**Department of Zoology**

# Ecology of key cerithioidean gastropods in the mangroves of the iSimangaliso Wetland Park, KwaZulu-Natal South Africa

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Submitted in fulfilment of the requirements for the degree of Philosophiae Doctor to be awarded in the Faculty of Science at the Nelson Mandela Metropolitan University

April 2017

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# Declaration I

I, Jacqueline Leoni Raw (s213476967) declare that, in accordance with Rule G5.6.3 of the Nelson Mandela Metropolitan University, this thesis submitted in fulfilment of the requirements for the degree Philosophiae Doctor is my own work and that all relevant sources have been duly acknowledged in the text. This thesis has not previously been submitted for any degree, diploma or examination.

The following publications form the research chapters presented in this thesis:

Raw JL, Perissinotto R, Bird MS, Miranda NAF, Peer N (In review) Variable niche size of the giant mangrove whelk, *Terebralia palustris* (Linnaeus, 1767) in a subtropical estuarine lake. *Hydrobiologia*

Raw JL, Perissinotto R, Miranda NAF, Peer N (2016) Diet of *Melanoides tuberculata* (Müller, 1774) from subtropical lakes: Evidence from stable isotope ($\delta^{13}$C and $\delta^{15}$N) analyses. *Limnologica* 59: 116-123.

Raw JL, Perissinotto R, Miranda NAF, Peer N (In press) Feeding dynamics of *Terebralia palustris* (Gastropoda: Potamididae) from a subtropical mangrove ecosystem. *Molluscan Research*

Raw JL, Perissinotto R, Miranda NAF, Peer N (2016) Feeding dynamics of *Melanoides tuberculata*. *Journal of Molluscan Studies* 82: 328-335.

Raw JL, Perissinotto R, Adams JB (In review) Resilience of *Cerithidea decollata* (Gastropoda: Potamididae) to environmental change and limited connectivity in subtropical estuarine mangroves. *Wetlands Ecology and Management*

Signature:........................................ Date: 10 · Apr · 2017

# Declaration II

This research was carried out under a research agreement entitled "Ecology of key cerithioidean gastropods in the mangroves of the iSimangaliso Wetland Park, KwaZulu-Natal, South Africa". All gastropods were collected accordingly on integrated Environmental and Fisheries Research Permits (RES2013/13, RES2015/31) issued by DAFF (South African Department of Agriculture, Forestry and Fisheries) under Section 83 of the Marine Living Resources Act. Clearance to conduct this research was obtained from the Research Ethics Committee of the Nelson Mandela Metropolitan University (ref: A14-SCI-ZOO-009). No endangered, threatened or protected species were used in this research.

**Signature:**........................................................ **Date:**.......10 - Apr - 2017..............

# Abstract

Gastropods are one of the most diverse species groups in mangrove habitats, however, many of their specific roles in relation to ecological patterns and processes are currently largely unknown. The overall aim of this research project was to provide basic ecological information for key gastropod species from subtropical mangroves within a protected area. South African mangroves cover relatively small areas and are restricted to estuaries, these habitats therefore present unique opportunities and challenges to the species that occur in them. Three gastropod species, *Terebralia palustris*, *Cerithidea decollata*, and *Melanoides tuberculata*, all occur at their natural southernmost range limit within South Africa and were selected based on their prominence and occurrence in mangrove habitats of the iSimangaliso Wetland Park, a UNESCO World Heritage Site. Trophic linkages and resource partitioning, resource utilization rates, and ecological resilience were investigated respectively using: 1) a stable isotope ($\delta^{15}$N and $\delta^{13}$C) approach; 2) an experimental approach to quantify feeding dynamics (ingestion rate, consumption/digestion efficiency and grazing impact); and 3) a mixed-effects modelling approach to relate population responses to environmental variables. The diet of *T. palustris* was seasonally variable and a number of sources were incorporated by different sized snails, but their grazing impact on microphytobenthos was not significant. The results also indicated an ontogenetic shift in the dietary niche for *T. palustris* through robust partitioning of resources between different size classes. The diets of *C. decollata* and *M. tuberculata* were dominated by different primary resources as a function of where they occurred in the mangroves. *Melanoides tuberculata* consumed a wide variety of primary resources, a typical trait of an opportunistic generalist species. The ingestion rate of *M. tuberculata* was not dependent on the availability of microphytobenthos, and was highest when conditions were oligotrophic. The resilience of *C. decollata* was related to the tree-climbing behaviour of this species and its occurrence was best explained by sediment conductivity. These responses were considered in conjunction to what has previously been reported on the resilience of the mangrove trees. The results of this research project have provided new basic ecological information for all three gastropod species in this data-deficient subtropical region.

This information can potentially be used in comparative studies for these species in other regions or in broader scale ecological studies. *Terebralia palustris* has recently experienced a range contraction along the South African coastline. This research project has shown that the diet of this species is highly variable and that food limitation and competition for resources should be considered as potential drivers of the local decline. *Cerithidea decollata* has in contrast expanded its distributional range in this region. This research project has shown that this species has a generalist diet and exhibits traits in relation to tolerance that are expected to have facilitated its expansion into temperate saltmarsh habitats that occur in dynamic estuaries. *Melanoides tuberculata* is a globally invasive species, and as South African populations are within its native range, ecological information from this region is valuable as it can be used to investigate the potential ecological effects following introduction into new habitats beyond the native range. Biological drivers have a significant impact on mangrove ecosystem functioning, particularly in relation to recycling and the retention of organic carbon generated through primary productivity. Understanding the ecological linkages that maintain ecological functioning and stability is therefore an important step towards conserving and sustainably managing threatened ecosystems such as mangrove forests.

# Acknowledgements

I would not have achieved everything I have without the love, support and encouragement from my family, Leoni and Carolynn Raw, and to them I am eternally grateful. I would also like to thank my close friends Michelle Risi and Michel Bengtson for their support despite being thousands of kilometres away. Finally, I must thank Christopher Nolte for his endless support, continuous positive attitude and at times much needed sense of humour. He has made a significant contribution to the culmination of this thesis by never letting me give up. At times his love was all that kept me going and for that I will always be indebted.

*"To stand at the edge of the sea,*
*to sense the ebb and flow of the tides,*
*to feel the breadth of a mist moving over a great salt marsh,*
*to watch the flight of shore birds that have swept up and down the surf*
*lines of the continents for untold thousands of years,*
*to see the running of the old eels and the young shad to the sea,*
*is to have knowledge of things that are as nearly eternal as any earthly*
*life can be"*

Rachel Carson – The Edge of the Sea

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# Chapter 1: General Introduction

Mangrove forests are iconic features of tropical and subtropical coastlines around the world. These ecosystems have an ancient history as the characteristic foundation tree species date back to the Late Cretaceous and Early Palaeocene periods (Saenger 1998). The modern mangrove genera were indeed well established by about 50 Ma in the Middle to Late Eocene along the shores of the Tethys Sea (Ellison et al. 1999). This impressive persistence of mangroves through the millennia is attributed to their remarkable ecological stability during periods of environmental inconstancy (Alongi 2015). Despite this, as is the case for almost all natural systems on Earth, numerous anthropogenic activities have had pronounced negative impacts on mangrove forests (Duke et al. 2007). Recent research suggests that mangrove ecosystems are potentially able to persist even through current predictions of escalated global change (Alongi 2015, Lovelock et al. 2015, Ward et al. 2016). However, this persistence is expected to be limited within certain specific conditions and the anticipated rapid environmental changes would have a serious impact on the ecological integrity of these surviving mangrove ecosystems. Conservation of mangroves as functional ecosystems should therefore not focus solely on the trees but should also include the associated fauna. Mangrove fauna, and the invertebrate species in particular, have been increasingly recognized as significant biological drivers of these ecosystems (Cannicci et al. 2008, Alongi 2009b). Current mangrove ecology is therefore focussed on linking attributes of fauna at different levels (individuals, populations, communities) to large scale ecosystem functioning. This research project therefore focuses on providing information on the ecology of a key group of mangrove invertebrates from a region that is data deficient in this regard.

## 1.1 Distribution, importance and threats related to mangrove ecosystems

The term "mangrove" refers to the distinct woody halophytic plant species that due to unique adaptations are able to inhabit the interface between terrestrial, estuarine and near-shore marine environments (Tomlinson 1999). Globally, the distributional range of mangrove tree species is linked to sea surface temperature, with occurrence being limited to tropical and sub-tropical regions by the winter 20 °C isotherm (Alongi

2009a). This gives these species a general latitudinal distribution between 30 °N and 30 °S (Giri et al. 2011). Mangrove trees establish between mean sea level and the highest spring tide (Alongi 2009a) and their occurrence in these areas has a significant influence on the formation of structurally unique habitats that support a large diversity of faunal species (Nagelkerken et al. 2008). The ecological communities supported within mangroves are often distinct and have a close association with the habitat type (Kathiresan & Bingham 2001). Mangrove forests are considered to be resilient and stable (Alongi 2008, 2015), and therefore even at their range extremities are able to provide suitable habitat to typical tropical species at higher subtropical latitudes (Macnae 1963).

South African mangroves are subtropical and occur at one of the southernmost limits of the global distribution range for this ecotype (Traynor & Hill 2008). Along the high energy South African coastline, mangroves are limited to occur within sheltered estuarine areas (Steinke 1999). Early studies on these ecosystems were largely descriptive (Macnae 1963, Ward & Steinke 1982) and focused on the coastal distribution of mangrove tree species and the associated fauna. Within this geographical region, mangroves only contribute 0.05 % of the total mangrove forest area of the entire east African coast (Adams et al. 2004). Similarly, the diversity of mangrove trees is relatively low as only six species of the ~ 50 taxa that occur in the Indo-West Pacific region are found along the South African coastline (Duke et al. 1998, Steinke 1999). The diversity of mangrove associated macrofauna is generally correlated with the diversity of the flora (Alongi 2009b). However, the structure of mangrove macrobenthic assemblages is largely influenced by local environmental conditions (Lee 2008). Historical records for South African mangrove fauna indicate similarities with the diverse communities from Inhaca Island, Mozambique (Macnae & Kalk 1962, Macnae 1963). The southern extension of these typically tropical species within this region is supported by the warm and fast-flowing Agulhas Current that not only ameliorates sea surface temperature, but also provides an efficient dispersal mechanism for viable propagules of mangrove trees and larvae of macrofauna through the formation of eddies (Steinke & Ward 2003, Teske et al. 2011). South African mangroves therefore offer a unique opportunity to assess ecological attributes of a large number of species occurring at their global distribution limits. Populations such as these that occur at the edge of their species' distributional

range may exhibit local adaptation and acclimation to environments that could be considered as unfavourable (Bennett et al. 2015b). However, as populations at their distributional limits are also generally fragmented, they are expected to have a lower adaptive potential and fitness as a consequence of reduced genetic diversity (Pearson et al. 2009). These factors are important when considering the implications for potential range expansions under predicted global change.

Besides their biodiversity value, mangrove ecosystems are also globally recognized for their economic importance as they provide a large number of ecosystem goods and services (Barbier et al. 2011). These are defined as the attributes of an ecosystem that benefit, sustain and support human well-being (Fisher et al. 2009). Ecosystem goods and services are therefore given an economic valuation that assigns quantitative values to these naturally provided benefits (Vo et al. 2012). The total economic value of mangrove habitat globally has previously been estimated at US $ 181 billion or US $ 10 000 ha$^{-1}$(Alongi 2002). Such a comprehensive economic valuation of all mangrove forests along the South African coastline has not been completed. However, the mangroves at the Mngazana Estuary in the Eastern Cape, which represent the third largest forest in terms of area in the country, have been conservatively estimated to have an economic value of ZAR 7.4 million (= 0.5 million US $, De Wet 2004). Important natural services that are evaluated in these assessments include the provision of coastal protection against erosion and storm surges (Dahdouh-Guebas et al. 2005, Arkema et al. 2013), as well as flood protection, nutrient processing and sediment retention (Alongi 2002, Lee et al. 2014). The provisional services of mangroves also include resources for utilization (wood, charcoal) as well as consumption (fruits, honey, fish and invertebrates) (Vo et al. 2012). The types of goods and services provided by mangrove ecosystems are, however, dependent on a large number of factors (Ewel et al. 1998). As unsustainable utilization degrades ecosystem functioning there is an inevitable negative effect on the provision of these ecosystem goods and services (Duke et al. 2007, Lee et al. 2014). Small mangrove forests such as those found along the South African coastline do provide valuable ecological goods and services, but they may be at a higher risk of exploitation as a result of their size. Recent research activities have therefore focussed on collecting baseline data for key South African mangrove forests (Adams et al. 2004, Rajkaran et al. 2009, Rajkaran & Adams 2011) as well as

identifying natural and anthropogenic factors that influence the resilience and stability of these ecosystems (Rajkaran et al. 2004, Hoppe-Speer et al. 2013, Adams & Human 2016).

Despite the ecological and economical importance of mangroves, these forests are globally one of the most threatened ecosystem types (Polidoro et al. 2010, Sandilyan & Kathiresan 2012), with losses estimated at between 20-35 % of the total area within the past three decades (Valiela et al. 2001, Giri et al. 2011). These losses are largely attributed to anthropogenic factors, such as clearance for development, aquaculture and extractive resource use (Duke et al. 2007, Polidoro et al. 2010). Along the South African coastline, the mangrove forest area has been reduced mainly through direct removal of the trees to allow for industrial, residential or agricultural development in areas where coastal wetlands naturally occurred (Rajkaran et al. 2004). Most notably the largest removal occurred in Durban Bay, where approximately 200 ha of mangrove forest was sacrificed for the development of one of the largest industrial ports in the country (Moll et al. 1971). Further large scale removal should however be prevented, as under current legislation estuaries that harbour mangroves are prioritized for conservation (Turpie et al. 2002). However, these ecosystems still face a multitude of threats, particularly in the form of extensive harvesting of trees for fire-making as well as for use as building materials (Rajkaran et al. 2004, Traynor & Hill 2008). Furthermore, land use practices, including the abstraction of freshwater for agriculture, input from waste-water treatment plants and the building of dams have a significant impact on the flow regime of rivers (Schlacher & Wooldridge 1996, Richter et al. 2003). Severe changes in flow regime and dynamics can have a detrimental effect on estuarine mangroves, as they may suffer die-back after prolonged inundation or persistent low water levels (Edwards 1969, Naidoo 2016). Current mangrove conservation challenges are therefore intricately linked with the threats faced by the estuarine and coastal areas in which they occur.

Besides the immediate anthropogenic impacts on mangrove forests, these habitats are also vulnerable to threats associated with global climate change (Gilman et al. 2008). Global change factors such as sea-level rise, increases in temperature, precipitation and $CO_2$ and changes in ocean currents are inter-related and spatially variable, which presents a challenge for estimating synergistic impacts on global

mangrove forests (Ward et al. 2016). As South African mangroves exist at a southern continental limit, it is predicted that mangroves will expand their distribution further south along this coastline as global temperatures continue to rise (Quisthoudt et al. 2013, Saintilan et al. 2014). However, as South African mangroves are limited to occurring in estuarine areas, the potential for recruitment of both mangrove fauna and flora will be influenced by a number of physical and environmental variables associated with these ecosystems. For example, recruitment might be limited by the intermittent connectivity of many estuaries with the Indian Ocean (Whitfield et al. 2012). As global climate change is one of many pressures acting on estuaries, it should be viewed as an additional form of anthropogenic alteration. It is therefore essential to have baseline ecological data that describe the current dynamics of mangrove ecosystems as climate change continues to accelerate.

As the loss of mangrove habitat has a significant effect on ecological functioning, the biodiversity of benthic fauna as well as associated fish species is also threatened both directly and indirectly (Blaber 2007, Ellison 2008). South African legislation recognizes the importance of ecological biodiversity in the National Environmental Management Act (Biodiversity Act, No. 10 of 2004) which furthermore prioritizes the conservation of mangroves as important coastal ecosystems (National Environmental Act: Integrated Coastal Management Act, No. 24 of 2008). Biodiversity research in South African mangroves has however focussed on larger taxa such as fish and birds. As mangroves provide important feeding and nursery areas, these habitats are used by a wide diversity of these species (Hockey & Turpie 1999, Whitfield & Marais 1999). Most importantly, mangrove areas provide critical habitat to juvenile fish and crustaceans that are targeted by both recreational and commercial fisheries (Mann 2013). Globally, the ecological and economical value of fisheries species that are dependent on mangroves has been long recognized (Rönnbäck 1999). Therefore, a large amount of research has focussed on understanding the links between mangrove primary productivity and the lower invertebrate taxa that form the base of mangrove ecosystem food webs (Bouillon et al. 2002, Kristensen et al. 2008). However, in South Africa relatively little research has focussed on the ecology of mangrove invertebrates, and in particular on their role as trophic links within these important ecosystems. One of the goals of this research project was therefore to provide new information and insight on these key

ecological interactions within mangrove ecosystems that are significantly influenced by their occurrence within estuaries.

*1.2 Background: Ecological role of mangrove gastropods and their occurrence within the mangroves of the iSimangaliso Wetland Park*

The faunal communities associated with mangrove habitats are not diverse in comparison to tropical rocky shores and coral reefs (Alongi 2002), and relatively few species are completely restricted to occurring only in these environments (Ellison et al. 1999). However, one of the prominent groups that occurs globally throughout mangrove forests and adjacent habitats is the gastropod molluscs (Vermeij 1973). Gastropods that typically occur in mangrove habitats are classified within three superfamily groups: Cerithioidea Férussac, 1819; Ellobioidea Pfeiffer, 1854; and Littorinoidea Children, 1834. Of these groups, the cerithioideans are often dominant in terms of abundance and biomass (Strong et al. 2011) and thus are considered to be key components of the ecological communities in which they occur. These gastropods are most commonly represented in mangrove ecosystems by members of the family Potamididae H. Adams & A. Adams, 1854 (mudwhelks or mud creepers). As the potamidids occur almost exclusively within mangroves, they are considered to be specialized inhabitants of these ecosystems (Reid et al. 2008). As such, the majority of these species have extensive distributions, often extending across entire biogeographical regions where mangrove habitat is established (Houbrick 1991, Madeira et al. 2012).

Within mangrove habitats, potamidid species have complex and variable ecological roles. As benthic deposit feeders, most of these species consume a combination of algae and detritus and thus form important linkages with both autochthonous and allochthonous carbon sources to higher trophic levels (Lee 2008). Species that consume mangrove leaf litter directly contribute towards the retention of primary production within these ecosystems (Cannicci et al. 2008). Additionally, the movement of large gastropods over the soft muddy sediments of mangrove habitats has a significant effect on the structure of epipsammic meiofaunal and microbial communities (Carlén & Ólafsson 2002). Interactions between mangrove gastropods and brachyurans are also diverse. Crabs such as *Thalamita crenata* Rüppell, 1830; *Epixanthus dentatus* (White, 1848); *Eurycarcinus natalensis* (Krauss, 1843); and

*Scylla serrata* (Forskål, 1775) all predate opportunistically on mangrove gastropods (Dahdouh-Guebas et al. 1999, Thimdee et al. 2001). In contrast, grapsid crabs, such as *Neosarmatium smithi* (H. Milne Edwards, 1853), consume mangrove leaf litter actively and aggressively compete with gastropods for these resources (Fratini et al. 2000). The functional roles of both gastropods and ocypodid crabs of the genus *Uca* Leach, 1814 are also comparable, as both groups are primary consumers of benthic microalgae and particulate detritus. The occurrence of potamidids within mangrove environments has also been related to the specific reliance of some species on mangrove trees for the provision of substrate and shelter (Reid et al. 2008). Certain species characteristically migrate up the trees with the incoming tide to escape predation (Vannini et al. 2006, Belgrad & Smith 2014), while others actively seek shaded areas to avoid desiccation stress (Lasiak & Dye 1986, Wells & Lalli 2003). These close associations between potamidids and mangrove ecosystems inform on the nature of their closely linked evolutionary histories (Reid et al. 2008). Understanding the ecological roles of these gastropods within mangroves can therefore provide insight to their importance for ecosystem functioning at larger scales.

Within South African mangroves, there are two prominent cerithioidean gastropods from the potamidid family: *Terebralia palustris* (Linnaeus, 1767), the giant mangrove whelk; and *Cerithidea decollata* (Linnaeus, 1767), the climbing mangrove whelk (Figure 1.1 A, B). *Terebralia palustris* has the most extensive global distribution of all mangrove potamidids, as it occurs across the entire Indo-Pacific region (Houbrick 1991), while the distribution of *C. decollata* is limited to the West Indian Ocean along the eastern coast of Africa (Madeira et al. 2012; Reid 2014). However, both species occur at their southern distribution limits along the South African coastline. Although mangrove potamidids have seldom been observed spawning (Reid et al. 2008), the life cycles of both *T. palustris* and *C. decollata* are assumed to include a pelagic larval stage that is dispersed by oceanic currents. This is supported by evidence of genetic homogeneity between populations at regional biogeographic scales (Madeira et al. 2012, Ratsimbazafy 2012). The potential limitation of occurring in estuaries that have intermittent connectivity to the marine environment is yet to be elucidated for these species.
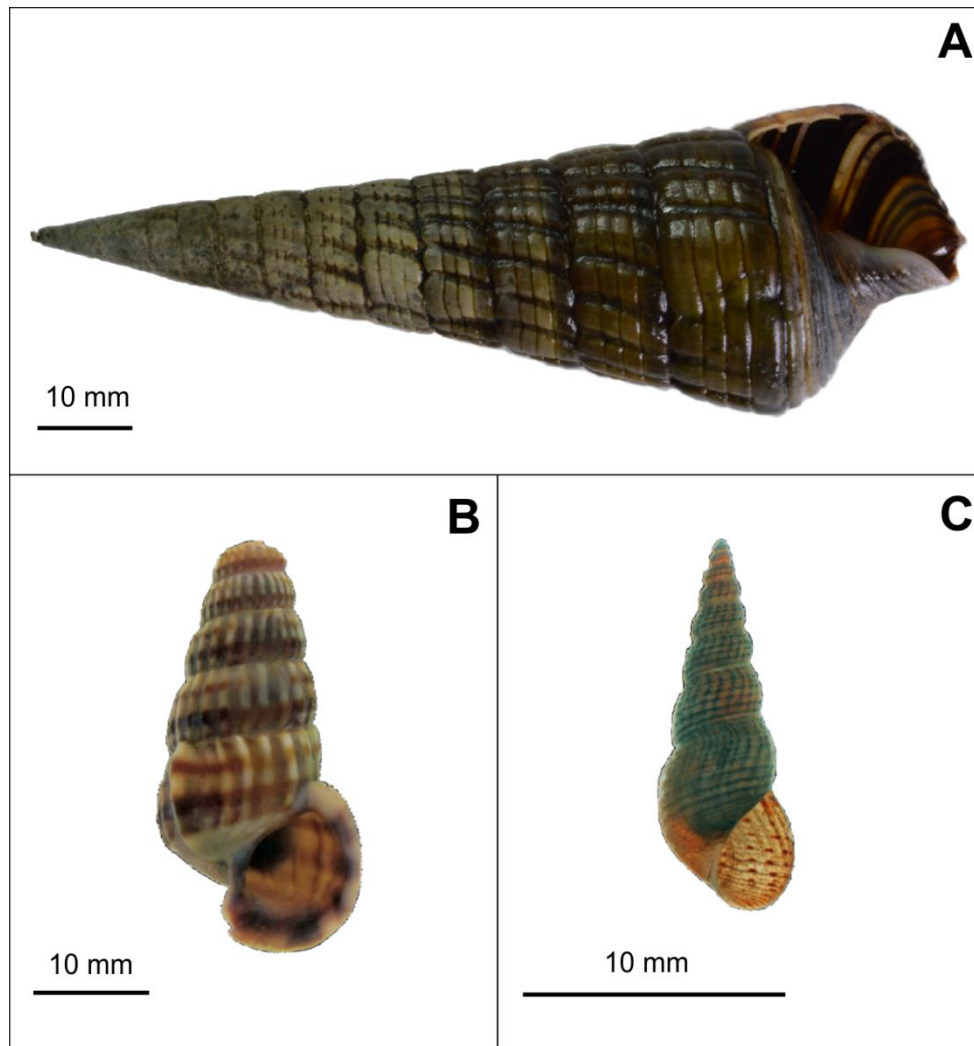
**Figure 1.1** Key cerithioidean gastropods that occur within the mangroves of the iSimangaliso Wetland Park in KwaZulu-Natal, South Africa: (**A**) *Terebralia palustris* (Linnaeus, 1767), (**B**) *Cerithidea decollata* (Linnaeus, 1767), and (**C**) *Melanoides tuberculata* (Müller, 1774). Photographs were adapted from Perissinotto et al. (2014) and Raw et al. (2014).

Considering their South African distributions, *T. palustris* and *C. decollata* were both historically recorded in at least six estuarine mangroves along the coast (Macnae 1963). At present, the distribution of *T. palustris* has declined and the species has only been detected in two mangrove systems on the subtropical east coast (Raw et al. 2014). Although there have been no comprehensive recent studies on the distribution of *C. decollata*, this species has been reported to have expanded its range into saltmarsh estuaries along the southern temperate coast (Hodgson & Dickens 2012). These distribution shifts can be considered as ecological indicators

of changes in environmental conditions. The recent assessment of *T. palustris* has found that the range of this species has contracted northwards along the South African coastline (Raw et al. 2014). The precise cause of this is not known, but *T. palustris* is sensitive to wastewater input (Cannicci et al. 2009). In contrast, *C. decollata* has been considered a pioneer species that has expanded its range southwards in response to temperature increases (Whitfield et al. 2016).

Ecological research in South Africa has considered both *T. palustris* and *C. decollata* within broad scale assessments. However, studies focussing on the specific ecological role of these species in South African mangroves are lacking. Although these species have been extensively studied on a global scale, the South African populations are unique representations as they occur at a southern continental limit. Furthermore, the restriction to occurring within estuarine areas will relate to potential differences in responses to environmental fluctuations and resource availability, as these habitats are strongly influenced by seasonal dynamics (Schumann et al. 1999). To assess some aspects of the ecological roles of key cerithioidean gastropods in South African mangroves, this study was carried out in systems within the protected area of the iSimangaliso Wetland Park.

The iSimangaliso Wetland Park was declared as South Africa's first UNESCO World Heritage Site in 1999, as it protects an expanse of unique coastal habitats, including four Ramsar Wetlands of International Importance (Figure 1.2). The Park covers an extensive 330 000 ha along 220 km of the KwaZulu-Natal provincial coastline and in total encompasses 9% of the entire South African coastline (Department of Environmental Affairs and Tourism 2009). The conservation value of this region is intricately linked to the diversity of the region, as a consequence of the unique geographical features that create mosaics of fluvial, lacustrine, estuarine, high-energy beach and coastal dune systems (Botha 2015). iSimangaliso falls within the subtropical climatic zone of Africa that is characterized by year-round high relative humidity and increased rainfall during the austral summer months of September to March.

The mangrove ecosystems within the iSimangaliso Wetland Park each have a distinct history relating to their management that must be considered in order to understand their current ecological conditions. These mangrove forests are also

amongst the most extensive in the country, and have had relatively minimal exposure to prolonged detrimental anthropogenic impacts as a result of formal protection. This provides a sound platform and important opportunity to carry out basic ecological research.
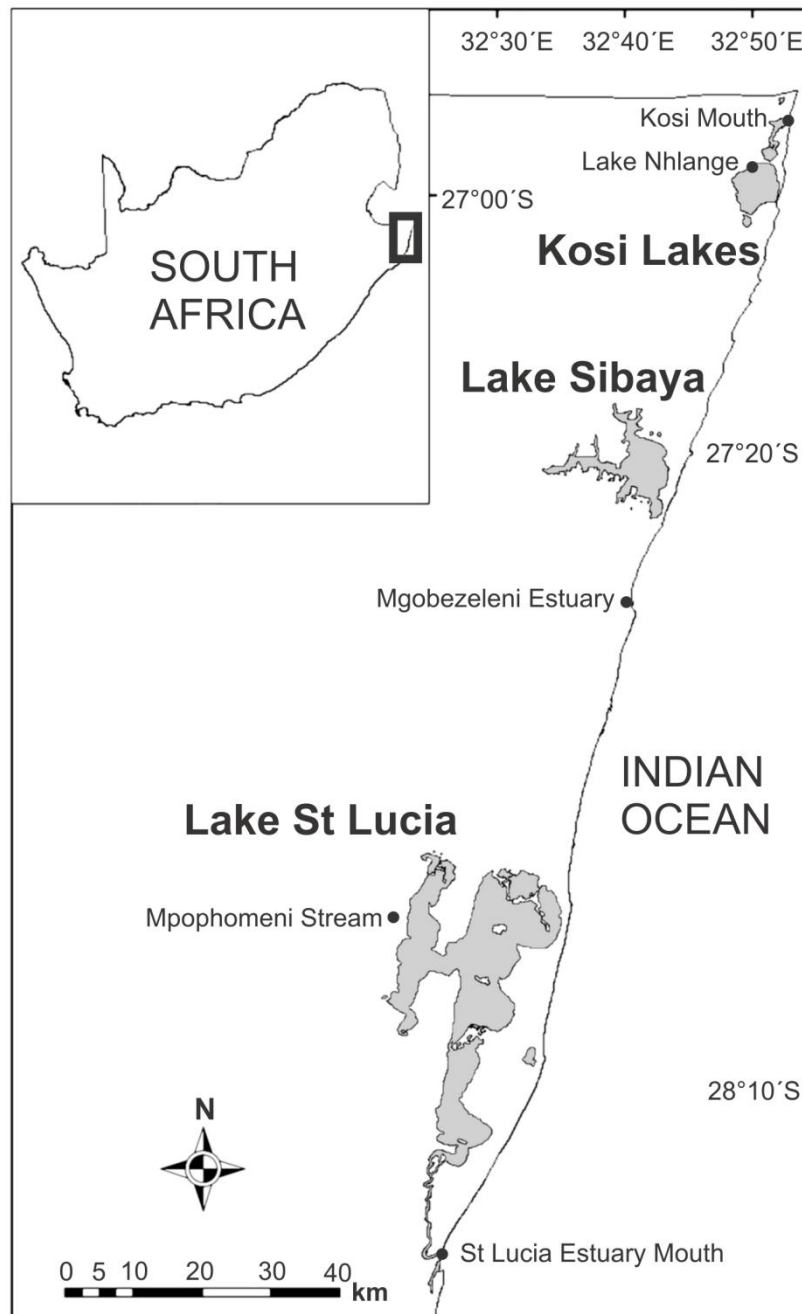


**Figure 1.2** Map of the iSimangaliso Wetland Park indicating the major Ramsar Wetlands of International Importance (Lake St Lucia, Lake Sibaya, Kosi Lakes). Estuaries that support mangrove ecosystems and sites that were sampled in this study are also indicated. This figure was adapted from Miranda et al. (2011).

The northernmost mangroves in the country are situated within the sheltered estuarine bay that forms the connection between the Kosi Bay lake complex (26°53'37''S; 32°52'52''E) and the Indian Ocean (Figure 1.3). This mangrove forest is the most diverse in terms of tree species, as *Avicennia marina* (Forssk. Vierh), *Bruguiera gymnorhiza* (L.) Lam, *Rhizophora mucronata* Lam, *Lumneritza racemosa* Willd and *Ceriops tagal* Perr. C.B. Robinson are all present here. The only *Xylocarpus granatum* König tree within South African borders also occurs within this forest. The mangroves at Kosi Bay experienced a large scale mortality event in 1965, as the result of prolonged inundation following closure of the mouth for a period of five months (Breen & Hill 1969). However, subsequent reports indicate that the forest has largely recovered since then (Begg 1980, Rajkaran & Adams 2011). At present one of the largest impacts on this mangrove forest is the harvesting of trees by the local fishermen who use them to build traditional fish traps. These traps are placed permanently within the tidal basin of the estuary. Besides the disturbance caused by the direct removal of mangrove material from the forest (Rajkaran & Adams 2011), the establishment of the fish traps also has a significant effect on sedimentation and thus on hydrodynamics and even recruitment of mangrove propagules within the tidal basin (Green et al. 2006). As a consequence of the relatively low latitude, the macrofauna species that occur within the Kosi Bay mangroves most closely resemble the assemblages of warmer tropical regions. Ten crustacean and six mollusc species have been previously recorded from this mangrove forest (Macnae 1963). Both *T. palustris* and *C. decollata* occur at Kosi Bay but appear to be spatially partitioned within the mangroves. *Terebralia palustris* is dominant on the lower shore regions and large individuals are targeted at low tide by local fishermen for use as bait (Raw et al. 2014).

Historically, mangroves were also established within the Mgobezeleni Estuary (27°32'10''S; 32°40'17''E) (Figure 1.1). Macnae (1963) described the mangroves at this location as "of great interest" because the *B. gymnorhiza* trees reached over 18 m in height. In this report he also commented on the very large size of *T. palustris* that occurred here. Unfortunately, by the time of the survey by Bruton & Appleton (1975), the construction of a bridge over the estuary had significantly constricted the flow and reduced the tidal connectivity within the estuary. There was a subsequent build-up of freshwater that inundated the mangroves, essentially drowning the trees

as their aerial roots remained submerged for an extended period of time (Bruton 1980). The associated mangrove fauna were not able to survive the regime shift to a freshwater-dominated ecosystem (Bruton & Appleton 1975). Although the bridge was re-constructed to better facilitate tidal connectivity and flow within the estuary, the mangrove ecosystem has since not become re-established. Mgobezeleni therefore stands as an important reminder of the significant impact of certain anthropogenic activities, which influence environmental conditions that are particularly sensitive to change.
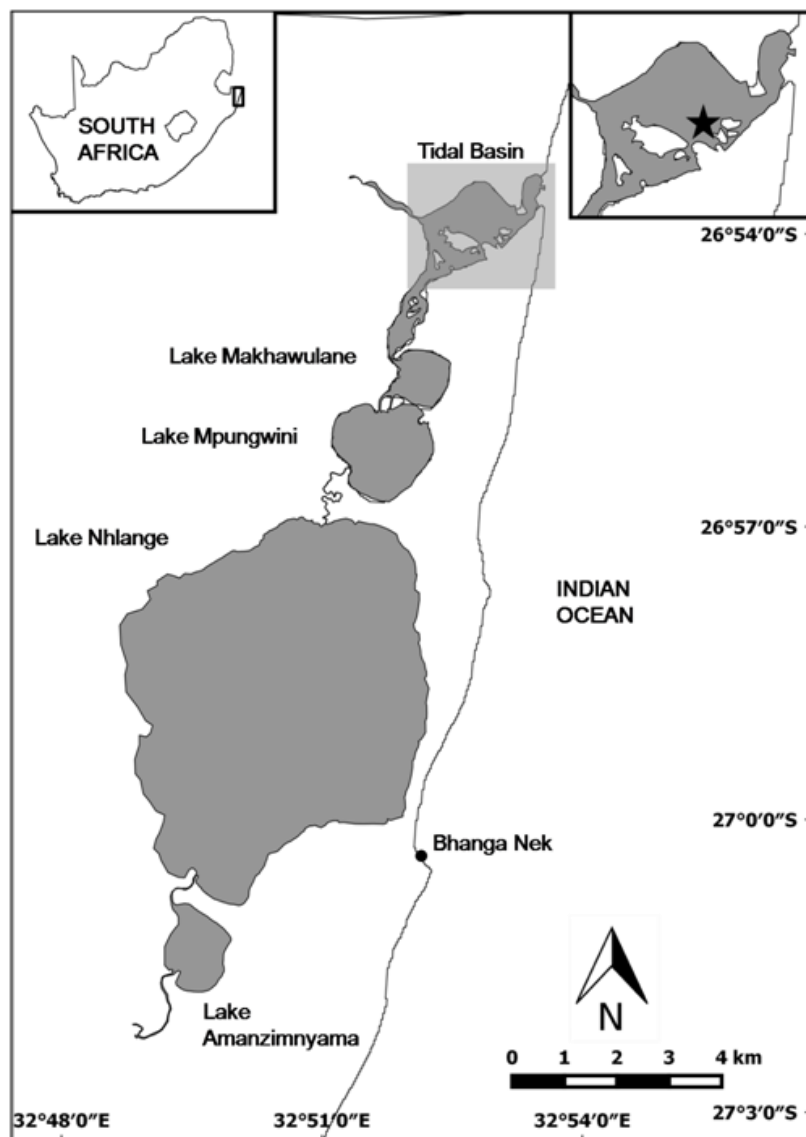


**Figure 1.3** Map of the Kosi Bay estuarine lake complex, with focus on the area where mangroves occur at the mouth of the estuary. (Credit: CR Nolte).

The southernmost mangroves of the iSimangaliso Wetland Park occur within the lower reaches of the St Lucia Estuary (28°22'55''S; 32°25'32''E) and the estuarine areas of the adjoining Mfolozi River (Figure 1.4). The mangroves within the St Lucia Estuary are unique in that they have persisted despite irregular and limited marine connectivity for an extended period of time (Hoppe-Speer et al. 2013). This unusual and complicated scenario has been the focus of a large amount of scientific research over recent decades (Perissinotto et al. 2013b).
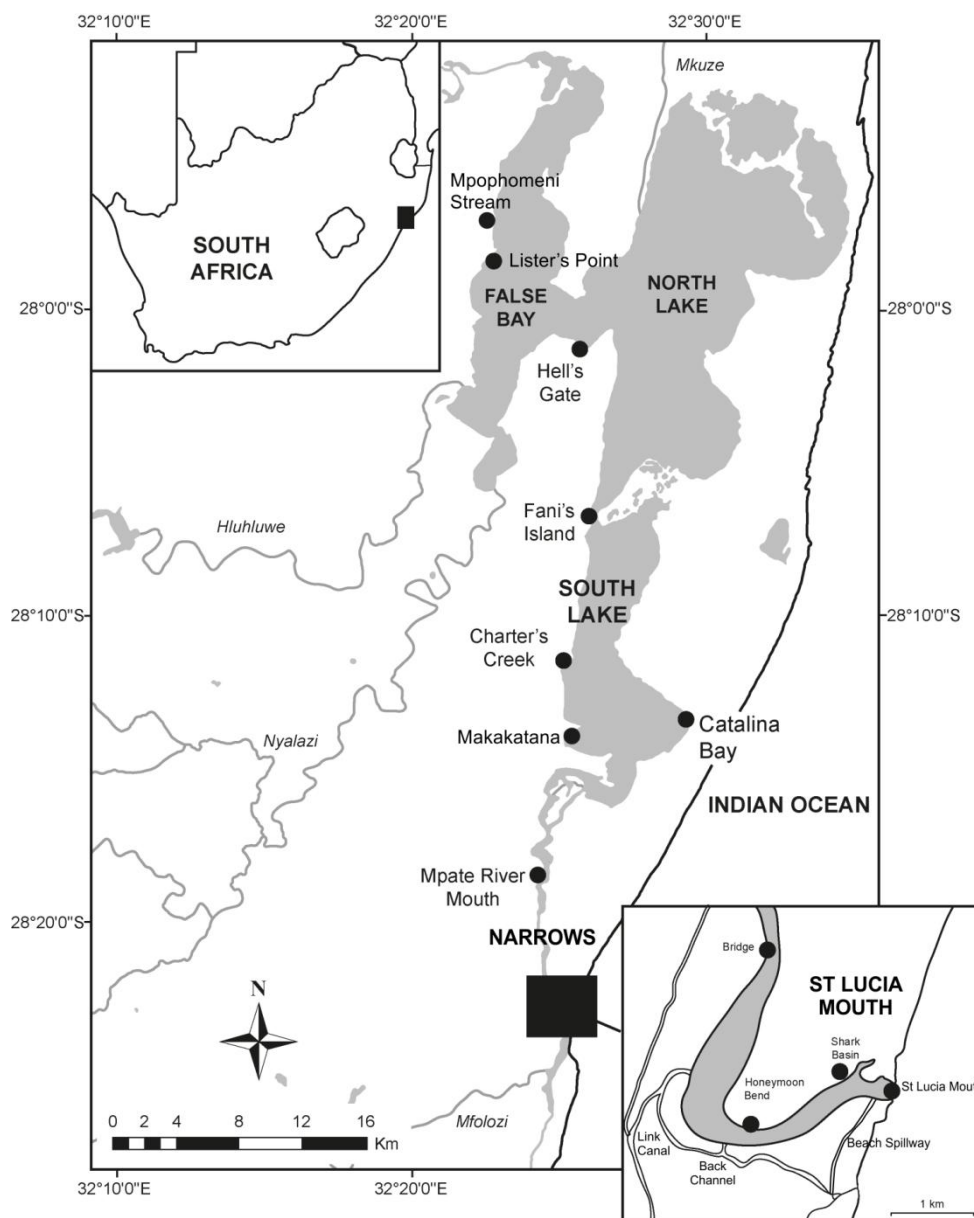


**Figure 1.4** Map of the St Lucia Estuary and adjoining Mfolozi River. The recently established re-connection is shown in the inset and consists of a backchannel as well as a beach spillway. This figure was adapted from Peer et al. (2014).

Historically, the St Lucia and Mfolozi estuarine systems formed a shared connection to the Indian Ocean (Taylor 2013). However, the establishment of sugar cane agriculture at the beginning of the 20th century within the Mfolozi floodplain required taking extensive measures to prevent flooding and inundation of low-lying farms (Whitfield & Taylor 2009). These measures included draining swamp areas and excavating canals to divert floodwaters towards the combined mouth for deposition into the marine environment. The swamp had until that point provided important ecological services by retaining sediment and allowing the flow of filtered fresh water into the St Lucia Estuary (Taylor 1993). The rate of sedimentation in the combined St Lucia/Mfolozi mouth became a cause for concern in the 1940s and this was further exacerbated by the effects of a drought in the 1950s which resulted in the development of a berm that prevented connectivity with the ocean (Whitfield & Taylor 2009). As low-lying farms were threatened with inundation by backed-up water in the Mfolozi River and connectivity to the ocean was seen as a necessity to maintain ecological functioning of the estuary, the decision was made to excavate a canal to allow the outflow of water to the sea (Kriel 1966). The mouths of the Mfolozi River and St Lucia Estuary were thus artificially separated (Whitfield & Taylor 2009). In the absence of the Mfolozi linkage, St Lucia became deprived of the single most important source of freshwater and this had a significant effect on the health of the system, particularly during periods of drought (Whitfield et al. 2013). A series of re-linkages with the Mfolozi were therefore established in a precautious manner that would allow freshwater inflow without excessive deposition of sediment into the St Lucia Estuary (Whitfield & Taylor 2009, Taylor 2013). At present the systems are managed with a priority to prevent further deterioration and maintain ecological functioning.

Recent research suggests that the health of the mangroves varies spatially within the lower reaches of the St Lucia Estuary and is dependent on a number of environmental variables (Adams & Human 2016). Presently the largest driver of ecological change in the St Lucia Estuary is the tentative connection with the Mfolozi River (Whitfield et al. 2013). The effects of this connection on the diversity and ecological structure of different invertebrate groups, including zooplankton, brachyurans and gastropods, have also been documented (Peer et al. 2014, Perissinotto et al. 2014, Carrasco & Perissinotto 2015). Interestingly, *T. palustris* has

not previously been recorded within the St Lucia/Mfolozi mangroves, despite historical and recent occurrence records from mangroves further to the south (Macnae 1963, Raw et al. 2014). In contrast, *C. decollata* has persisted in St Lucia, even through the drastic ecological changes that have occurred during recent decades (Perissinotto et al. 2014). A third cerithioidean gastropod, *Melanoides tuberculata* (Müller, 1774) (Figure 1.1 C), also occurs within the mangroves at St Lucia. This is a typically freshwater species from the family Thiaridae Gill, 1871 that has some tolerance for salinity and is therefore able to inhabit a wide variety of freshwater and brackish aquatic environments including wetlands, streams, rivers, lakes and pans (Appleton 1996, Brown 1994). This species has an extensive native distribution that includes East Africa, the Middle East and Southeast Asia (Facon et al. 2003). Although *M. tuberculata* is not a characteristic mangrove species, the unique non-tidal conditions within St Lucia have allowed these snails to establish dense populations in mangrove areas that are adjacent to freshwater seepage zones (Perissinotto et al. 2014). The ecological significance of *M. tuberculata* within a mangrove environment was considered as an important component of this research project as this species has been introduced to many locations in the New World, where it has subsequently become invasive (Facon et al. 2003). The opportunistic occurrence of *M. tuberculata* in a mangrove habitat provided an interesting opportunity to determine the nature of ecological interactions, including the partitioning of resources and potential niche overlap, between this species and typical mangrove gastropods.

*1.3 Key research questions, objectives and thesis structure*

The sustainable management of threatened habitats such as mangroves is most effectively achieved through ecosystem-based management built on information provided by economics as well as ecological and social sciences (Christensen et al. 1996, Slocombe 1998). Ecological research that informs ecosystem-based management must however be carried out at different temporal and spatial scales, as different processes at each level of organization are strongly linked (Levin 1992, Leslie & McLeod 2007). For instance, processes that determine ecosystem-scale factors such as ecological functioning and stability are informed by studies carried out at the community level (Massol et al. 2011). These include biodiversity assessments and studies that elucidate the dynamics and structure of the ecological

community (Tilman 1999, Loreau et al. 2001, Hooper et al. 2005). These ecological aspects are in turn based on information gained from basic ecological studies conducted at the levels of species and individuals (Violle et al. 2012). Research that is focussed on the interactions among species, as well as between species and their environment, is therefore critical for understanding larger scale implications, including the ecological role of each species within the ecosystem (DeAngelis & Mooij 2005). This research project provides new information on ecological aspects at the levels of species and individuals to inform on patterns and processes at larger scales. Three ecological aspects for mangrove gastropods, which were then formulated into the primary key research questions, were considered in this research project and are indicated in Figure 1.5. The ecological aspects that were considered were related to the ecological roles of mangrove gastropods and their resilience in these ecosystems.

First, the role of mangrove gastropods as trophic links to different sources of primary carbon was investigated. The contribution of carbon derived from different primary sources to estuarine and marine food webs associated with mangroves has been continuously revised and debated. Although mangrove trees are considered to be productive (Komiyama et al. 2008), their direct contribution to the trophic web has been considered to be minimal (Connolly et al. 2005). Instead, research has shown that there is a significant contribution of carbon from imported (allochthonous) sources (Bouillon et al. 2002). However, as South African mangroves are limited to occur in estuaries that may have restricted connectivity to the marine environment, allochthonous sources may not be readily available. This led to the formulation of the second research question which was related to resource utilization rates by the dominant mangrove gastropods in each of the two estuarine mangrove ecosystems that were considered in this study. The productivity of benthic microalgal assemblages in mangrove environments has generally been considered to be quite minimal, as mangrove sediments are unfavourable for their growth (Alongi 1994). This is largely attributed to the high particulate content and small grain size of the sediment, the high tannin content and the shading provided by the canopy of the mangrove trees (Alongi & Sasekumar 1992, Cahoon et al. 1999). However, when benthic microalgae do establish under certain conditions, they become a nutritious food source to benthic invertebrates within the mangroves (Newell et al. 1995,

Bouillon et al. 2004a). The role of mangrove gastropods in exerting top-down control of benthic primary productivity was therefore investigated. The third ecological aspect that was considered in this research project is related to resilience of mangrove gastropod species in response to ecosystem changes. Mangroves are considered to be stable and resilient habitats (Alongi 2002), however the resilience of the fauna associated with mangroves also needs to be investigated. Although the mangrove trees that are established in estuaries may be able to withstand certain environmental fluctuations associated with threats to estuaries, including changes in mouth dynamics and flow regimes, the effects of these factors on the mangrove fauna are less clear. Changes to population parameters over time were therefore assessed for a key mangrove species, in relation to annual environmental fluctuations related to both natural and anthropogenic impacts.

The key research questions, and the corresponding aims and objectives, of this project can thus be formulated as:

**1. Do gastropods within estuarine mangroves represent trophic links to both autochthonous and allochthonous sources?**

AIM: To determine the contribution of different primary sources to the diets of key gastropods from different estuarine mangrove ecosystems.

OBJECTIVES:

A stable isotope approach was used to determine the contribution of different sources to the diets of key gastropod species within estuarine mangroves. At Kosi Bay, as *T. palustris* dominates the benthos, the diet of this species was compared between different size classes in both the wet and dry seasons (CH 2). As *M. tuberculata* only occurs opportunistically within the mangroves at St Lucia, the diet of this population was compared to those of other populations from different aquatic environments (CH 3). The diets of *M. tuberculata* and *C. decollata* were also compared (CH 3)

**2. Do gastropods in estuarine mangroves have a significant grazing impact on available benthic microalgal sources?**

AIM: To determine the role of dominant mangrove gastropods in exerting top-down control on benthic primary productivity in estuarine mangrove environments

OBJECTIVES:

An experimental approach was used to determine the feeding dynamics (ingestion rate, consumption/digestion efficiency, grazing impact) of dominant mangrove gastropod species. At Kosi Bay, the feeding dynamics were assessed and compared for juvenile *T. palustris* through a daily and tidal cycle in different rainfall seasons (CH 4). At St Lucia, the feeding dynamics were assessed for *M. tuberculata* in the mangroves and compared with those from populations in other aquatic environments in which this species typically occurs (CH 5).

**3. What is the relationship between large-scale environmental fluctuations and the occurrence of a resilient mangrove gastropod species?**

AIM: To determine which environmental factors influence the occurrence and abundance of a resilient mangrove gastropod.

OBJECTIVES:

*Cerithidea decollata* has been able to persist in the St Lucia Estuary despite long-term changes in environmental conditions as a result of different management practices that have attempted to maintain ecological functioning of the estuary. The effects of environmental fluctuations on the abundance of *C. decollata* were assessed in the St Lucia Estuary (CH 6) using a mixed-effects modelling approach.
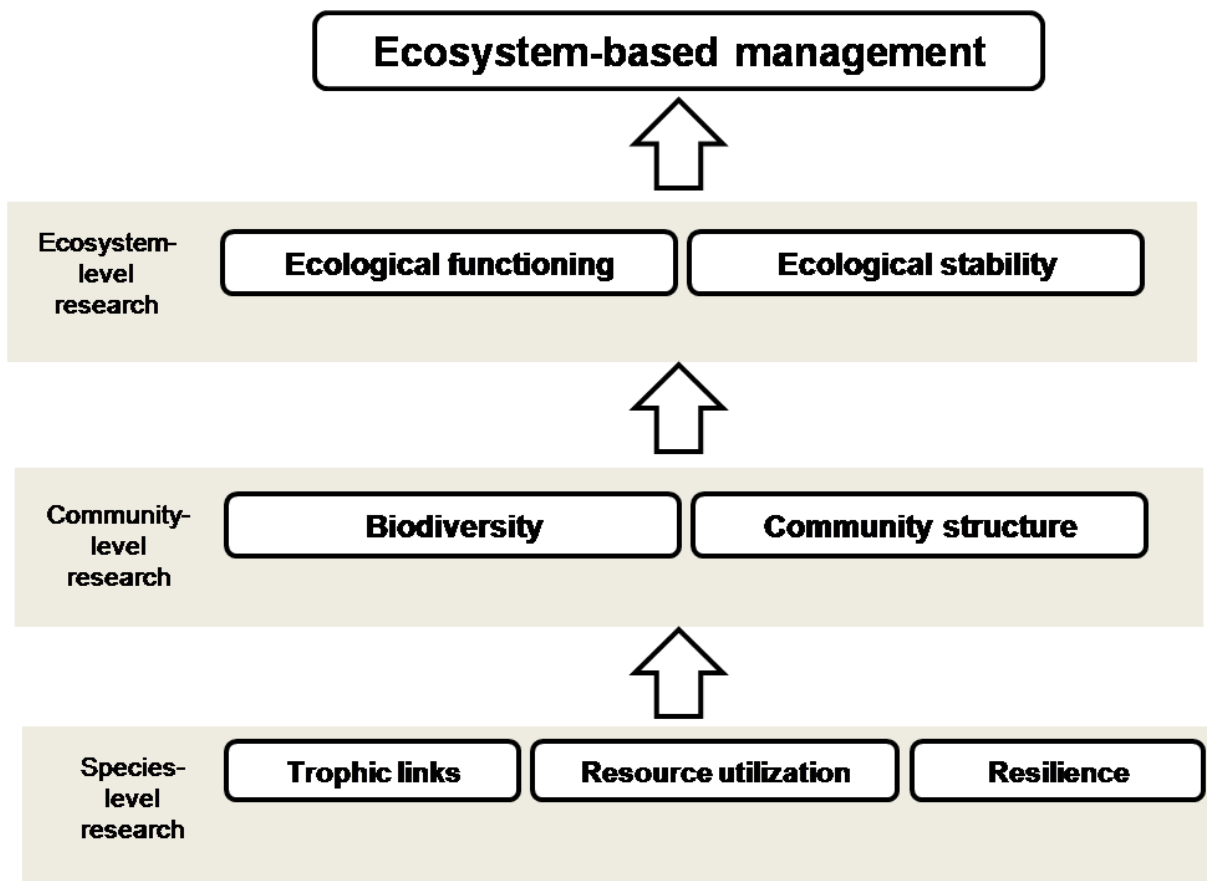
**Figure 1.5** Schematic diagram outlining the relationship between the species-level research of this project and larger scale ecological attributes that are used to inform on the ecological science component of ecosystem-based management.

# Chapter 2: Diet of *Terebralia palustris* at Kosi Bay

## 2.1 Introduction

A key paradigm of modern mangrove research is the high degree of internal recycling of mangrove-derived carbon (Alongi 2009b; Lee et al. 2014). This is an important indicator of ecosystem functioning, as it is a biologically-driven process relying on both macrofauna to mechanically break down the leaf litter, as well as microbial activities to enrich the organic content of the sediment by the break-down of detritus (Alongi 2009b). Species that consume mangrove leaf litter are therefore considered to be integral components of mangrove ecosystems (Lee et al. 2014), and are often used as bioindicators in assessments of mangrove health following restoration or rehabilitation efforts (Pagliosa et al. 2016). Initially, brachyurans were largely accredited as the primary consumers of mangrove leaf litter (Lee 1998), but the role of gastropods has also been increasingly recognized (Bouillon et al. 2004b; Cannicci et al. 2008). Detritivores and deposit-feeders are considered to be functionally redundant (Levin et al. 2001), and these taxa can support ecosystem stability through efficient resource partitioning when biodiversity is high (Balvanera et al. 2006; Finke & Snyder 2008). As ecological theory predicts that niches are conserved through evolutionary time to retain ecological function (Pearman et al. 2008; Wiens et al. 2010), mangrove ecosystems provide an opportunity to investigate aspects of the ecological niche as many co-occurring species have similar functional roles.

The ecological niche is generally identified within a resource utilization framework (Pianka 1976) and this can be quantitatively assessed using stable isotopes (Bearhop et al. 2004; Newsome et al. 2007; Turner et al. 2010). The conservation of isotopic ratios of $\delta^{13}C$ through the food web, and the predictable shifts in $\delta^{15}N$ with each trophic level (DeNiro & Epstein 1978, 1981; Vanderklift & Ponsard 2003) allow

for trophic structures to be identified (Peterson & Fry 1987; Middelburg 2014). Stable isotope studies have been particularly useful for investigating trophic linkages and determining the contribution of mangrove-derived carbon to higher trophic levels (Newell et al. 1995; Bouillon et al. 2002; Hsieh et al. 2002). However, recent work has highlighted the importance of determining accurate enrichment factors for mangrove invertebrates, or the degree to which the isotopes are fractionated by metabolic processes (Herbon & Nordhaus 2013; Bui & Lee 2014). In their experimental study, Bui & Lee (2014) found that enrichment factors for detritivorous crabs are significantly different from those commonly applied in the literature and that using their refined enrichment values produced a model that supported observations of *Parasesarma erythodactyla* consuming large quantities of mangrove-derived detritus. As enrichment factors are variable between species depending on their trophic level, feeding mode and excretory system (McCutchan et al. 2003), developing a reliable mixing model requires careful consideration of many factors and can otherwise result in a model that is either not informative or difficult to interpret (Phillips et al. 2014).

An alternative and recommended approach is to assess trophic dynamics using a quantitative measure of isotopic niche space (Bearhop et al. 2004; Layman et al. 2007). This allows direct conceptualization of the ecological niche as defined by the variability of the $\delta^{13}$C and $\delta^{15}$N signatures for the consumer in question (Jackson et al. 2011). The size and overlap of the isotopic niches for different consumers can also be statistically compared, thus allowing for inferences relating to dietary overlap, resource partitioning and competitive interactions. Spatial and temporal comparisons of the isotopic niche for a specific consumer can also provide information regarding changes in resource availability (Newsome et al. 2007). This is particularly useful for assessing trophic linkages in ecosystems, such as estuaries, that are dynamic and experience fluctuations in resource availability as a result of physical and biological processes (Flint & Kalke 1986; Yang et al. 2008). Changes or shifts to the isotopic niches of species that have integral ecological roles relate to larger scale studies that aim to assess community-level dynamics or factors that influence ecosystem functioning.

In this study we assessed the isotopic niche for the giant mangrove whelk *Terebralia palustris* (Linnaeus, 1767), a key consumer of mangrove leaf litter within these

habitats across the Indo-Pacific region (Houbrick 1991). Previous work in Kenya has shown that adult *T. palustris* consume significant quantities of leaf litter (Slim et al. 1997; Fratini et al. 2004), while juveniles consume detritus and benthic microalgae (Fratini et al. 2004; Pape et al. 2008). This corresponds with their spatial distribution across the shore, as juveniles generally occur on the seaward edge, while larger snails are found beneath the canopy (Pape et al. 2008; Penha-Lopes et al. 2009; Raw et al. 2014). The ecological role of this species is therefore variable through ontogeny, and partitioning of resources is maintained even if there is no spatial segregation between different sized snails within the mangroves (Fratini et al. 2004).

Using a stable isotope approach, Penha-Lopes et al. (2009) found that adult *T. palustris* at Inhaca Island, Mozambique, incorporated sources besides mangrove leaf litter into their diets. As mangrove leaf litter is nutritionally poor (Bosire et al. 2005), many invertebrates that consume this source supplement their diets with alternative sources (Bouillon et al. 2002). Therefore, the aim of this study was to quantify the size and variation of the isotopic niche of *T. palustris* to provide a measurable estimate of how this species contributes towards recycling of mangrove leaf litter in a subtropical estuarine ecosystem. A stable isotope approach was used to quantify isotopic niche shifts of *T. palustris* in a subtropical estuarine mangrove forest on the east coast of South Africa. As this region experiences a seasonal rainfall regime, it was possible to make temporal comparisons of the isotopic niche of *T. palustris* in response to resource quality and availability. The results of this study therefore provide important information regarding the variability of the dietary niche of a species with a key ecological role within a threatened ecosystem. Furthermore, the information gained from baseline studies such as this will be valuable for future assessments of responses to contemporary global change.

## 2.2 Materials and Methods

### 2.2.1 Site description

Globally, the southern distribution limit for *Terebralia palustris* is along the east coast of South Africa (Houbrick 1991). A survey by Raw et al. (2014) found that although *T. palustris* has declined in this region, a healthy population still persists at the mangroves of Kosi Bay (26°53'37''S; 32°52'52''E) (Figure 1.3), which is within the iSimangaliso Wetland Park, a UNESCO World Heritage Site. The mangrove trees at Kosi Bay are characteristically stunted (Rajkaran & Adams 2011) as the absence of fine organic deposits and low mud content are suboptimal for the establishment of large trees (Begg 1980; Wright et al. 1997). Samples for stable isotope analysis were collected from an area of the mangrove forest on the south shore of the embayment formed at the mouth of the estuary. This area was dominated by *Avicennia marina, Bruguiera gymnorhiza*, and *Rhizophora mucronata* trees.

Within this subtropical region there are two climatic seasons that are characterized by differences in rainfall. Samples were collected in November 2013 (early summer, wet season) and in July 2014 (mid-winter, dry season). The South African coastline has a limited tidal range and is classified as microtidal, as the spring tides range between 1.8 and 2.0 m (Cooper 2000; Harris et al. 2011). Both sampling excursions (in November and July) took place on a morning spring low tide. A YSI 6600 multiprobe system was used to measure the physical and chemical properties (temperature, salinity, dissolved oxygen and pH) of water samples (collected in triplicate) from a shallow channel at the sampling site.

### 2.2.2 Sample collection and processing

For stable isotope analysis, samples were collected for *T. palustris* as well as any potential food sources which were present at the time of sampling. Previous assessments on the spatial distribution of *T. palustris* at Kosi Bay have shown that the highest average (± SD) density of snails (97.7 ± 57.1 ind.m$^{-2}$) occurs in the lower shore region and that this zone is dominated by juveniles, as the average (± SD) shell height is 27.3 ± 10.2 mm (Raw et al. 2014). Fewer individuals (17.8 ± 8.7 ind.m$^{-2}$) of a much larger average size (53.5 ± 20.7 mm) occur in the high shore region beneath the canopy (Raw et al. 2014). There is clear evidence for spatial

segregation of *T. palustris* at this site. Therefore, to investigate ontogenetic dietary shifts in *T. palustris*, the gut contents and isotopic signatures of three size classes were compared (< 30 mm, 30 – 60 mm, > 60 mm). The size at maturity for *T. palustris* depends on a number of factors but is usually reported at around 50 mm (Houbrick 1991).

Potential food sources that were collected included epiphytic macroalgae that were attached to mangrove pneumatophores – termed the bostrychietum community (Steinke et al. 2003), microphytobenthos (MPB), fresh and newly fallen mangrove leaves, pneumatophores, detritus, sedimentary organic matter (SOM) and particulate organic matter (POM). Fresh mangrove leaves (green) as well as newly fallen leaves (orange) were collected from *B. gymnorhiza*, and *R. mucronata* trees in the sampling area. Initial comparisons of the isotopic compositions of these leaves were however found to be indistinguishable. As Fratini et al. (2008) have shown that *T. palustris* does not show a strong selective feeding preference between *B. gymnorhiza* and *R. mucronata*, subsequent samples were later homogenized into representatives of "fresh" and "fallen" leaves.

Macroalgae were collected depending on their occurrence. Detritus was composed of decayed macrophyte material. MPB was collected by scraping the upper 1 cm of sediment and re-suspending it in filtered estuarine water (Whatman GF/F, 0.7 µm pore size). The sediment settled to the bottom while the MPB in suspension was filtered onto pre-combusted (450 °C, 6 h) filters (Whatman GF/F 0.7 µm pore size). POM was collected in a similar manner by filtering estuarine water onto pre-combusted filters. SOM was collected using a 20 mm diameter corer. The upper 1 cm of the core was discarded (as this fraction would contain MPB) and the remainder was retained as the sample. MPB, POM and SOM were collected in triplicate on each sampling occasion. All samples were frozen after collection until laboratory processing.

In the laboratory, gastropods were examined under a dissecting microscope (40× magnification). Recent feeding preferences were assessed by identifying different constituents within the gut contents of individual snails and classifying them based on gross morphology as "Algae", "Detritus", "Filament", or "Sediment" (Alfaro 2008; Miranda & Perissinotto 2012). Muscle tissue was excised from the foot of individual

gastropods and treated for lipids that may have been retained from the skin using a 2:1:0.8 solution of methanol: chloroform: distilled water (Bligh & Dyer 1959). Generally, lipids are removed as they can significantly influence the isotopic signature of the consumer in question (Logan et al. 2008; Tarroux et al. 2010). In the case of the gastropod tissue, lipids would be expected to occur at a higher density in the skin, which was removed by dissection. The treatment for lipids was therefore precautionary and preliminary results indicated that it did not significantly influence the isotopic signatures of the excised muscle tissue. This has previously been reported for aquatic consumers (Ingram et al. 2007).

The mangrove leaves and macroalgae samples were thoroughly rinsed in distilled water to remove residual sediment and visible epifauna. The filters for MPB and POM as well as the SOM cores and the detritus samples were all treated with 2 % HCl until all bubbling had ceased, an indication that biogenic carbon in the form of calcium carbonate ($CaCO_3$) was completely removed. All samples for stable isotope analysis were subsequently dried in an air-circulated oven at 60 °C for at least 48 h.

After drying, the samples were prepared for stable isotope analysis following standard protocols. Each dried tissue sample was ground into a homogenous powder using a mortar and pestle which was sterilized between subsequent samples with 70 % ethanol. The samples were weighed (~ 0.5 mg for animal tissue and ~ 1.0 mg for plant, algal and detrital matter) and packaged into 5 x 9 mm tin capsules (SÄNTIS Analytical AG, Switzerland). Gastropod tissue from up to 5 individuals was pooled only in cases where individual snails were too small to contribute enough muscle tissue for the stable isotope samples to be successfully analysed. SOM samples were homogenized and packaged into Eppendorf microcentrifuge tubes. Five replicates were processed for each gastropod size class and each source item in each season.

### 2.2.3 Stable isotope analysis

Samples were analyzed by the Environmental Isotope Laboratory at iThemba Laboratories in Pretoria, South Africa. The stable isotope analyses were carried out using a Flash HT Plus elemental analyzer coupled to a Delta V Advantage isotope ratio mass spectrometer by a ConFloIV interface (ThermoFisher, Bremen, Germany).

The isotopic ratios are expressed using the standard delta notation (δ) as the relative per mil (‰) difference between samples and the international standards of Vienna PeeDee Belemnite for carbon and atmospheric $N_2$ for nitrogen. The ratio is therefore defined as:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000$$

where $X$ is $^{13}C$ or $^{15}N$ and $R$ is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ respectively. Merck Gel was used as the in-house standard ($\delta^{13}C$ = -20.57 ‰; $\delta^{15}N$ = +6.80 ‰).

### 2.2.4 Data analysis

The $\delta^{13}C$ signatures of the potential food sources were compared for each season using separate Kruskal-Wallis rank sum tests as the data were found to be non-parametric. Nemenyi *post hoc* tests with Tukey distribution were used for subsequent pair-wise comparisons. This indicated whether primary sources could be distinguished based on their $\delta^{13}C$ signatures. Univariate parametric assumptions and the non-parametric tests were run using the packages "car" (Fox & Weisberg 2014) and "PMCMR" (Pohlert 2014) in R v 3.2.5 for Windows (R Development Core Team 2016).

Seasonal and ontogenetic differences in the $\delta^{13}C$ and $\delta^{15}N$ for *T. palustris* individuals were compared using a two-way non-parametric permutational MANOVA (PERMANOVA, Anderson 2001). The $\delta^{13}C$ and $\delta^{15}N$ data were first normalized and then combined into a multivariate resemblance matrix (Euclidean distance measure). Differences between size classes (fixed factor, three levels: large, > 60 mm; medium, 30-60 mm; and small, < 30 mm) and between the sampling occasions (fixed factor, two levels: November and July), were tested using 999 permutations of the residuals under a reduced model. The PERMANOVA+ add-on (Anderson et al. 2008) to PRIMER v6 software (Clarke & Warwick 2001; Clarke & Gorley 2006) was used to carry out these multivariate analyses.

To further explore differences in the feeding niche of *T. palustris* individuals of different sizes, and between sampling occasions, the Stable Isotope Bayesian Ellipses in R (SIBER, Jackson et al. 2011) model was used. The Bayesian Inference

method allows the error associated with fitting ellipses to each group to be calculated using the number of samples as well as their distribution. Thus, the standard ellipse area (SEA) for a set of bivariate data (in this case $\delta^{13}C$ and $\delta^{15}N$ isotope space) is calculated using a MCMC algorithm to generate a distribution of covariance matrices that describe the observed data in terms of likelihood. The SEA contains approximately 40% of the data (Jackson et al. 2011), hence revealing the core niche area that is largely insensitive to sample size fluctuations and extreme values. SEA is then corrected ($SEA_C$) to minimize bias caused by small sample sizes (Jackson et al. 2011) using the equation:

$$SEA_c = SEA * \left[ \frac{(n-1)}{(n-2)} \right]$$

Ellipse areas were subsequently compared using pair-wise tests that calculated the probability that the posterior distribution of one group (Group 1 = large snails; Group 2 = medium snails; Group 3 = small snails) is larger than that of another. This allowed significant differences in niche sizes among size classes to be inferred.

The stable isotope niche model was run using the package "SIBER" developed by Jackson et al. (2011) for R v 3.2.5 for Windows (R Development Core Team 2016).

*2.3 Results*

*2.3.1 Habitat characteristics*

There were some differences between the sampling occasions for the physical and chemical properties measured at the shallow water channel near the sampling site (Table 2.1). Most notably, higher temperature and lower salinity were recorded in November.

**Table 2.1** Differences in environmental conditions at Kosi Bay, as indicated by the mean (± SD) estimates for physical and chemical variables measured from the water column in November 2013 and July 2014. The mean (± SD) shell heights of *Terebralia palustris* from different size classes that were collected for stable isotope analyses are also presented.

| Environmental Parameter | November | July |
|---|---|---|
| Temperature (° C) | 32.9 ± 0.3 | 24.5± 0.2 |
| Salinity | 23.6± 0.6 | 35.2 ± 0.1 |
| Dissolved $O_2$ (mg/L) | 8.8± 1.3 | 9.9 ± 0.6 |
| pH | 8.2± 0.4 | 8.7± 0.03 |
| *Terebralia palustris* **size classes** | | |
| > 60 mm | 69.4 ± 8.9 | 84.3 ± 4.7 |
| 30 – 60 mm | 44.0 ± 7.3 | 47.9 ± 3.7 |
| < 30 mm | 21.3 ± 3.6 | 25.7 ± 2.8 |

Regarding *T. palustris*, the same size classes (< 30 mm, 30 – 60 mm, > 60 mm) were targeted for collection on both sampling occasions. However, snails collected in the July were slightly larger on average, particularly those that measured > 60 mm. This might have been a consequence of reduced harvesting pressure of the largest individuals by local fishermen for use as bait in the cooler winter season. This was not expected to influence the stable isotope signatures, as the dietary transition in this species occurs at around 50 mm (Houbrick 1991).

## 2.3.2 Gut content analyses

Gut content varied between snails of different size classes, but appeared to be relatively similar between sampling occasions (Figure 2.1). Distinct pieces of orange leaf material were only found in the gut contents of snails > 30 mm. Filamentous algae also occurred less frequently within the gut contents of snails < 30 mm. Sediment and detrital matter was present within the gut contents of most individuals, irrespective of size. The fresh algal material within the gut contents could not be clearly identified as either microalgae (MPB) or fragments of macroalgae and was therefore grouped together. This source was mostly present within the guts of smaller individuals.
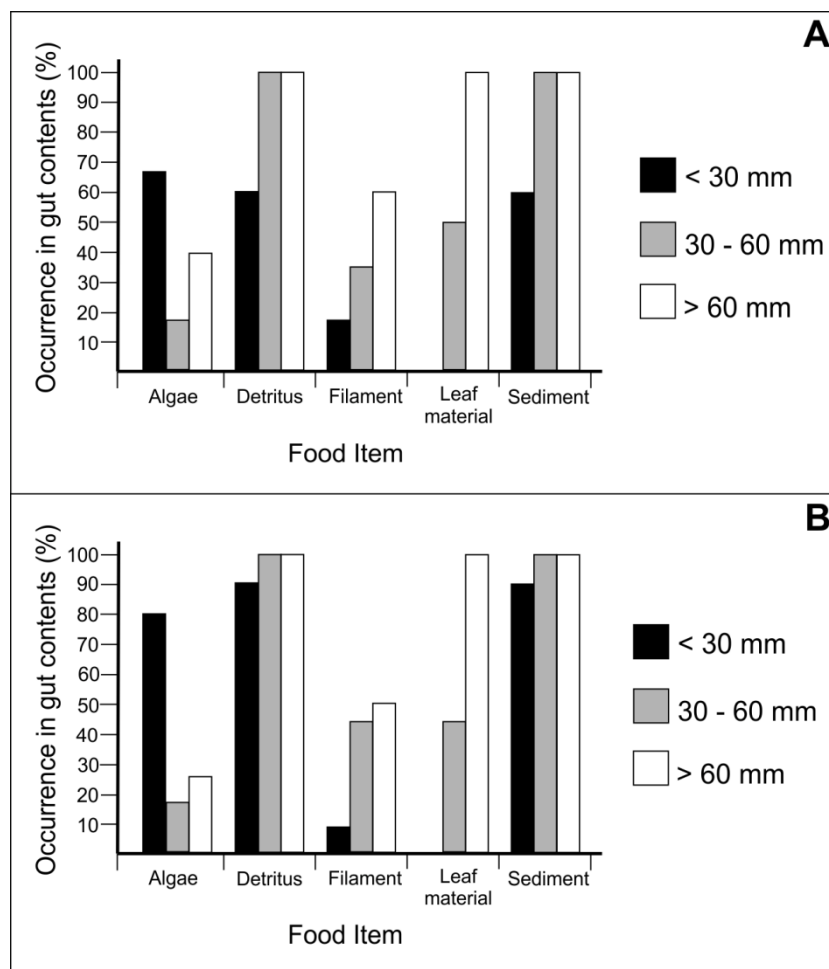


**Figure 2.1** Percentage occurrence of items within the gut contents of *Terebralia palustris* individuals (*n* = 15 for each size class) collected for stable isotope analyses in the November 2013 (**A**) and July 2014 (**B**) at Kosi Bay. Gut contents were categorized based on gross morphology.

### 2.3.3 Seasonal variation in source signatures

Source signatures for $\delta^{13}C$ were significantly different in both November (Kruskal Wallis $\chi^2$ = 22.493, *df* = 7, *p* = 0.0021) and July (Kruskal Wallis $\chi^2$ = 25.714, *df* = 8, *p* = 0.0012). On both sampling occasions the available sources were generally $^{15}N$-depleted (Figure 2.2, Table 2.2). In November, the mean (± SD) $\delta^{13}C$ signatures for sources ranged from -30.32 ± 0.04 ‰ for fresh mangrove leaves to -12.66 ± 0.09 ‰ for *Cladophora* sp. In July, *Cladophora* sp. was the most enriched in $\delta^{13}C$ (-16.16 ± 0.44 ‰), while orange mangrove leaves were most depleted (-27.98 ± 0.04 ‰).
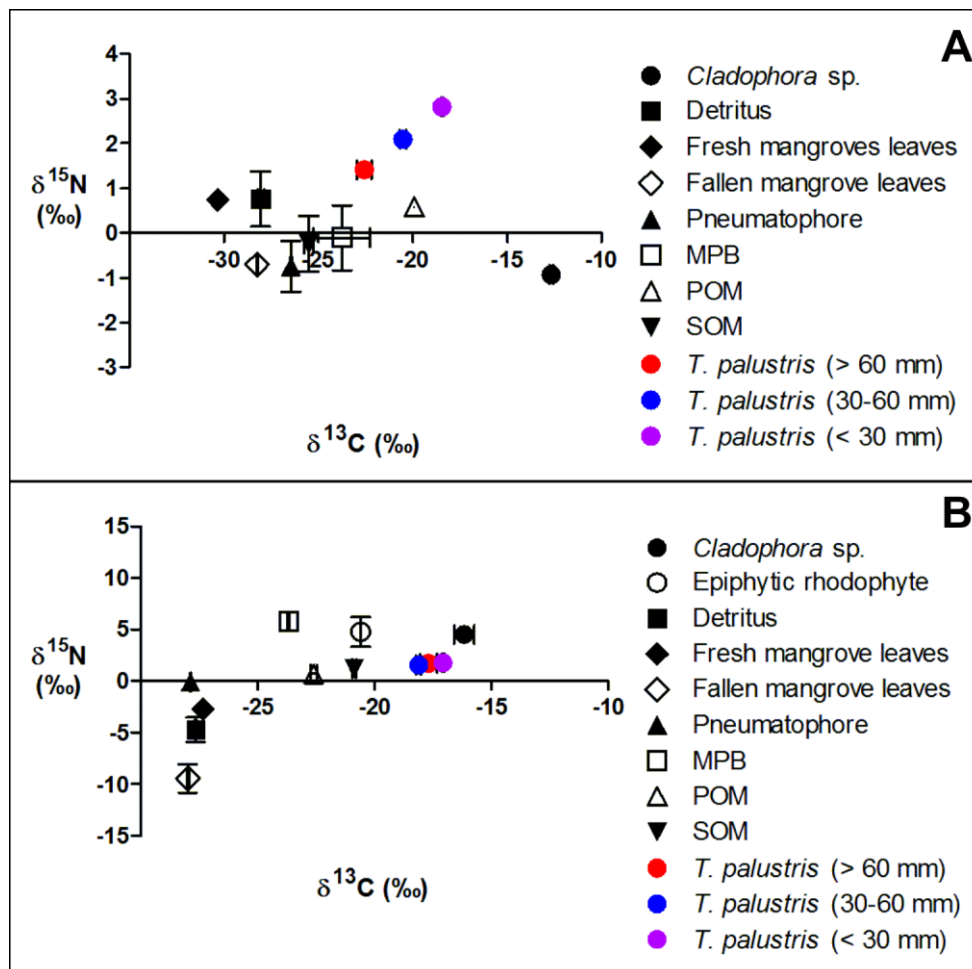


**Figure 2.2** Biplot of the mean (± SD) $\delta^{15}N$ and $\delta^{13}C$ signatures of *Terebralia palustris* and the available food items at Kosi Bay in November 2013 (**A**) and July 2014 (**B**) (*n* = 5 for each potential food source and each snail size class).

**Table 2.2** Mean (± SD) δ$^{15}$N and δ$^{13}$C signatures of *Terebralia palustris* and the available food items at Kosi Bay in November 2013 and July 2014. The mean (± SD) C:N ratio is also provided.

| Sources | November 2013 | | | July 2014 | | |
|---|---|---|---|---|---|---|
| | δ$^{15}$N (‰) | δ$^{13}$C (‰) | C:N | δ$^{15}$N (‰) | δ$^{13}$C (‰) | C:N |
| *Cladophora* sp. | -0.930 ± 0.12 | -12.66 ± 0.09 | 7.88 ± 0.08 | 4.50 ± 0.55 | -16.16 ± 0.44 | 24.52 ± 2.35 |
| Epiphytic rhodophyta | - | - | - | 4.76 ± 1.45 | -20.58 ± 0.01 | 68.55 ± 4.35 |
| Detritus | 0.766 ± 0.61 | -28.05 ± 0.17 | 66.78 ± 2.95 | -4.72 ± 1.21 | -27.65 ± 0.04 | 40.51 ± 2.69 |
| Fresh mangrove leaves | 0.742 ± 0.12 | -30.32 ± 0.04 | 26.41 ± 0.36 | -2.72 ± 0.44 | -27.33 ± 0.05 | 69.08 ± 2.85 |
| Fallen mangrove leaves | -0.707 ± 0.15 | -28.24 ± 0.02 | 59.34 ± 0.91 | -9.44 ± 1.38 | -27.98 ± 0.04 | 201.66 ± 4.50 |
| Pneumatophore | -0.747 ± 0.57 | -26.44 ± 0.06 | 34.92 ± 1.25 | -0.09 ± 0.54 | -27.87 ± 0.03 | 93.89 ± 0.01 |
| MPB | -0.106 ± 0.72 | -23.75 ± 1.50 | 11.75 ± 0.31 | 5.80 ± 0.86 | -23.67 ± 0.03 | 17.11 ± 1.24 |
| SOM | -0.241 ± 0.62 | -25.50 ± 0.24 | 13.75 ± 0.79 | 0.72 ± 0.55 | -22.60 ± 0.13 | 28.78 ± 2.23 |
| POM | 0.579 ± 0.12 | -19.91 ± 0.01 | 9.16 ± 0.03 | 1.24 ± 0.15 | -20.87 ± 0.09 | 18.48 ± 3.50 |
| *Terebralia palustris* | | | | | | |
| > 60 mm | 1.41 ± 0.07 | -22.55 ± 0.38 | 3.62 ± 0.04 | 1.70 ± 0.20 | -17.68 ± 0.37 | 5.26 ± 0.36 |
| 30 – 60 mm | 2.09 ± 0.11 | -20.51 ± 0.15 | 3.57 ± 0.01 | 1.53 ± 0.33 | -18.11 ± 0.10 | 4.45 ± 0.05 |
| < 30 mm | 2.82 ± 0.05 | -18.44 ± 0.05 | 3.60 ± 0.01 | 1.78 ± 0.17 | -17.06 ± 0.05 | 4.48 ± 0.02 |

*2.3.4 Isotopic signatures for Terebralia palustris and estimates of niche width*

The isotopic composition of *T. palustris* individuals varied between sampling occasions and amongst size classes (Table 2.2, Table 2.3, Figure 2.2). The highly significant interaction between these two factors indicates that differences were not consistent across the sampling occasions. This is evident in the pair-wise tests which showed that isotopic composition was significantly different among all size classes in November, but in July there was only a significant difference between the medium (30-60 mm) and small (< 30 mm) size classes (Table 2.3).

**Table 2.3** PERMANOVA comparisons for muscle tissue isotopic composition of *Terebralia palustris* individuals from different size classes collected in November 2013 and July 2014 at Kosi Bay. Pair-wise comparisons for each size class in each season are also provided.

| PERMANOVA | df | SS | MS | F | p |
|---|---|---|---|---|---|
| Sampling occasion | 1 | 22.330 | 22.330 | 154.170 | 0.001 |
| Size | 2 | 18.912 | 9.456 | 65.287 | 0.001 |
| Sampling occasion× Size | 2 | 13.283 | 6.642 | 45.856 | 0.001 |
| Residual | 24 | 3.476 | 0.144 | - | - |
| Total | 29 | 58 | - | - | - |

| PAIR-WISE COMPARISONS | November 2013 | July 2014 |
|---|---|---|
| (> 60 mm) vs (30-60 mm) | $t = 11.175, p = 0.012*$ | $t = 1.136, p = 0.249$ |
| (> 60 mm) vs (< 30 mm) | $t = 29.798, p = 0.011*$ | $t = 1.407, p = 0.236$ |
| (30-60 mm) vs (< 30 mm) | $t = 15.521, p = 0.008*$ | $t = 2.191, p = 0.003*$ |

Figure 2.3 shows the bivariate isotope-space for different size classes of *T. palustris* in both November and July. Pair-wise tests indicated that the ellipse for large snails (> 60 mm) was larger than the ellipse for medium-sized snails (30 – 60 mm) in November as well as in July (Table 2.4). Similarly, on both sampling occasions the ellipses for medium-sized snails were larger than the ellipses for small (< 30 mm) snails (Figure 2.3, Table 2.4).
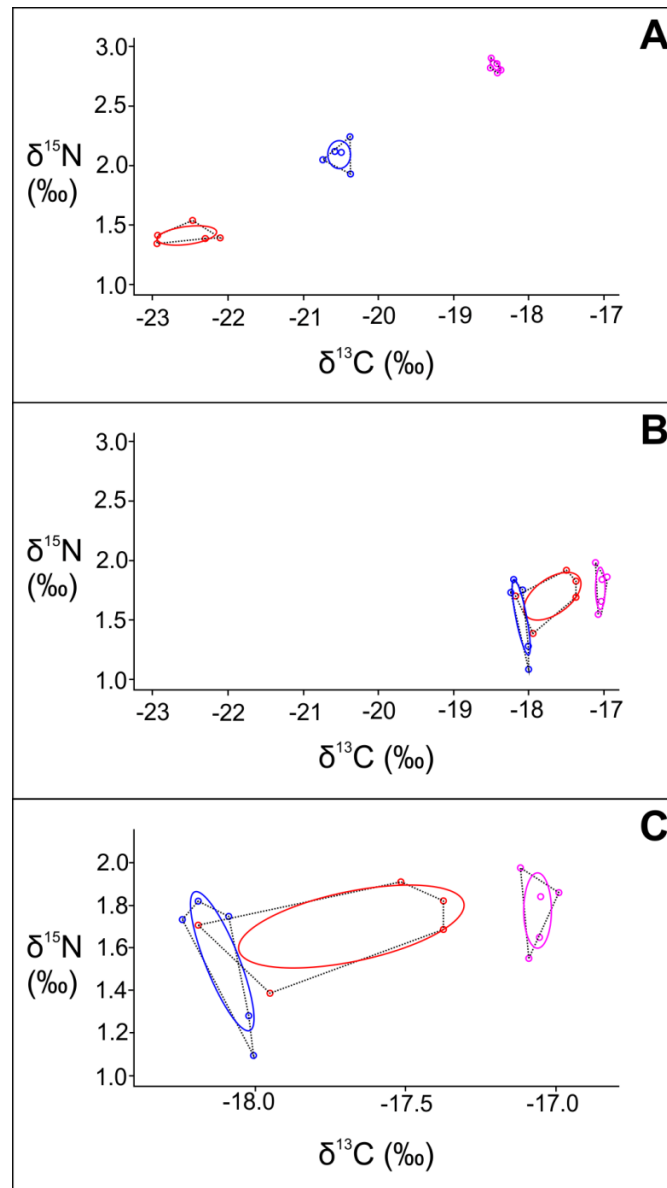


**Figure 2.3** Variation in $\delta^{15}N$ and $\delta^{13}C$ for different size classes of *Terebralia palustris* (> 60 mm = red, 30-60 mm = blue, < 30 mm = magenta) in November 2013 (**A**) and July 2014 (**B**), a focus on the converged ellipses for July is also provided (**C**). Standard ellipses were based on maximum likelihood estimates and were corrected for small sample sizes. The convex hulls (dotted lines) are also included.

In November, the ellipses for each size class were clearly separated in isotope-space (Figure 2.3). Although there was a convergence of the ellipses in isotope-space in July (Figure 2.3B), there was still no overlap between the ellipses for different size classes of *T. palustris* (Figure 2.3C).

**Table 2.4** Pair-wise comparisons of posterior distributions for the ellipses that illustrate the isotopic niches of large (> 60 mm), medium (30 – 60 mm) and small (< 30 mm) *Terebralia palustris* (Groups 1, 2, and 3 respectively) in November 2013 and July 2014 at Kosi Bay.

| PAIR-WISE COMPARISONS | Wet | Dry |
|---|---|---|
| Group 1 Ellipse > Group 2 Ellipse | probability = 0.751 | probability = 0.931 |
| Group 1 Ellipse > Group 3 Ellipse | probability = 0.999 | probability = 0.999 |
| Group 2 Ellipse > Group 3 Ellipse | probability = 0.998 | probability = 0.959 |

*2.4 Discussion*

*Terebralia palustris* is widely recognized as an integral component of Indo-Pacific mangroves because its consumption of leaf litter contributes significantly towards recycling within these ecosystems (Fratini et al. 2004; Cannicci et al. 2008). Previous research has described the diet of *T. palustris* in mangrove habitats in relation to the size of the snails, as well as their spatial distribution across the shore (Slim et al. 1997; Penha-Lopes et al. 2009). However, this is the first study to report on the size and associated variability of the dietary niche for this species. The results of this study indicate that changes in nutritional quality of available resources have a significant impact on the dietary niche size of *T. palustris*. This may be an important factor determining the persistence of this species in subtropical estuarine mangroves that are characterized by seasonal regime shifts.

*2.4.1 Ontogenetic shifts in diet in relation to spatial resource availability and partitioning*

Ontogenetic niche shifts occur in many species (Werner & Gilliam 1984) and have been reported to drive the dynamics and structure of populations, communities and ecosystems (Polis & Strong 1996; Claessen et al. 2002). These shifts are characterized by a change in diet, habitat range, or a combination of the two (Werner & Gilliam 1984). The ontogenetic dietary shift in *T. palustris* has been well documented, as it is distinguished by a morphological change to the structure of the radula as individuals mature (Houbrick 1991). This change in radula structure is related to the general spatial distribution of *T. palustris* in the mangroves as larger snails consume mangrove leaf litter when they occur in higher shore regions beneath the canopy (Houbrick 1991). Isotopic signatures for *T. palustris* have been previously reported by Slim et al. (1997) who found a significant difference in the $\delta^{13}$C signatures of juvenile and adult snails in Kenya. Furthermore, Penha-Lopes et al. (2009) compared both $\delta^{13}$C and $\delta^{15}$N signatures for *T. palustris* of different sizes at Inhaca Island, Mozambique, as a function of their occurrence across the shore and thus in relation to microhabitat and potential resource availability.

Quantitative measures to identify shifts in niche width, niche position and niche overlap using stable isotope data have been recently recommended

(Hammerschlag-Peyer et al. 2011). The application of a hypothesis-testing framework, using both univariate and multivariate statistical approaches to analyze the stable isotope data, provides information that is more valuable than simple qualitative observations or inferring shifts based on correlations of isotopic signatures with body size (Hammerschlag-Peyer et al. 2011). In this study we found clear support for an ontogenetic niche shift in *T. palustris* at Kosi Bay, South Africa, using both qualitative and quantitative approaches. First, based on the observed spatial segregation of different sized individuals, we hypothesized that an ontogenetic dietary shift did occur for this population. Second, we found differences in the gut contents of snails from different size classes. Furthermore, isotopic signatures were significantly different between size classes, and were similar to those reported by Penha-Lopes et al. (2009). Third, the application of the Bayesian ellipse model to the isotope data allowed a direct assessment of isotopic niche size that can be used to quantitatively infer an ontogenetic dietary shift.

The differences in the isotopic niche sizes, as indicated by the ellipses, provide some important insight regarding resource partitioning between the size classes of *T. palustris*. In both seasons, the small individuals (< 30 mm) had the smallest isotopic niche, indicating consumption of relatively fewer sources in comparison to the large individuals (> 60 mm). This was reflected in the gut contents, as smaller individuals were found to consume mainly detritus and algal material, while large snails were also feeding upon filamentous algae and mangrove leaf litter. However, the occurrence of certain items within the gut contents could also be related to digestibility. Generally, food items that have greater structural complexity take longer to be digested and are assimilated less efficiently (Hargrave 1970; Brendelberger 1997). For example, macroalgal material that contains complex carbohydrates often requires specific enzymes in order to be fully digested (Galli & Giese 1959, Linton & Greenway 2007). The high prevalence of detritus within the gut contents of all size classes of *T. palustris* might therefore be an indication of a reduced ability to digest this source.

Previous studies have reported that juveniles are generalist deposit-feeders that consume a variety of sources, while adults consume predominantly leaf litter (Fratini et al. 2004; Pape et al. 2008). However, mangrove leaf litter has a low nutritional quality and large-scale studies have shown that it only significantly contributes to the

diets of relatively few specialist invertebrate consumers (Bouillon et al. 2004a; Imgraben & Dittmann 2008; Mazumder & Saintilan 2010). Alternative primary carbon sources that are consumed by mangrove invertebrates, such as benthic microalgae and epiphytic macroalgae, have been identified using stable isotope approaches (Bouillon et al. 2002). For *T. palustris*, the results of this study corroborate those of Penha-Lopes et al. (2009): the depletion of $\delta^{13}C$ signatures of large snails in comparison to those of smaller individuals does not signify a complete reliance on mangrove leaf litter, and other enriched sources contribute significantly to the diet of these individuals.

Habitat shifts related to ontogenetic dietary shifts have been shown to contribute to niche partitioning frameworks (Schellekens et al. 2010). Loreau & Ebenhoh (1994) showed that where a habitat shift in a population optimized resource use, it prevented intraspecific competition across these habitats and within the population. Predation is also expected to influence habitat shifts and foraging patterns as explicit predator avoidance behaviours are often exhibited by gastropods that are prey species (Turner 1996; Dalesman et al. 2009; Mach & Bourdeau 2011). Predation could therefore be an important factor that drives dietary shifts of primary consumers both directly and indirectly through trophic cascades (Rosenzweig 1991; Huxel et al. 2002). In the case of *T. palustris*, larger individuals generally do not have natural predators, but they are harvested by humans for use as bait or for consumption (Wells & Lalli 2003, Raw et al. 2014). This could influence the population structure and also the partitioning of resources between size classes, but further research is needed to directly test these effects. Predation of juvenile *T. palustris* by brachyuran predators could be restricting their occurrence to certain foraging areas, but this is yet to be investigated.

Within mangrove forests, the variability in environmental conditions on small spatial scales has a significant impact on resource availability, and thus on the diets of benthic invertebrates (Guest & Connolly 2004; Kon et al. 2007; Kon et al. 2011). Most significantly, the lower shore regions support the growth of benthic microalgae (Alongi 1994; Liu et al. 2013), while upper shore regions are characterized by higher organic content within the sediment (Cahoon et al. 1999). This variability in sediment characteristics has been related to the occurrence and diet of *T. palustris* that are spatially segregated across the shore by Penha-Lopes et al. (2009). Dietary shifts

could therefore be interpreted as a consequence of spatial distribution, but Fratini et al. (2004) have shown that diets differ even when there is spatial overlap between size classes.

Fratini et al. (2001) have also demonstrated that large *T. palustris* actively respond to chemical compounds that are released when fallen mangrove leaves are mechanically damaged. This indicates that they forage selectively, and do not only consume leaves that are encountered by chance on the substrate (Fratini et al. 2001). However, *T. palustris* is not an obligate consumer of mangrove leaf litter as evidenced by our results as well as those of Penha-Lopes et al. (2009) and Fratini et al. (2004). This species has also been reported to occur outside of mangrove habitats by Feulner (2000). The selective incorporation of a nutritionally poor resource, particularly when superior alternatives are available, is potentially driven by an evolutionary mechanism to support resource partitioning between the different size classes. It is expected that, as suggested by Schellekens et al. (2010), the ontogenetic shift provides juveniles with a large supply of a nutritious resource, while adults incorporate resources that are less readily available and nutritionally inadequate, in order to reduce intraspecific competition.

### 2.4.2 Seasonal shifts in source signatures and diet of Terebralia palustris

Primary productivity in estuarine systems is largely reliant on terrestrially-derived nutrients (Knoppers 1994; Alongi 1998), and is therefore significantly influenced by seasonal changes in temperature and precipitation (Nozais et al. 2001; Perissinotto et al. 2002). This relates to significant variability in terms of resource availability for primary consumers (Cloern & Jassby 2008). Furthermore, stable isotope signatures of primary producers are seasonally influenced by changes in nutrient availability (Vizzini & Mazzola 2003). The temporal differences in consumer stable isotope signatures can therefore be attributed to either large-scale shifts in environmental signatures, or to the consumption of different resources in different seasons depending on availability (Peterson & Fry 1987; Vizzini & Mazzola 2003; Baeta et al. 2009).

The mean annual precipitation for the Kosi Bay region is 939 mm/year, as measured by the South African Weather Service at the Ingwavuma meteorological stations at Kosi Bay and Manguzi (Ndlovu & Demlie 2016). According to data collected between

1972 and 2015, the largest portion of this rainfall is received during the wet summer months, with the mean monthly precipitation ranging from 100 mm in November to 150 mm in January (Ndlovu & Demlie 2016). In contrast, in the drier winter period, the mean monthly precipitation ranges from 40 mm in June to 35 mm in August (Ndlovu & Demlie 2016). As a result, there is a strong inflow of fresh water from the head of the estuary during the summer period (Kyle & Ward 1995).

The Kosi Bay system is naturally oligotrophic (Begg 1980) and there are no significant nutrient inputs from anthropogenic sources (Kyle & Ward 1995). Therefore, in winter, when rainfall is reduced, the system has a significantly reduced input of freshwater and nutrients. This was reflected in the depleted $\delta^{15}N$ signatures and higher C:N ratios that were recorded for mangrove leaves in July 2014. The C:N ratios of mangrove leaves and detritus vary seasonally as they are influenced by decomposition rates, moisture and the availability of inorganic nutrients (Ehleringer et al. 2000; Bosire et al. 2005; Bouillon et al. 2008). High C:N ratios may be driven by very low nitrogen content, as the $\delta^{13}C$ signatures at Kosi Bay were within the expected range of -35.1 to -21.9 ‰ for mangrove leaves (Bouillon et al. 2008). Nitrogen content of mangrove leaves has been shown to be significantly reduced in low rainfall periods (Bosire et al. 2005) and negative $\delta^{15}N$ signatures have previously been recorded for mangrove sources in other regions (Fogel et al. 2008). The C:N ratio of freshly fallen leaves from *Rhizophora mucronata* and *Bruguiera gymnorhiza* at Kosi Bay in July was considerably higher than the C:N ratios recorded for *R. mucronata* and *Sonneratia alba* in Kenya (Bosire et al. 2005) further emphasizing the oligotrophic state of the Kosi Bay system. In contrast, algal sources are highly productive with relatively fast turn-over rates and therefore exhibit high temporal variability in $\delta^{15}N$ and $\delta^{13}C$ (Post 2002b; Oakes et al. 2010). At Kosi Bay, we found that MPB and the filamentous *Cladophora* sp. were comparatively N-enriched in July, as indicated by higher $\delta^{15}N$ signatures.

For *T. palustris*, we found that signatures for both $\delta^{15}N$ and $\delta^{13}C$ were more similar between the different size classes in July in comparison to November. Also, the $\delta^{13}C$ signatures for *T. palustris* of all size classes were enriched in July, while the $\delta^{15}N$ signatures were enriched for the large individuals, but depleted for medium- and small-sized snails. This could indicate that all size classes were consuming sources that had relatively similar $\delta^{13}C$ signatures. Variability in the $\delta^{15}N$ signatures of

primary consumers has been used to assess trophic niche width, as it indicates high diversity in the diet when a number of different sources can be incorporated (Bearhop et al. 2004). The increased range of $\delta^{15}N$ signatures for different size classes of *T. palustris* in July could therefore be interpreted as an increase in the size of the dietary niche. As the $\delta^{15}N$ for large snails became enriched in July, this could indicate a shift to consuming a source with a lower C:N ratio. Considering only the isotopic signatures, it could be interpreted that the diet of large *T. palustris* had shifted to overlap with those of smaller sized snails in July. However, the comparisons of isotopic niches (represented by the ellipses) indicated that the significant differences in the sizes of the niches were retained in July and that there was no overlap between the isotopic niches of different sized snails.

Shifts in the isotopic signatures of *T. palustris* could be the result of snails consuming different resources, or perhaps different proportions of the primary sources depending on availability or nutritional quality. Alternatively, the $\delta^{15}N$ signature of larger snails may also be influenced by internal metabolic processes that assist digestion of nutritionally poor macrophyte material. Linton & Greenway (2007) reported on the ability of herbivorous land crabs to internally recycle N, as they predominantly consume plant material and detritus that has high levels of cellulose and tannins. Within subtropical mangroves, the availability of mangrove leaf litter varies seasonally as leaf fall is dependent on rainfall patterns (Tomlinson 1999). Furthermore, as decomposition rates are driven by temperature, the availability of mangrove-derived detritus is also variable (Mackey & Smail 1996). In contrast, the availability of MPB is relatively similar between the wet and dry seasons at Kosi Bay (unpubl. data), and Steinke et al. (2003) have reported that *Cladophora* sp. is a diagnostic component of the epiphytic macroalgal community found on the pneumatophores of mangroves in the lower tidal basin. The low C:N ratios of the algal sources indicate that they are of higher nutritional quality than the macrophyte-derived sources, a general trend within both mangrove and salt marsh ecosystems (Bouillon et al. 2002; Hart & Lovvorn 2003). However, analysis of the gut contents indicated that algal sources were not very prevalent in the diets of larger snails. Instead, detritus was a prominent component of the gut contents, and this source had a relatively low C:N ratio in the dry season. The C:N ratios of sources and gastropods presented in this study therefore indicate that sources other than

mangrove leaf litter may be incorporated by *T. palustris* in the dry season, either by direct selective feeding on these resources or selective assimilation within the digestive tract (Doi et al. 2006; Pape et al. 2008).

*2.4.3 Ecological role of Terebralia palustris in subtropical mangroves*

The decline in productivity and biomass of mangrove trees with increasing latitude is expected to be the result of a number of inter-related physiological challenges experienced beyond the equatorial region (Komiyama et al. 2008). The biological and environmental processes that drive nutrient and carbon cycling in mangroves are influenced by many factors (Feller et al. 2010) and as a result there is considerable within-region variation in the productivity of mangroves at higher latitudes (Imgraben & Dittman 2008; Morrisey et al. 2010). Reduced productivity may directly result in smaller proportions of mangrove-derived carbon and nutrients being incorporated into higher trophic levels (Morrisey et al. 2010). Some studies have indeed indicated that mangrove leaves and mangrove-derived detritus do not make a significant contribution to the diets of prominent benthic macrofauna, such as brachyurans, at higher latitudes (Mazumder & Saintilan 2010; Gladstone-Gallagher et al. 2014). At tropical latitudes, *T. palustris* consumes a significant proportion of mangrove leaf litter (Slim et al. 1997; Fratini et al. 2004) and is therefore considered as having an integral ecological role (Cannicci et al. 2008). Fratini et al. (2004) found that mangrove leaf litter was the main component (62.5 %) of the gut contents of large *T. palustris* in Kenya and Slim et al. (1997) reported that under wet conditions these snails could remove up to 41.6 % of available leaf litter. This is also reflected in the $\delta^{13}C$ signatures for *T. palustris* in this region, as adults have been reported to have values ranging from -20.2 to -21.82 ‰ (Pape et al. 2008).

However, at subtropical latitudes, the ecological function of *T. palustris* as a consumer of mangrove leaf litter may be less pronounced, as indicated by the variability of the dietary niche reported in this study, as well as the findings of Penha-Lopes et al. (2009) for this species in Mozambique. Penha-Lopes et al. (2009) found that the average$\delta^{13}C$ signature of large *T. palustris* (>50 mm) was 21.3 ± 0.9 ‰, while in this study large snails were even further depleted in $^{13}C$ (-22.55 ± 0.38 ‰). The contribution of mangrove leaf litter towards the diet of *T. palustris* was not directly quantified in this study. Although this source was always present within the

gut contents of large individuals, other sources (detritus, filament and algae) were also consistently present.

Mangrove leaf litter in the form of detritus is consumed by a number of gastropod species, however *T. palustris* is one of the few species that directly consumes freshly fallen mangrove leaves (Cannicci et al. 2008), and is therefore directly competing with brachyurans for these resources (Slim et al. 1997; Fratini et al. 2000). Competition could therefore be driving the dietary shifts and thus influencing the ecological role of *T. palustris* at higher latitudes. Fratini et al. (2000) reported on strong competitive interactions between these snails and the herbivorous crab *Neosarmatium smithi*. In South African mangroves, the closely related *N. meinterti* has been described as having a similar ecological role to that of *N. smithi* (Emmerson & McGwynne 1992). Mangrove leaf litter has been reported to constitute over 70 % of the diet of *N. meinerti* (Steinke et al. 1993), and this species has been estimated to consume over 40 % of the available leaf litter in the mangroves of the warm temperate Mngazana Estuary (31°41'29''S; 29°25'24''E) (Emmerson & McGwynne 1992). This species is therefore responsible for retaining a large proportion of mangrove leaf litter, particularly in high shore mangroves such as those along the South African coastline (Ólafsson et al. 2002). The latitudinal distribution of mangroves along the South African coastline also extends beyond the range limits of *T. palustris* (Raw et al. 2014). Therefore, although *T. palustris* may make some contribution towards retention of mangrove leaf litter at subtropical latitudes when it is present, this ecological role is evidently dominated by the grapsid crabs in this region. This is a trend which has been globally reported upon (Lee 1998).

*2.5 Conclusion*

The observed plasticity in the diet of all size classes of *T. palustris* is related to niche variation of this species and is expected to contribute towards partitioning of resources through ontogeny. This partitioning is particularly important for the sustainability of this population in a dynamic estuarine mangrove ecosystem subject to oligotrophy and seasonal fluctuations. Ellipse-based stable isotope models provided a quantitative assessment of the dietary niche allowing for direct inferences regarding seasonal dietary shifts and potential overlap. As mangrove ecosystems are variable across latitudinal gradients, the results of this study highlight the importance of conducting basic research in different regions to provide information about key ecological aspects that contribute to larger scale processes and ecosystem functioning.

# Chapter 3: Diet of *Melanoides tuberculata*

## 3.1 Introduction

The vast majority of freshwater gastropods are benthic crawlers that forage by a combination of scraping (for epipelic and epilithic algae and bacterial films) and deposit feeding (for episammic algae and detritus). Besides direct top-down control on benthic primary productivity, gastropod grazing also influences nutrient demand and recycling processes in established algal mats (Hillebrand et al. 2002; Vanni 2002). Furthermore, as freshwater gastropods are important prey items to fish and crustaceans, they serve as integral trophic links to higher consumers (Vermeij & Covich 1978; Covich et al. 1999). Considering their broad ecological roles and their widespread global distribution, freshwater gastropods are often key components in a multitude of diverse habitats (Strong et al. 2008).

Grazing gastropods generally exhibit a degree of plasticity in their diets and this is attributed to their unselective feeding modes. Dietary plasticity is considered an indicator of niche breadth, as the range of items consumed is related to the level of dietary specialization (Feinsinger et al. 1987; Bolnick et al. 2002). These attributes, which underlie many general ecological principles, can be directly elucidated with data from stable isotope analysis (SIA) (Bearhop et al. 2004; Turner et al. 2010). As isotopic ratios of $\delta^{15}$N and $\delta^{13}$C are conserved through the food web with predictable shifts at each trophic level (DeNiro & Epstein 1978, 1981; Vanderklift & Ponsard 2003), changes in trophic structure and energy flow can be tracked with SIA (Peterson & Fry 1987; Middelburg 2014). However, there is evidence that the shifts in isotopic ratios are not always predictable, and may depend on a number of factors such as diet type, feeding mode and digestion/assimilation efficiencies (McCutchan et al. 2003; Yokoyama et al. 2005; Caut et al. 2009; Robbins et al. 2010, Remien 2015). This has recently been highlighted for detritivores that consume nutritionally

poor resources, such as herbivorous crabs that feed on mangrove leaf litter (Herbon & Nordhaus 2013; Bui & Lee 2014). Despite this, SIA is still a powerful tool for ecologists and a number of procedures and models are therefore being developed in order to improve the efficiency and accuracy of this technique (Moore & Semmens 2008; Parnell et al. 2010; Remien 2015; Brett et al. 2016).

SIA can also be used to assess dietary overlap between consumers and therefore provide insight into potential competitive interactions (Bootsma et al. 1996). This aspect of SIA has been widely applied within the field of invasion ecology to determine the degree of dietary overlap between introduced and native species (Miranda & Perissinotto 2012; Hill et al. 2015). Using SIA to determine the dietary composition of primary consumers, such as gastropods, supplies essential information to larger scale ecosystem studies (Layman et al. 2007). Furthermore, benthic organisms are considered effective isotopic indicators as they provide a representative baseline of energetic inputs to higher trophic levels (Grey 2006).

*Melanoides tuberculata* (Müller, 1774) is a freshwater thiarid gastropod that is considered to be a generalist, non-selective deposit feeder (Madsen 1992). Globally, this species is one of the two most important invasive thiarid gastropods (Facon et al. 2003). This species has established across the New World, including regions of the United States (Karatayev et al. 2009), the Caribbean (Pointier et al. 2011) and South America (De Marco 1999; Peso et al. 2011). *Melanoides tuberculata* has an extensive native range along eastern Africa and across the Middle East to Southeast Asia (Brown 1994; Facon et al. 2003) where it inhabits a wide variety of aquatic environments (de Kock & Wolmarans 2009; Perissinotto et al. 2014). Like many freshwater gastropods, *M. tuberculata* is an important primary consumer and serves as an integral trophic link as it is predated upon by fish, crustaceans and birds (Chimbari & Madsen 2003; Escobar et al. 2009; Evers et al. 2011; Peer et al. 2015b).

A number of genetically and phenotypically distinct morphs are found within the native range of *M. tuberculata* (Samadi et al. 1999; Facon et al. 2003). However, there have been no reports on variation in ecological traits; such as reproductive capacity, feeding rates and diet, between different morphs. The aim of this study was to provide baseline information on the dietary composition of three distinct *M.*

*tuberculata* populations from different habitats within subtropical lakes on the north-eastern coast of South Africa. This was achieved through SIA of natural $\delta^{13}$C and $\delta^{15}$N abundances for sources and gastropod consumers within the different habitats. Within the study region, *M. tuberculata* has a substantial grazing impact on available microphytobenthos (Raw et al. 2016b). However, the degree of dietary plasticity and potential niche breadth of *M. tuberculata* from this region have not previously been assessed. The diet of *M. tuberculata* was hypothesized to vary in two ways. Firstly, as *M. tuberculata* is expected to feed indiscriminately on benthic resources, the diet would vary seasonally depending on resource availability. Secondly, as *M. tuberculata* inhabits a variety of diverse habitats, the diet would differ between populations and therefore indicate trophic plasticity. This estimation of diet should provide useful information relating to the potential competitive interactions between *M. tuberculata* and other co-occurring benthic gastropods.

*3.2 Materials and Methods*

*Melanoides tuberculata* were collected for stable isotope analyses from three distinct populations (Lake Nhlange, the Mpophomeni Stream and St Lucia Estuary Mouth) within coastal lakes of the iSimangaliso Wetland Park (Figure 1.2). This region is within the native range of *M. tuberculata* (Brown 1994), however, there is preliminary evidence that several morphologically distinct populations exist within South Africa (Appleton & Miranda 2015). In this study, snails from the St Lucia Estuary Mouth and those from the Mpophomeni Streamhave been identified as the indigenous form (see Appleton 1996), while those from Lake Nhlange are cryptic and appear to have Asiatic origins when characterized following the guidelines of Facon et al. (2003). This is the subject of ongoing work and the true origins of these snails will only be confirmed through molecular genetics studies.

### *3.2.1 Description of study sites*

Collection sites (Figure 3.1) represented different habitat types and therefore varied in terms of physico-chemical parameters (Table 3.1). Lake Nhlange (26°57'56''S 32°49'77''E) of the Kosi Bay estuarine lake complex is a predominantly freshwater oligotrophic lake that spans an area of approximately 32 km$^2$ (Allanson & van Wyk 1969; Begg 1980). Here *M. tuberculata* was associated with the submerged macrophyte, *Ceratophyllum* sp. within the shallow littoral zone. The Mpophomeni Stream (27°57'17''S 32°22'37''E) is a small, brackish stream with a muddy bed that passes through an area dominated by sand forest vegetation that is unique to the region (Kirkwood & Midgley 1999). The stream flows into the False Bay basin of Lake St Lucia, the largest estuarine lake in Africa (Whitfield et al. 2013). *Melanoides tuberculata* at the Mpophomeni Stream were sometimes associated with the filamentous algae, *Cladophora* sp. At the St Lucia Estuary Mouth (28°22'48''S 32°25'18''E), *M. tuberculata* were collected from a channel that carries freshwater dune seepage through the mangrove forest on the northern bank of the estuary. There is a salinity gradient along the channel, ranging from fresh at the upper reaches to brackish at the point where it empties into the mouth of the estuary. This mangrove area, consisting of *Avicennia marina* and *Bruguiera gymnorhiza* trees, is unique in that it persists despite limited tidal connectivity to the Indian Ocean (Whitfield & Taylor 2009; Hoppe-Speer et al. 2013).
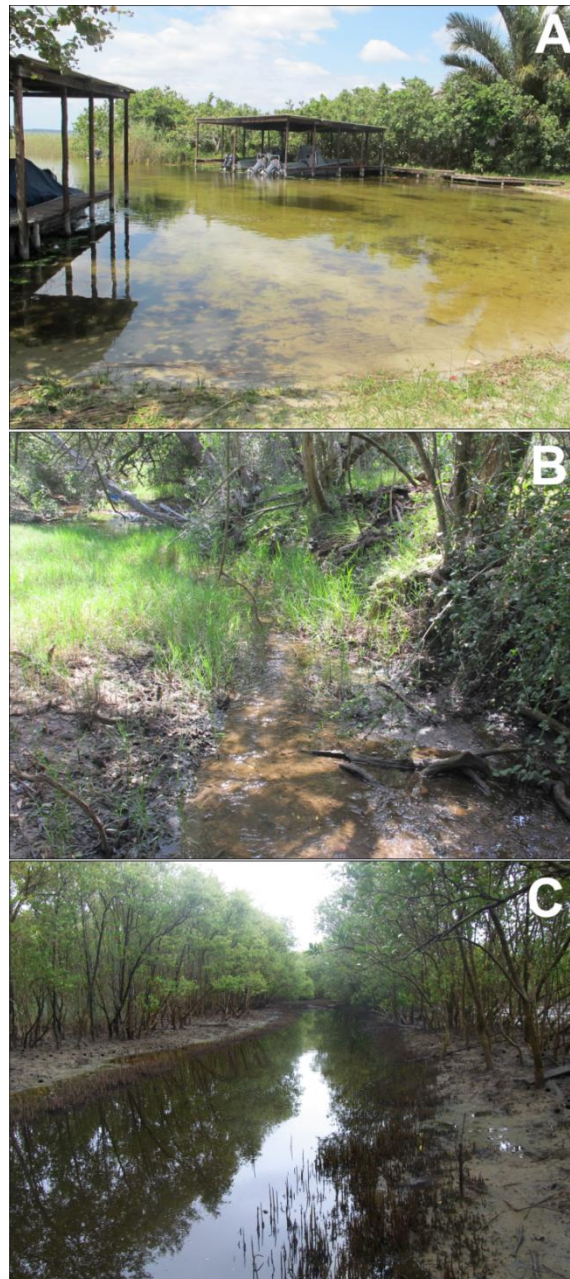
**Figure 3.1** Photographs of sites (**A** – Lake Nhlange, **B** – Mpophomeni Stream, **C** – St Lucia Estuary Mouth) from which *Melanoides tuberculata* and relevant primary sources were collected for stable isotope analyses. Photo credit: L Clennell.

The subtropical climate of this region is characterized by a high rainfall (wet) season between October and April (summer) and a low rainfall (dry) season between May and September (winter). As the iSimangaliso Wetland Park covers an expansive area, the mean annual precipitation is variable between the three sites. For Lake St Lucia, this has been estimated as 890 mm (Stretch et al. 2013), while the Kosi Lakes

receive approximately 940 mm (Ndlovu & Demlie 2016). Rainfall for the St Lucia Estuary has previously been reported to range from approximately 250 mm per month in December and January to below 50 mm per month in August and September (Tirok & Sharler 2013). The area near the Mpophomeni Stream is characterized by a lower monthly rainfall on average, with approximately 200 mm per month in December and January and below 20 mm per month in August and September, as reported by Tirok & Sharler (2013).

To determine any seasonal shifts in dietary composition, samples for stable isotope analysis were collected from each location during both rainfall seasons over the 2013-2014 period. A YSI 6600-V2 multiprobe was used to measure physico-chemical parameters at each location at the time of sample collection. Besides *M. tuberculata*, any other prominent aquatic gastropods present at the time of sampling were also collected for stable isotope analysis. The climbing mangrove whelk, *Cerithidea decollata* (Linnaeus, 1767), was collected at St Lucia Estuary Mouth while the invasive thiarid, *Tarebia granifera* (Lamarck, 1822), was collected at Lake Nhlange. No other aquatic gastropods were detected at the Mpophomeni Stream.

### 3.2.2 Sample collection and processing

Gastropods were collected by hand or by using a sweep net, depending on water depth. The snails were frozen after collection until processing in the laboratory. After careful removal of the shell, muscle tissue of the foot was excised, homogenized and defatted in a solution of methanol : chloroform : distilled water (2 : 1 : 0.8; Bligh & Dyer 1959) to remove any residual lipids retained from the skin. This was a precautionary treatment as lipids would influence the measured isotopic signature (Logan et al. 2008; Tarroux et al. 2010). The tissue was oven dried at 60 °C for at least 48 h before further processing.

Microphytobenthos (MPB) was collected by scraping the upper 1 cm of sediment and suspending this sediment in filtered water (0.7 µm Whatman GF/F) from the respective site. The sediment settled and the suspended MPB was vacuum filtered onto pre-combusted (450 °C, 6 hr) glass fibre filters (0.7 µm Whatman GF/Fs). Water samples were collected to obtain a representative of particulate organic matter (POM). This was collected as a representative of phytoplankton and suspended particulate detritus that may settle on the substrate and therefore become available

to grazing gastropods. POM was collected by the same filtration method onto pre-combusted GF/Fs. Other potential food sources, including fringing vegetation, submerged macrophytes, macroalgae and detritus, were also collected. For sedimentary organic matter (SOM) analysis, 20 mm diameter cores were taken and the upper 1 cm was discarded (as it would contain predominantly microalgae). All samples collected in the field were frozen until laboratory processing. The filters (containing MPB and POM) were acid washed (2% HCl) to remove any carbonates. The acid treatment was also applied to the detritus and sediment samples until all visible bubbling had ceased. The macroalgal and macrophyte samples were carefully rinsed with distilled water to remove sediment and visible associated fauna. All source samples were subsequently placed in an air-circulated oven (60 °C, 48 h) for drying.

### 3.2.3 Stable isotope analysis

After drying, all samples were independently homogenized using a mortar and pestle and then weighed to the appropriate mass for stable isotope analysis. Source material including detritus, roots, leaves and macroalgae was weighed to approximately 2.5 mg per sample and gastropod tissue was weighed to approximately 1 mg per sample. Each sample was packaged into a 5 x 9 mm tin capsule (SÄNTIS Analytical AG, Switzerland). For sediment, approximately 20 mg was packaged into Eppendorf microcentrifuge tubes. Five replicates were packaged for each source item and each gastropod species collected from each site.

The packaged samples were sent to IsoEnvironmental cc at Rhodes University, Grahamstown, South Africa. The samples were analyzed on a Europa Scientific 20-20 isotope ratio mass spectrophotometer linked to an ANCA Prep Unit. The ratios were expressed in delta notation (δ) as parts per thousand (‰) deviation from the accepted international standards of atmospheric nitrogen and Vienna Pee Dee Belemnite for the nitrogen and carbon isotopes respectively. The following equation was used to determine delta values:

$$\delta X = \left[ \left( \frac{R_{sample}}{R_{standard}} \right) - 1 \right] \times 1000$$

where $X = {}^{13}C$ or ${}^{15}N$ and $R =$ corresponding ratio of ${}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

### 3.2.4 Statistical analyses and source contribution

Statistical analyses were conducted using R v 2.11.1 for Windows (R Development Core Team 2010). MANOVAs were run using the "car" package (Fox & Weisberg 2014) to test for significant temporal differences in carbon and nitrogen stable isotope ratios of potential food items and gastropod consumers.

The mixing model SIAR v 4.0 (Stable Isotope Analysis in R, package "siar" by Parnell & Jackson 2013) was used to estimate the proportionate contribution of each potential food item to the diet of gastropods at the different sites in each season. Following the guidelines of Parnell et al. (2010) and Inger et al. (2010), diagnostic matrix plots were used to assess the performance of the model. Sources that consistently had a minimal contribution to the diet were therefore systematically removed to achieve the most parsimonious model. The $\delta^{15}$N and $\delta^{13}$C values of all sources were corrected with the trophic enrichment factors (mean ± SD) of 2.2 ± 1.61 and 0.4 ± 1.34 respectively. These values follow the recommendation of McCutchan et al. (2003) for consumers with plant-based diets.

*3.3 Results*

*3.3.1 Habitat characteristics*

There was an observable seasonal difference in the physico-chemical parameters at each site (Table 3.1). These variations in environmental conditions would be expected to influence resource availability. Although this was not quantified directly, there were some notable differences between seasons. At Lake Nhlange, the filamentous alga *Cladophora* sp., was absent from the sampled littoral zone in the dry season. Similarly, at the Mpophomeni Stream, *Cladophora* sp. was less extensive in the dry season leading to a patchy distribution along the stream bed. The St Lucia Estuary Mouth appeared to remain stable in terms of resource availability.

**Table 3.1** Physico-chemical measurements at Lake Nhlange, Mpophomeni Stream and St Lucia Estuary Mouth at the time of stable isotope sample collection.

| | Lake Nhlange | | Mpophomeni Stream | | St Lucia Estuary Mouth | |
|---|---|---|---|---|---|---|
| | *Wet* | *Dry* | *Wet* | *Dry* | *Wet* | *Dry* |
| **Salinity** | 3.1 | 3.1 | 7.5 | 9.1 | 7.6 | 3.3 |
| **Temperature (°C)** | 29.8 | 21.9 | 26.6 | 19.8 | 25.9 | 20.0 |
| **Dissolved O$_2$ (mg/L)** | 7.6 | 9.7 | 8.1 | 10.0 | 4.2 | 5.4 |
| **pH** | 8.5 | 8.4 | 8.4 | 7.4 | 8.2 | 6.3 |

*3.3.2 Stable isotope analysis*

The $\delta^{15}N$ and $\delta^{13}C$ signatures were significantly different (MANOVA) between available sources in both rainfall seasons at each respective site. This allowed for appropriate differentiation between sources in the SIAR mixing models.

During the wet season at Lake Nhlange ($F_{4,14}$= 29.596, Pillai's Trace = 1.858, $p <$ 0.05), mean (± SD) source signatures for $\delta^{13}C$ ranged from -31.32 ± 0.04 ‰ in *Phragmites* sp. to -22.36 ± 0.01 ‰ in detritus while those for $\delta^{15}N$ ranged from 1.06 ± 0.45 ‰ in *Cladophora* sp. to 7.65 ± 0.07 ‰ in the submerged macrophyte,

*Ceratophyllum* sp. (Table 3.2). Similarly, source signatures were different ($F_{4,12}=$ 29.771, Pillai's Trace = 1.836, $p < 0.05$) in the dry season and ranged from -31.29 ± 0.09 ‰ to -24.4 ± 0.5 ‰ for $\delta^{13}C$ and -1.89 ± 0.33 ‰ to 8.98 ± 1.36 ‰ for $\delta^{15}N$ (Table 3.2).

**Table 3.2** Mean (± SD) $\delta^{15}N$ and $\delta^{13}C$ signatures of available food items and gastropods from Lake Nhlange in both the wet and dry seasons.

| Sources | Wet | | Dry | |
|---|---|---|---|---|
| | $\delta^{15}N$ (‰) | $\delta^{13}C$ (‰) | $\delta^{15}N$ (‰) | $\delta^{13}C$ (‰) |
| *Phragmites* sp. | 5.50 ± 0.05 | -31.32 ± 0.04 | 2.88 ± 0.12 | -31.29 ± 0.09 |
| *Ceratophyllum* sp. | 7.65 ± 0.07 | -24.83 ± 0.06 | 8.98 ± 1.36 | -30.69 ± 0.07 |
| *Cladophora* sp. | 1.06 ± 0.45 | -25.85 ± 0.04 | - | - |
| Detritus | 2.11 ± 0.73 | -22.36 ± 0.01 | -1.89 ± 0.33 | -25.06 ± 0.14 |
| MPB | 2.98 ± 0.42 | -24.50 ± 0.20 | 7.22 ± 1.95 | -24.4 ± 0.50 |
| SOM | 1.83 ± 0.50 | -24.51 ± 0.16 | 7.28 ± 0.46 | -25.27 ± 0.11 |
| POM | 4.36 ± 0.16 | -25.96 ± 0.02 | 6.82 ± 1.07 | -26.55 ± 0.37 |
| **Gastropods** | | | | |
| *M. tuberculata* | 6.53 ± 0.05 | -23.26 ± 0.07 | 6.14 ± 0.62 | -24.07 ± 0.11 |
| *T. granifera* | 7.41 ± 0.13 | -20.63 ± 0.26 | 7.28 ± 0.27 | -21.30 ± 0.10 |

At the Mpophomeni Stream, source signatures were different in both the wet ($F_{4,16}=$ 28.083, Pillai's Trace = 1.837, $p < 0.05$) and dry ($F_{4,16}=$ 42.486, Pillai's Trace = 1.879, $p < 0.05$) seasons. The benthic algal sources were most enriched in both $\delta^{13}C$ and $\delta^{15}N$ at this site. MPB was the most enriched in $\delta^{13}C$ in both the wet and dry seasons (-20.17 ± 0.17 ‰ and -21.78 ± 0.7 ‰ respectively) (Table 3.3). MPB was also most enriched with $\delta^{15}N$ in the dry season (10.57 ± 3.09 ‰), while *Cladophora* sp. was most $\delta^{15}N$ enriched (13.17 ± 0.2 ‰) in the wet season (Table 3.3).

**Table 3.3** Mean (± SD) $\delta^{15}$N and $\delta^{13}$C signatures of available food items and gastropods from Mpophomeni Stream in both the wet and dry seasons.

| Sources | Wet | | Dry | |
|---|---|---|---|---|
| | $\delta^{15}$N (‰) | $\delta^{13}$C (‰) | $\delta^{15}$N (‰) | $\delta^{13}$C (‰) |
| Macrophytes | 8.50 ± 0.12 | -28.03 ± 0.04 | 3.93 ± 0.13 | -27.69 ± 0.003 |
| *Cladophora* sp. | 13.17 ± 0.20 | -28.53 ± 0.06 | 9.08 ± 0.10 | -36.01 ± 0.18 |
| Detritus | 8.07 ± 0.33 | -22.82 ± 0.61 | -3.47 ± 2.86 | -26.91 ± 0.13 |
| MPB | 8.09 ± 0.15 | -20.17 ± 0.17 | 10.57 ± 3.09 | -21.78 ± 0.70 |
| SOM | 6.55 ± 0.12 | -20.52 ± 0.06 | 5.27 ± 0.96 | -23.49 ± 0.55 |
| POM | 10.15 ± 0.41 | -24.14 ± 0.11 | 5.92 ± 1.27 | -25.36 ± 0.07 |
| **Gastropods** | | | | |
| *M. tuberculata* | 13.87 ± 0.09 | -27.19 ± 0.007 | 14.02 ± 0.44 | -27.12 ± 0.31 |
| *M. tuberculata*[a] | - | - | 16.83 ± 0.12 | -25.85 ± 0.14 |

[a]indicates *M. tuberculata* collected specifically from outside *Cladophora* sp. patches.

At the St Lucia Estuary Mouth, source signatures were also different between the wet ($F_{4,14}$= 76.255, Pillai's Trace = 1.936, $p < 0.05$) and dry ($F_{4,14}$= 9.702, Pillai's Trace = 1.623, $p < 0.05$) seasons. For $\delta^{13}$C, mangrove leaves were most depleted (-28.81 ± 0.05 ‰) in the wet season while SOM was most enriched (-21.56 ± 0.64 ‰). In comparison, dry season $\delta^{13}$C signatures ranged from -29.42 ± 0.15 ‰ to -21.29 ± 0.33 ‰ (Table 3.4). Interestingly, wet season mangrove leaves were most depleted in $\delta^{15}$N (-0.21 ± 0.2 ‰), while dry season mangrove leaves were most enriched (4.75 ± 0.41 ‰).

**Table 3.4** Mean (± SD) $\delta^{15}$N and $\delta^{13}$C signatures of available food items and gastropods from St Lucia Estuary Mouth in both the wet and dry seasons.

| Sources | Wet | | Dry | |
|---|---|---|---|---|
| | $\delta^{15}$N (‰) | $\delta^{13}$C (‰) | $\delta^{15}$N (‰) | $\delta^{13}$C (‰) |
| Mangrove leaves | -0.21 ± 0.20 | -28.81 ± 0.05 | 4.75 ± 0.41 | -28.01 ± 0.05 |
| *Cladophora* sp. | 1.13 ± 0.39 | -22.55 ± 0.19 | 2.26 ± 0.10 | -29.42 ± 0.15 |
| Detritus | 2.16 ± 0.21 | -28.72 ± 0.02 | -8.75 ± 1.56 | -27.64 ± 0.05 |
| MPB | 3.23 ± 0.07 | -22.05 ± 0.20 | 1.18 ± 0.51 | -24.04 ± 0.02 |
| SOM | 2.25 ± 0.27 | -21.56 ± 0.64 | 4.15 ± 0.07 | -21.29 ± 0.33 |
| POM | 3.56 ± 0.36 | -27.08 ± 0.08 | 0.18 ± 0.06 | -27.56 ± 0.17 |
| **Gastropods** | | | | |
| *M. tuberculata* | 3.60 ± 0.03 | -24.41 ± 0.07 | 3.86 ± 0.28 | -27.42 ± 0.02 |
| *C. decollata* | 4.49 ± 0.06 | -20.84 ± 0.05 | 4.48 ± 0.16 | -20.74 ± 0.24 |

Seasonal comparisons (ANOVA) between $\delta^{15}$N and $\delta^{13}$C signatures for gastropods yielded different results for each site. At Lake Nhlange (Table 3.2, Figure 3.2), both *M. tuberculata* ($F_{1,10}$= 186.44, $p < 0.05$) and *T. granifera* ($F_{1,10}$= 28.49, $p < 0.05$) were enriched with $\delta^{13}$C in the wet season. However, $\delta^{15}$N remained relatively constant for both species between seasons (Table 3.2). Although *Cladophora* sp. was available during the wet season, this source made a minimal contribution to the diets of both *M. tuberculata* and *T. granifera* (95 % CIs [0, 0.26] and [0, 0.32] respectively) (Figure 3.2). Detritus dominated the diet of *M. tuberculata* in both the wet and dry seasons (95 % CIs [0.10, 0.51] and [0.23, 0.45] respectively). In the wet season, the diet of *T. granifera* was also dominated by detritus (95 % CI [0, 0.46]) while in the dry season this species consumed a marginally higher proportion of SOM (95 % CI [0.22, 0.50]) (Figure 3.2).
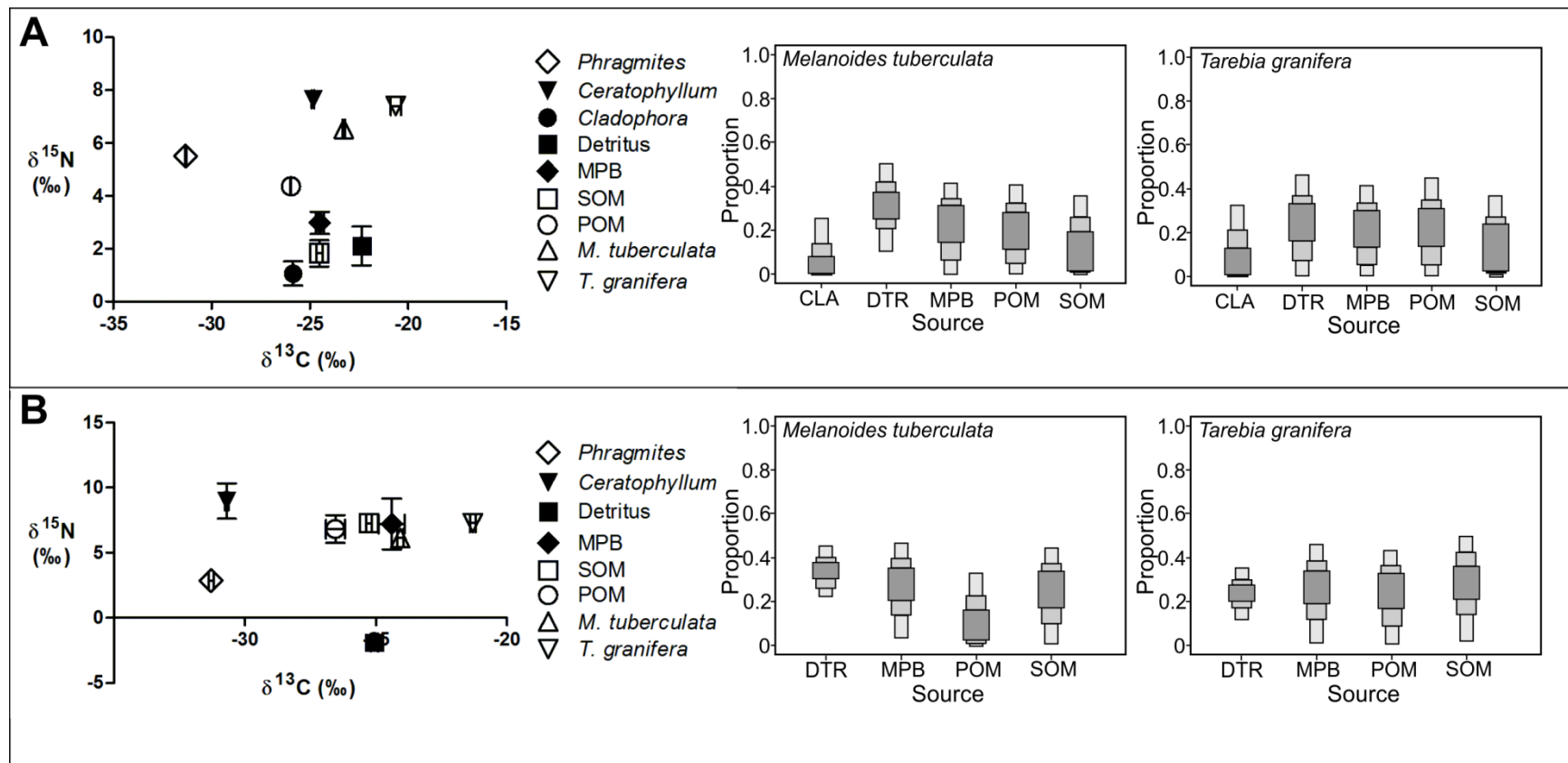
**Figure 3.2** Gastropods and food sources at Lake Nhlange. Stable isotope ($\delta^{15}$N and $\delta^{13}$C) biplots show the signatures (error bars represent SD) of sources and gastropods in both the wet (**A**) and dry (**B**) seasons. SIAR boxplots indicate the proportionate contribution (25, 75, and 95% CIs) of dominant sources to the diet of *M. tuberculata* and *T. granifera* in both seasons. CLA = *Cladophora* sp., DTR = detritus, MPB = microphytobenthos, POM = particulate organic matter, SOM = sedimentary organic matter.

For *M. tuberculata* at the Mpophomeni Stream, both δ$^{15}$N and δ$^{13}$C signatures were similar ($F_{1,10}$= 0.557, *p* > 0.05 and $F_{1,10}$= 0.249, *p* > 0.05 respectively) between seasons (Table 3.3). However, in the dry season, individuals collected from outside patches of *Cladophora* sp. were significantly enriched with both δ$^{15}$N ($F_{1,10}$= 150.18, *p* < 0.05) and δ$^{13}$C ($F_{1,10}$= 56.36, *p* < 0.05) (Table 3.3). *Cladophora* sp. clearly made the largest proportionate contribution towards the diet of *M. tuberculata* in the wet season (95% CI [0.47, 0.84]) (Figure 3.3). In the dry season, MPB contributed towards the diet of individuals both within and outside of *Cladophora* sp. patches (95 % CIs [0.02, 0.45] and [0.02, 0.42] respectively). Furthermore, *Cladophora* sp. had a larger contribution to the diet of individuals collected from within these patches (95 % CI [0.21, 0.40]) in comparison to those collected outside of the patches(95% CI [0.08, 0.29]).

At the St Lucia Estuary Mouth, δ$^{15}$N signatures were similar between seasons for both *M. tuberculata* ($F_{1,10}$= 6.221, *p* > 0.05) and *C. decollata* ($F_{1,10}$= 0.001, *p* > 0.05) (Table 3.4). However, δ$^{13}$C was significantly different ($F_{1,10}$= 3359.3, *p* < 0.05) between seasons for *M. tuberculata* (Table 3.4). The proportionate contribution of various sources to the diet varied seasonally for both gastropod species (Figure 3.4). In the wet season, both detritus and *Cladophora* sp. made prominent contributions towards the diet of *M. tuberculata* (95 % CIs [0.12, 0.43] and [0.04, 0.45] respectively). The proportionate contribution of *Cladophora* sp. to the diet (95 % CI [0.14, 0.51]) was similar in the dry season. POM also made a notable contribution to the diet in the dry season (95 % CI [0, 0.43]). In contrast, in both the wet and the dry seasons detritus made a minimal contribution to the diet of *C. decollata* (95 % CIs [0, 18. 0.24] and [0, 0.24] respectively). Instead, these snails consumed larger proportions of SOM and MPB in both the wet (95 % CIs [0.04, 0.58] and [0.02, 0.49] respectively) and dry (95 % CIs [0.06, 0.60] and [0, 0.43] respectively) seasons.
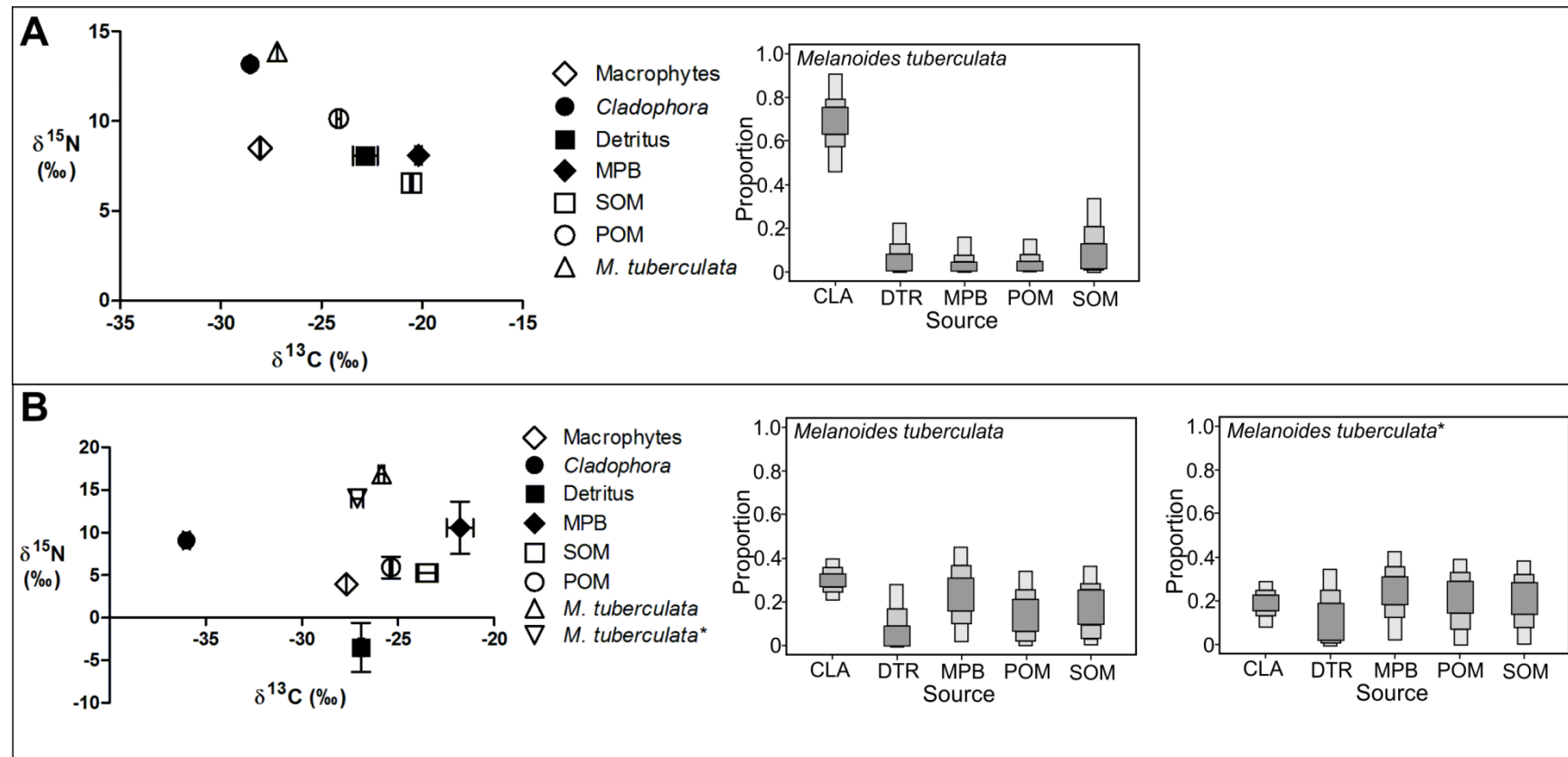
**Figure 3.3** Gastropods and food sources at the Mpophomeni Stream. Stable isotope ($\delta^{15}$N and $\delta^{13}$C) biplots show the signatures (error bars represent SD) of sources and gastropods in both the wet (**A**) and dry (**B**) seasons. SIAR boxplots indicate the proportionate contribution (25, 75, and 95% CIs) of dominant sources to the diet of *M. tuberculata* in both seasons (* indicates snails collected specifically from outside *Cladophora* sp. patches). CLA = *Cladophora* sp., DTR = detritus, MPB = microphytobenthos, POM = particulate organic matter, SOM = sedimentary organic matter.
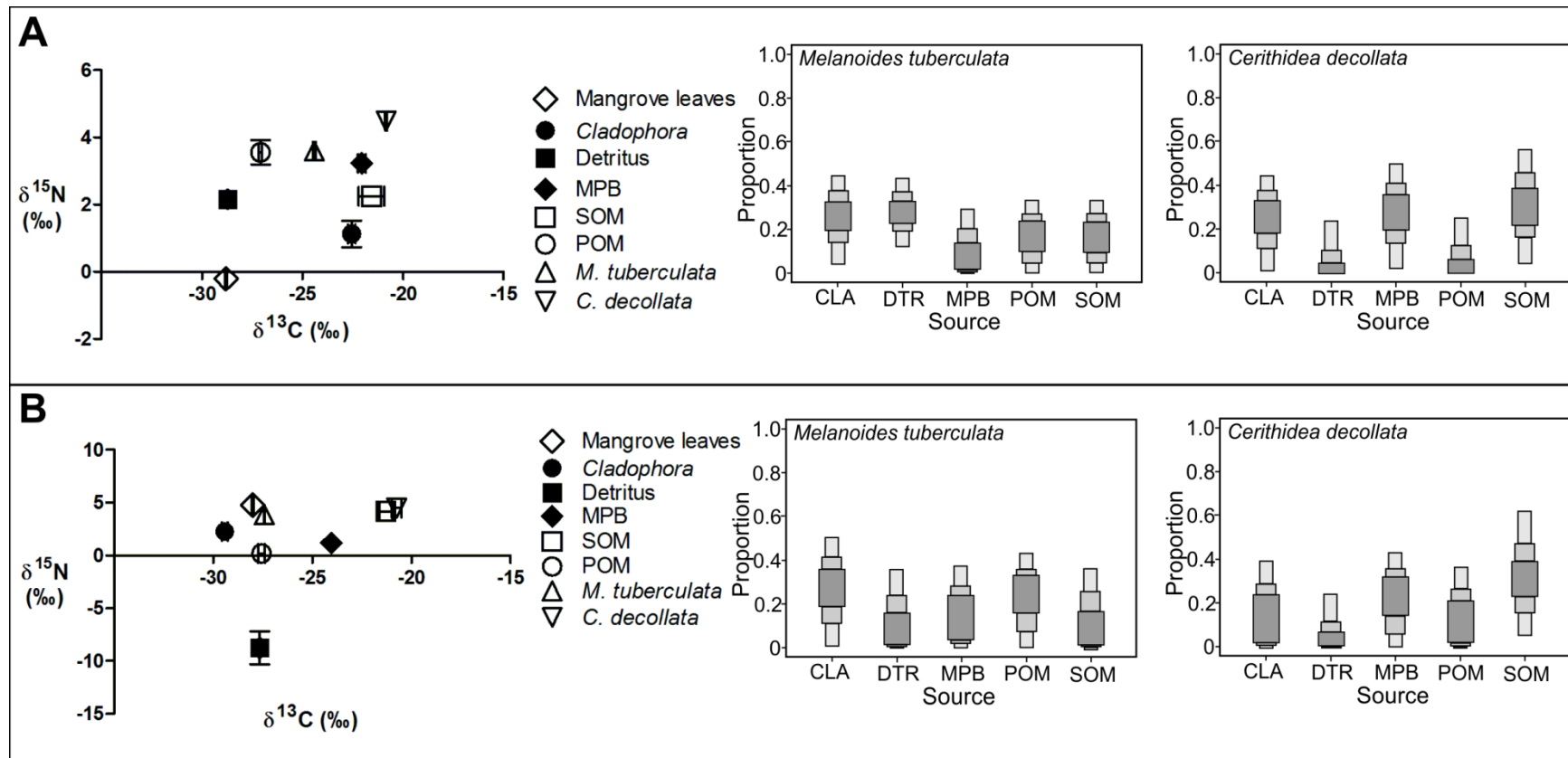
**Figure 3.4** Gastropods and food sources at St Lucia Estuary Mouth. Stable isotope ($\delta^{15}N$ and $\delta^{13}C$) biplots show the signatures (error bars represent SD) of sources and gastropods in both the wet (**A**) and dry (**B**) seasons. SIAR boxplots indicate the proportionate contribution (25, 75, and 95% CIs) of dominant sources to the diet of *M. tuberculata* and *C. decollata* in both seasons. CLA = *Cladophora* sp., DTR = detritus, MPB = microphytobenthos, POM = particulate organic matter, SOM = sedimentary organic matter.

*3.4 Discussion*

*Melanoides tuberculata* has previously been incorporated into broader stable isotope studies (Coat et al. 2009; Peer et al. 2015b). However, this is the first to focus on the potential dietary plasticity and niche breadth of this species. *Melanoides tuberculata* is well recognized as a generalist deposit feeder that indiscriminately consumes microalgae, detritus and periphyton (Madsen 1992; Vasconcelos et al. 2013). Besides supporting these observations, we also found that the diet of *M. tuberculata* is to some extent influenced by resource availability, limiting the potential for opportunistic or optimal foraging strategies.

### *3.4.1 Variation in diet in response to resource availability*

The feeding and mobility habits of benthic gastropods limit the number of sources accessible to them for foraging. As such, similar sources were sampled as potential dietary components for *M. tuberculata* in each of the different habitats. The diet of *M. tuberculata* was however variable between sites. This may indicate potential adaptive and plastic traits related to feeding ecology. As a habitat generalist, *M. tuberculata* occurs in diverse environments that vary in terms of hydroperiod, salinity, substrate type, and water flow (Appleton 1996; de Kock & Wolmarans 2009; Perissinotto et al. 2014). The persistence of *M. tuberculata* under these different conditions directly relates to the ability of this species to cope with varying levels of resource availability.

Availability of benthic resources is influenced by numerous factors, gastropod grazing being one of the most prominent (Blanchard et al. 2001; Vasconcelos et al. 2013). However, environmental parameters also significantly influence resource availability. In shallow freshwater environments irradiance and nutrient availability directly affect the productivity and biomass of periphyton (Rosemond et al. 2000). At the Mpophomeni Stream, which is well shaded within the established sand forest, nutrient availability varies seasonally in relation to rainfall and runoff (Peer et al. 2015b). It has also been established that the $\delta^{15}$N signatures of consumers is related to whether the ecosystem as a whole is eutrophic or oligotrophic (Woodland et al. 2012). However, at the Mpophomeni Stream the source of $\delta^{15}$N enrichment has not yet been identified. In the dry season, there was an observable decrease in the cover extent of the filamentous *Cladophora* sp. that may have been related to

reduced nutrient inputs. At this time, snails consumed a larger proportion of MPB both within and outside of *Cladophora* sp. patches. As MPB biomass and productivity is strongly negatively correlated with the presence of filamentous algae (Nozaki 2001), it is apparent that *M. tuberculata* most likely consumes more MPB in the dry season as it becomes more available.

The seasonal comparison of diet for *M. tuberculata* at the St Lucia Estuary Mouth also showed a clear difference in the proportionate contributions of detritus and POM. Within mangrove forests, mangrove leaf litter and benthic microalgae are the dominant sources of autochthonous carbon, while phytoplankton and seagrass detritus provide supplementary sources (Kristensen et al. 2008). At the time of the study, the detrital material collected at St Lucia Estuary Mouth consisted almost entirely of decomposing mangrove leaves. The severely depleted $\delta^{15}N$ signature for detritus in the dry season is worth noting, although the cause was not investigated as part of this study. Microbial processes generally enrich detrital sources in mangroves (Tremblay & Benner 2006), while physical processes such as leaching can drive depletion (Hill & McQuaid 2009). This could also influence the availability of this resource to gastropod consumers. Mangrove leaf fall varies seasonally in this subtropical region, with increased leaf fall occurring during the wet summer months (Steinke 1999). In contrast, POM would be consistently available. The increased proportionate contribution of POM to the diet of *M. tuberculata* during the dry season may simply be due to increased settling of suspended particulate material on the substrate due to seasonally reduced flow (as a consequence of lower rainfall) within the channel. In contrast, at Lake Nhlange, although the filamentous *Cladophora* sp. was available during the wet season, this source only made a minimal contribution to the diet of *M. tuberculata*. In this case, the *Cladophora* sp. was most likely not readily consumed because it was not easily accessible to the snails in deeper water. Interestingly, although *M. tuberculata* was associated with the submerged macrophyte, *Ceratophyllum* sp., at Lake Nhlange this plant did not make any detectable contribution to the diet of these snails.

## 3.4.2 Variation in $\delta^{15}N$ and trophic plasticity

Large ecosystem-scale stable isotope studies usually aim to provide an assessment of food web dynamics by using $\delta^{15}N$ (and the appropriate enrichment factors) to determine trophic position for secondary and tertiary consumers (Vander Zanden & Rasmussen 2001). Generally, $\delta^{15}N$ signatures of consumers are directly related to their trophic position as a consequence of isotopic fractionation through each trophic level (Post 2002b). However, because organisms such as gastropods are unanimously recognized as primary consumers, temporal and spatial differences in $\delta^{15}N$ signatures are not truly a reflection of their trophic level (Riera 2010). Instead, these differences in $\delta^{15}N$ reflect high diversity in the diet as a number of different sources can be incorporated over time. The variation associated with $\delta^{15}N$ can therefore be used to assess trophic niche width (Bearhop et al. 2004).

*Melanoides tuberculata* did exhibit generalist feeding habits, as shown by the temporal and spatial differences in the proportionate contribution of various sources to the diet. Furthermore, the variance associated with $\delta^{15}N$ was always greater in the dry season. A greater diversity of sources is therefore incorporated into the diet at this time. This may reflect a seasonal change in resource partitioning to optimize utilization when there is a change in availability (possibly as a consequence of less favourable environmental conditions). Although resources are most optimally exploited in communities that have a higher diversity of specialist consumers (Finke & Snyder 2008), it has been proposed that the limitations of "generalist" consumers faced with intraspecific competition can be overcome through individual-level dietary diversity (Bolnick et al. 2002; Doi et al. 2010). Although the overall trophic niche of *M. tuberculata* is relatively broad, it is likely that individual snails utilize the different sources in different proportions and at variable rates. These trends have previously been reported for stream macroinvertebrates under variable resource levels (Rosi-Marshall & Wallace 2002). Habitat heterogeneity and differences in microhabitat resource availability may explain these individual-level differences in diet (Doi et al. 2010). This was evident at the Mpophomeni Stream, as the diet of snails varied over a small spatial scale. Trophic plasticity should therefore not be considered as a singular trait exhibited by a species, but rather as a flexible measure of potential resource use that is largely influenced by external factors.

### 3.4.3 Potential competitive interactions

As the variation associated with $\delta^{15}$N is used to assess trophic niche width, it can also be used to infer on potential competition (Svanbäck & Bolnick 2007). Species with overlapping isotopic signatures would occupy similar trophic niches and are therefore considered to be in competition for similar resources. The stable isotope biplots show a clear difference in the $\delta^{15}$N and $\delta^{13}$C signatures for *M. tuberculata* and *C. decollata* at the St Lucia Estuary Mouth, indicating minimal dietary overlap. In contrast, at Lake Nhlange, although *M. tuberculata* and *T. granifera* did not have definitively overlapping isotopic signatures, there were no clear differences in the proportionate contributions of the various sources to the diets of these two species. Both MPB and SOM made similar proportionate contributions to the diets of these species in both seasons. Previous work has suggested that these species may be competing for MPB at this site as they are able to feed at comparable rates (Miranda et al. 2011; Raw et al. 2016b). As Lake Nhlange is oligotrophic, it appears that detrital sources may be consumed more readily by both species despite this source being of poorer nutritional quality in comparison to MPB.

Invasive gastropods have been repeatedly reported as generalist consumers that efficiently compete with native species through resource exploitation (Miranda et al. 2011; Hill et al. 2015; Larson & Black 2016). Both *M. tuberculata* and *T. granifera* have been assessed as efficient competitors following their establishment as alien species in new habitats (Pointier et al. 2011; Miranda & Perissinotto 2012). However, the competitive interactions between *M. tuberculata* and *T. granifera* remain unclear and are yet to be fully investigated. The introduction and establishment of *T. granifera* within coastal lakes of the iSimangaliso Wetland Park has been associated with the decline of historic *M. tuberculata* populations, with the exception of those from Lake Nhlange (Miranda & Perissinotto 2014). Differences in behaviour have also been recorded between *M. tuberculata* from Lake Nhlange and those from St Lucia Estuary Mouth (Raw et al. 2015). As individuals from Lake Nhlange appear cryptic in their morphology and potentially have Asiatic origins, a shared evolutionary history with *T. granifera* may explain these variations. Asiatic morphs of *M. tuberculata* may therefore be more efficient competitors than their African

counterparts. This has important implications for human-mediated introductions of this species, even within its native range.

## 3.5 Conclusion

The invasion success of *M. tuberculata* is expected to be influenced by a combination of traits relating to tolerance, feeding and reproductive capacity. Here we found that diet was variable and was largely dependent on resource availability. Seasonal differences in diet indicate that the species exploits different resources at variable rates. Future work should focus on determining the degree to which individual-level dietary diversity contributes to the species overall generalist niche.

# Chapter 4: Feeding dynamics of *Terebralia palustris*

## 4.1 Introduction

Benthic microalgal assemblages, collectively termed microphytobenthos (MPB), which occur within the surface sediment of shallow marine and freshwater environments, have been largely acknowledged for their significant contribution towards primary productivity (MacIntyre et al. 1996). In contrast, within tropical mangrove forests, the contribution of MPB to primary productivity is expected to be minimal due to growth limitation by shading and the high concentrations of tannins within the muddy sediments (Alongi 1994). Macrophyte-derived detritus has therefore been considered as the major basal resource that is available for benthic primary consumers in these habitats (Bouillon et al. 2004b). However, numerous studies have shown that the contribution of mangrove detritus to higher trophic levels is highly variable (Kruitwagen et al. 2010; Giarrizzo et al. 2011). Alternative autochthonous and allochthonous basal resources have subsequently been identified as providing nutrition to primary consumers that serve as trophic links within mangrove ecosystems (Newell et al. 1995; Bouillon et al. 2002; Abrantes & Sheaves 2009). One such autochthonous source is MPB (Bouillon et al. 2004a), which is a crucial component in comparable estuarine mud flat and salt marsh ecosystems (Sullivan & Currin 2000; Lemley et al. 2016)

The prevalence of MPB within mangrove forests is largely dependent on the physical environment and is therefore highly variable between and within these systems. Larger grain sizes and lower particulate organic content of the sediment are correlated with increased MPB biomass (Alongi 1994; Cahoon et al. 1999). The presence of these conditions in mangrove habitats will be largely dependent on the local geomorphological features. The required sediment and environmental characteristics that favour MPB are therefore generally found in the lower intertidal

region. This zone is favourable for MPB because it is regularly flushed by the tide, there is minimal shading by the canopy and a lower density of pneumatophores prevents the accumulation of fine particulate material (Liu et al. 2013). The resources consumed by mangrove macrofauna are largely dependent on their microhabitat and considerable variation may exist across relatively small spatial scales (Guest & Connolly 2004; Kon et al. 2011; Pratt et al. 2015). Therefore, consumption of MPB in mangrove habitats would be limited to benthic primary consumers that occupy the lower intertidal zone, including gastropod molluscs and brachyurans such as fiddler crabs (Macnae 1969). The importance of MPB as an autochthonous source within mangroves is also expected to vary across a latitudinal gradient. Leaf fall is largely correlated with rainfall patterns and therefore varies between regions (Tomlinson 1999). Decomposition rates of mangrove leaf litter are significantly influenced by temperature, and thus by seasonality (Mackey & Smail 1996). Seasonality at subtropical latitudes therefore has a large effect on the availability of mangrove leaf litter for consumption by deposit feeders. Alternative resources may therefore be of higher importance to benthic consumers in these regions (Gladstone-Gallagher et al. 2014).

*Terebralia palustris* (Linnaeus, 1767), the largest and most widespread of the extant Potamididae family (Houbrick 1991; Strong et al. 2011), is considered a major component of Indo-Pacific mangrove macrofauna assemblages (Cannicci et al. 2008). A large number of studies have therefore investigated the ecological role of *T. palustris*. Most notably, adult *T. palustris* are known to be avid consumers of freshly fallen mangrove leaf litter (Slim et al. 1997; Fratini et al. 2000), as an ontogenetic change in the structure of the radula enables them to mechanically graze on these resources (Houbrick 1991). Generally, juveniles occur within the lower intertidal zone while adults occupy higher regions of the shore, but this is not always the case (Fratini et al. 2004). The spatial segregation of *T. palustris* within the mangroves has however been related to the ontogenetic niche partitioning of the diet for this species. Juvenile *T. palustris* that occupy the lower intertidal zone have been reported to consume mainly MPB (Pape et al. 2008; Penha-Lopes et al. 2009). In contrast, juveniles that occur in higher shore regions when there is no spatial segregation between age classes have detritus-based diets (Fratini et al. 2004). The ecological role of *T. palustris* as a benthic consumer within Indo-Pacific mangroves is therefore

complex and variable, particularly as these gastropods are able to attain very high densities (Pape et al. 2008; Penha-Lopes et al. 2009; Raw et al. 2014). The potential impact that grazing may have on MPB resources in intertidal mangrove habitats should therefore be quantified.

The aim of this study was to provide an assessment on the rates at which juvenile *T. palustris* are able to consume MPB. A seasonal comparison of feeding activity was also made as this study was carried out within an estuarine mangrove ecosystem at a subtropical location that is characterized by different rainfall periods. Feeding activity was therefore hypothesized to vary at two different temporal scales. Firstly, for a large number of intertidal organisms, feeding activity is limited by abiotic (e.g. desiccation) and biotic (e.g. predation) factors (Chapperon & Seuront 2013). Therefore, it was hypothesized that the feeding activity of *T. palustris* juveniles would vary over the course of 24 h depending on light and tidal conditions. Secondly, seasonal rainfall patterns have a large impact on nutrient availability, and thus on primary productivity within subtropical estuarine environments (Whitfield et al. 2012). Therefore, it was hypothesized that the consumption of MPB by *T. palustris* would be influenced by the availability of this resource and would therefore vary seasonally.

## 4.2 Materials and Methods

### 4.2.1 Site description and gastropod collection

The Kosi Bay estuarine lake system (26°53'37''S; 32°52'52''E) (Figure 1.3) is one of three major Ramsar wetlands within the iSimangaliso Wetland Park, a UNESCO World Heritage Site on the northern coast of the KwaZulu-Natal Province of South Africa. There is an extensive mangrove forest on the south shore of the sandy embayment at the mouth. However, the mangrove trees in this area are stunted with an average height of below 300 cm and an average diameter at breast height (DBH) of less than 4 cm (Rajkaran & Adams 2011).This is the result of a weak foundation as the area is characterized by a lack of mud and fine sediment deposits (Begg 1980; Wright et al. 1997).

The relatively flat and sandy physical features of Kosi Bay are therefore suitable for the establishment of MPB communities. This locality is one of the southernmost limits for the global distribution of *T. palustris* (Houbrick 1991) and previous assessments have shown that there is a spatial segregation of size classes within the mangrove habitat (Raw et al. 2014). The size at maturity for *T. palustris* varies depending on environmental conditions (Houbrick 1991; Nishihira et al. 2002) but the ontogenetic dietary shift generally occurs around 50 mm total shell length. As the population structure at Kosi Bay closely resembles that reported by Penha-Lopes et al. (2009) in Mozambique, we only used snails < 30 mm total shell length as representatives of juvenile deposit feeders. These individuals were collected for experiments from amongst the pneumatophores on the seaward side of the mangrove area dominated by *Rhizophora mucronata* and *Brugueira gymnorhiza* trees*.*

As there are two climatic seasons characterized by rainfall patterns in this subtropical region, experiments were carried out in February 2015 (late austral summer, wet season) (mean monthly rainfall of 150 mm – Ndlovu & Demlie 2016) and in July 2015 (mid austral winter, dry season) (mean monthly rainfall of 50 mm – Ndlovu & Demlie 2016), to allow for seasonal temporal comparisons. The South African coastline is classified as microtidal (Cooper 2000; Harris et al. 2011), therefore both experiments were carried out during a full moon phase, beginning on the first day with the spring low tide occurring in the morning.

The physico-chemical parameters of salinity, temperature (°C), dissolved oxygen (mg. L$^{-1}$), pH and turbidity (NTU) were measured in the water column of a narrow channel adjacent to the study site upon arrival using a YSI 6600-V2 multiprobe system.

### 4.2.2 Gastropod grazing experiment

The natural variations in gut pigment content were estimated by collecting five gastropods every 3 hours over a 24 hour period. After collection, the gastropods were dissected and their whole guts were placed in 8 mL of 90 % acetone. The samples were stored in darkness at 4 °C for 48 hours to allow for chlorophyll *a* extraction of the gut contents. The total pigments (chlorophyll *a* and phaeopigments) were measured with a 10-AU Turner Designs fluorometer using the non-acidification method (Welschmeyer 1994). These measurements were then expressed as chlorophyll-*a* equivalents (µg pigm. ind$^{-1}$).

The relationship between gut chlorophyll and shell height (SH) was compared between seasons using an Analysis of Covariance, as larger individuals would be expected to consume greater quantities of microalgae. However, the linear relationship, as indicated by linear regression, between SH and gut chlorophyll was different between seasons ($F_{(1,40)}$ = 3.563, $p$ = 0.067 in the wet season and $F_{(1,43)}$ = 1.371, $p$ = 0.248 in the dry season). Therefore, gut chlorophyll measurements were size-standardized across both seasons (to allow for suitable comparisons) using the mean SH as follows:

$$Gut\ pigment\ content = chlorophyll_a\ equivalents \times \left(\frac{mean\ SH}{individual\ SH}\right)$$

Differences in the average gut pigment content between seasons were compared using an independent samples *t*-test. For each season, the gut pigment content was compared between tidal phases (Low, Flood, High, Ebb) and between time periods (Day, Night) using a two-way ANOVA. Statistical comparisons were performed using the "car" package (Fox & Weisberg 2014) in R v 2.11.1 (R Development Core Team 2010) for Windows after testing that the parametric assumptions (Shapiro Wilks test for normality, Levene's test for homoscedasticity) were met.

The feeding rate of *T. palustris* juveniles was estimated with the *in situ* gut fluorescence technique (Mackas & Bohrer 1976). This method has previously been successfully adapted for gastropods (Miranda et al. 2011) and allows for the daily ingestion rate ($I$, mg pigm. $ind^{-1}$ $day^{-1}$) to be estimated as follows:

$$I = \frac{kG}{(1-b)}$$

Here $k$ is the gut evacuation rate ($h^{-1}$), $G$ is the integrated average size-standardized gut pigment concentration (mg pigm. $ind^{-1}$) over 24 h and $b$ is an index of pigment consumption/digestion within the gut (Wang & Conover 1986). The calculated ingestion rates for *T. palustris* juveniles were compared between the two rainfall seasons.

### Gut evacuation rate (k)

Freshly collected *T. palustris* juveniles were brushed and rinsed to remove sediment and epiphytes from their shells before being isolated in 250 mL plastic jars. Individual snails were each placed in 100 mL of water that had been collected *in situ* and filtered through a Whatman GF/F (0.7 μm) and a Millipore filter (0.2 μm) to ensure removal of all particulate material. Non-fluorescent cornstarch was added to the filtered water. This provided a food source to promote continuous gut evacuation (Pakhomov & Perissinotto 1996; Carrasco & Perissinotto 2010). Five individuals were processed (as outlined above) to provide an estimate of gut pigment content at the start of the experiment. For the first hour of the experiment, five individuals were removed from their jars and processed every 10 minutes. For the final two hours (total duration 3 h), five individuals were processed every 30 minutes. As the snails continuously consumed the cornstarch, their gut pigment content decreased over time. The linear slope of this change in gut pigment over time was then used to estimate the gut evacuation rate (Pakhomov & Perissinotto 1996). A maximum gut evacuation rate ($k_{max}$) was calculated from the first 30 min of the experiment. This value was subsequently used to estimate a maximum ingestion rate ($I_{max}$).

*Pigment consumption/digestion (b)*

A two compartment pigment budget approach (Mayzaud & Razouls 1992) was used to estimate the efficiency at which *T. palustris* is able to consume/digest photosynthetic pigments within the gut. Twenty freshly collected individuals were isolated as described above in 600 mL plastic jars containing 200 mL of the filtered estuarine water and cornstarch mixture. After the first 12 hours, the water-cornstarch solution was replaced to maintain favourable conditions within the jars. After the second 12 hours (total duration 24 h), ten of the individuals were processed as described above to estimate their residual gut pigment content. The remaining ten individuals were each placed in a 2 L bucket containing 200 mL of pure filtered estuarine water. MPB that had been collected from the substrate at the collection site were suspended in filtered estuarine water and provided in aliquots of 20 mL to each bucket. A series of 10 control buckets were set up in the same manner but without the addition of gastropods. The snails were allowed to consume the settled microalgae for a period of one hour. After this time period the snails were processed and the water from each respective bucket (including the controls) was filtered separately (Whatman GF/F 0.7 μm). The filters were placed in 8 mL of 90 % acetone for extraction of chlorophyll-*a*. The snails did not produce any faecal pellets during the time spent feeding on the microalgae. The efficiency of *T. palustris* to consume/digest pigments within the gut was therefore calculated as the difference in pigment concentration between the water and snail compartments.

### 4.2.3 Gastropod abundance and impact on microphytobenthos

Gastropod abundance was estimated in triplicate using a 0.25 m$^2$ quadrat. The number of individuals within the frame was counted to estimate population density (ind.m$^{-2}$). This was replicated three times within the lower region of the shore on each sampling occasion. The average population density was then multiplied by the calculated average and maximum ingestion rates in order to estimate the potential average and maximum feeding impacts, respectively (*FI* and *FI*$_{max}$ in mg pigm.m$^{-2}$d$^{-1}$).

The amount of microphytobenthos (MPB) available on the substrate (mg pigm.m$^{-2}$) was estimated in triplicate. A 20 mm internal diameter corer was used to collect sediment cores of which the upper 2 cm containing the MPB was retained. Each

sample was placed in 30 mL of 90 % acetone at 4 °C for 48 hours to allow for chlorophyll extraction. After this period, the pigment concentrations were measured fluorometrically as described above. The calculated feeding impact was then expressed as a percentage of the MPB available for consumption by the snails. Per capita resource availability (mg pigm. $m^{-2}$ $ind^{-1}$) was also calculated for comparison between seasons.

*4.3 Results*

*4.3.1 Seasonal variation in environmental conditions*

There were clear seasonal trends in the environmental conditions at Kosi Bay, as indicated by the measured physico-chemical parameters (Table 4.1). As expected, temperature was considerably lower at the time of the winter experiment. As rainfall is higher in summer, a lower salinity was recorded in the estuary during this season, while in winter the environmental conditions reflected characteristics of the marine environment.

**Table 4.1** Average (± SE) physico-chemical parameters measured in each season from the water column of the Kosi Bay estuary. The average (± SE) shell height (SH) of individuals collected on each sampling occasion is also provided.

|  | **Austral summer** **(February 2015)** | **Austral winter** **(July 2015)** |
|---|---|---|
| **Time** | 12h00 | 13h00 |
| **Temperature (°C)** | 32.9 ± 0.2 | 24.5± 0.2 |
| **Salinity** | 23.6± 0.4 | 35.2 ± 0.1 |
| **pH** | 8.2± 0.2 | 8.7± 0.02 |
| **Turbidity (NTU)** | 2.3 ± 0.1 | 1.8 ± 0.8 |
| **Dissolved oxygen (mg.L$^{-1}$)** | 8.8± 0.7 | 9.9 ± 0.3 |
| **Shell height (mm)** | 20.3 ± 2.5 | 24.7± 3.7 |

*Terebralia palustris* juveniles that were collected for the winter experiment were also larger on average than those collected the previous summer (Table 4.1).

*4.3.2 Seasonal, diel and tidal variations in gut pigment content*

The average gut pigment content of *T. palustris* varied between seasons, between day and night hours and also between tidal phases. Seasonal differences in daily average gut pigment content were significant ($t = -3.878$, *df* = 85, *p* = 0.0002) with higher gut pigment content recorded from snails collected during the drier winter period (Table 4.2, Figure 4.1). Although the average gut pigment content of *T.*

*palustris* varied throughout the day (Figure 4.1), a significant difference ($t = 3.072$, *df* = 38, *p* = 0.004) between day and night hours was only found in winter.

The average gut pigment content measured during each tidal phase was different between seasons. In summer, the gut pigment content was highest during high tide and lowest at flood tide (Table 4.2). In contrast, in winter the highest gut pigment content was recorded from snails collected at ebb tide and the lowest was recorded during high tide (Table 4.2). However, there were no significant differences for gut pigment content between tidal phases in summer ($F_{3,37} = 2.069$ $p = 0.123$) or in winter ($F_{3,40} = 0.213$, $p = 0.887$) (Table 4.2).

When considering time of day (Day, Night) and tidal phase (Low, Flood, High, Ebb) as categorical predictors of gut pigment content there were no significant interactions between these factors either in summer ($F_{3,37} = 1.527$ $p = 0.228$) or winter ($F_{3,40} = 2.500$, $p = 0.077$). In summer, gut pigment content was generally similar between corresponding day and night tidal phases (Figure 4.1C). In contrast, during the winter experiment there was a clear, although not statistically significant, difference in gut content between day and night tidal phases (Figure 4.1D).
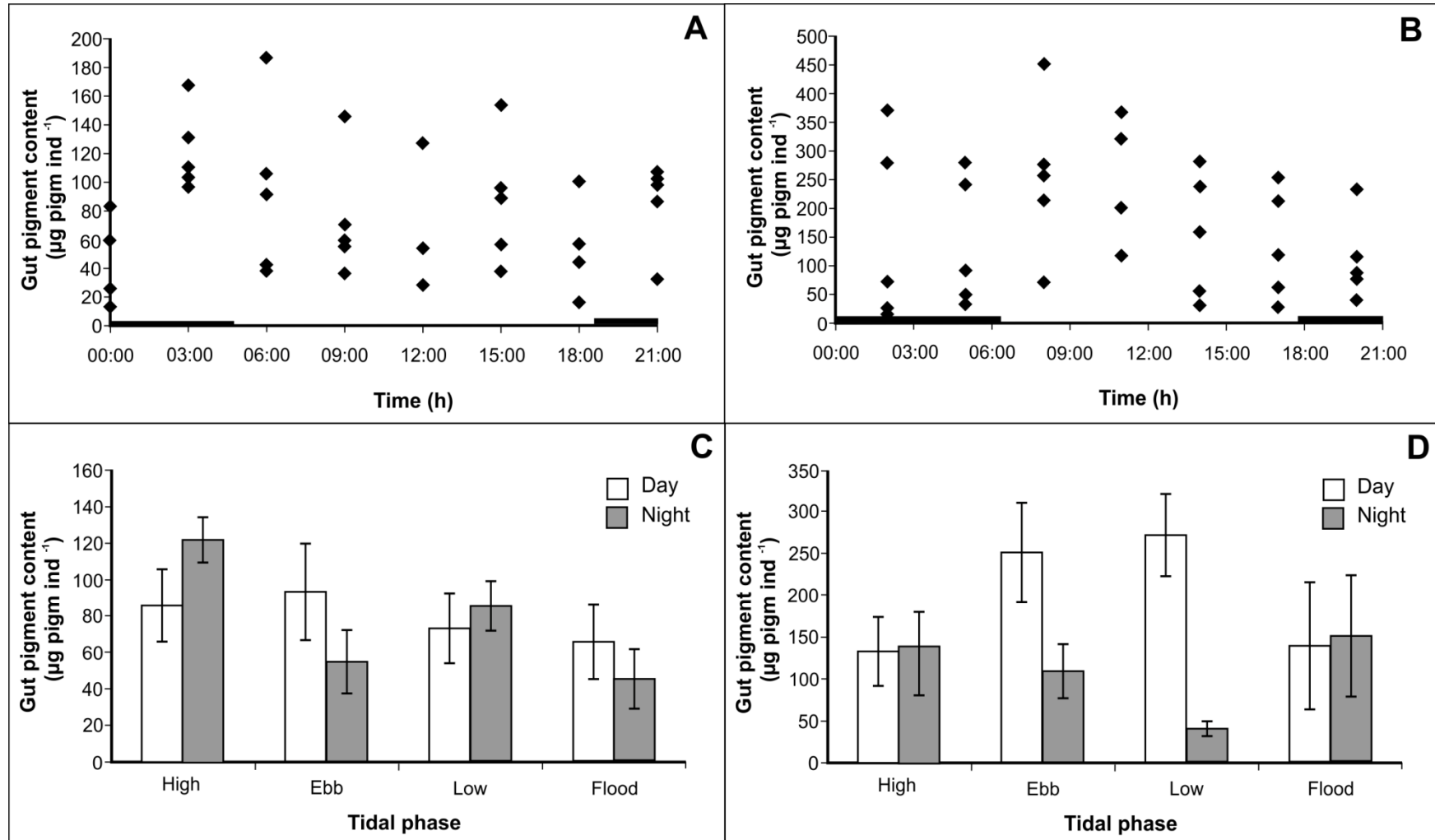
**Figure 4.1** Diel and tidal variations in gut pigment content for *Terebralia palustris* at Kosi Bay recorded in austral summer (**A, C**) and austral winter (**B, D**). Thicker line on horizontal axes (**A, B**) indicates night time hours. Error bars (**C, D**) represent the standard error of the mean.

**Table 4.2** Seasonal, diel and tidal variations in the average (± SE) gut pigment content measured for *T. palustris* juveniles in summer and winter of 2015 at Kosi Bay, South Africa.

| | Gut pigment content (µg pigm.ind$^{-1}$) | | | | | | |
|---|---|---|---|---|---|---|---|
| | | **24 h cycle** | | **Diel variation** | | **Tidal variation** | |
| | | **Day** | **Night** | **High** | **Ebb** | **Low** | **Flood** |
| **Summer** | 76.1 ± 6.6 | 76.1 ± 9.1 | 87.2 ± 11.2 | 104.3 ± 12.6 | 76.2 ± 17.2 | 79.5 ± 11.2 | 56.1 ± 12.9 |
| **Winter** | 153.9 ± 18.9 | 225.6 ± 31.9 | 113.9 ± 20.7 | 135.6 ± 31.4 | 180.7 ± 40.4 | 156.0 ± 45.7 | 144.6 ± 49.3 |

*4.3.3 Ingestion rates and feeding impact*

The feeding parameters that were used to calculate ingestion rate varied seasonally for juvenile *T. palustris* (Table 4.3). A larger quantity of chlorophyll was consumed by snails over a 24 h period in winter, as indicated by the integrated gut pigment content (*G*). However, a faster gut evacuation rate was recorded during the summer experiment (Table 4.3, Figure 4.2). The efficiency at which snails were able to consume/digest pigments within the gut also varied between seasons (Table 4.3). The higher consumption/digestion efficiency in winter, coupled with the larger quantity of chlorophyll consumed (*G*), resulted in a faster calculated ingestion rate for snails in this drier season (Table 4.3).

**Table 4.3** Integrated size-standardized average gut pigment content (*G*) measured over 24 h; maximum gut evacuation rate ($k_{max}$) and corresponding gut passage time (GPT); and pigment consumption/digestion efficiency (*b*) calculated for for juvenile *Terebralia palustris* at Kosi Bay, South Africa in both seasons.

| Season | (*G*) | ($k_{max}$) | GPT | (*b*) |
|---|---|---|---|---|
| | (mg pigm.ind$^{-1}$) | (h$^{-1}$) | (h) | (%) |
| **Summer** | 0.63 | 0.84 | 1.19 | 35.9 |
| **Winter** | 1.25 | 0.66 | 1.52 | 51.0 |
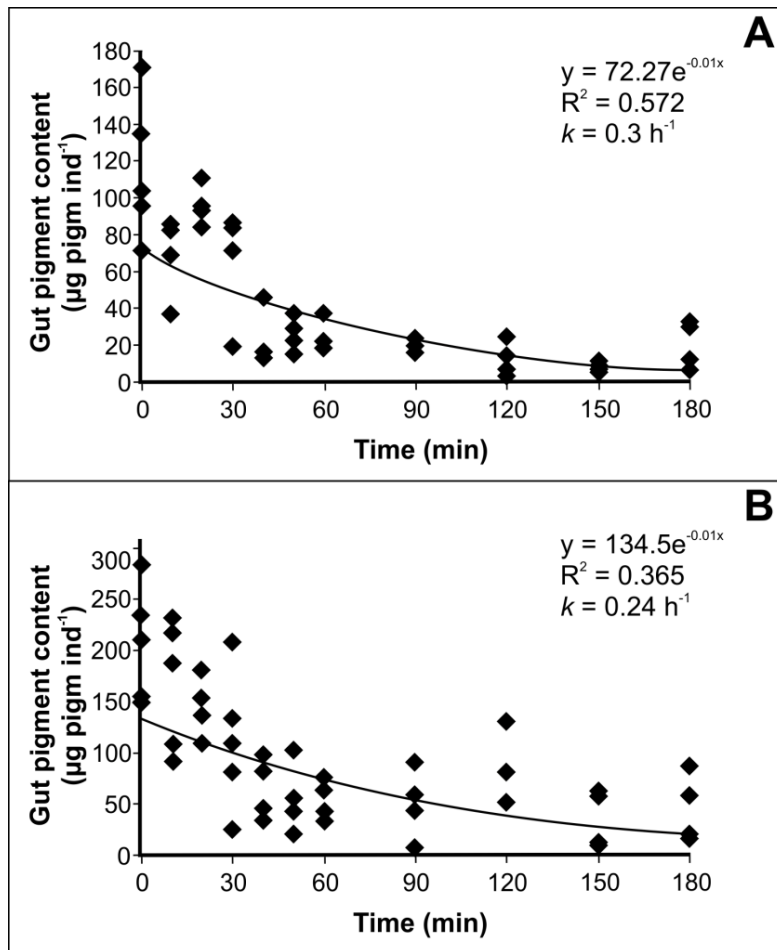
**Figure 4.2** Decline in gut pigment content over a three hour period for *Terebralia palustris* in austral summer ($t_0$ = 15:00)(**A**) and in austral winter ($t_0$ = 14:00)(**B**) at Kosi Bay. The average gut evacuation rate (*k*) was calculated from the linear slope of the log-transformed gut pigment values measured over the 180 min experiment.

In winter, *T. palustris* occurred at a higher population density (Table 4.4). As the calculated ingestion rate was also higher during this season, the potential feeding impact was higher in winter (Table 4.4). The total available biomass of MPB was similar between seasons. The potential daily consumption of MPB was much higher in winter and this resulted in lower per capita resource availability in this season (Table 4.4).

**Table 4.4** Calculated average and maximum values for feeding impact of *Terebralia palustris* as estimated from population density and calculated ingestion rates ($I$, $I_{max}$) at Kosi Bay, South Africa. Microphytobenthos (MPB) biomass (average ± SE) and per-capita availability of MPB for each season are also provided.

| Season | Density | Ingestion rate | | Feeding impact | | MPB biomass | Daily consumption | Per capita available MPB |
|--------|---------|----------------|---|----------------|---|-------------|-------------------|--------------------------|
| | $(ind.m^{-2})$ | $(mg\ pigm.ind^{-1}\ d^{-1})$ | | $(mg\ pigm.\ m^{-1}\ d^{-1})$ | | $(mg\ pigm.\ m^{-2})$ | (%) | $(mg\ pigm.\ m^{-2}\ ind^{-1})$ |
| | | $I$ | $I_{max}$ | $FI$ | $FI_{max}$ | | | |
| **Summer** | 60 ± 20 | 0.29 | 0.82 | 17.62 | 49.34 | 116.77 ± 17.02 | 15.1 | 1.95 |
| **Winter** | 100 ± 40 | 0.61 | 1.67 | 61.03 | 167.82 | 120.42 ± 16.33 | 50.7 | 1.20 |

*4.4 Discussion*

*Terebralia palustris* is a conspicuous component of Indo-Pacific mangroves, because of its large size and the high densities at which at occurs (Fratini et al. 2004; Pape et al. 2008; Penha-Lopes et al. 2009). The ecological importance of this species to these systems has already been highlighted as adult snails consume a significant proportion of mangrove leaf litter and are therefore in direct competition with large sesarmid brachyurans for food resources (Slim et al. 1997; Fratini et al. 2000). Furthermore, their movement on the surface of the sediment has a significant impact on meiofaunal and bacterial communities (Carlén & Ólafsson 2002), and their deposit-feeding activities have much larger scale consequences in terms of nutrient dynamics and recycling of carbon (Cannicci et al. 2008; Penha-Lopes et al. 2010). This is however the first quantitative report on the rates at which juvenile *T. palustris* are able to consume available benthic photosynthetic resources in the form of MPB. Differences in the feeding activity of *T. palustris* did not strictly correlate with daily environmental fluctuations; however differences across the seasonal temporal scale were more predictable. There was, however, some variability that could be associated with differences in resource availability between seasons.

### 4.4.1 Temporal differences in feeding dynamics

Daily feeding activity (as indicated by gut pigment content) of *T. palustris* was expected to vary with tidal and light conditions; however this was not always the case. Higher environmental temperatures coupled with increased insolation and longer emergence times during day time spring low tides in the summer significantly raise the risk of desiccation to intertidal gastropods (McMahon & Britton 1983; Davenport & Davenport 2005). In the case of *T. palustris*, individuals generally aggregate in shady areas or within shallow pools during day time low tides (Slim et al. 1997; Wells & Lalli 2003). However, at Kosi Bay we found that the feeding activity of juvenile *T. palustris* remained relatively constant irrespective of tidal and light conditions in the summer season.

Nocturnal foraging by intertidal gastropods is generally driven by lower desiccation stress. Predation risk may however be higher for these periods, particularly during full moon phases. Larger *T. palustris* do forage in all light and tidal conditions (Fratini et al. 2001; Fratini et al. 2008). However, they generally occur within well shaded

regions of the mangroves and due to their size they are more tolerant to desiccation (Soemodihardjo & Kastoro 1977) and have fewer predators. In contrast, juveniles can be predated upon by larger brachyurans (Vannini et al. 2001; Wells & Lalli 2003) and their occurrence on the lower region of the shore has been related to their lower desiccation tolerance, as this zone receives run-off and seepage from upper regions and is characterized by shorter emergence times (Penha-Lopes et al. 2009). At Kosi Bay, we found that feeding activity was only greatly reduced during the night time low tide of the winter experiment. Although the prevalence of potential brachyuran predators at Kosi Bay has not been quantified, gastropods are generally driven by the chemical and mechanical cues of their potential predators (Mach & Bourdeau 2011). In our study, the observed patterns in feeding activity of juvenile *T. palustris* are therefore most likely to be driven by the seasonal subtropical climate.

As a consequence of these temperature-driven activity patterns, seasonal differences in parameters relating to the feeding dynamics of *T. palustris* were also observed. As warmer summer temperatures increase the metabolic rate of the snails, their continuous feeding throughout the course of the day resulted in a faster gut evacuation time for this season. Although winter feeding activity was reduced and gut evacuation time was slower, higher consumption/digestion efficiency was recorded for this season. The estimated consumption/digestion efficiency for *T. palustris* consuming MPB was however lower than what has been reported for other mangrove deposit-feeding gastropods, such as *Cerithidea cingulata* when feeding on bacteria (Dye & Lasiak 1987). If traits that are related to consumption/digestion efficiency are plastic, this may promote the ability of this species to survive during unfavourable conditions. This trend was previously reported for the fiddler crab, *Uca annulipes*, within a subtropical mangrove forest (Peer et al. 2015a). Greater consumption/digestion efficiency may therefore enable the snails to meet their energetic requirements despite the reduction in feeding activity over the course of 24 hours.

Measuring feeding activity over a synodic month in both the summer and winter seasons will indicate how these snails respond to short local scale fluctuations. A comparison between neap and spring tides may further indicate whether activity at spring tide was in fact reduced, particularly in the summer when the gut chlorophyll content was much lower. Slim et al. (1997) found that feeding activity of *T. palustris*

was reduced when the inundation period was shorter and this is presumably a strategy to conserve water by reducing mucous trails. Differences in the cross-shore distribution of juveniles between the two climatic seasons should also be considered. To mitigate the effects of desiccation, in summer juvenile *T. palustris* may occur relatively higher up on the shore in shaded areas where detrital sources are more available, thus reducing their gut chlorophyll content in this season.

### 4.4.2 Feeding dynamics in response to resource availability

Along high energy coastlines, such as the east coast of South Africa, mangrove forests are restricted to occur within sheltered estuarine areas (Macnae 1963). Within this region, estuaries are dynamic and are largely influenced by seasonal drivers (Scharler 2012). For instance, seasonal increases in flow, as a result of increased rainfall, have a significant influence on the availability of inorganic nutrients and thus on the primary productivity within the estuary (Nozais et al. 2001; Perissinotto et al. 2002; Collins & Melack 2014). However, at Kosi Bay we found that the biomass of MPB was relatively similar in summer and in winter. Despite this, there was a clear difference in the utilization of this resource by juvenile *T. palustris*.

Juvenile *T. palustris* consumed a much lower proportion of the total available MPB biomass in summer when they were slightly smaller and occurred at a lower density. Alternative sources may have therefore been available for consumption during this warmer season. For instance, increased flow is known to transport fluvial organic matter downstream (Whitfield et al. 2012). Mangrove leaf litter is also more readily available during summer at subtropical latitudes, as the warmer temperatures facilitate the rate of decomposition into detritus (Mackey & Smail 1996; Tomlinson 1999). These sources would not be detected by the fluorometric approach. As deposit-feeding gastropods are largely considered to be non-selective generalists, their diets generally reflect the availability of resources. However, there is evidence that selective assimilation of nutritional sources occurs within the gut (Doi et al. 2006). Pape et al. (2008) suggested that juvenile *T. palustris* selectively assimilate benthic microlagae such as diatoms based on their $\delta^{13}C$ isotopic signature. However, prevailing low salinity conditions may promote the growth of different algal groups that are less favourable for consumption by *T. palustris*, resulting in a dietary switch to non-fluorescent material such as detritus. A stable isotope study is needed

to reveal whether there is in fact a seasonal dietary shift and a lower incorporation of MPB into the diet during summer for juvenile *T. palustris* at Kosi Bay.

The per capita resource availability of MPB was however lower in winter, because *T. palustris* occurred at a higher density and had a faster ingestion rate. Direct intraspecific competition for benthic microalgal resources is therefore expected to be higher during this period. In winter the maximum potential feeding impact ($FI_{max}$) of *T. palustris* juveniles on the total available MPB biomass was more than three times higher than in summer. Grazing by gastropods has been shown to have significant effects on the biomass and productivity of MPB (Pillay et al. 2009; Pratt et al. 2015). However, even if the snails consistently grazed at their maximum ingestion rate ($I_{max}$) for 24 h they would only reduce the available MPB biomass at Kosi Bay by around half. However, the productivity dynamics of MPB fluctuate throughout the course of the day and stocks are replenished by the tide (Blanchard et al. 2001), therefore the actual feeding impact that these snails have on available MPB at Kosi Bay is likely not very substantial.

*4.5 Conclusion*

Although the feeding activity of *T. palustris* was largely influenced by temperature, it appears that this species is well suited to the subtropical climatic regime. *Terebralia palustris* is able to utilize resources at variable rates and their potential maximum consumption rates did not exceed the available MPB biomass. Although juvenile *T. palustris* do consume mangrove derived detritus, their occurrence on the lower regions of the shore also enables them to incorporate MPB into their diets. The importance of MPB to the diet of *T. palustris* appears to be highly variable and dependent on a number of factors. Undoubtedly, the consumption of sources that are not derived from mangroves allows this species to inhabit coastal areas that do not support these macrophytes (Feulner 2000). The consumption of this autochthonous resource should therefore be considered as an integral part of the ecological role for this widespread and charismatic species.

# Chapter 5: Feeding dynamics of *Melanoides tuberculata*

## *5.1 Introduction*

Benthic primary producers provide an essential autochthonous resource in shallow water ecosystems. This resource is ultimately linked to higher trophic levels through deposit-feeders, such as gastropods. Deposit-feeders are generally indiscriminate while feeding and thus often exhibit a large degree of trophic plasticity. The degree of trophic plasticity evident in most benthic aquatic gastropods is considered an important trait influencing the success of some species following their introduction into habitats outside their native range. The invasion success of apple snails (Ampullariidae), such as *Pomacea canaliculata* and *P. maculata*, the New Zealand mud snail *Potamopyrgus antipodarum*, and the thiarid *Tarebia granifera*, has been attributed at least in part to the broad generalist diets of these species (Baker et al. 2010; Miranda & Perissinotto 2012; Bennett et al. 2015a). Grazers at high densities have a substantial impact on available resources (Hillebrand 2009), including top-down control on primary productivity and effects on community structure of benthic macrofauna as a result of competition (Kerans et al. 2010).

*Melanoides tuberculata* (Müller, 1774) is renowned as one of two globally invasive thiarid gastropods (Facon et al. 2003). The native range of *M. tuberculata* extends through East Africa, across the Middle East and to Southeast Asia (Brown 1994; Facon et al. 2003). Within this range it is possible to find genetically and phenotypically distinct morphs (Samadi et al.1999), which may have either African or Asian evolutionary origins due to human-mediated spread (Facon et al. 2003). *Melanoides tuberculata* typically occurs in a wide variety of perennial or temporary, freshwater or brackish habitats including rivers, streams, springs, wetlands, pans and coastal lakes (Brown 1994; Appleton 1996; de Kock & Wolmarans 2009; Perissinotto et al. 2014). It is currently unknown whether the generalist habitat and dietary traits recorded for *M. tuberculata* are in fact due to intrinsic variations

between genetically distinct morphs. Regardless, following establishment *M. tuberculata* attains high population densities (Work & Mills 2013) and successfully displaces native gastropods, presumably through interspecific competition (Guimarães et al. 2001).

Relatively little is known about the role *M. tuberculata* plays as a benthic consumer of primary production except that individuals feed by indiscriminately scraping the substrate for detritus, sedimentary organic matter and photosynthetic benthic microalgae (Madsen 1992; Coat et al. 2009; Miranda & Perissinotto 2012). Laboratory studies report that grazing by *M. tuberculata* influences the species richness and density of periphyton (Vasconcelos et al. 2013). However, the potential feeding impact of *M. tuberculata* on standing stocks of microphytobenthos has not previously been investigated. The aim of this study was to estimate the feeding dynamics of *M. tuberculata* and to determine the impact of this species on available benthic resources. Feeding dynamics were assessed and compared for three distinct populations from environments that are representative of the variety of habitats in which the species occurs. It was predicted that feeding dynamics would differ between populations in different habitats in two ways. First, as *M. tuberculata* is a generalist deposit feeder, the average gut pigment content of individuals would be related to the available biomass of microalgae in each habitat. Second, the rate at which *M. tuberculata* consumed microalgae would vary with population density. Variation in feeding dynamics between different populations of *M. tuberculata* would be indicative of plasticity in these traits. This plasticity could be intrinsic or in response to environmental parameters, such as resource availability. The estimation of the potential feeding impact of *M. tuberculata* on microalgal resources should provide useful information relating to the invasion success of this species.

*5.2 Materials and Methods*

    *5.2.1 Site description and gastropod collection*

The iSimangaliso Wetland Park, a UNESCO World Heritage Site on the north coast of KwaZulu-Natal Province, South Africa, protects a wide range of coastal habitats including three major Ramsar Wetlands of International Importance (Figure 1.2).

For this study, *in situ* experiments were carried out with *Melanoides tuberculata* collected from three different habitats: (1) the mangrove forest on the north shore of the St Lucia Estuary Mouth; (2) the muddy bed of the Mpophomeni Stream in the False Bay region of Lake St Lucia; (3) the sandy shores of Lake Nhlange in the Kosi Bay lake system. These habitats are representative of the range of environments in which *M. tuberculata* typically occurs in terms of temperature, salinity and substrate type. Although *M. tuberculata* is indigenous to South Africa (Brown 1994), preliminary conchological analyses using the categorical scoring system of Facon et al. (2003) indicate that there are currently several morphologically distinct populations. In this study (Figure 5.1), *M. tuberculata* from the St Lucia Estuary Mouth (A) as well as the Mpophomeni Stream (B) have been identified as the characteristic tuberculate form, which is considered to be indigenous (see Appleton, 1996). However, those from Lake Nhlange (C) display a smooth sculpture and have a distinct columellar band, resembling the Asian genotype/morph illustrated by Genner et al. (2004). This is the subject of an ongoing study in South Africa (Appleton & Miranda 2015).
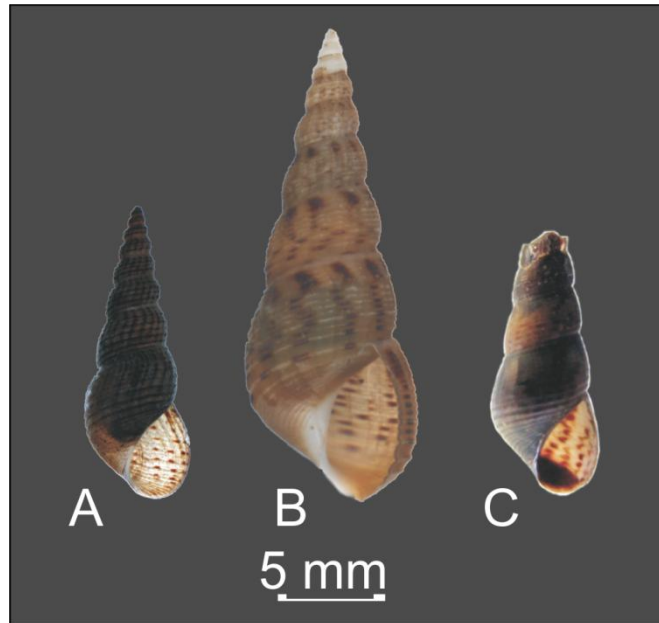
**Figure 5.1** *Melanoides tuberculata* collected from (**A**) St Lucia Estuary Mouth, (**B**) Mpophomeni Stream, and (**C**) Lake Nhlange of the iSimangaliso Wetland Park, South Africa. Photo: N. Miranda

The experiments with *M. tuberculata* from the St Lucia Estuary Mouth and the Mpophomeni Stream were carried out on 21 and 23 February 2014, respectively. The experiments with *M. tuberculata* from Lake Nhlange were carried out on 31 January 2015. Physico-chemical parameters were measured upon arrival at each site using a YSI 6600-V2 multiprobe. Approximately 10 individual snails were collected and then processed to obtain an estimate of gut pigment content at that time.

**Table 5.1** Average (± SE) values of physico-chemical variables, population parameters and gut pigment content for *Melanoides tuberculata* at St Lucia Estuary Mouth, Mpophomeni Stream and Lake Nhlange.

| Site | Date and time | Salinity | Temperature (°C) | Gut pigment content* ($\mu$g pigm.ind$^{-1}$) | Average SH (mm) | Density (ind.m$^{-2}$) |
|---|---|---|---|---|---|---|
| St Lucia Estuary Mouth | 21 Feb 2014 10:00 | 7.6 ± 0.04 | 25.9 ± 0.25 | 83.36 ± 13.15 | 13.37 ± 0.58 | 288 ± 15 |
| Mpophomeni Stream | 23 Feb 2014 16:00 | 8.8 ± 0.02 | 24.6 ± 0.07 | 338.86 ± 39.18 | 26.17 ± 0.92 | 67 ± 7 |
| Lake Nhlange | 31 Jan 2015 14:00 | 2.9 ± 0.03 | 32.4 ±0.11 | 255.07 ± 69.94 | 13.22 ± 0.56 | 104 ± 34 |

* Gut pigment content estimated from the 10 individuals collected immediately upon arrival at each site. SH, shell height.

Abbreviation SH: Shell height

## 5.2.2 Gastropod grazing experiments

*Gut contents*:

To determine the dominant constituents in the diet of *M. tuberculata*, the gut contents of 15 randomly selected individuals from each site were examined under a dissecting microscope. Gut contents were classified by gross morphology (microalgae, filamentous algae, detritus, sediment) and the percentage of snails that contained these items in their guts was calculated.

To determine natural variations in the pigment in the gut (a proxy for ingested photosynthetic material), individuals were collected at 3-h intervals over a period of 24 h. Five individuals were collected after each time interval and the shell height (SH) of each snail was measured with Vernier callipers. The gastropods were dissected and each whole gut was placed in 8 ml of 90% acetone and then stored in the dark at 4 °C for 48 h to extract chlorophyll *a*. The total pigments (chlorophyll *a* and phaeopigments) were subsequently measured using the non-acidification method with a 10-AU Turner Designs fluorometer (Welschmeyer 1994) and expressed as chlorophyll *a* equivalents (µg pigm.ind$^{-1}$).

Gut chlorophyll content was expected to vary with shell size. Therefore, to determine whether gut chlorophyll content varied over the course of the day at each site, time period (morning, afternoon, evening, night) was used as a categorical predictor variable in a general linear model (GLM), which incorporated shell height as a continuous covariate. The slope of the linear relationship between gut chlorophyll content and shell size was not consistent between sites. Therefore, to compare the overall difference in gut pigment content in µg pigm.ind$^{-1}$ between sites the measurements were size-standardized across all three populations to allow for suitable comparisons using the mean SH as follows:

$$Gut\ pigment\ content = chlorophyll_a\ equivalents \times \left(\frac{mean\ SH}{individual\ SH}\right)$$

ANOVA with Tukey's HSD *post hoc* test was used to compare gut pigment content between populations. Size-standardized gut pigment values were used to calculate all subsequent parameters in order to make these values directly comparable between populations.

The feeding rate of *M. tuberculata* was estimated using the *in situ* gut-fluorescence technique developed by Mackas & Bohrer (1976), which has since been adapted for gastropods (Miranda et al. 2011; Díaz et al. 2012). The daily ingestion rate ($I$, mg pigm.ind$^{-1}$ d$^{-1}$) was estimated as follows:

$$I = \frac{kG}{(1-b)}$$

Where $k$ is the gut evacuation rate (h$^{-1}$), $G$ is the integrated average size-standardized gut pigment concentration (adjusted to mg pigm.ind$^{-1}$) over 24 h and $b$ is an index of pigment consumption/digestion within the gut (Wang & Conover 1986; see below). The calculated values for $I$ were compared between populations using Pearson's chi square test.

*Gut evacuation rate (k)*:

The gut evacuation rate was measured with freshly collected *M. tuberculata*. Individuals were isolated in 100 ml plastic vials containing water collected *in situ* and filtered through a Whatman GF/F (0.7 µm) and a Millipore filter (0.2 µm), to ensure removal of all particulate material. To promote continuous gut evacuation, nonfluorescent cornstarch was added as a source of food to the filtered water (Carrasco & Perissinotto 2010). The gut pigment content was measured (see above) from five gastropods at the beginning of the experiment. Five individuals were subsequently processed every 10 min for the first hour and every 30 min for the following 2 h (total duration 3 h). The gut evacuation rate was estimated from the linear slope of the change in gut pigment over time (Pakhomov & Perissinotto 1996). To determine maximum potential ingestion rates ($I_{max}$), the maximum gut evacuation rate ($k_{max}$) was estimated from the rate of pigment decline over the first 30 min of the experiment.

*Pigment consumption/digestion (b)*:

The efficiency of *M. tuberculata* in consuming/digesting photosynthetic pigments in the gut was determined using the two-compartment pigment-budget approach (Mayzaud & Razouls 1992). Twenty individuals were isolated in 100 ml of the filtered water and cornstarch mixture described above for a period of 24 h. The water-cornstarch solution was replaced after 12 h to avoid a build-up of waste products.

After the 24-h period, the gut pigment content was measured from ten individuals. A 20-ml suspension of microalgae was added to each of ten 2L buckets containing 300 ml of pure filtered water (no cornstarch) collected *in situ*. After the microalgae had settled, the remaining ten snails were each placed in a bucket and allowed to feed for a period of 1 h. A control was set up in the same manner but without the addition of gastropods. After the incubation period of 1 h, the snails were processed as described above. The water from each replicate was filtered (Whatman GF/F 0.7 μm) and the filter was placed in 8 ml of 90% acetone for extraction as described. No faecal pellets were produced during the incubation period. The differences in pigment concentration between the water and snail compartments were therefore attributed to consumption or digestion within the gut.

### *5.2.3 Gastropod abundance, resource availability and impact on microphytobenthos*

Gastropod abundance was measured quantitatively using a corer with an internal diameter of 42 mm at the St Lucia Estuary Mouth and the Mpophomeni Stream. The corer was pushed into the sediment and all individuals within the area were counted. This method could not be employed at Lake Nhlange where *M. tuberculata* occurs in deeper water. Instead, a net of 0.3 m diameter was swept across 5 m of the substrate where *M. tuberculata* occurred. Abundance sampling was replicated in triplicate at each site to estimate population density ($ind.m^{-2}$).

The potential feeding impact ($mg\ pigm.m^{-2}\ d^{-1}$) was calculated as the product of the daily ingestion rate and the density of gastropods for each population. The average available microphytobenthos (MPB) standing stock ($mg\ pigm.m^{-2}$) was estimated from triplicate cores (20 mm internal diameter) placed in 30 ml of 90% acetone at 4 °C for 48 h. After chlorophyll *a* extraction, the pigment concentrations were measured fluorometrically as described above. The feeding impact of gastropods was then expressed as a percentage of the average available MPB standing stock. The biomass of MPB available per individual snail ($mg\ pigm.m^{-2}\ ind^{-1}$) was estimated as an indication of resource availability at each site. The estimates for feeding impact were compared between populations using Pearson's chi square tests.

*5.3 Results*

  *5.3.1 Gut pigment content*

The gut contents of *Melanoides tuberculata* were dominated by microalgae and detritus for snails from all three populations (Table 5.2). Filamentous algae only occurred in the guts of snails from the Mpophomeni Stream, although their percentage was relatively low.

**Table 5.2** Percentage occurrence of gut content items for *Melanoides tuberculata* from the St Lucia Estuary Mouth, Mpophomeni Stream and Lake Nhlange.

| Site | Microalgae | Filamentous algae | Detritus | Sediment |
|------|-----------|-------------------|----------|----------|
| St Lucia Mouth | 73.3 | - | 80 | 6.7 |
| Mpophomeni Stream | 72.2 | 16.7 | 61.1 | 33.3 |
| Lake Nhlange | 64.3 | - | 78.6 | 42.9 |

The average gut-pigment content of individuals collected immediately upon arrival differed between sites. The average size of individuals was relatively similar at the St Lucia Estuary Mouth and Lake Nhlange, while those at the Mpophomeni Stream were double this size (Table 5.1). Although shell height was a significant covariable of gut chlorophyll content at St Lucia Estuary Mouth ($F_{1,37}$ = 4.249, $P$ = 0.047), Mpophomeni Stream ($F_{1,38}$ = 5.515, $P$ = 0.025) and Lake Nhlange ($F_{3,36}$ = 6.2716, $P$ = 0.017), these parameters were in fact poorly correlated at each site ($r^2$ = 0.162; $r^2$ = 0.145 and $r^2$ = 0.228 respectively).

Gut chlorophyll content did not differ significantly during the course of the day for *M. tuberculata* at Lake Nhlange (GLM: $F_{3,36}$ = 0.982, $P$ = 0.413), Mpophomeni Stream (GLM: $F_{3,38}$ = 451, $P$ = 0.718) or St Lucia Estuary Mouth (GLM: $F_{3,37}$ = 1.362, $P$ = 0.271) (Figure 5.2). However, the average size-standardized gut chlorophyll measured over 24 h (*G*) between snails was higher at the Mpophomeni Stream

(ANOVA: $F_{2,126} = 27.745$, $P = 0.001$) in comparison with those from the St Lucia Estuary Mouth and Lake Nhlange (Table 5.3).
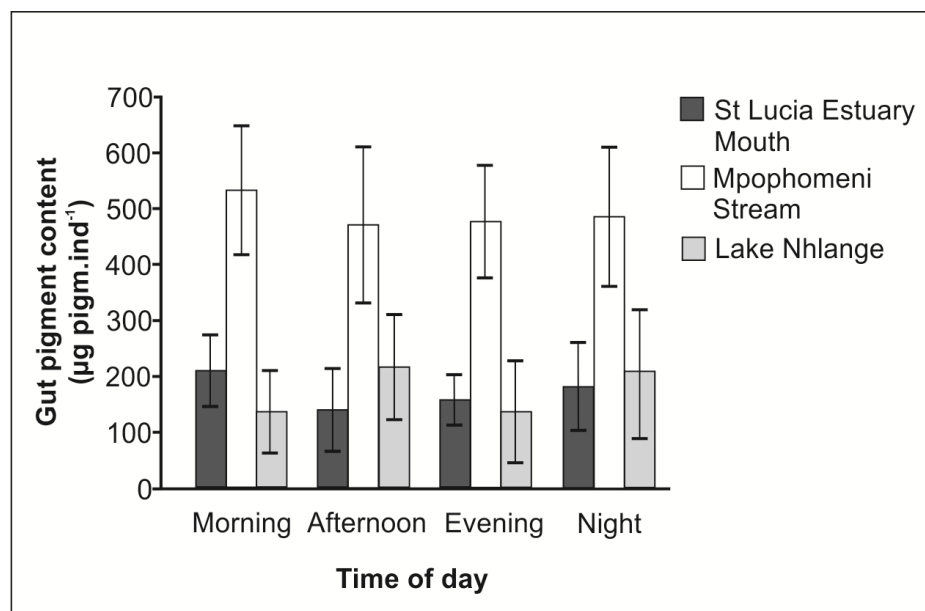


**Figure 5.2** Diel variation in gut pigment content for *Melanoides. tuberculata* at the St Lucia Estuary Mouth, the Mpophomeni Stream and Lake Nhlange.

**Table 5.3** Integrated size standardized average gut pigment content (*G*) measured over 24 h; maximum gut evacuation rate ($k_{max}$) and corresponding gut passage time (GPT); and pigment consumption/digestion efficiency (*b*) calculated for *Melanoides tuberculata* from different localities.

| Site | (*G*) (mg pigm.ind$^{-1}$) | ($k_{max}$) (h$^{-1}$) | GPT (h) | (*b*) (%) |
|---|---|---|---|---|
| St Lucia Estuary Mouth | 1.38 | 0.48 | 2.08 | 11.1 |
| Mpophomeni Stream | 3.93 | 0.42 | 2.38 | 87.7 |
| Lake Nhlange | 1.40 | 0.54 | 1.85 | 84.1 |

## 5.3.2 Ingestion rates, feeding impact and resource availability

A negative exponential model provided the best fit for the rate of pigment decline over a 3-h period for all experiments (Figure 5.3). The maximum gut evacuation rate ($k_{max}$) varied between sites and was highest for snails at Lake Nhlange and lowest at the Mpophomeni Stream (Table 5.3). Both the average gut evacuation rate ($k$) (Figure 5.3) and the calculated average ingestion rate ($I$) were similar ($\chi^2 = 1.455$, *df* = 2, *P* = 0.483) between populations (Table 5.4). This was the result of the variation in the consumption/digestion efficiency ($b$) and the size-standardized gut chlorophyll content ($G$) between snails from different sites (Table 5.3). As a product of density and ingestion rate, the average feeding impact did differ significantly ($\chi^2 = 36.602$, *df* = 2, *P* < 0.0001) between sites (Table 5.4). The maximum potential feeding impact (estimated from $I_{max}$) was also significantly different between sites ($\chi^2 = 471.077$, *df* = 2, *P* < 0.0001) (Table 5.4). Biomass of MPB was similar at the St Lucia Estuary Mouth and the Mpophomeni Stream (Table 5.4). As *M. tuberculata* occurred at the lowest density at the Mpophomeni Stream where MPB biomass was relatively high, the per capita resource availability (mg pigm.m$^{-2}$ ind$^{-1}$) was greatest at this site (Table 5.4). The average potential daily consumption of MPB differed significantly between sites ($\chi^2 = 39.942$, *df* = 2, *P* < 0.0001) and was highest at Lake Nhlange (Table 5.4).
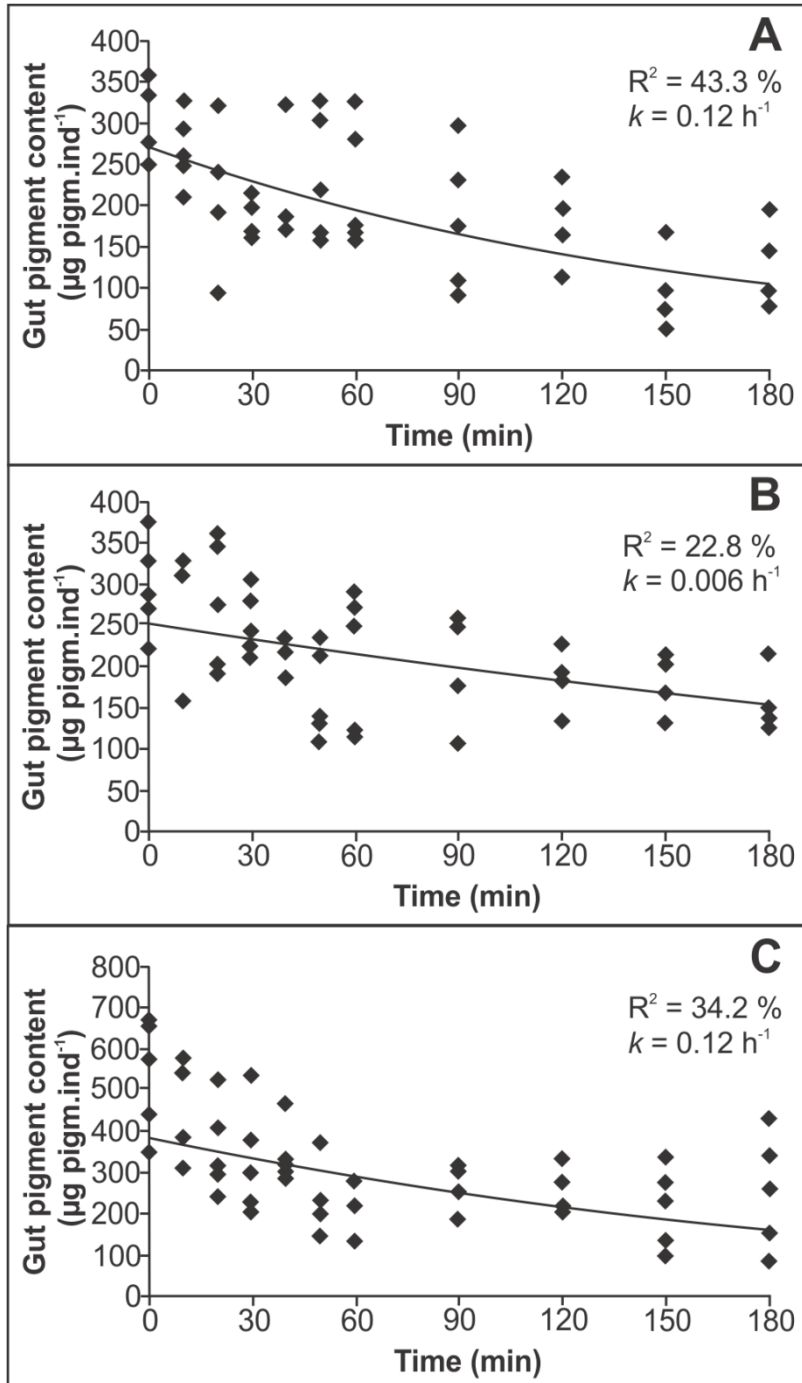
**Figure 5.3** Decrease in gut pigment content over time for *Melanoides tuberculata* from St Lucia Estuary Mouth ($t_0$ = 12:00) (**A**), Mpophomeni Stream ($t_0$ = 14:00) (**B**) and Lake Nhlange ($t_0$ = 16:00) (**C**). Average gut evacuation rate ($k$) calculated as the linear slope of log-transformed gut pigment content over the entire 180 min.

**Table 5.4** Calculated average and maximum values for ingestion rate and feeding impact for *Melanoides tuberculata* at St Lucia Estuary Mouth, the Mpophomeni Stream and Lake Nhlange. Average (± SE) available microphytobenthos (MPB) biomass, potential daily MPB consumption and per-capita availability of MPB at each site are also given.

| Site | Ingestion rate | Feeding impact | MPB biomass | Daily MPB consumption | Per-capita available MPB |
|---|---|---|---|---|---|
| | $(mg\ pigm.ind^{-1}\ d^{-1})$ | $(mg\ pigm.m^{-2}\ d^{-1})$ | $(mg\ pigm.m^{-2})$ | (%) | $(mg\ pigm.m^{-2}ind^{-1})$ |
| St Lucia Estuary Mouth | 0.17 | 48.30 | 436.82 ± 213.72 | 11.06 | 1.52 |
| | 0.67 | 193.19 | | | |
| Mpophomeni Stream | 1.91 | 128.0 | 415.14 ± 76.46 | 30.83 | 6.20 |
| | 13.37 | 896.02 | | | |
| Lake Nhlange | 1.05 | 109.86 | 173.25 ± 35.08 | 63.41 | 1.67 |
| | 4.75 | 494.39 | | | |

*5.4 Discussion*

*Melanoides tuberculata* has been reported to consume periphytic biofilms (Vasconcelos et al. 2013) as well as detritus and microalgae (Coat et al. 2009). However, this is the first report on the rate at which *M. tuberculata* is able to consume available MPB. Remarkably, this species was able to consume over 60% of the total available microalgal biomass in one of the three different systems (Lake Nhlange) investigated in this study. There was, however, a large degree of variability in the feeding dynamics of *M. tuberculata* from the different habitats.

### 5.4.1 Differences in the feeding dynamics between populations

*Food availability and quality of resources*:

The consumption of benthic microalgae by *M. tuberculata* was not directly related to the biomass of available MPB. However, when considering the variation in per-capita available MPB between sites there is a clear trend in relation to gut pigment content (*G*). Population density has the potential to influence ingestion rates of deposit-feeding gastropods, as the result of interference competition through space limitation and an increase in the frequency of interactions between individuals (Blanchard et al. 2000). These effects were, however, not recorded for snails at natural densities (Barnes 2001). Lower gut pigment content measured at high population density (when per-capita available MPB was low) at the St Lucia Estuary Mouth was related to a lower ingestion rate and subsequently a lower potential impact on available stocks. However, a high pigment consumption/digestion efficiency coupled with a fast gut passage time resulted in a high calculated ingestion rate at Lake Nhlange. Under these conditions when the total available biomass of MPB was lower, which also resulted in a low per-capita availability of MPB, the potential feeding impact of snails was in fact very high.

As *M. tuberculata* is a generalist deposit feeder, the lower ingestion rates measured at higher population densities may be the result of these individuals consuming a lower proportion of photosynthetic material. Detritus was indeed recorded in the gut contents from a large percentage of the snails examined from all three habitats. The constituents of particulate detritus can differ significantly among habitats (Yee & Juliano 2006). However, detritus is a nutritionally poor food source for gastropods in

comparison with benthic microalgae (Levinton et al. 1984). In the mangrove habitat, *M. tuberculata* may be fulfilling their energetic requirements by feeding predominantly on sediment enriched with organic detritus and microbes, which are common alternatives to photosynthetic microalgae for deposit feeding gastropods (Sheldon & Walker 1997).

The nutritional quality of food, as well as the physical structure and complexity of food particles, have been related to variations in gut passage time and the efficiency with which individuals consume/digest pigments within the gut (Taghon & Jumars 1984). Gut passage time is generally positively correlated with this consumption/digestion efficiency (Hawkins et al. 1990). Therefore, a long gut passage time could be indicative of either poor food quality or high structural complexity of the food consumed. Similarly, different algal groups are digested in the gut at different rates and efficiencies by gastropods (Brendelberger 1997). In the case of *M. tuberculata* from the Mpophomeni Stream, filamentous *Cladophora* was recorded in the gut contents from some individuals even though they were collected from outside the patches of this alga. Although microalgae were most commonly found in the guts, the incorporation of *Cladophora* potentially leads to higher consumption/digestion efficiency in these snails. Therefore, although the gut passage time was longer for *M. tuberculata* from the Mpophomeni Stream, their high efficiency contributed to a faster ingestion rate and thus to a significantly larger potential feeding impact on available MPB.

*Environmental variation*:

The variation in feeding dynamics observed for *M. tuberculata* from different habitats is potentially driven by a range of environmental conditions. Temperature is positively correlated with ingestion rates in gastropods (Foster et al.1998; Sanford 2000). As temperature drives metabolic processes, it would be expected also to influence gut passage time and consumption/digestion efficiency. The fastest gut passage time (estimated from $k_{max}$) and highest consumption/digestion efficiency were recorded from Lake Nhlange where environmental temperature was indeed the highest. The calculated ingestion rate was not, however, directly correlated with the temperature differences between habitats. Ingestion rates were in fact highest under the highest environmental salinity, which was recorded at the Mpophomeni Stream.

The feeding activity of benthic invertebrates generally varies within optimal ranges of salinity (Irlandi et al. 1997; Pascal et al. 2008). Although *M. tuberculata* is considered to be a predominantly freshwater species, it has been repeatedly reported from estuarine habitats and the species has a broad salinity tolerance (da Silva & Barros 2015). The relationship between salinity and ingestion rate may therefore determine the extent to which *M. tuberculata* is able to affect benthic assemblages following introduction.

Substrate type and, in particular, grain size determine the surface area available for colonization and thus influence the biomass of MPB in aquatic habitats (Cahoon et al. 1999). Sediment particles are also indirectly ingested by grazers (Levinton et al.1984) with implications for digestion/consumption efficiency within the gut (Broekhuizen et al. 2001). A third of the individuals examined from the Mpophomeni Stream contained sediment particles within their guts. However, for *M. tuberculata*, sediment was most frequently found in the gut contents of individuals collected from the sandy habitat at Lake Nhlange. A fast gut passage time for these snails may therefore facilitate fast removal of indigestible particles.

Finally, a difference in the predation pressure ateach of the sites could also be driving the observed variability in feeding dynamics by influencing foraging behaviour. Freshwater snails are sensitive to the cues of their predators and often exhibit a range of avoidance strategiesthat influence their behaviour (Covich et al. 1994; Chivers & Smith 1998; Dalesman et al. 2006). Predation can therefore influence habitat use as well as foraging patterns and feeding rates (Turner 1996; Premo & Tyler 2013; Dalesman et al. 2015). At the Mpophomeni Stream, *M. tuberculata* is known to be predated upon by the freshwater crab *Potamonautes sidneyi* Rathburn, 1904 (Peer et al. 2015b). However, at the St Lucia Estuary Mouth and Lake Nhlange the deeper water would facilitate predation by molluscivorous fishes, as has been reported in Zimbabwe and Lake Malawi (Chimbari & Madsen 2003; Evers et al. 2011). A specific study is therefore needed to quantify how different predators influence the behaviour of *M. tuberculata* and thus determine the role of predation in regulating foraging behaviour for this species.

## 5.4.2 Evolutionary significance of variation in feeding dynamics

The large degree of variation in feeding dynamics recorded for *M. tuberculata* suggests that traits related to feeding may be plastic and therefore that they may differ between environments. However, this can only be concluded following a specific experimental investigation, which was beyond the scope of this study. Phenotypic plasticity arises when individuals of a similar genotype express different traits depending on environmental conditions (Scheiner 1993). This is often difficult to assess in natural populations, except in the situation of clonal species in which populations tend to be dominated by closely related individuals (Jackson 1986). In the case of *M. tuberculata*, which reproduces through ovoviviparous parthenogenesis, populations may indeed be genetically similar (Myers et al. 2000). The existence of genetically distinct but highly plastic morphs within this species (Samadi et al. 1999) complicates this scenario. Although certain traits may be expected to be plastic, there may be genetic differences between morphs that have experienced different selective pressures.

Differences in physiology and other traits that would influence competition have not been directly compared between African and Asian morphs of *M. tuberculata*. However, at the time of their study, Genner et al. (2004) reported that morphs of Asiatic origin presently occur in areas of Lake Malawi that were previously occupied by native African morphs. This suggests that Asian morphs have displaced their African counterparts. Within the iSimangaliso Wetland Park, *M. tuberculata* has been displaced by the alien invasive *Tarebia granifera* (Miranda & Perissinotto 2014), with the exception of those at Lake Nhlange. Individuals of *M. tuberculata* from Lake Nhlange also behave differently from those from St Lucia Estuary Mouth (Raw et al. 2015). A shared Asian evolutionary origin between *T. granifera* and certain *M. tuberculata* morphs may explain these variations.

Globally, *M. tuberculata* has been introduced to many subtropical and tropical locations such as the southeastern United States (Karatayev et al. 2009), the Caribbean (Pointier et al. 2011) as well as areas of South America in Brazil, Argentina and Paraguay (De Marco 1999; Peso et al. 2011). The invasion success of *M. tuberculata* has largely been attributed to advantageous functional traits including wide physiological tolerance of desiccation (Facon et al. 2004), temperature (Mitchell

& Brandt 2005) and salinity (Weir & Salice 2012). If traits relating to feeding are indeed plastic, this would be advantageous to the success of *M. tuberculata* as an invasive species. The variation in feeding dynamics suggests that these snails utilize resources at different rates depending on their availability. However, individuals exhibit a degree of trophic plasticity as indicated by the various gut content items. As such, *M. tuberculata* has the ability to occupy a relatively broad trophic niche. Therefore, the invasion success of *M. tuberculata* may in part be attributed in the ability of this species to exploit a range of resources at variable rates.

### 5.4.3 Comparisons with other globally invasive species

High densities of invasive gastropod species such as *Potampopyrgus antipodarum*, *T. granifera* and *M. tuberculata* are considered competitive threats to native species when food resources are limited (Rader et al. 2003; Appleton et al. 2009; Moore et al. 2012). Generally, although deposit feeders are effective at reducing MPB biomass, it is very seldom that consumption rates exceed the rate of MPB biomass generation (Pratt et al. 2015). Furthermore, MPB assemblages are highly variable in terms of biomass and species composition across different spatial scales (Underwood & Kromkamp 1999). It is therefore difficult to make reliable estimations of grazing pressure without using a dedicated *in situ* mesocosm approach. However, some estimates can be comparable, if the dynamics of MPB are also presented. Our results show that the daily consumption of available MPB by *M. tuberculata* is higher than what has been reported for the closely related *T. granifera* by Miranda et al. (2011) (63.4% and 35%, respectively). In contrast, *P. antipodarum* is potentially able to consume up to 75% of the daily available gross primary production (Hall et al. 2003).

Although ingestion rates are typically highest at low population densities, when per-capita resource availability is high, grazing impact on available algal stocks by *P. antipodarum* has also been positively correlated with primary productivity within areas of their introduced range (Riley et al. 2005). Similarly, for *T. granifera*, grazing impacts were positively correlated with available MPB biomass (Miranda et al. 2011). In contrast, a high grazing impact was recorded for *M. tuberculata* at Lake Nhlange, which is oligotrophic (Begg 1980), as the result of a fast ingestion rate and relatively high population density. It may be that snails from Lake Nhlange have higher

ingestion rates in order to maximize consumption of limited food resources. At Lake Nhlange in particular, Miranda et al. (2011) reported that *T. granifera* only consumed up to 27.4 % of the available MPB biomass (37.3 ± 25.7 mg pigm.m$^{-2}$) while present at a density of 282 ± 66 ind.m$^{-2}$ . In comparison, at a density of 104 ± 34 ind.m$^{-2}$, *M. tuberculata* was estimated to consume 63.4 % of available MPB (173.25 ± 35.1 mg pigm.m$^{-2}$). This possibly suggests that under conditions of low per-capita resource availability *T. granifera* has a higher carrying capacity within this oligotrophic habitat. This may be contributing to the disappearance of *M. tuberculata* from other water bodies within this biogeographic region following the introduction of *T. granifera* (Miranda & Perissinotto 2014).

*5.5 Conclusion*

The success of *M. tuberculata* following introduction and establishment is expected to be the result of a combination of traits. In this study, we found that the feeding dynamics of *M. tuberculata* was variable between populations from different habitats. This may be an important factor contributing towards the invasion success of this species, as it is able to utilize available resources at different rates. It is evident that these results should be complemented with a stable isotope analysis to determine both immediate and long term contributions of various food resources to the diet of *M. tuberculata* in different aquatic habitats. However, as microphytobenthos is generally the most important basal resource in aquatic environments, the *in situ* gut fluorescence method provides a good estimate of the potential impact of grazing snails.

# Chapter 6: Resilience of *Cerithidea decollata* in St Lucia

## 6.1 Introduction

Ecological resilience is a major component of numerous theoretical concepts and models that have been developed in an effort to incorporate complexity into understanding the potential effects of anthropogenic global change on natural systems. The concept of ecological resilience, as originally coined by Holling (1973), is related to the amount of disturbance that an ecosystem can withstand before self-organized processes and structures are changed. Resilience can also be considered in terms of the time it takes for an ecosystem to return to a stable state after a disturbance (Gunderson 2000). Investigating the resilience of an ecosystem can therefore provide important information with regards to natural thresholds and how these may be perturbed by anthropogenic activities (Grimm & Berger 2016). Ecological resilience can also be estimated in relation to natural disturbances, as is evident in the persistence of certain ecosystems through millennia despite fluctuating trends in global climate and sea level (Moritz & Agudo 2013). Mangrove forests are a prominent example of such an ecosystem, as the modern genera have been established at least since the Middle to Late Eocene (Ellison et al. 1999). The persistence and stability of mangrove forests has been attributed to a number of adaptations that enable a few woody plant species to colonize the interface between terrestrial, estuarine and marine environments and thus provide a unique habitat to a large number of organisms that have become adapted to these conditions (Alongi 2008, Nagelkerken et al. 2008).

The notable ecological resilience and stability of mangroves is predicted to allow these ecosystems to persist to some degree even through contemporary anthropogenic global change (Alongi 2015, Ward et al. 2016). However, it is expected that this will come with a cost of reduced ecological integrity (Alongi 2015)

and that the future occurrence of mangroves will be severely limited to certain regions (Lovelock et al. 2015). The regional and local attributes that will determine the persistence of mangrove trees under predicted global change have been identified as those that influence sediment accretion, allow for landward migration and enhance sediment distribution as well as propagule dispersal (McLeod & Salm 2006). Factors influencing the resilience of the associated mangrove fauna have been identified by comparing the assemblages of planted and natural mangrove stands (Pagliosa et al. 2016). The colonization of planted mangrove sites by characteristic faunal species has led to their presence being used as a qualitative indication of successful rehabilitation (Bosire et al. 2008). Unfortunately, recent work by Pagliosa et al. (2016) has shown that although the fauna may re-colonize planted sites, the ecological resilience is not comparable to that of natural mangroves. This occurs as a result of stressors that are generally related to hydroperiod, nutrient inputs as well as soil chemistry (Pagliosa et al. 2016), as they have a significant impact on the mangrove macrofauna that drive ecosystem processes (Cannicci et al. 2008, Lee 2008). Conservation of ecologically functional mangrove ecosystems therefore requires an integrated approach towards identifying areas that will allow establishment or persistence of the trees as well as the associated fauna.

Estuarine areas can promote the persistence of mangrove ecosystems if these environments are able to offer ample supplies of freshwater and sediment, have available low-lying retreat areas, and experience a tidal range that promotes thorough flushing (Gilman et al. 2008). However, as they are coastal ecosystems, estuaries are also vulnerable to a number of threats associated with anthropogenic activities, climate change, and extreme events (Crain et al. 2009, Jennerjahn & Mitchell 2013). Furthermore, as estuarine environments are characteristically dynamic and variable, it has been challenging to quantify their responses (Elliott & Quintino 2007) and thus their potential to provide suitable areas for mangroves to persist in under global change scenarios (Quisthoudt et al. 2013, Godoy & Lacerda 2015). Research has therefore focussed on monitoring mangroves that currently occur in estuaries and investigating their resilience and responses within these dynamic environments (Hoppe-Speer et al. 2013, Costa et al. 2015, Asbridge et al. 2016). The responses of mangrove fauna to factors associated with global change have also been investigated, but studies have generally been focussed on distinct

threats such as increased temperature (Chapperon & Seuront 2010) or nutrient enrichment by wastewater (Cannicci et al. 2009). Monitoring estuarine macrofauna has however provided important insight to the responses of assemblages, in terms of productivity and biomass, to environmental change (Currie & Small 2005, de Paz et al. 2008). The responses of mangrove macrofauna to environmental variability should therefore be included in studies that aim to assess the resilience of estuarine mangroves.

The St Lucia Estuary, which is located on the northern coast of the KwaZulu-Natal coast of South Africa, provides a unique opportunity to investigate the responses of estuarine mangrove ecosystems to dynamic fluctuations that are driven by both natural and anthropogenic factors. As it is the largest estuarine lake on the African continent (Cyrus et al. 2011), it is also the most extensively researched system in southern Africa (Whitfield & Taylor 2009). The St Lucia Estuary is therefore considered as an important model for estuarine ecology and conservation as the large amount of research and long term monitoring has provided valuable information on many aspects that are globally applicable (Perissinotto et al. 2013b). The St Lucia Estuary has been characterized by extensive management programs that have attempted to maintain the ecological functioning of the system in response to both natural and anthropogenic impacts (for a detailed review see Whitfield & Taylor 2009, Taylor 2013). The most notable impacts have occurred as a result of the natural sub-decadal flood-drought cycle that can be exacerbated by anthropogenic activities that influence flow (Perissinotto et al. 2013a, Stretch et al. 2013). This results in large scale regime shifts from hypersaline to freshwater-dominated phases as well as the persistence of largely non-tidal conditions as a result of limited marine connectivity (Whitfield et al. 2013). A strategic monitoring program has therefore been implemented since 2010 with the specific aim to investigate the responses of mangroves within the St Lucia Estuary to these environmental fluctuations and provide information relating to their resilience (Hoppe-Speer et al. 2013, Rautenbach 2015, Adams & Human 2016). These studies have provided valuable information with regards to the resilience of the mangrove trees within the St Lucia Estuary. It is therefore evident that the resilience of mangrove fauna that have key ecological roles should also be considered. The overall aim of the present study was therefore to provide a complementary

assessment for the responses of a dominant mangrove faunal species over the same time period.

*Cerithidea decollata* (Linnaeus, 1767), commonly known as the climbing mangrove whelk, has a widespread distribution along the East African coastline from Kenya to South Africa (Reid 2014). As a benthic deposit feeder, *C. decollata* contributes towards the recycling of carbon and transferral of benthic primary production to higher trophic levels (Bouillon et al. 2004b, Kruitwagen et al. 2010). It is also one of the few species that has been recorded to persist within the mangrove habitats of the St Lucia Estuary through previous regime shifts (Perissinotto et al. 2014) and is therefore considered to be resilient. The occurrence of *C. decollata* within the mangroves of St Lucia has been broadly correlated with sediment moisture (Hoppe-Speer et al. 2013). However, as this species undergoes planktotrophic development (Reid 2014), connectivity with the marine environment should also be considered as an important factor that enables its populations to persist (Madeira et al. 2012).

The objectives of this study therefore were: 1) to compare the density of *C. decollata* from mangrove sites within St Lucia that differ in terms of marine connectivity; 2) to determine whether the relative level of the lake (as a proxy for flood or drought conditions) has a significant impact on the populations of *C. decollata*; and 3) to determine which local environmental variables, if any, are significantly related to the density of *C. decollata* within the St Lucia Estuary.

Assessing the relationship between *C. decollata* and environmental conditions has the potential to provide insight to the use of this species as a bioindicator for the health of mangrove habitats in estuaries that are impacted by regime shifts, particularly in relation to freshwater inflow and marine connectivity. This study also provides information on the resilience of this mangrove species in relation to large scale environmental variability associated with an estuary.

## 6.2 Materials and Methods

### 6.2.1 Study sites

The St Lucia Estuary (Figure 1.4) contains a variety of habitats and thus supports complex ecological networks and high biodiversity, it has therefore been assigned as a Ramsar Wetland of International Importance and is situated within the iSimangaliso Wetland Park, South Africa's first UNESCO World Heritage Site (Porter 2013). Mangroves (*Avicennia marina* and *Bruguiera gymnorhiza*) are present within the lower reaches of the estuary and have been reported to cover an area of 571 ha (Rajkaran & Adams 2011). The average height of *A. marina* trees in the St Lucia Estuary has been reported around 600 mm, while the average height of the *B. gymnorhiza* trees is approximately 300 mm (Rajkaran & Adams 2011).

The monitored sites that were selected for comparison in this study were determined by the presence of *Cerithidea decollata*. A comprehensive assessment and comparison of the population structure of the mangrove trees at the different sites has been presented by Adams & Human (2016). The sites were all situated within the lower reaches of the estuary but were variable in terms of their potential for connectivity with the marine environment. The Back Channel site (28°23'44.28'' S, 32°25'6.59'' E) is located within the artificially constructed channel that connects the Mfolozi River with the St Lucia Estuary. This site experiences exposure to seawater at spring high tide when the mouth of the Mfolozi is open to the Indian Ocean (Hoppe-Speer et al. 2013). The Shark Basin site (28°22'6.01'' S, 32°25'23.72'' E) is located within a freshwater seepage area on the northern bank of the St Lucia Estuary. This site exhibits limited influence from the marine environment, however intrusion of saline water from the main body of the estuary can occur. The Honeymoon Bend site (28°23'12.60'' S, 32°24'14.65''E) is the furthest upstream and is located along the main water channel of the Narrows. Four randomly selected quadrats (25 m$^2$) (see Hoppe-Speer et al. 2013) were sampled at each site in each year. In order to capture the variability within each site, the quadrats were qualitatively classified as "Dry", "Waterlogged", "Submerged", or "Flooded" on each sampling occasion.

Data for this study were collected in 2010, 2013, 2014 and 2015 as part of a long term monitoring program for the mangrove habitats of the St Lucia Estuary. The St

Lucia Estuary is dynamic and as a result of the geomorphology of the catchment, it is sensitive to factors that influence water inflow (Stretch et al. 2013). As a result, each sampling occasion represented a different relative water level and salinity for the estuary (Figure 6.1).
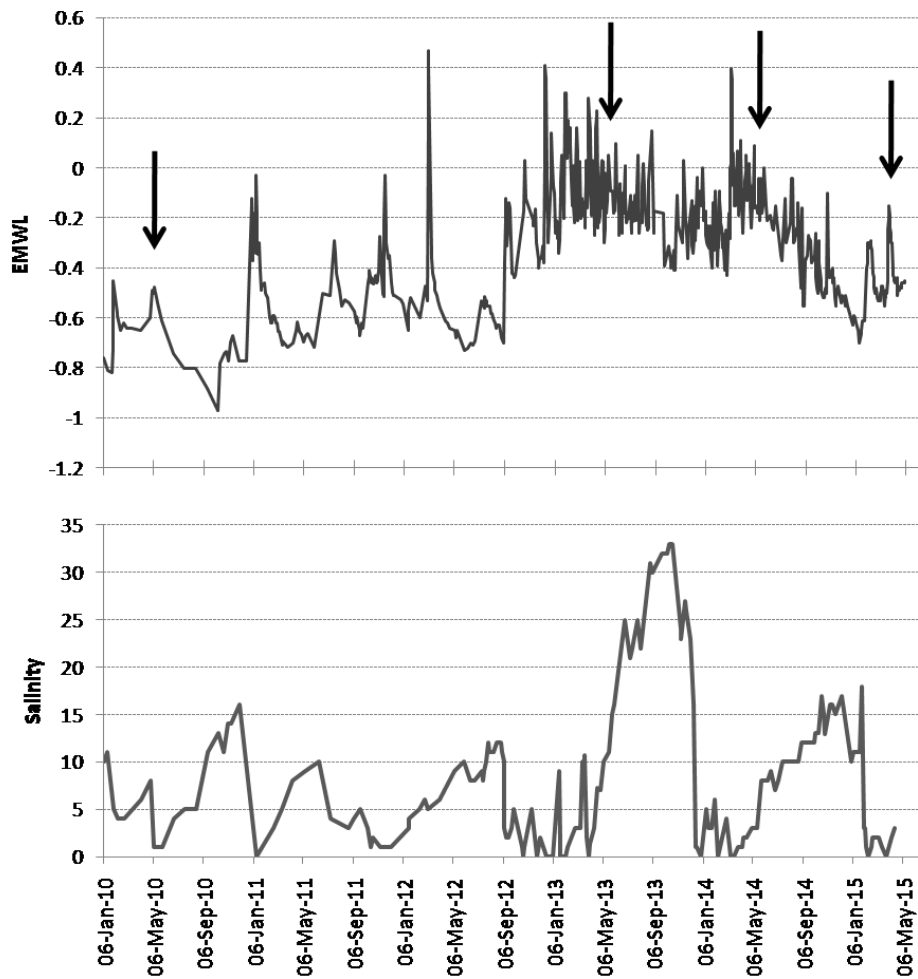


**Figure 6.1** Estuary Mean Water Level (EMWL) and salinity measured for the St Lucia Estuary over the period of Jan 2010 to May 2015. EMWL was calculated following Lawrie & Stretch (2011) by calibrating water level measurements taken at the Bridge which crosses the lower Narrows region. Arrows indicate sampling occasions.

### 6.2.2 Sample collection and processing

*Sediment characteristics*

Samples of surface sediment were collected in triplicate per quadrat using an auger. The samples were retained for further processing in the laboratory. This included the measurement of sediment moisture content, sediment organic matter and sediment conductivity (Adams & Human 2016).

After the removal of visible detritus and debris, the sediment was divided, weighed to approximately 15 g and placed into crucibles. These were then oven dried (100 ° C, 48 h) and subsequently re-weighed (Black 1965) so that sediment moisture was calculated as:

$$Sediment\ moisture\ (\%) = \left[\frac{(Wet\ mass - Dry\ mass)}{Wet\ mass}\right] X\ 100$$

Sediment organic matter was measured in a similar manner. Each crucible was weighed before (M1) and after (M2) placing approximately 10 g of sediment in it. The crucibles were then placed in a muffle furnace (600 °C, 8 h) for combustion (Briggs 1977) and then cooled to room temperature before being re-weighed (M3). Organic matter was subsequently calculated following Adams & Human (2016) as:

$$Sediment\ organic\ matter\ \left[\frac{(M2 - M3)}{(M2 - M1)}\right] X\ 100$$

Sediment conductivity was measured following the method of Barnard (1990). This entailed air drying the sediment and then suspending it in 100 ml of distilled water. The solution was then filtered (Whatman No. 1) and the conductivity of the filtrate was measured using a hand-held conductivity meter (CyberScan, Eutech) calibrated at 20 °C.

*Gastropod abundance*

The abundance of *C. decollata* was estimated on each sampling occasion by counting the number of individual snails present on each tree within the respective quadrats. Generally, *C. decollata* climbs up the trunks of mangrove trees, in order to avoid submergence by the incoming high tide (Vannini et al. 2006). However, the St Lucia Estuary is largely non-tidal and the long term absence of tidal exchange has

resulted in a breakdown of these typical rhythmic migrations. This has been shown to be the case for snails that inhabit high shore regions that are only reached by the highest spring tides (Vannini et al. 2008). It was therefore assumed to be just as likely to find individuals on the substrate as on the tree trunks. As the number of snails counted was confounded by the number of trees within each quadrat, snail density was calculated to take this into account as follows:

$$Snail\ density = \frac{total\ number\ of\ snails}{number\ of\ trees\ on\ which\ snails\ occurred\ per\ 25m^2\ quadrat}$$

### 6.2. 3 Statistical analyses

A two-way ANOVA was performed (fixed factors: Site, Year) to test differences in density of *C. decollata* at St Lucia. "Year" was considered a fixed factor as it represented the relative water level and salinity on each sampling occasion (Figure 6.1). After running the ANOVA, Tukey-HSD post-hoc comparisons were subsequently used to identify significant pair-wise differences. The parametric assumptions of normality and homoscedasticity were tested using Shapiro Wilk's test and Levene's test respectively. These univariate statistical analyses were performed using the packages "car" (Fox & Weisberg 2014) and "agricolae" (de Mendiburu 2016) in R v 3.2.5 for Windows (R Development Core Team 2016).

The environmental variables (sediment moisture, sediment organic matter and sediment conductivity) were compared between sites and sampling years using multivariate analyses. Principal Components Analyses were therefore used to visualize the data which were first log(x+1)-transformed and normalized. A multivariate resemblance matrix was then generated using Euclidean distances. The resemblance matrix was used in a two-way permutational MANOVA (PERMANOVA, (Anderson 2001). This tested differences in environmental variables between sites (fixed factor, three levels: Back Channel, Shark Basin, Honeymoon Bend) and years sampled (fixed factor, four levels: 2010, 2013, 2014, 2015). Pair-wise tests were used to determine spatial trends (only differences between sites in each year) in environmental variables as well as trends in relation to estuary water level and salinity (only differences between years for each site). Multivariate comparisons of environmental data were performed in PRIMER v 6 (Clarke & Warwick 2001), using the PERMANOVA+ add-on (Anderson et al. 2008).

Finally, a linear regression model was developed to relate the density of *C. decollata* to the environmental variables. All continuous environmental variables, their potential ecologically relevant interactions, as well as the categorical factors were considered as predictors. The model was developed following Zuur et al. (2009) using the package "nmle" (Pinheiro et al. 2016) for R v 3.2.5 for Windows (R Development Core Team 2016). After preliminary data exploration, a log(x) transformation was applied to the variable "Conductivity". To allow for heterogeneity between sites, an identity variance structure was applied to the factor "Site". A general least squares regression was therefore selected as the appropriate model type. The optimal model was selected using the "MuMIn" package (Barton 2016) based on the corrected Aikake Information Criterion (AIC) for small sample sizes (Hurvich & Tsai 1991). The model was validated using the appropriate plots of the residuals to assess normality and homoscedasticity, with reference to the expected values as well as the explanatory variables (Zuur et al. 2009).

*6.3 Results*

*6.3.1 Environmental variability*

There were significant differences in the measured environmental variables (sediment moisture, sediment organic matter, sediment conductivity) when comparing between sites and years sampled (Table 6.1).

**Table 6.1** PERMANOVA output showing significance of main effects and interaction between "Site" and "Year" as categorical predictors of environmental variables (sediment moisture, sediment organic matter, sediment conductivity) measured at mangrove sites within the St Lucia Estuary.

| PERMANOVA | *df* | *SS* | *MS* | *F* | *p* |
|---|---|---|---|---|---|
| Site | 2 | 83.857 | 41.928 | 30.858 | 0.001 |
| Year | 3 | 61.393 | 20.464 | 15.061 | 0.001 |
| Site x Year | 6 | 62.252 | 10.375 | 7.636 | 0.001 |
| Residual | 115 | 156.26 | 1.359 | - | - |
| Total | 126 | 378 | - | - | - |

Pair-wise comparisons (Table 6.2) between the sites for each year showed that in 2010 environmental conditions were similar between the Back Channel and Shark Basin. However, environmental conditions were significantly different between these two sites and those at Honeymoon Bend. In all other years sampled the environmental conditions were significantly different ($p < 0.05$) between all sites (Table 6.2).

**Table 6.2** Pair-wise comparisons illustrating spatial trends for environmental variables measured at different sites (BC: Back Channel; SB: Shark Basin; HB: Honeymoon Bend) in each year at the St Lucia Estuary. Comparisons were determined using PERMANOVA and grouping observations of "Site" by levels of the factor "Year".

| Pair-wise comparisons | 2010 | 2013 | 2014 | 2015 |
|---|---|---|---|---|
| BC : SB | $t = 1.584$, $p = 0.104$ | $t = 2.833$, $p = 0.001$ | $t = 11.044$, $p = 0.001$ | $t = 3.007$, $p = 0.001$ |
| BC : HB | $t = 9.657$, $p = 0.001$ | $t = 7.389$, $p = 0.001$ | $t = 11.752$, $p = 0.001$ | $t = 4.615$, $p = 0.001$ |
| SB : HB | $t = 2.754$, $p = 0.007$ | $t = 2.216$, $p = 0.025$ | $t = 6.790$, $p = 0.001$ | $t = 3.898$, $p = 0.002$ |

Environmental conditions were also variable when compared between different years for each site (Figure 6.2). The Principal Components (PC) scores allowed a characterization of each site over all sampling occasions in terms of the measured environmental variables (Table 6.3). The first PC (PC 1) explained more than 70 % of the variation in the data at the Back Channel, but only 50 % of the variation for Shark Basin and Honeymoon Bend (Table 6.3). The loading of the environmental variables (sediment moisture, sediment organic matter and sediment conductivity) on PC 1 was also different between sites. The highest loading on PC 1 for the Back Channel was associated with sediment conductivity, while for Shark Basin and Honeymoon Bend it was sediment moisture (Table 6.3).
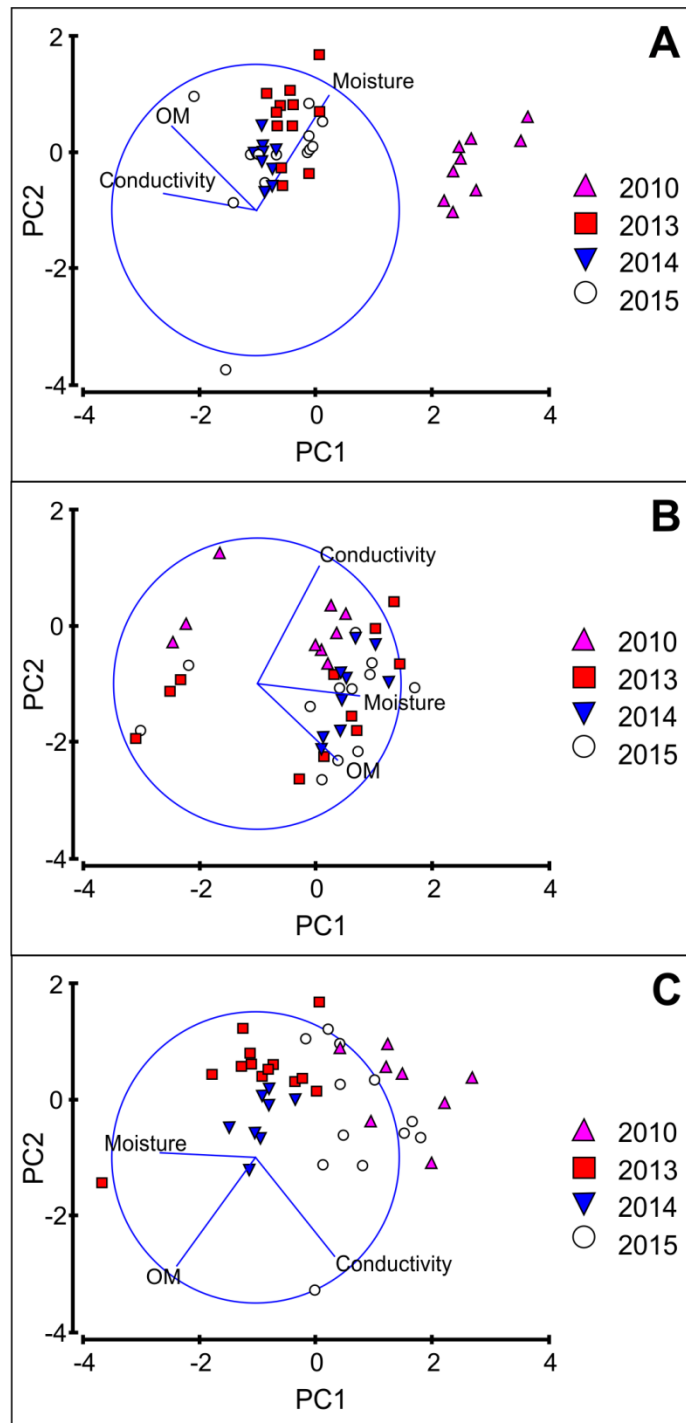
**Figure 6.2** Principal Components Analyses (PCA) illustrating temporal trends for environmental variables (sediment moisture, sediment organic matter, sediment conductivity) measured at mangrove sites of the St Lucia Estuary at **A**: Back Channel; **B**: Shark Basin; and **C**: Honeymoon Bend. Data were first log(x+1)-transformed and normalised before applying the PCA.

**Table 6.3** Principal Component loadings for sediment moisture, sediment organic matter and sediment conductivity for each mangrove site sampled in the St Lucia Estuary. The eigenvalue and percentage contribution of each Principal Component to the variation in the data are also provided. Principal components were calculated for each site across all years that were sampled.

|  | PC 1 | PC 2 | PC 3 |
|---|---|---|---|
| **Back Channel** | | | |
| Moisture content | 0.510 | 0.804 | -0.307 |
| Organic matter | -0.576 | 0.584 | 0.572 |
| Conductivity | -0.639 | 0.115 | -0.760 |
| Eigenvalue | 2.11 | 0.67 | 0.22 |
| % variability | 70.3 | 22.2 | 7.5 |
| **Shark Basin** | | | |
| Moisture content | 0.678 | -0.068 | 0.732 |
| Organic matter | 0.589 | -0.546 | -0.596 |
| Conductivity | 0.440 | 0.835 | -0.330 |
| Eigenvalue | 1.63 | 0.91 | 0.46 |
| % variability | 54.2 | 30.3 | 15.5 |
| **Honeymoon Bend** | | | |
| Moisture content | -0.638 | 0.039 | 0.769 |
| Organic matter | -0.534 | -0.742 | -0.405 |
| Conductivity | 0.555 | -0.669 | 0.494 |
| Eigenvalue | 1.7 | 0.78 | 0.52 |
| % variability | 56.7 | 26.0 | 17.3 |

*6.3.1 Variation in gastropod density*

Considering "Site" and "Year" as categorical predictors of snail density, the 2-way ANOVA showed a significant interaction between these factors ($F_{6,35}$ = 2.978, $p$ = 0.019). This is evident when considering the change in snail density at each site measured on different sampling occasions (Figure 6.3).
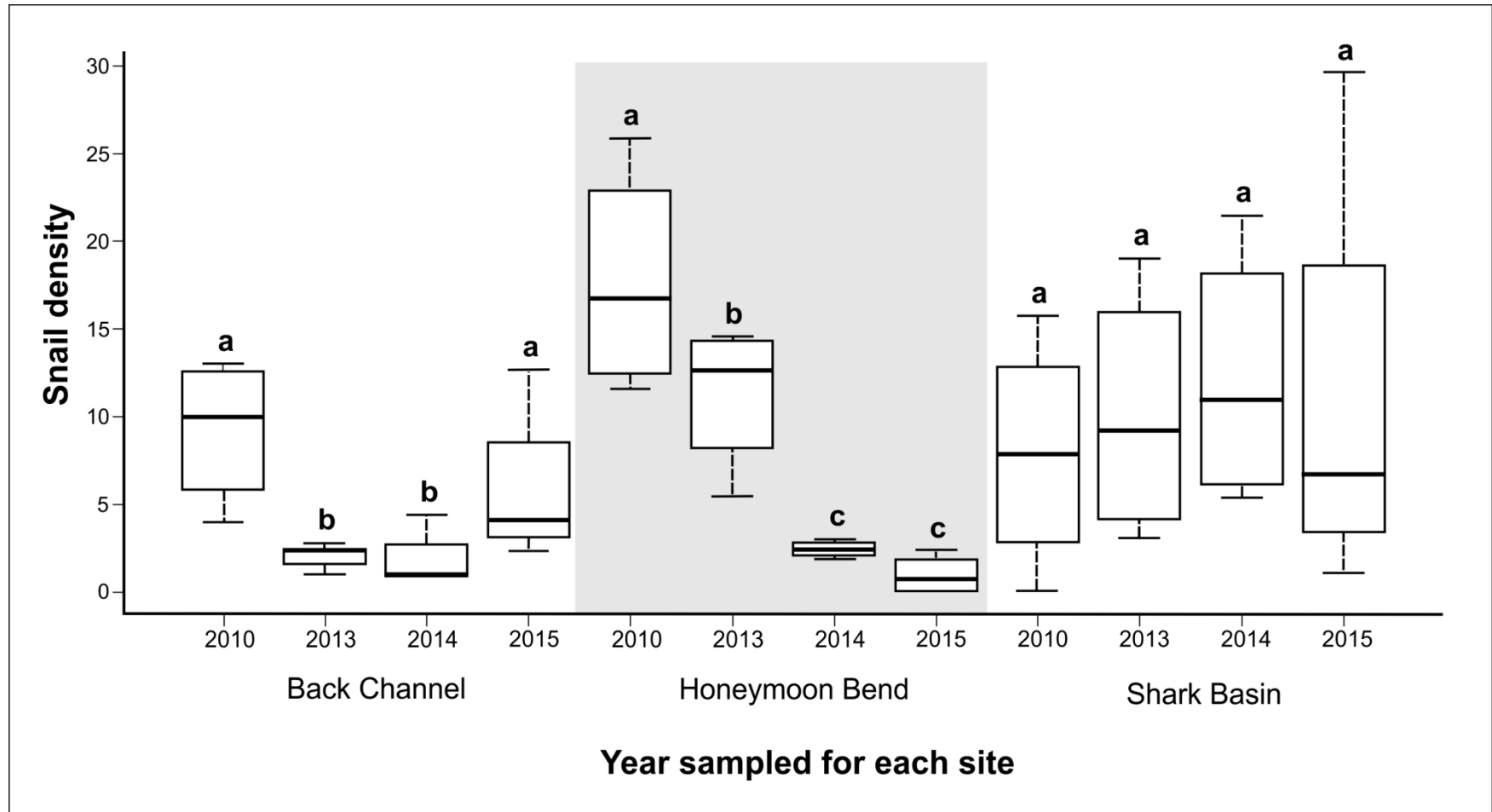
**Figure 6.3** Box-plot of the mean density (thickened line) of *Cerithidea decollata* at mangrove sites (Back Channel,Honeymoon Bend, Shark Basin,) of the St Lucia Estuary measured in different years. Boxes and error bars represent 25, 75 and 95 % Confidence Intervals of the mean. Trends for each separate site are indicated by Tukey post-hoc groupings (*p* > 0.05) using lower case letters. Shading is used to assist visual separation of sites.

Tukey-HSD post-hoc tests were used to compare snail density at each site for different years. These comparisons showed that the population at Shark Basin was the most stable (Figure 6.3). In contrast, *C. decollata* was most variable at Honeymoon Bend, with the density of snails in 2010 and 2013 being significantly different from each other, as well as from both 2014 and 2015 (Figure 6.3). There were no clear trends when snail density was compared between sites within the same year (Figure 6.3). Tukey-HSD post-hoc tests also showed that snail density was not significantly different ($p > 0.05$) between: the Back Channel and Shark Basin in 2010 and 2015; Shark Basin and Honeymoon Bend in 2013; and the Back Channel and Honeymoon Bend in 2014.

### *6.3.3 Relationship between gastropod density and environmental variability*

There was considerable variability in the environmental conditions and snail density between different sites as well as in relation to lake level. It was therefore difficult to directly infer any trends or whether any particular environmental conditions were driving snail density at different sites and on different sampling occasions. Snail density was first considered in relation to the qualitative category assigned to each quadrat at the time of sampling (Figure 6.4). This visualization provided further support for the variability that exists between sites.

**Back Channel**

|      | Q1    | Q2    | Q3   | Q4    |
|------|-------|-------|------|-------|
| 2010 | 7.72  | 13    | 3.96 | 12.13 |
| 2013 | 2.33  | 2.78  | 1    | 0     |
| 2014 | 1     | 1     | 1    | 4.38  |
| 2015 | 12.60 | 3.86  | 2.33 | 4.36  |

**Shark Basin**

|      | Q1    | Q2   | Q3    | Q4    |
|------|-------|------|-------|-------|
| 2010 | 0     | 5.57 | 15.62 | 9.94  |
| 2013 | 3     | 5.35 | 12.81 | 18.98 |
| 2014 | 14.80 | 5.22 | 21.39 | 6.97  |
| 2015 | 29.50 | 7.62 | 5.75  | 1     |

**Honeymoon Bend**

|      | Q1    | Q2    | Q3    | Q4    |
|------|-------|-------|-------|-------|
| 2010 | 13.38 | 25.75 | 19.82 | 11.43 |
| 2013 | 14.07 | 10.93 | 14.43 | 5.33  |
| 2014 | 2.55  | 2.92  | 1.80  | 2.13  |
| 2015 | 2.33  | 0     | 1.33  | 0     |

- Flooded
- Submerged
- Waterlogged
- Dry
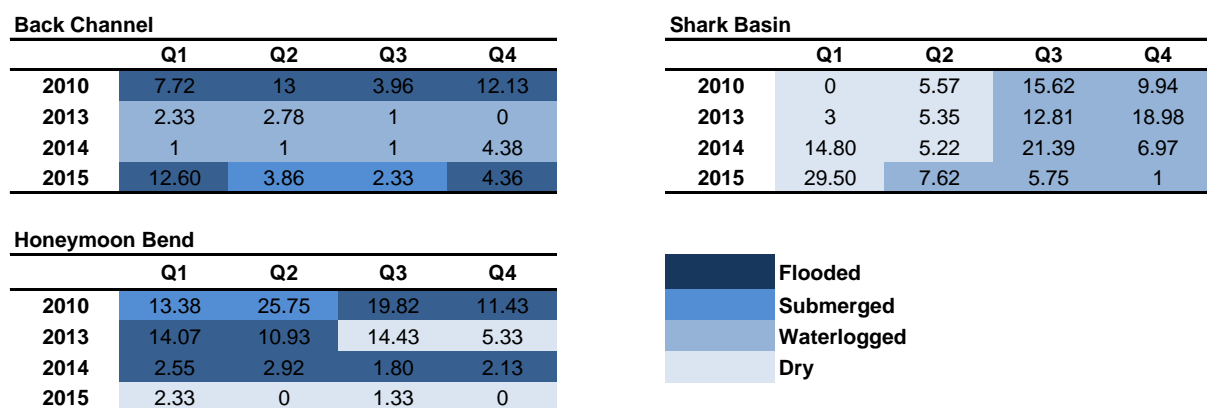
**Figure 6.4** Calculated density of *Cerithidea decollata* in relation to the qualitative category (Flooded, Submerged, Waterlogged, Dry) assigned to each specific quadrat on respective sampling occasions at Back Channel, Shark Basin and Honeymoon Bend mangrove sites of the St Lucia Estuary.

The formation of a global model incorporating all possible predictors that could be statistically tested for significance was applied to investigate the drivers of snail density. The qualitative category assigned to a quadrat ("Dry", "Waterlogged", "Submerged", or "Flooded") at the time of sampling was not included in the model because as a factor it was shown to be a proxy for sediment conductivity, sediment moisture and sediment organic matter (positive correlations, $R^2 > 0.5$). The model selection process therefore found that snail density could best be described by the following generalized least squares model, fit by REML (restricted maximum likelihood estimation):

$$y = -2.43x + 13.12$$

where $y$ is Snail Density and $x$ is the log(x)-transformation of sediment conductivity. This model also took into account the deviation in variance between sites (Table 6.4).

**Table 6.4** Summary of optimal generalized least squares model for density of *Cerithidea decollata* at the St Lucia Estuary.

| Coefficients | Value | Std Error | *df* | *t* | *p* | Correlation |
|---|---|---|---|---|---|---|
| (Intercept) | 13.120 | 2.677 | - | 4.901 | 0.0001 | - |
| log(Conductivity) | -2.432 | 0.840 | - | -2.894 | 0.0061 | -0.951 |
| Residual | - | 3.669 | 41 | - | - | - |
| Total | - | - | 43 | - | - | - |

| Variance function | Different standard deviations per site |
|---|---|
| Site 1 | 1.000 |
| Site 2 | 2.325 |
| Site 3 | 2.240 |

The variability of sediment conductivity measured at the different sites on each sampling occasion is illustrated in Figure 6.5. The trends in sediment conductivity are comparable to those recorded for the density of *C. decollata* (Figure 6.3), when considering that the model allowed for variability between sites. At the Back Channel, high sediment conductivity in 2014 corresponded with lower densities of *C. decollata*. In contrast, at Honeymoon Bend the highest snail density was recorded when sediment conductivity was also high, in 2010. At Shark Basin both sediment conductivity and snail density were relatively stable.
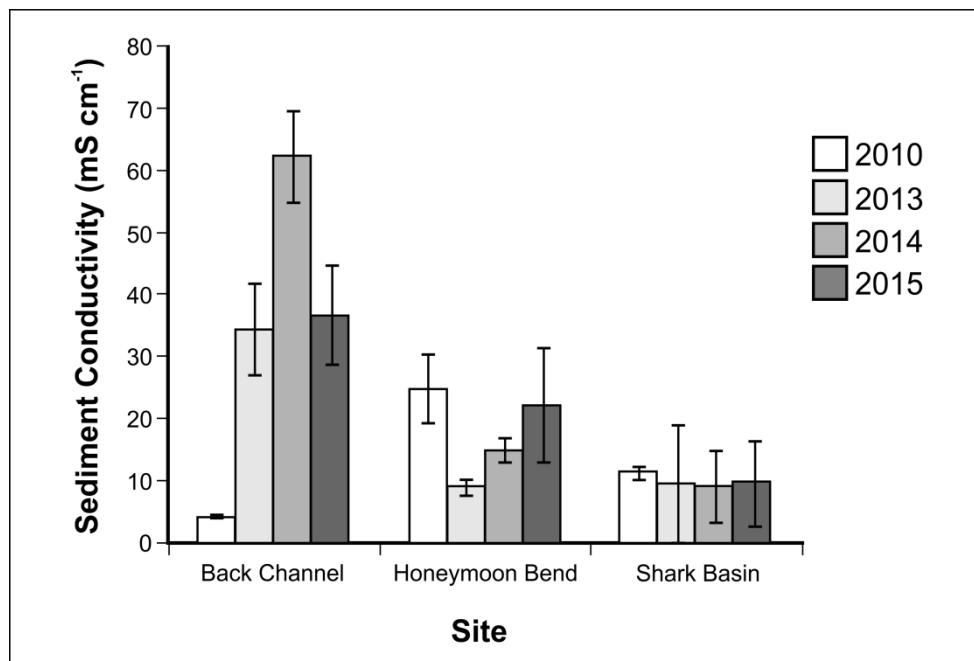


**Figure 6.5** Average (± SD) sediment conductivity measured from mangrove sites (Back Channel, Honeymoon Bend, Shark Basin) in the St Lucia Estuary in different years.

*6.4 Discussion*

The resilience of mangrove trees in response to factors associated with contemporary global change has been increasingly highlighted (Gilman et al. 2008, Ward et al. 2016). However, a limited number of studies have simultaneously reported on the responses of associated mangrove fauna to these stressors (Ellison 2008). This study has therefore provided a complementary assessment for a dominant mangrove gastropod in an estuarine system where the resilience of the mangrove trees has already been assessed. As *C. decollata* is known to be adapted to variable habitats, the responses recorded in this study are able to inform on some of the limiting environmental thresholds. The responses of *C. decollata* to local and long term environmental change within the St Lucia Estuary indicated that this species is resilient to relatively large fluctuations and variability in factors associated with the dynamics of the estuary.

*6.4.1 Interpreting responses to changes in marine connectivity and estuary water level*

Adams and Human (2016) reported that the persistence of mangrove trees within the St Lucia Estuary was most significantly influenced by the water level of the estuary. Mangroves are sensitive to changes in inundation duration and frequency (Ball 1988), as both prolonged inundation or extensive emersion are detrimental to the established trees as well as to any potential propagule recruits (Delgado et al. 2001, Hoppe-Speer et al. 2011). Significant die-back of mangroves occurred in the St Lucia Estuary as a result of prolonged inundation, as indicated by the flooded quadrats between 2013 and 2014 at Honeymoon Bend. Superficially, the responses of *C. decollata* appear to be similar to those of the mangrove trees as there was a significant decline in density at Honeymoon Bend in 2013 and 2014. However, the mangrove trees were reported to respond well to changes that had occurred at the Back Channel during this time as there was successful recruitment of seedlings (Adams & Human 2016). In contrast, the density of *C. decollata* recorded at the Back Channel was significantly lower in 2013 and 2014. Furthermore, while *C. decollata* remained stable at Shark Basin during the monitoring period, there was an increase in the percentage of dead mangrove trees recorded at this site in 2013 due to the loss of a seedling cohort (Adams & Human 2016). This mismatch in recorded responses may reflect true differences between the resilience of the trees and the

snails to environmental changes, however, discrepancies may also result from different response times to these changes.

*Cerithidea decollata* exhibits an innate behavioural response to changes in water level and this behaviour can be modified over a relatively short period of time (Vannini et al. 2008). Interestingly, Cockcroft & Forbes (1981) noted that *C. decollata* is able to survive submergence in seawater for at least two weeks. The vertical migration by *C. decollata* has therefore been described as a predator avoidance strategy (Vannini et al. 2006). *Cerithidea decollata* is mostly predated upon by mangrove brachyurans, with strong evidence of predation by *Epixanthus dentatus* (White, 1848) reported by Vannini et al. (2001). This species is predominantly nocturnal and ambushes its prey on the subtrate or on the roots of the mangrove trees (Cannicci et al. 1998; Vannini et al. 2001). Other potential brachyuran predators include the pilumnid *Eurycarcinus natalensis* (Krauss, 1843) and the portunids *Thalamita crenata* Rüppell, 1830 and *Scylla serrata* (Forskål, 1775) which are significant threats during high tide (Vannini et al. 2006).

The climbing behaviour of *C. decollata* has also been described as a mechanism to cope with physiological stress (McGuinness 1994). Vertical migrations by *Cerithideopsis scalariformis* have also been linked with parasite avoidance (Belgrad & Smith 2014). It might therefore be expected that a higher density of snails would be recorded on the trees when the relative water level was higher, resulting in flooding of the quadrats. While this did occur at the Back Channel, the same trend was not recorded at Honeymoon Bend or Shark Basin. We expect that fewer *C. decollata* were recorded on the trees at the Back Channel site in 2013 and 2014, as increased marine connectivity and the influence of a tidal regime would drive a migration to the substrate. This is likely, as *C. decollata* are able to establish their rhythmic migration after exposure to between 5 and 6 consecutive high tides (Vannini et al. 2008) and by this time a canal had been constructed along the beach to establish a connection between the St Lucia Estuary and the Indian Ocean via the Mfolozi River (Whitfield et al. 2013).

As the construction of the beach canal coincided with a natural regime shift towards a freshwater-dominated phase in the St Lucia Estuary between 2012 and 2014 (Whitfield et al. 2013), it is not possible to attribute the fluctuations in water level

measured at the Bridge to either tidal movements or increased river inflow. The location of the site selected at Honeymoon Bend along the main channel of the Narrows made these quadrats particularly susceptible to changes in the water level during this period. At this site, flooded quadrats did not correspond with higher densities of *C. decollata*. It is currently unknown whether prolonged inundation of the mangroves would drive these snails to forage on submerged sediment or whether they remain inactive on the trunks of the trees until their death. This complicates the interpretation of the further decline in snail density at this site in 2015, when low water levels resulted in the quadrats becoming dry. Dry sediment conditions are expected to be detrimental to mangrove gastropods as low sediment moisture content is directly related to physiological stress (Iacarella & Helmuth 2011), and furthermore does not support regeneration of their benthic algal food sources (Underwood & Paterson 1993). Hoppe-Speer et al. (2013) did report on the total absence of *C. decollata* from mangrove sites in St Lucia that were completely dry. However, dry sediment conditions in some quadrats did not prevent the persistence of *C. decollata* at the Shark Basin site, for instance. The stability of this site has been attributed to the local freshwater seepage acting as a buffer to the potentially extreme fluctuations experienced in other areas of the Narrows (Taylor et al. 2006, Hoppe-Speer et al. 2013, Adams & Human 2016). It is clear that these conditions ameliorate potential stressors to *C. decollata* at this site, as it appears to be largely unaffected by changes in the water level of the estuary.

### 6.4.2 Sediment conductivity as a predictor of Cerithidea decollata density at the St Lucia Estuary

There is clearly an overwhelming amount of variability associated with the different mangrove sites in the St Lucia Estuary. One component that was not included in the model was sediment granulometry, as the data were not available for all sites on each sampling occasion. Adams & Human (2016) have reported that sediment composition was variable during the sampling period. There was overall a decrease in the percentage of sand at the Back Channel in 2013 and 2014. A similar trend was reported for Shark Basin and Honeymoon Bend in 2014. As a result, higher clay content was measured at all three sites in 2013 and 2014. Silt content was reported to remain relatively stable (Adams & Human 2016). Although the variability of this

physical attribute could have influenced the results of the model, it is likely that this variable would have been correlated with sediment conductivity.

It is important to consider whether instantaneous sampling can provide a meaningful assessment of trends between biological and physico-chemical parameters in such a dynamic estuarine system (Legendre & Demers 1984). In the case of mangrove trees, an annual sampling event can provide meaningful data as the responses that are recorded (growth, seedling recruitment and die-back) can inform on relatively long term trends (Schmitt & Duke 2014). However, the results of this study suggest that this time frame may be insufficient to capture the responses of *C. decollata* to environmental change. For example, in 2010 the sampling event coincided with an unseasonably high rainfall event (Hoppe-Speer et al. 2013) and thus quadrats sampled at both Honeymoon Bend and the Back Channel were categorized as "Flooded". However, this time period in fact represented the end of a long drought phase (Whitfield et al. 2013) during which the Narrows region remained relatively stable and thus able to support high densities of *C. decollata*. Subsequent categorization of "Flooded" quadrats at Honeymoon Bend did not correspond with high snail density, as already discussed. The ideal recommendation is therefore to improve the sampling design by increasing sampling frequency to capture potential seasonal variability and have a better resolution of responses to extreme events. However, this is often a logistical constraint, particularly if: 1) the study is focussed on monitoring mangrove trees that respond over longer time periods; and 2) the study area is remote and the sites are not easily accessible. In an attempt to compensate for this, it was possible to use an alternative approach to examine the trends in snail density. This was achieved by identifying a physical variable that is related to snail density at the time of sampling, but also provides some indication of the prevailing environmental conditions. The use of mathematical models to describe biological observations in relation to the environment has become an invaluable tool in ecology to resolve complex patterns in order to understand the key processes that drive ecosystems (Underwood et al. 2000, DeAngelis & Mooij 2005). This approach was therefore used to understand the density trends of *C. decollata* in the St Lucia Estuary.

The model selection process was able to resolve the complexity, and the final optimal model described snail density as a function of sediment conductivity with the

described relationship being variable between sites, as is clearly evident from the results in this study. Sediment salt-load in the St Lucia Estuary is highly variable and is significantly influenced by both large scale events, such as floods and droughts, as well as by local factors, such as groundwater intrusion and bioturbation (Bate & Taylor 2008). Therefore, the relationship between snail density and sediment conductivity is driven by different processes at the different sites. For example, high sediment conductivity (and low snail density) measured at the Back Channel site in 2014 was the result of an increased flow of seawater via Mfolozi River (Adams & Human 2016). In contrast, high sediment conductivity (and low snail density) measured at Honeymoon Bend in 2015 was likely the result of evaporation of the water column resulting in the deposition of salts (as suggested to occur by Bate & Taylor 2008).

Sediment salinity has been considered as a driving factor of community composition for deposit-feeding meiofauna (Whitlatch 1981, Ingole & Parulekar 1998). However, studies that focus on deposit-feeding gastropods generally consider water salinity as a primary factor that influences feeding activities (Hylleberg 1975, Chaparro et al. 2008). This is preferable for physiological tolerance experiments, as the salinity of fine sediments in estuaries is relatively stable in comparison to fluctuations in the water column (Chapman 1981). However, as the St Lucia Estuary undergoes periodic drought periods, the salt load of the sediment can be significantly high following evaporation - an excess of 2 million tonnes of salt was estimated to be contained within sediments to a depth of 20 cm during the drought period of 2002-2006 (Bate & Taylor 2008). Furthermore, overtopping from the marine environment as a result of Cyclone Gamede in 2007 was estimated to have introduced an additional 12 million tonnes of salt into the St Lucia Estuary (Bate & Taylor 2008). As *C. decollata* is able to occupy a wide range of habitats besides mangroves, such as salt marsh, salt pans, and creeks in fully marine or brackish conditions (Reid 2014) this species appears to have a relatively broad tolerance to water salinity. However, the physiological effect of consuming sediment that has excessively high salt content has not been investigated for *C. decollata*. Generally, species that inhabit high salinity environments have evolved a range of hypo-osmostic regulatory mechanisms to survive in these stressful conditions (Herbst 2001). As estuaries are increasingly facing threats related to reduced freshwater inflow (Alber 2002),

changes to the hydrodynamics of these systems may be inevitable (Gibson et al. 2003). If estuaries are considered to be potential refuge areas for the colonization of mangroves, it is essential to consider the potential physiological challenges that may be encountered under different scenarios.

### 6.4.3 On the resilience of Cerithidea decollata

The resilience of mangrove fauna has largely been considered in relation to their tolerance to increased environmental temperatures and the physiological stress associated with desiccation (Chapperon & Seuront 2010, Alongi 2015). Tropical species are considered to be particularly at risk because predicted temperature increases in equatorial regions are expected to be beyond their physiological limits (Tewksbury et al. 2008). Populations that occur at the edge of a tropical species' distributional range may therefore be critical for contributing towards persistence and potential range expansion (Hardie & Hutchings 2010). However, as marginal populations tend to be fragmented they are also expected to be susceptible to edge effects, including reduced genetic diversity as a result of limited gene flow (García-Fernández et al. 2012). This can however be advantageous, if local adaptation results in an enhanced potential to deal with environmental fluctuations beyond those experienced by populations at the centre of the distributional range (Eckert et al. 2008).

The results of this study have shown that *C. decollata* is able to persist through relatively large fluctuations of environmental conditions in the St Lucia Estuary. This may indicate local acclimation or plasticity (Hofmann & Todgham 2010), however *C. decollata* does reach its southern range limit on the South African coastline (Reid 2014). There is also evidence for genetic variation between southern, central, and northern populations of *C. decollata* along the east African coastline between Kenya and South Africa (Madeira et al. 2012). Along the high energy South African coastline, mangroves and salt marshes are limited to occurring in sheltered estuarine areas (Steinke 1999). As *C. decollata* occurs in both these habitat types in this region, it is not unlikely that this species has become locally adapted to conditions that are characteristic to these estuarine habitats. One of the most prominent characteristics of estuaries along the east coast of South Africa is that they are naturally temporarily open-closed systems that only have an established connection

with the marine environment when rainfall increases the flow and causes a breach (Whitfield 1992). This has been identified as a major factor that has limited the distribution and expansion of mangroves in this region (Saintilan et al. 2014), as closure of the estuary mouth results in rising water levels that in turn causes mangrove die-back through persistent inundation (Hoppe-Speer et al. 2015). However, the distribution of *C. decollata* extends beyond that of mangroves along the South African coastline as it has been recorded from salt marsh habitat within the temperate Knysna Estuary (Hodgson & Dickens 2012). The occurrence of *C. decollata* as far south as Knysna (34°04'38''S; 23°03'33''E) has been attributed to recent trends of rising sea temperatures as a result of climate change (Whitfield et al. 2016). This further highlights the potential resilience of this species and indicates that future research should focus on identifying specific tolerance ranges to conditions that are expected to prevail in estuaries under global change scenarios, such as increased temperature, higher sediment salinities and prolonged periods of inundation or limited connectivity to the marine environment.

## 6.5 Conclusion

Estuaries have been prioritized as areas that could provide suitable habitat for mangroves under predicted global change. It is therefore important to understand the responses of mangrove species to environmental conditions that could be experienced in estuaries under global change scenarios. The results of this study have shown that the responses of mangrove trees and the associated fauna to these environmental conditions can be variable and an integrated approach towards monitoring the resilience of these ecosystems is required. Furthermore, *C. decollata* has a wide tolerance for fluctuating environmental conditions beyond those that generally occur in estuaries that have a permanent connection to the marine environment. This study provides further support for the resilience of this species and indicates that further work should focus on investigating the specific tolerance of key mangrove species to conditions that they might experience in dynamic estuaries.

# Chapter 7: General Discussion

Anthropogenic global change in relation to climate, land use, and resource utilization has defined the focus of ecological studies at least since the Millennium Ecosystem Assessment (Alcamo et al. 2003). Marine and coastal ecosystems in particular have been identified as vulnerable to anthropogenic threats and thus effective management plans that focus on sustainability have been prioritized at a global scale (Crain et al. 2009, Visbeck et al. 2014, Rickels et al. 2016). Research has shown that many of these ecosystems are generally resilient and this has been related to their ecological complexity in the form of multiple interactions at different scales that collectively maintain ecosystem stability (Peterson et al. 1998, Hughes et al. 2005). As many processes in these ecosystems are interdependent and interactions can be nonlinear, it is possible for relatively small changes to facilitate regime shifts or collapses (Levin & Lubchenco 2008). Ecosystem-based management therefore aims to sustain the production of goods and services by using a multisectoral and multidisciplinary approach that considers ecological processes at multiple scales from a long term perspective (Lubchenco 1994, Turpie et al. 2008, Sherman 2014). By considering ecosystems from a holistic perspective, rather than as a collection of separate species, ecosystem-based management goals are able to incorporate ecological complexity and the dynamic characteristics of natural systems (Slocombe 1998).

To provide support to these ecosystem-based management approaches, general concepts, theories and models that incorporate ecological complexity have been prioritised for development by recent research efforts (Crowder & Norse 2008, Grimm & Berger 2016). However, understanding large scale processes requires a basis of ecological research that explains the underlying patterns (Underwood et al. 2000). Research that provides new ecological information for data-deficient species, ecosystems, or regions is therefore valuable, as it can be used to determine suitable indicators of ecosystem state (Levin et al. 2009, Ward et al. 2016). This research project has therefore contributed towards this call for the generation of new scientific

knowledge by providing basic ecological information for species that occur in threatened coastal ecosystems within a data-deficient region.

*7.1 Conceptual synthesis, summary of the research and contribution to new scientific knowledge*

The key research questions for this project were focused on three ecological themes: trophic linkages and resource partitioning, resource utilization rates, and ecological resilience.

Trophic linkages, in the form of food webs, identify pathways through which energy and matter are transferred within ecological communities (Paine 1988). Classical food web theory was developed around the argument provided by MacArthur (1955), who described community stability in relation to the number of trophic links as well as the number of species within the community. The relationship between food webs, species diversity, structure and stability has since become one of the most extensively debated and revised aspects in the field of ecology (May 1973, Paine 1980, Hastings 1988, Hall & Raffaelli 1993, Tilman 1999, Link 2002, Dunne 2006). Most recently, ecological research has focussed on determining whether the strength of trophic interactions influences community stability (Berlow et al. 2004, Rooney & McCann 2012). Food web models are however focussed on predation and rarely consider the importance of non-trophic interactions, such as facilitation and competition (Dodds 1997, Chase et al. 2002, Berlow et al. 2004). Other extrinsic factors, such as disturbance, environmental stress, productivity, and recruitment, also influence food web structure by regulating distribution and abundance (Dayton 1971, Bertness & Callaway 1994, Polis & Strong 1996, Post 2002a). The partitioning of primary resources among basal consumers should also be considered in food web models, as competition for these resources can structure the assemblages of both primary producers and primary consumers (Tilman 1982, Schoener 1983, Hooper 1998, Berlow et al. 2004).

In Chapters 2 and 3, a stable isotope approach ($\delta^{13}$C and $\delta^{15}$N) was used to investigate resource partitioning and to identify trophic linkages between different primary sources and mangrove gastropods. In the case of *Terebralia palustris* at Kosi Bay (Chapter 2), the diets of juvenile and adult snails were distinctly different. Analyses of the gut content showed that leaf litter only made a direct contribution to

the diet of larger snails, while juveniles consumed a variety of algal and detrital sources. Juveniles are predated upon (Vannini et al. 2001, Wells & Lalli 2003), while large adults are mostly protected by their thickened shells (Houbrick 1991). The results of Chapter 2 therefore indicate that different primary sources that are available in the mangroves are not equally transferred to higher trophic levels through *T. palustris* as a result of this partitioning. In contrast, the diet of *Melanoides tuberculata* (Chapter 3) generally reflected the availability of primary resources and therefore showed high levels of plasticity by including the filamentous algae *Cladophora* sp., detritus, and particulate organic matter that settled on the substrate from the water column. From a stable isotopes perspective, *M. tuberculata* can therefore be used to establish a suitable baseline for food web studies (Grey 2006). In comparison, the diet of *Cerithidea decollata* was restricted to microphytobenthos and sedimentary organic matter (Chapter 3). The role of mangrove gastropods as trophic links is therefore dependent on how these species utilize and partition the primary sources that are available to them in these environments. As discussed in Chapter 2, the importance of primary sources (besides mangrove leaf litter) to benthic invertebrate consumers, and higher trophic levels, has already been elucidated using stable isotope approaches (Bouillon et al. 2002, Bouillon et al. 2004a). The results of these chapters are therefore corroborative, but also provide new information with regards to how these resources can be partitioned among key mangrove gastropods.

Resource partitioning forms the basis of niche theory (Vandermeer 1972), a fundamental ecological concept that was first put forward following observations of species coexisting and utilizing the same resources by Grinnell (1924). Elton (1927) then described the niche of a species in relation to the abiotic environment and availability of food resources, and Gause (1934) provided empirical evidence that "no two species can occupy the same ecological niche". Resource partitioning studies therefore focussed on elucidating the limits of interspecific competition (Schoener 1974), as the concept was developed to relate species' responses to the evolutionary selection pressures of coexistence (Walter 1991). Recent research has considered resource partitioning as a mechanism that stabilizes species coexistence (Chesson 2000) and enhances overall resource consumption in communities (Finke & Snyder 2008).

Efficient resource utilization by coexisting species drives both regulatory and recycling processes in ecosystems, and therefore contributes towards stability and resilience (Chapin et al. 1997, Huxel et al. 2002). Although detrital pathways are often significant in many ecosystems (Wetzel 1995, Moore et al. 2004), studies on the trophic regulation of primary sources have chiefly considered the relationship between consumers and primary productivity (Yee et al. 2007). Primary productivity can be regulated directly by grazers or by the availability of nutrients and sunlight, as well as indirectly by predators through trophic cascades (Carpenter & Kitchell 1988, Huryn 1998, Borer et al. 2005, Kerimoglu et al. 2013). In shallow water ecosystems, the biomass of microphytobenthos (MPB) is often much greater than that of the phytoplankton (MacIntyre et al. 1996), and these benthic communities have been estimated to contribute as much as 50 % of the total primary production in estuarine environments (Underwood & Kromkamp 1999). At small spatial scales, benthic grazers exert a significant top-down control on MPB biomass (Pratt et al. 2015), and this potentially influences both inter- and intraspecific competition and resource partitioning (Blanchard 1991, Aberle et al. 2005).

In Chapters 4 and 5, rates of MPB consumption were determined by quantifying the feeding dynamics for the dominant gastropod species in the mangroves at Kosi Bay and the St Lucia Estuary respectively. This research is the first to quantify ingestion rates, assimilation efficiencies and potential feeding impacts for both *T. palustris* and *M. tuberculata*. For juvenile *T. palustris* at Kosi Bay (Chapter 4), the consumption of MPB was temporally variable, and was influenced by daily tidal cycles. The results of Chapter 4 showed that the maximum potential grazing impact that could be exerted by *T. palustris* juveniles would not be limited by the total available MPB biomass. The flat and sandy geomorphology of Kosi Bay promotes the growth of MPB, which would be a preferable food resource as it has a higher nutritional quality in comparison to autochthonous detritus derived from the mangrove leaf litter (as shown in Chapter 2). However, MPB is an important resource to a number of macrofaunal taxa on the intertidal flats of estuaries and mangroves (Sommer 1999, Bouillon et al. 2004a, Peer et al. 2015a). The partitioning of MPB at Kosi Bay between different macrofauna species could therefore explain the results of Chapters 2 and 4, because although juvenile *T. palustris* do consume MPB, their

diets are seasonally variable and are therefore not completely dependent on this source.

The feeding dynamics of *M. tuberculata* were also found to be variable (Chapter 5) but consumption of MPB was not related to the total available biomass of this resource. Grazing impact by *M. tuberculata* on MPB was highest when conditions were oligotrophic, which could indicate that this species prioritizes resources based on nutritional quality. As primary productivity of MPB can be limited by nutrient availability (Miller et al. 1996), when conditions were oligotrophic the biomass of MPB was relatively low. As a result, the potential daily consumption of MPB by *M. tuberculata* exceeded 60 % of the available biomass (Chapter 5). This could be interpreted as a top-down control of benthic primary production by *M. tuberculata*. Ingestion rates increased with higher per capita availability of MPB, which suggests that intraspecific competition may be driving the variability in feeding dynamics between populations of *M. tuberculata*. The results of Chapter 5 support those of Chapter 3, as they confirm that *M. tuberculata* exhibits a high degree of trophic plasticity, which may be an adaptive trait for this generalist deposit feeder.

Generalist species are defined as having broad trophic niches or being tolerant to a wide range of environmental conditions (Richmond et al. 2005). Therefore, when conditions are variable or unpredictable, generalist species are expected to cope better than specialists because they have increased behavioural, physiological and phenotypic plasticity (Bergman 1988, Parsons 1994, Rutherford et al. 1995). The diversity of species' responses to disturbances is one of the most important ways in which biodiversity increases ecosystem resilience (Yachi & Loreau 1999, Elmqvist et al. 2003, Bernhardt & Leslie 2013), which is defined as the capacity of an ecosystem to maintain functioning, structure, and feedbacks following disturbance events (Folke et al. 2004). Ecological resilience also assumes that an ecosystem can be functional in alternative states, each of which is defined by a unique set of processes (Peterson et al. 1998, Gunderson 2000). Ecosystems with low biodiversity are therefore at higher risk of being perturbed by disturbances, as key ecological processes are maintained by a relatively low number of species (Peterson et al. 1998, Loreau et al. 2001, Naeem 2002, Rosenfeld 2002, Hooper et al. 2005).

In Chapter 6, the population responses of *C. decollata* in mangrove habitats of the St Lucia Estuary were assessed in relation to fluctuating environmental conditions and disturbances. The St Lucia Estuary is renowned for its high biodiversity of benthic macrofauna (Nel et al. 2012, Peer et al. 2014, Perissinotto et al. 2014). However, *C. decollata* is one of the few species that has persisted in the mangroves through both hypersaline and freshwater regimes (Perissinotto et al. 2014). *Cerithidea decollata* is considered to be a generalist species as these snails have a wide salinity tolerance (Reid 2014) and can occur in temperate salt marsh habitats (Hodgson & Dickens 2012). Elucidating the population responses of this species to unpredictable environmental conditions, therefore, provided important new information for a resilient key mangrove species. The results of Chapter 6 show that sediment conductivity is the best predictor of *C. decollata* density in the St Lucia Estuary. However, the tree-climbing behaviour of these snails allows escape from unfavourable water or sediment conditions, and therefore mitigates the effects for a certain period of time. This study provided important information for this species that can be used in assessing the resilience of the mangrove ecosystem in the St Lucia Estuary.

*7.2 Global relevance of the research projects' findings*

This research project had a regional focus, on key mangrove gastropods from two estuaries on the eastern subtropical coast of South Africa. However, the gastropod species examined all have broad geographical distributions that extend beyond South African borders. Considering the two mangrove potamidids, *T. palustris* occurs in mangrove habitats across the entire Indo-West Pacific (Houbrick 1991) and *C. decollata* is distributed along the east African coastline as far as Kenya (Reid 2014). The distribution of *M. tuberculata* is the most extensive, as this species has a native range from East Africa to South East Asia, but has also been introduced to many areas in the New World where it has become invasive (Facon et al. 2003). South Africa therefore represents the southernmost global distribution limit for naturally occurring populations of all three gastropod species examined in this research project.

The range limits of species can be defined ecologically in relation to their niche, but an evolutionary perspective of range limits considers local adaptation and gene flow

(Kirkpatrick & Barton 1997). If species at the edge of their range are able to adapt to novel habitats or conditions, this is considered to be a form of niche evolution (Holt et al. 2004). Range limits can therefore be considered as 'testing grounds' and studies on edge populations can provide information with regards to whether the species could adapt to novel conditions or not (Sexton et al. 2009). Edge populations have therefore become the focus of many climate change studies that aim to determine the potential for range expansions in response to rising temperatures (Gibson et al. 2009, VanDerWal et al. 2013, Chuang & Peterson 2016). This has led to the development of bioclimatic models that predict temperature-induced shifts in the geographic range of a species based on thermal tolerances (Pearson & Dawson 2003, Xavier et al. 2010). However, in reality the ability of a species to expand to new suitable habitats is restricted by additional intrinsic and extrinsic factors. First, by the intrinsic traits of the populations that exist on the 'expanding edge' (*sensu* Hampe & Petit 2005) which are related to dispersal, colonization, and resource utilization as they will influence establishment (Angert et al. 2011). Second, by the extrinsic rapid hydroclimatic fluctuations that individuals will experience while dispersing, colonizing and establishing in the new habitat (Chapperon & Seuront 2010). It is therefore important to include available physiological and ecological data, that will inform on these responses, within predictive niche models of range expansion (Helmuth 2009, Kearney & Porter 2009, Cavanaugh et al. 2015).

This research project has therefore provided useful and new ecological information for three key mangrove gastropods at their southern distribution limit that have the potential for poleward range expansions. As *T. palustris* has previously occurred as far south as the Mngazana Estuary (31°41'26''S; 29°25'24''E) (Macnae 1963), the potential for a poleward range expansion of this species is not limited by temperature tolerance. The recent range contraction along the South African coastline for *T. palustris* and its decline in mangrove habitats has instead been related to reduced food availability (Berjak 2011, Raw et al. 2014). This is a cause for concern, as populations at lower tropical latitudes are expected to be faced with increasingly stressful conditions associated with rising temperatures (Tewksbury et al. 2008). If southern mangrove habitats are also not suitable for *T. palustris*, this species could face a "squeeze" in its global distribution range (Raw et al. 2014). The results of this research project have highlighted the importance of resource diversity (Chapter 2)

and the variability of consumption rates (Chapter 3) for *T. palustris*. Any range expansion predictions for this speciesshould therefore also consider these specific trophic requirements when identifying new potential habitats for colonization.

As discussed in Chapter 6, a poleward range expansion has already been recorded for *C. decollata* along the South African coastline (Whitfield et al. 2016). The temporarily-open closed conditions of many South African estuaries limit the occurrence of mangrove trees along the coastline (Saintilan et al. 2014). However, *C. decollata* also occurs beyond the range of the mangroves (Hodgson & Dickens 2012). It is therefore clear that this species possesses certain generalist traits that have enabled this range expansion, and in particular to survive the dynamic conditions of estuarine environments. These include pelagic larval dispersal and a wide salinity tolerance (Reid 2014). The results of this research project have provided new information with regards to traits that would facilitate establishment in a new habitat, such as a non-restrictive diet (Chapter 3), or enable persistence in unfavourable conditions, such as resilient responses to changing environmental conditions (Chapter 6). *Cerithidea decollata* could therefore be considered as an opportunistic species.

Similarly, *M. tuberculata* is a generalist species that occurs in a variety of habitats (de Kock & Wolmarans 2009) and its occurrence in the mangroves of the St Lucia Estuary is considered to be opportunistic (Perissinotto et al. 2014). Although South Africa does represent the southern distribution limit for naturally occurring populations of *M. tuberculata* (Appleton 1996; Brown 1994), invasive populations of this species have been reported to occur as far south as New Zealand (Duggan 2002). Some mangrove areas of the St Lucia Estuary have been colonized by the closely related *Tarebia granifera*, which is native to South East Asia (Perissinotto et al. 2014). At the time that sampling was carried out for this project, *M. tuberculata* did not co-occur with *T. granifera* within the St Lucia Estuary. However, rising water levels and predominating freshwater conditions are likely to allow further expansion of *T. granifera* into new areas of the estuary in the near future (Miranda et al. 2010). Interactions between *T. granifera* and *M. tuberculata* are expected to lead to the displacement of the latter based on previous introductions of *T. granifera* to other water bodies in the region (Raw et al. 2013, Miranda et al. 2014, Raw et al. 2015).

Many of the intrinsic and extrinsic ecological and evolutionary factors that allow species to naturally expand their ranges in response to climate change also allow opportunistic species to colonize and establish in new habitats to which they have been either intentionally or accidentally introduced (Colautti & MacIsaac 2004). There has indeed been some debate regarding whether range expansions into adjacent habitats should be considered as a form of biological invasion (Thompson et al. 1995, Davis & Thompson 2000). Valéry et al. (2008) therefore argue that a conceptual definition of biological invasions should not be based purely on a geographical criterion, but should instead focus on the ecological aspects of the phenomenon.

Different intrinsic and extrinsic ecological and evolutionary factors are considered to facilitate invasion success (Kolar & Lodge 2001, Colautti et al. 2014). Examples of intrinsic factors include species traits related to tolerance, reproductive capacity and niche breadth (Rosecchi et al. 2001, McMahon 2002, Raw et al. 2016a). As discussed in Chapter 5, the invasion success of *M. tuberculata* has been attributed to a number of specific traits. In this research project, trophic niche width (Chapter 3) and resource utilization rates (Chapter 5) have been identified as traits that enable *M. tuberculata* to inhabit different environments that are variable in terms of resource availability. *Melanoides tuberculata* is a successful invasive species (Pointier 2001, Facon et al. 2005, Karatayev et al. 2009, Peso et al. 2011, Weir & Salice 2012) and ecological research relating to its ability to establish and persist in new environments is therefore globally relevant.

*7.3 Conclusions & recommendations for further research*

Mangrove ecosystems are globally threatened (Duke et al. 2007, Giri et al. 2011), and within South Africa these habitats are prioritized for conservation as the national legislation recognizes their ecological and economic value (Turpie et al. 2002). Marine and coastal research in South Africa has therefore focussed on applied science that can be directly used to inform management (McQuaid 2010). However, a recent review of the global state of mangroves in response to factors associated with global change has highlighted that this region is data-deficient in this regard (Ward et al. 2016). In order to carry out these vulnerability assessments, basic ecological research must first provide relevant information in relation to ecosystem

functioning (Williams et al. 2008). Fortunately, there have been some recent advances to promote basic research in marine and coastal ecosystems of South Africa (Scott 2013).

Recent ecological research has stressed the importance of ecological studies to disentangle observed responses and trends from the potential effects of factors associated with anthropogenic global change (Thuiller 2007, Quisthoudt et al. 2013, Flombaum et al. 2016). Research trends have therefore focussed on relating the responses of threatened or key species in certain habitats to these factors (Gilman et al. 2008, Moritz & Agudo 2013). This research project did not aim to directly relate any of the findings to factors associated with global change. However, the new ecological information developed through this research project is relevant and can be used to inform larger scale studies as already discussed. This project has highlighted the importance of carrying out basic ecological research for populations that occur at their distributional range limit, as a number of factors may cause responses to be different to those recorded for individuals at the centre of the distribution. The results of this project have also provided further support for the importance of gastropods as primary consumers in mangrove forests, a role which was previously attributed largely to the brachyurans. Finally as South African mangroves are subtropical, the diversity of the fauna is considerably lower in comparison to lower latitudes. Therefore, important functional roles must be carried out by a fewer number of species. This research project has therefore provided an assessment of how the dominant gastropods which do occur in these ecosystems contribute towards ecosystem functioning.

Recommendations for future research have been outlined in the specific chapters and are related to further ecological studies and linking the findings of this project to broader scale patterns and processes. In brief:

- An important recurring theme was the significance of resource availability for the ecological roles of these deposit-feeding gastropods. As mentioned, the dynamic characteristics of estuaries that are only temporarily open to the marine environment influence this availability and should therefore be investigated as drivers of ecological functioning in mangroves.

- One of the most pertinent aspects that should be further investigated is the regional range retraction of *T. palustris*, which could also potentially be explained by sensitivity to certain conditions (salinity regime, high sedimentation, prolonged inundation) experienced within temporarily open estuaries.

- Resource partitioning and potential competitive interactions for MPB should be investigated for *T. palustris* and deposit-feeding brachyurans at Kosi Bay. This may provide insight into the biological drivers of *T. palustris*' regional decline.

- The possibility that Asiatic *M. tuberculata* have become established in South Africa should be investigated using a molecular genetics approach. Specific ecological and biological comparisons between these morphs and those of African origin can then be carried out.

- The occurrence of individual dietary specialization in *M. tuberculata* should also be determined. The South African populations could provide particularly interesting insight as to whether there is morphological plasticity or perhaps adaptive traits relating to radula morphology and whether this influences the feeding habits of the snails. There is also the opportunity to compare radula morphologies between African and Asian morphs of *M. tuberculata*.This could provide more direct evidence for dietary plasticity of this successful invasive species.

- The occurrence of *M. tuberculata* in the St Lucia Estuary should be monitored in relation to the predicted expansion of *T. granifera*. Continuous basic ecological work is important to track changes to these communities and provide insights for management actions directed at alien invasive species.

- Monitoring of the *C. decollata* populations of the St Lucia Estuary should continue, as current management practices are aiming to restore marine connectivity and natural tidal regimes. This could have a significant impact on the occurrence of *M. tuberculata* in the mangroves if there is salt intrusion to the freshwater seepage areas. The disappearance of *M. tuberculata* could result in a shift in the resources utilized by *C. decollata* and a follow-up study may be required.

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