaling exponents scaled allometrically with body mass across all species and life stages. There were no differences in metabolic scaling exponents for megalopae, while values varied for the zoeae according to taxon. Invertebrate larvae associated to specific mangrove microhabitats exhibited differences in their metabolic responses to increasing temperatures, which became more pronounced in the advanced developmental stages. Megalopae had a higher scaling exponent than zoeae, as well as an increased activation energy when compared to sesarmid zoeae. These results support the theory of a biphasic life cycle in crustacean larvae, where the mass-scaling coefficient changes with larval development (Jensen et al. 2013). The mass-scaling coefficient however increased with life stage, which is in contrast to other studies on crustacean larvae, where a transition from isometric to allometric scaling with advancing developmental stage was underlined (Jacobi and Anger 1985, Jensen et al. 2013, Alter et al. 2015, Small et al. 2015, Leiva et al. 2018). This transition seems to derive from the decrease in surface area to volume ratio of the respiratory organs as ontogeny

progresses, a phenomenon common in aquatic invertebrates with complex life cycles (Glazier, 2006; Leiva *et al.*, 2018). The increased scaling exponent of megalopae in comparison to zoeae is counterintuitive as both stages mainly uptake oxygen through diffusion, with megalopae possibly having only weak oxyregulating capabilities (Tankersley and Wieber 2000, Alter et al. 2015). Additionally, zoeae have shorter diffusion distances and a smaller surface area of respiratory organs than megalopae in relation to size and energetic demand, for cutaneous gas exchange to take place (Fitzgibbon et al. 2015, Leiva et al. 2018). An increase in the metabolic scaling coefficient with advancing development has however been observed in larval spiny lobster (Fitzgibbon et al. 2015), scyphomedusae (Cnidaria: Scyphozoa) (Kinoshita et al. 1997), ctenophores (Svetlichny et al. 2004), fish (Yagi and Oikawa 2014) and penaeid prawns (Kurmaly et al. 1989). These studies have shown that increased metabolic scaling suggests a phase shift in behavioural traits to compensate for increased motility, rapid growth and anti-predator adaptation. Furthermore, the patterns in the metabolic scaling coefficients observed here and particularly where scaling coefficients were significantly different could be attributed to taxon-specific environmental constraints as well as larval behaviour, a factor that can affect the metabolic scaling exponent of animals the most (Crear and Forteath 2001, Carey et al. 2013, Jensen et al. 2013). Additionally, oxyregulatory capacities through well-developed gills may only develop post-zoeal stage in the taxa tested in this study.

At the low range of experimental temperatures, larvae from both study sites showed no difference in MO_2 among microhabitats, with the exception of *M. thukuhar* at Mngazana. At increased temperatures however, differences in MO_2 among microhabitats became evident. These differences reaffirm how the effect of an organisms' environmental history can shape the physiological performance of individuals after short-term exposures to increased temperature (Castillo and Helmuth 2005, Leiva et al. 2016, 2018). Interestingly, temperature

and salinity measurements were homogenous within the months in which the study was carried out, postulating that additional factors, not taken into account in this study (e.g. water depth, dissolved oxygen, turbidity, prey availability, state of the tide), could play a role in affecting the larval metabolic rates of brachyurans. The capacity to regulate the respiratory metabolism under different oxygen tension in different stages of larvae has been recorded for the intertidal porcelain crab *Petrolisthes laevigatus*, reflecting the conditions recorded in the habitats they were collected (Leiva et al. 2018). Decreases in MO_2 with decreasing oxygen tension have also been observed for the early stage larvae of other decapods (Belman and Childress 1973, Spicer and Strömberg 2003, Alter et al. 2015, Fitzgibbon et al. 2015).

Larvae collected from the control microhabitats exhibited higher metabolic rates at increasing temperatures than larvae collected from any other mangrove microhabitats. The constant inundation of water at the control sites as compared to the other microhabitats (except the tidal creek) could be a result of the quantity of quality (oxygen enriched due to tidal flushing) water influencing metabolic rates. Furthermore, the lack of celerity and physical forcing of tidal water within the tidal creeks as compared to the control areas could negatively affect the dissolved oxygen availability, possibly explaining the depressed metabolic rates of larvae from this microhabitat (Knight et al. 2013).

Control microhabitats were the most exposed environments among all selected and most likely to support a large density of larval predators due to the increased water depth, constant inundation of water and the lack of complex structures associated with the other microhabitats in this study (Mumby et al. 2004, Granek and Frasier 2007). In the case of sesarmid zoea at Mngazana and the megalopa at Mlalazi, the increased MO_2 in specimens originating from the

control could be in response to an elevated level of kairomones. Predation cues due to the secretion of kairomones can alter the behaviour of several zooplankton species and even the morphology of crab larvae (Cohen and Forward 2009; Charpentier et al. 2017). Furthermore, short-term exposure to predator cues has resulted in the increased oxygen consumption of tadpoles (Steiner and Van Buskirk 2009) and fish larvae (Robison et al. 2018). Conditions as such, could therefore have a (prolonged and consistent) effect and influence the increased $M\mathrm{O}_2$ in larvae that originated from a predator-rich area, where more energy would have been allocated to elicit a flight-type swimming behaviour (Mitchell et al. 2017, Briceño et al. 2018).

Metabolic responses to increased temperature changed according to ontogeny. Only the eA of *Pinnotheres* sp. megalopa (0.64 eV) was compatible with the previously reported interspecific mean of (0.65 eV) eA for aquatic organisms (Gillooly et al. 2001), with zoeae and other megalopae exhibiting lower values ranging from (0.45 to 0.57 eV) (Gillooly et al. 2001). The eA values observed indicate that all taxa in this study have lower activation energy and therefore a lower dependence on temperature for metabolic reactions than the interspecific mean for aquatic organisms (Gillooly et al. 2001, Clarke 2004). The differences in significant eA among taxa and stages could also be due to different selective pressures owing to an organisms environmental history or life-history strategy (Tagliarolo et al. 2018).

At Mlalazi, sesarmid and *Pinnotheres* sp. zoea exhibited a decline in $M\mathrm{O}_2$ at the maximum temperature tested when compared to the average experimental temperatures, while at Mngazana, sesarmid zoea showed increased metabolic rates at maximum experimental temperatures. *Pinnotheres* sp. zoea indicated no difference between 24°C and 30°C at Mngazana. In addition, *Pinnotheres* sp. and *M. thukuhar* megalopa showed a plateau in their

respiratory ability between 28°C and 33°C at Mlalazi, and between 19°C and 24°C at Mngazana. The depression in MO_2 at the maximum experimental temperature indicates the energetic limitations of zoeae within the Mlalazi Estuary (Schiffer et al. 2014, Small et al. 2015, Leiva et al. 2018). The metabolic rates of crustaceans living above their thermal optimums have indeed been observed to plateau or decrease (Frederich and Pörtner 2000, Magozzi and Calosi 2015). The optimum temperature for an organism's metabolic rate is usually in the centre of its thermal tolerance range. As such, a decrease in metabolic rates generally occurs when organisms experience temperatures beyond their optimum (pejus temperatures); yet survival is still possible, but becomes deleterious (Frederich and Pörtner 2000, Pörtner et al. 2000, Pörtner 2001, 2002). Due to thermally induced limitations in the respiratory capacity of organisms, at increasing temperatures, a progressive mismatch in the supply and demand of oxygen for maintenance eventually leads to anaerobic metabolism beyond its critical limit (Frederich and Pörtner 2000). Furthermore, the trend observed here also suggests that organisms with a reduced ability to consume oxygen had reached or surpassed their pejus temperatures, where optimal physiological performance ceases (Pörtner 2001).

The thermal sensitivity of zoeae at the temperature extremes within mangrove systems is likely influenced by their early life-history strategy. Recently hatched sesarmid crab zoea in particular employ a rapid export of larvae seaward for continued development in neritic waters (Dittel and Epifanio 1990, Papadopoulos et al. 2002, Paula et al. 2004a). This migration from the intertidal mangroves to more stable environmental conditions offshore (Paula et al. 2004a), suggests that early stage larvae that are exported, are not evolutionary equipped to cope with acute temperature increases within intertidal systems. The duration of short-residence within the mangrove before export is thus dependent on the environmental conditions (temperature,

salinity, hydrostatic pressure, turbidity, state of the tide) and is of particular importance for population persistence if zoeae experience deleteriously high temperatures more regularly.

In contrast, competent megalopae, after having developed offshore, return back to their settlement areas within mangroves, using the nocturnal flood tide (Dittel and Epifanio 1990, Paula et al. 2004a, Ragionieri et al. 2015). Megalopae returning to the intertidal mangroves to settle could be better adapted to acute temperature changes as they prepare for settlement and in turn possibly have weak oxyregulatory capacities due to advanced gill development in preparation for the juvenile life stage (Fitzgibbon et al. 2015, Leiva et al. 2018).

Sesarmid megalopae, such as *N.africanum* and *P. catenatum* in this study showed no signs of metabolic failure when exposed to the highest temperatures, confirming that stage-specific changes contribute to the thermal ranges within which mangrove crab larvae survive (Sastry and McCarthy 1973, Small et al. 2015). An ontogenetic shift in optimum temperature can be attributed to specific energetic demands linked to a specific early life stage, coupled with the development of osmoregulatory, respiratory and cardiovascular structures and functions (Spicer and Strömberg 2003, Small et al. 2015). The results in this study contradict previous observations, as zoeae indicated a lower optimum temperature for growth and survival than megalopae at Mlalazi. This suggests that limitations in the aerobic pathway in early stage larvae could possibly be responsible for the narrow range of optimum temperatures in which they are able to grow efficiently and survive to further their ontogenetic development through moulting (Weiss et al. 2012). Previous studies on stage-specific metabolism of crabs have reported a potential bottleneck for successful recruitment of crabs in the megalopal stage, reporting that,

as crab larvae develop, they become increasingly stenothermic (Jacobi and Anger 1985, Schiffer et al. 2014, Alter et al. 2015, Small et al. 2015, Leiva et al. 2018) .

In summary, this study demonstrates that the metabolic scaling coefficients of mangrove-associated brachyuran larvae are largely stage-specific, but can be taxon-specific for zoeae. The ontogenetic patterns observed in the metabolic responses according to the microhabitat from which they originated provides further evidence to how the environmental history (even short-term) of an organism can influence its physiology to short-term acute temperature changes. These stage-specific metabolic responses are perhaps useful to inform and corroborate the life history dynamics of mangrove decapod larvae, which in turn can be linked to the environment they experience which informs their physiology.

The metabolic limitations of zoeae at Mlalazi at maximum experienced temperatures indicate that larvae are developing and functioning at their upper limits and have very little room to adjust for further temperature increases (Weiss et al. 2012). Sesarmid zoea deriving from subtropical populations are therefore increasingly vulnerable to acute temperature rises, if they coincide with spawning. Crossing thresholds for temperature limitation in specific habitats may induce carryover effects that could result in damage accumulation or short-term acclimatisation in larvae (Williams et al. 2016). The magnitude of these carryover effects will depend on the frequency, the duration and intensity of acute temperature exposures (Somero 2010). Thus, if extreme temperature rises are frequent, even though they may be of short duration, the acclimatisation benefits will only serve as to reduce fitness differences within populations if individual larvae survive the initial stress. Alternatively, if stress or damage are accumulated, it will result in mass-mortality events (Williams et al. 2016). Either way, even short-term acute

and real exposures to extreme high temperatures in this sub-tropical region will negatively impact the fitness, if not survival, of the individuals and ultimately the functioning and persistence of the populations.

Chapter 5: General discussion and synthesis

The work presented in this thesis investigated the role mangrove microhabitats play in the early life history stages of invertebrates and fish. Specifically, this was done by characterising the generic dissimilarity in 3D root complexity provided by mangrove tree species', analysing the composition, abundance and distribution of larvae among microhabitats and examining how mangrove microhabitat and ontogeny of mangrove-associated brachyuran larvae respond metabolically to rapid temperature variations.

The metrics used in quantifying habitat complexity range in importance and suitability for reasonable interpretation of the effects exerted on the biotic structuring and enhancement of populations. For instance, when considering the microhabitat selection of mobile fauna and larval settlement on an open rocky shore, quantifying the available microhabitat using fractal dimensions of the surface is appropriate. This is due to the benthic nature of organisms that inhabit rocky shores where microhabitat availability is directly proportional to surface complexity (Kostylev et al. 2005). Alternatively, the volume of interstitial spaces has been widely used to infer habitat use in subtidal ecosystems to determine the body-size spectra that effectively take advantage of the complexity provided by foliose algae and submerged macrophytes (Hacker and Steneck 1990). Separately these metrics are informative to explain specific phenomena of interest that will transpire due to complex interactions, however, when used in unison, they provide a more useful estimate of which aspects of complexity and at what scale they will have specific outcomes (Warfe et al. 2008). The present study suggests that the interstitial spaces within and among the roots are the primary measurable parameter to realistically gauge how species use microhabitats in 3-dimensions, while the surface area to volume ratio (S/V) and fractal dimension might be suitable to infer how these structures influence abiotic processes such as sediment trapping, nutrient retention and wave dissipation. The distribution and abundance of larval communities corroborate this observation. Here, small

sized larvae (e.g. sesarmid and *D. fenestrata* zoea and *P. catenatum* megalopa) were most abundant in microhabitats such as the pneumatophores, where the interstitial space was low, but appropriate for their body size, while sizeable larvae (e.g. fish and *V. litterata* megalopa) were found in areas such as the stilt roots with larger interstitial spaces. This trend suggests that the measure of interstitial volume within the structure in question informs which types of larvae can make use of such habitat. Nevertheless, here the S/V ratio and interstitial volume correlated negatively and can be used in unison, to infer both available habitat for resource use and implications to the physico-chemical processes resultant of structural complexity. These local proficiencies of realised environmental conditions, influence the metabolism, development and resource acquisition rates of organisms at the local and mesoscale, and ultimately drive how communities are structured (Márquez and Kolasa 2013, Mittelbach and Schemske 2015).

The presence of structures in three dimensions, specifically in aquatic systems, influences the gradient in which an organism experiences its environment (Kelaher et al. 2001, Taniguchi and Tokeshi 2004, Gingold et al. 2010, Carter et al. 2018). These effects are dependent on the configuration of structures that serve to either enhance or mediate: turbulence, water flow, UV radiation, temperature and desiccation stress (Bell et al. 1991). The present study indicated that invertebrate larvae associated to specific mangrove microhabitats exhibited differences in their metabolic responses to increasing experienced temperatures. In addition, larvae collected from the control microhabitats, which had a lower qualitative degree of structural complexity, exhibited higher metabolic rates at increasing temperatures than larvae collected from any other mangrove microhabitats. Habitat complexity is hence instrumental in determining (and perhaps improving) the actual environmental boundaries that an organism experiences. The consequences of environmental buffering impact community level processes through reducing

both the physical and chemical stress experienced and enhancing the resource acquisition of organisms that inhabit complex areas (Bell et al. 1991, Smith and Ballinger 2001, Smith et al. 2014). Furthermore, physiological variation resulting from environmental heterogeneity can result in a range of genotypic and phenotypic responses in individuals within a population (Jimenez et al. 2015). The costs of exposure to thermal stress may depend on environmental factors that covary in intertidal habitats, such as species-interactions, oxygen and food availability (Denny et al. 2011, Miller et al. 2015, Leiva et al. 2018). Theoretically, megalopae and zoeae tested/studied here may move into more structurally complex habitat for shelter from predation, thus reducing costly metabolic activities such as vigorous swimming to avoid predators. Furthermore, optimum metabolic rates associated with the reduced energetic demands of swimming, are likely to be observed in areas with reduced tidal forcing, such as in the tidal creeks or within the immediate vicinity of complex microhabitat structures (Epifanio and Cohen 2016). This pattern was observed during this study, where larvae occurring in complex microhabitats maintained lower oxygen consumptions at high temperatures than those from the control habitats. Nevertheless, when temperature is sufficiently stressful for organisms, the mere existence of microscale environmental variation experienced amplifies the physiological variation among individuals (Jimenez et al. 2015, Mota et al. 2015, Leiva et al. 2018). Thus, microscale variations in water velocity, turbulence and drag effects exerted on larvae within structurally complex microhabitats and decreased predator-prey interactions, could be driving the physiological variations observed.

This study shows how the invertebrate and fish larval communities differ at the microhabitat level both spatially, temporally, with certain species at different ontogenetic phases occurring in significantly higher numbers in certain microhabitat/s. Larvae utilising microhabitats throughout their ontogeny within an ecological seascape require ecosystem connectivity among

heterogeneous habitats (Nagelkerken et al. 2015). Furthermore, ontogenetic microhabitat shifts within a single ecosystem, require heterogeneity, yet connectivity, within a "microscape" of distinguishable habitat features, which enhance survival and persistence of larval communities. Larvae hatched in the system likely encounter a complex and connected matrix of root habitat while being exported by the ebbing tide. Here, the variable export of larvae out of estuaries is explained through a delaying process, facilitated by the availability of microhabitats of varying degrees of structural complexity, which affords a buffer against rapid seaward transport. A lag in export is aided through the encountering of a complex network of microhabitats, as recently spawned as well as returning larvae move through the ecological microscapes to environmentally favourable conditions for further growth and/or settlement. The movement of larvae among microhabitats throughout their developmental stages ensures that possible predation and deleterious environmental effects are avoided and could be crucial in supplying individuals to the adult population through the availability of microscapes.

Although overlooked, it is critical to relate how fine-scale processes translate into broader spatio-temporal patterns, and equally, how large-scale processes resemble small-scale phenomena to understand how disturbances that operate over multiple scales will affect ecosystem responses and resilience to perturbations (Allen et al. 2005, Nash et al. 2014). Taking into consideration how organisms use microhabitats is hence critical to understand the role of structural complexity at fine scales. The ability of small organisms such as larvae to exploit refugia offered by complex structures is scale dependent. This trend confirms the textural discontinuity hypothesis, which infers that animals exploit certain areas more efficiently as a consequence of their body size relative to the space offered within a microhabitat that contains complex structures (Holling 1992). Spatial complexity mediating ecological niches and refugia can be of specific importance to small sized individuals that are

generally more vulnerable to predation than larger ones (Klecka and Boukal 2014). Discontinuous patch mosaics of habitat result in incoherence in the available resources across temporal and spatial scales, this is further evidenced here, reflecting the patchiness and spatio-temporal variability in the larval communities inhabiting different microhabitats through variable space allocation and asynchronous spawning of both fish and macroinvertebrates. Ultimately, efficient use of microhabitat is driven by the utilisation of size-specific resources such as the accessibility to the interstitial space within microhabitats. Moreover, decreased microhabitat availability will result in the homogenisation of communities and functional groups at relevant scales due to organisms not being entrained to exploit the available space (Fischer et al. 2008). Habitat structures that afford different levels of available interstitial space for exploitation by variably sized organisms remain particularly relevant for larval community enhancement and persistence at the microhabitat scale. Additionally, phenomena occurring at the microscale affect the ecosystem features that emerge at the meso- and macroscale (predator-prey interactions, trophic dynamics, adult population and community structure). Thus, interactions among lower level entities, i.e. how larvae interact with their environment at the fine/pertinent scale, is facilitative to how the mangrove ecosystem functions, and is summarised in a hierarchical conceptual model below adapted from Parrot (2002) (Fig. 5.1).

Individual mangrove root systems provide a substrate for algae and other epibiota and more broadly increased available living space that acts as refuge for invertebrate and fish larvae (Fig 5.1). The increased spatial complexity and perhaps food resources are attractive to larvae, adult invertebrates and (small) fish to feed while avoiding predators, who are too large to navigate among the intricate structures. Species interactions are subsequently mediated by the available shelter within the microhabitat and allow for niche establishment and favourable development in an environment where mangrove root structure acts as an environmental buffer reducing

drag, velocity and flow of water that reduces the energetic demands of swimming (Fig. 5.1). The consequences of phenomena at the microhabitat scale emerge at the meso-scale, where populations have increased metabolic variation among individuals deriving from the same ecosystem experiencing nuanced physico-chemical settings. This variability is the result of the realised environmental conditions and interactions an individual experiences within a particular microhabitat. Subsequently, metabolic dissimilarity is likely interlinked with food web dynamics, because metabolic variation in populations have a stabilising effect on trophic dynamics as it promotes species survival by creating a large diversity of metabolic rates in response to available resources (Quévreux and Brose 2019). As competition for resources increase, individuals are excluded from the larval community through predation, starvation or harmful environmental conditions. This trophic-derived regulation of individuals at the population level, dictates the composition and abundance of larval communities that establish in either transient nursery areas or corridors as they move into suitable habitat for continued development and or recruitment. Furthermore, the linkages among microhabitats within the mangrove microscape results in multiple discrete habitats that organisms can utilise as their essential developmental conditions change throughout their ontogeny. This further influences the composition of larval communities on both a spatial and temporal scale. Larvae move among microhabitats resulting in high turnover rates in community composition due to older larvae moving on to different habitat and recently spawned larvae recruiting within to replace them. The collective processes within the micro- and mesoscales described above lead to the establishment of a mangrove faunal community through facilitating the successful development of early stages and the recruitment of juveniles into adult populations in the mangrove and adjacent habitat, networked through tidal creeks, estuaries or bays. Additionally, the variability of interactions (both physico-chemical and biological) that larvae encounter at lower hierarchical levels and smaller spatial scales will determine the resulting pathway of

community development, while at the macroscale the adult community composition is likely to be highly predictable and self-organised by biogeographic processes (Dizon and Yap 2006). The successful recruitment into adult populations enhance faunal community persistence, additionally, the diversity of functional groups within a persistent community drive ecosystem productivity availing more resources to be utilised efficiently through enhancing the rates of elemental cycling (Sodré and Bozelli 2019). High-level ecosystem processes such as adult population size and community stability ultimately affect and feedback upon the lower levels because larger, fitter populations produce greater numbers of viable offspring to be included into the larval pool to increase the probability of successful recruitment and support high genetic diversity (Bellwood and Hughes 2001) (Fig. 5.1).

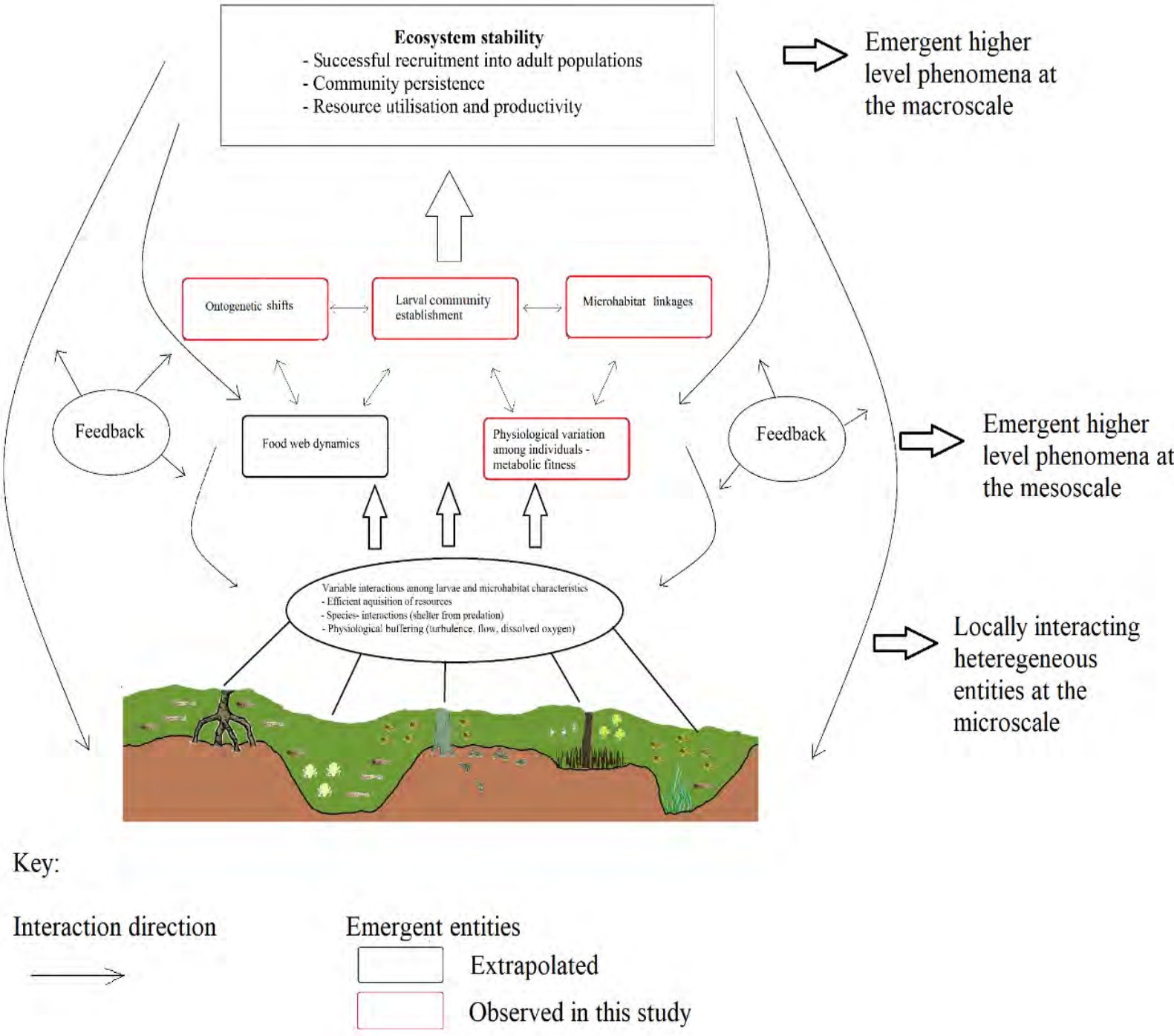

Fig. 5.1. Conceptual diagram of how low-level interactions within microhabitats contribute to emergent processes influencing meso- and macroscale dynamics through early faunal community establishment, physiological variation and persistence resulting in ecosystem stability. The locally interacting heterogeneous entities (drawing based on results in Chapter 3) show the association of larvae to certain microhabitats based on abundance; sesarmid zoea in the knee root and seagrass habitat; *D. fenestrata* zoea and *P. catenatum* megalopa in the pneumatophores, *V. litterata* in the tidal creeks and fish larvae in the knee roots, tidal creeks

and seagrass beds. Red-bordered boxes are empirical observations in this study; black bordered boxed are patterns extrapolated from the literature.

Habitat complexity through the compartmentalisation of microhabitats within mangrove forests provides linkages among ontogenetic stages of both invertebrates and fish, and should be more critically assessed for effective conservation of biodiversity (Kovalenko et al. 2012). Mangroves have been highlighted as one of the most important ecosystems that contribute to both human and environmental well-being, but are declining at a rapid rate of 1-3% per year (Friess et al. 2019). Efforts for mangrove rehabilitation have largely been focused on planting monospecific stands of *Rhizophora* spp. with a relatively low success rate (Primavera and Esteban 2008, Cormier-Salem and Panfili 2016). Here, I have highlighted how the structural diversity of mangrove tree species supports different larval communities and provides environmental buffering to larval metabolism. In that light, the protection of natural mangrove should be prioritised over rehabilitation efforts due to the nuances in fine scale processes of assorted habitat provided by tree species diversity that have an impact on the overall functioning of the ecosystem.

This thesis advances the knowledge on the facilitative structural and buffering role mangrove microhabitats play in the spatio-temporal occurrence and physiological performance of larvae. Moreover, it gives an insight into the importance of heterogeneous connected microhabitats over small spatial scales within an organism's home range for successful completion of their larval phase and recruitment into adult populations. Furthermore, structurally complex microhabitats influence the realised environmental conditions an organism experiences and the phenotypic adaptations to rapid temperature variations. Nevertheless, if stressful thermal conditions occur more frequently and with greater intensity and the buffering effect of

microhabitats are lost there is a serious risk of mass-mortality of larval communities that could reverberate up the ecological hierarchy and impair the optimum functioning of mangrove systems. Thus, maintaining and preserving the natural environmental heterogeneity within a system is vital for the contribution that fine scale processes have on how the entire system operates.

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Chapter 4 Appendices

Appendix 4.1. Number of individuals per taxon, microhabitat and site used for each temperature treatment.

Species	Temperature (°C)	CNT	KR /SR	PR	TC
Mlalazi					
Sesarmid zoea	20	25	11	-	-
	28	6	19	-	-
	33	-	6	-	6
Pinnotheres sp. zoea	20	4	15	17	12
	28	4	4	38	-
	33	-	14	-	-
Pinnixa sp. zoea	33	-	-	59	6
N. africanum megalopa	20	8	30	22	-
	28	3	-	8	38
	33	32	35	3	70
P. catenatum megalopa	20	8	13	28	16
	28	23	29	15	16
	33	14	15	11	4
Pinnotheres sp. megalopa	20	10	3	-	6
	28	11	-	3	-
	33	9	4	-	-
Mngazana					
Sesarmid zoea	19	30	45	33	35
	24	50	10	17	16
	30	28	-	21	27
Pinnotheres sp. zoea	24	8	16	-	-
	30	-	-	4	16
P. africanus zoea	30	-	4	4	12
P. catenatum megalopa	30	-	18	10	10
Pinnotheres sp. megalopa	19	-	5	4	20
	24	32	3	6	18
	30	37	37	14	11
M. thukuhar megalopa	19	-	12	27	-
	24	-	19	5	4

Appendix 4.2. Outcome of the generalised linear models testing for differences in MO_2 among microhabitats for each taxon and temperature, at each study site. (χ^2) chi-squared test statistics, (d.f) Degrees of freedom, (p) statistical significance and Posthoc test results are indicated for each linear model.

Species	Temperature (°C)	Fixed effect	χ^2	d.f	p	Posthoc
		Mlalazi				
Sesarmid zoea	20	Microhabitat	0.014	1	0.904	
	28	Microhabitat	0.001	1	0.992	
	33	Microhabitat	1.099	1	0.294	
Pinnotheres sp. zoea	20	Microhabitat	1.183	3	0.757	
	28	Microhabitat	11.074	2	0.003	CNT^{ab}, KR/SR^{b}, PR^{a}
Pinnixa sp. zoea	33	Microhabitat	0.069	1	0.791	
N. africanum megalopa	20	Microhabitat	1.0176	2	0.601	
	28	Microhabitat	16.763	2	**<0.001**	CNT^{b}, PR^{a}, TC^{b}
	33	Microhabitat	46.074	3	**<0.001**	CNT^{a}, KR/SR^{b}, PR^{bc}, TC^{c}
P. catenatum megalopa	20	Microhabitat	8.532	3	0.036	CNT^{ab}, KR/SR^{a}, PR^{ab}, TC^{c}
	28	Microhabitat	6.131	3	0.105	
	33	Microhabitat	42.711	3	**<0.001**	CNT^{c},KR/SR^{b}, PR^{a}, TC^{a}
Pinnotheres sp. megalopa	20	Microhabitat	5.406	2	0.066	
	28	Microhabitat	6.436	1	0.011	CNT^{b}, PR^{a}
	33	Microhabitat	6.091	1	0.013	CNT^{a}, KR/SR^{b}
		Mngazana				
Sesarmid zoea	19	Microhabitat	4.934	3	0.176	
	24	Microhabitat	4.729	3	0.193	
	30	Microhabitat	15.455	2	**<0.001**	CNT^{b}, PR^{a}, TC^{a}
Pinnotheres sp. zoea	24	Microhabitat	1.214	1	0.270	
	30	Microhabitat	0.874	1	0.349	
P. africanus zoea	30	Microhabitat	2.001	2	0.366	
P. catenatum megalopa	30	Microhabitat	7.795	2	**0.021**	KR/SR^{a} ,PR^{b}, TC^{ab}
Pinnotheres sp. megalopa	19	Microhabitat	5.278	2	0.071	
	24	Microhabitat	3.031	3	0.386	
	30	Microhabitat	17.995	3	**<0.001**	CNT^{b}, KR/SR^{b}, PR^{ab}, TC^{a}
M. thukuhar megalopa	19	Microhabitat	16.041	1	**<0.001**	KR/SR^{b}, PR^{a}
	24	Microhabitat	1.665	2	0.434	

Appendix 4.3. Number of individuals and the microhabitat/s they were pooled from to test for differences among each temperature treatment for each site.

Mlalazi						
Species	20 °C (n)	Microhabitat/s	28 °C (n)	Microhabitat/s	33 °C (n)	Microhabitat/s
Sesarmid zoea	36	CNT & KR/SR	25	CNT,KR/SR	12	KR/SR & TC
Pinnotheres sp. zoea	48	CNT, PR, KR/SR & TC	8	CNT, KR/SR	14	KR/SR
N. africanum megalopa	60	CNT, PR & KR/SR	41	CNT & TC	32	CNT
P. catenatum megalopa	52	CNT, PR, KR/SR & TC	83	CNT, PR, KR/SR & TC	14	CNT
Pinnotheres sp. megalopa	19	CNT, KR/SR & TC	11	CNT	9	CNT
Mngazana						
Species	19 °C (n)	Microhabitat/s:	24 °C (n)	Microhabitat/s:	30 °C (n)	Microhabitat/s:
Sesarmid zoea	108	CNT, PR & KR/SR	93	CNT, PR, KR/SR & TC	76	CNT, PR & TC
Pinnotheres sp. zoea	-	NA	24	CNT & KR/SR	20	PR & TC
P. africanus zoea	-	NA	-	NA	30	PR, KR/SR & TC
P. catenatum megalopa	-	NA	-	NA	38	PR, KR/SR & TC
Pinnotheres sp. megalopa	29	PR, KR/SR & TC	59	CNT, PR, KR/SR & TC	74	CNT & KR/SR
M. thukuhar megalopa	12	KR/SR	28	PR, KR/SR & TC	-	NA