
**Diversity and ecological role of true crabs
(Crustacea, Brachyura) in the St Lucia Estuary,
iSimangaliso Wetland Park, in response to global
change**

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Abstract

The St Lucia estuarine lake, located within the iSimangaliso Wetland Park, is one of South Africa's first UNESCO World Heritage Sites. The system has historically experienced natural and anthropogenic environmental change and is currently moving to a new dry phase, after a prolonged drought (2002-2011) and a brief wet phase (2012-2014), while still displaying limited connectivity to the marine environment. Several habitat types occur around the lake and, as expected, the diversity of true crabs around the lake is fairly extensive, although research surrounding this topic is lacking. Since the last survey conducted in 1965, when 26 species were found around the lake, many are now absent from the system, with only 15 species being recorded at present. Population distributions vary with species sensitivity to environmental change. In particular, two groups were expected to increase in distribution throughout the St Lucia system during the short wet phase. These are the freshwater crabs (*Potamonautes* spp.), which were expected to move through the lake in response to flooding, and the fiddler crabs (*Uca* spp.) which started recolonising the mangroves with increased connectivity of the St Lucia to the ocean.

New niches created through environmental change promote speciation. A new species of *Potamonautes* was described from the ephemeral pans on the western shore of False Bay. Endemic species are thought to be an indicator of high biodiversity and have traditionally been crucial to conservation planning. The most abundant freshwater crab around the lake is *Potamonautes sidneyi*. Stable isotope analyses showed that the species plays an important multi-trophic and adaptable role as an opportunistic consumer and detritivore.

Four species of fiddler crabs occur in South Africa at their poleward limit. The St Lucia populations persist despite the virtually non-tidal state of their habitat. This is a rare phenomenon around the world but one that is expected to increase with environmental change. The physiological response of a key fiddler crab species, *Uca annulipes*, was investigated by examining feeding dynamics using an *in situ* gut fluorescence technique. The feeding dynamics, usually influenced by sexual dimorphism, tide and diel rhythms, now only appear to be influenced by daylight hours and sexual dimorphism. Furthermore, the population had a significant impact on the MPB community consuming up to 10.73% of MPB stocks daily. Due to the lack of tidal influence, there is little recovery time for these communities and thus cumulative effects of fiddler crabs on MPB in non-tidal systems can be significant. However, although adults are able to survive in this environment, larvae require a marine connection and are unable to tolerate a wide fluctuation in salinity. The brackish environment of the St Lucia Narrows region is unsuitable and the populations can therefore not be self-sustaining.

This research contributes towards scientific knowledge of the response of true crabs to environmental change. Brachyurans are key factors to consider during conservation planning as they are crucial to maintain ecosystem function in the face of environmental change.

Declaration 1 - Plagiarism

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Declaration 2 – Publications

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis are as follows:

PUBLICATION 1:

Peer N, Perissinotto R, Taylor RH, Miranda NAF (2014). Temporal variations in the diversity of true crabs (Crustacea: Brachyura) in the St Lucia Estuary, South Africa. *African Invertebrates* **55**: 39-65.

Candidate's contribution: Bulk of conceptualization and design; Fieldwork; Laboratory analyses; Compilation of First draft.

PUBLICATION 2:

Peer N, Perissinotto R, Gouws, G, Miranda NAF (2015). Description of a new species of *Potamonautes* MacLeay, 1838, from the iSimangaliso Wetland Park, South Africa. *ZooKeys* **503**: 23 – 43.

Candidate's contribution: Conceptualization and design; Fieldwork; Laboratory analyses; Compilation of first draft.

PUBLICATION 3:

Peer N, Perissinotto R, Miranda NAF, Raw JL. (2015) A stable isotopic study of the diet of *Potamonautes sidneyi* (Brachyura: Potamonautidae) in two coastal lakes of the iSimangaliso Wetland Park, South Africa. *Water SA* **41**: 549 – 558.

Candidate's contribution: Bulk of conceptualization and design; Fieldwork; Laboratory analyses; Compilation of first draft.

PUBLICATION 4:

Peer N, Miranda NAF, Perissinotto R. (2015) A review of the ecology of fiddler crabs (genus *Uca*, Leach 1814), with emphasis on South African species. *African Zoology* **50**: 187 – 204.

Candidate's contribution: Bulk of conceptualization and design; Laboratory analyses; Compilation of first draft.

PUBLICATION 5:

Peer N, Miranda NAF, Perissinotto R, Raw JL. (2015) Feeding dynamics of the fiddler crab *Uca annulipes* (H. Milne Edwards, 1837) estimated from gut pigment contents. *Marine and Freshwater Research*: **online early** (<http://dx.doi.org/10.1071/MF15038>)

Candidate's contribution: Bulk of conceptualization and design; Fieldwork and experiments; Laboratory analyses; Compilation of first draft.

PUBLICATION 6:

Peer N, Miranda NAF, Perissinotto R. (in press). Suspended silt and salinity tolerances of the first zoeal stage of the fiddler crab *Uca annulipes* (Decapoda: Brachyura) and why marine connectivity is essential to the survival of this species. *African Journal of Marine Science* **38**.

Candidate's contribution: Bulk of conceptualization and design; Fieldwork and experiments; Laboratory analyses; Compilation of first draft.

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“Nature's creative power is far beyond man's instinct of destruction.”

20 000 Leagues under the Sea
Jules Verne

In his book entitled '*The Book of Barely Imagined Beings*', Caspar Henderson declares:

“And only recently have we begun to learn that the seas are rich with real rather than mythical beings that are strange and sometimes delightful in ways we would never have imagined – that there are, for example, creatures as tall as men which have no internal organs and thrive in waters that would scald us to death in moments, that there is a vast world of cold darkness in which almost all creatures glow with light, or that there are intelligent, aware animals that can squeeze their bodies through a space the width of one of their eyeballs.”

We can safely say that this holds true for not only the ocean but the various other biomes that make up this world as well.

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General introduction

Environmental change, both naturally and anthropogenically driven, is inevitable and involves both habitat transformation and climate change. In this thesis, global change refers to the environmental change experienced on a worldwide scale. The negative effects of environmental change have been well-documented, some of which include the loss of biodiversity, a depleted ozone layer, sea level rise, ocean acidification, habitat destruction and the increased susceptibility of ecosystems to invasive species and pathogens. However, the effects are not always negative (Hoffmann and Hercus 2000; Bellard et al. 2012). Examples of the positive effects of environmental change include speciation (Hua and Wiens 2013), favourable or reduced host-pathogen interactions (Voutilainen et al. 2012; Hicks et al. 2015), and the creation of more specialised habitats promoting diversity and abundance of associated biota (Ethier and Fahrig 2011; Sirami et al. 2013). Ecosystems are not always threatened and can be somewhat resilient to changes in the environment. Ecosystem resilience depends on a suite of ecological factors. Furthermore, the two-way relationship between ecology and environmental change is a complex one where a change in the environment influences the associated ecological structure and vice versa. Many ecological paradigms are thus linked closely to environmental change.

The diversity-function relationship in ecosystems is a well-studied one (MacArthur 1955; Goodman 1975; Loreau 2000) and basically states that a greater biodiversity promotes ecosystem stability and resilience through the assured maintenance of ecosystem processes and reduced susceptibility to species invasion. Ecosystem stability, or resistance, is defined as the ability of an ecosystem to return to its original stable state after a disturbance, while ecosystem resilience refers to the ability of an ecosystem to absorb changes and maintain the relationships between populations along with the ecosystem state (Holling 1973). Additionally, greater biodiversity insures the delivery of ecosystem goods and services which are economically valuable (Chapin et al. 2000). However, in order to efficiently conserve biodiversity and ecosystem function it is essential to understand how specific key components respond to these shifts (Dawson et al. 2011). Some organisms are more tolerant or adaptable to change and persist because of these qualities. These are the organisms that are most likely to create a stable and resilient ecosystem (Nelson et al. 2007; Côté and Darling 2010).

True crabs (brachyurans) are an example of such organisms. They are key components of many aquatic ecosystems and act as bio-engineers through burrowing activity and disturbance whilst feeding (Kristensen 2008; Araujo et al. 2012). In this way they directly impact their associated environment and indirectly impact all other sympatric counterparts (Retraubun 1998; Kristensen 2008). Brachyurans are opportunistic feeders and thus form integral trophic links usually as primary or secondary consumers (Dye and Lasiak 1986; Hill and O'Keefe 1992; Miller and Morgan 2014), or even as top predators (Klaus and Plath 2011) due to their ability to feed on a wide variety of food sources. Furthermore, they facilitate the decomposition process by breaking down detritus and organic matter whilst feeding on detritus and in this way are also responsible for the retention of nutrients in nutrient-poor environments (Lee 2008; Bui and Lee 2014). Due to their mobile nature, they also link various habitat types i.e. terrestrial and aquatic, benthic and pelagic, etc. (Morris and van Aardt 1998; Lee 2008). True crabs are highly adaptable, able to survive in extreme habitats (Guinot and Hurtado 2003; Klaus and Plath 2011) and subsequently show a high tolerance to environmental changes, both natural and anthropogenic (Cannicci et al. 2009; Fusi et al. 2014).

The St Lucia Estuary is situated on the east coast of South Africa and is the largest estuarine lake in Africa, covering an area of approximately 300 km² (Cyrus et al. 2011). It forms a crucial part of the iSimangaliso Wetland Park, South Africa's first UNESCO World Heritage Site, and is a RAMSAR Wetland of International Importance. The estuarine lake is a well-known biodiversity hotspot which falls within the Maputaland centre of endemism (Smith et al. 2008). The system experiences natural large-scale fluctuations between flood and drought events (Stretch et al. 2013). This leads to variations in water levels which in turn affect the salinity, evaporative water loss, hydrodynamics and the open or closed state of the estuary mouth (Perissinotto et al. 2013). Additionally, human influence and management of the system have exacerbated the impact of the climatic changes experienced by the lake during the past century. The adjacent Mfolozi River was once connected to the St Lucia Estuary at the mouth. Prior to 1952, this river was an important freshwater source to the St Lucia system and created a more stable mouth condition (Lawrie and Stretch 2011). The increase in agriculture and plantation practices created a demand for freshwater in the region, a demand that was met through canalisation of the Mfolozi River. Increased agricultural practices led to the degradation of the Mfolozi swamps and, subsequently, the filtering service provided by this habitat was diminished. Increased sediment flow into the Mfolozi

River adversely affected the St Lucia estuarine system and the two waterbodies were separated. The St Lucia mouth was artificially maintained open until 2002, when human intervention ceased and the mouth naturally closed. The mouth remained closed permanently except for a 6-month breach caused by Cyclone Gamede in May 2007. Recently a management decision has been taken to reconnect the St Lucia and Mfolozi mouths (Whitfield et al. 2013). Anthropogenic change and management are still heavily incumbent on the St Lucia system, despite its current heavily-protected status (Whitfield and Taylor 2009).

Currently, two main changes are occurring in the St Lucia estuarine lake. The first is the climatic change from a prolonged drought phase (2002-2011) to a brief freshwater-dominated phase (van Elden et al. 2014) (2012-2014) and eventually back to a new dry spell (2015-present). As a result, the entire system experienced lower salinity and a rapid increase in water level during the wet phase, alleviating the desiccation and hypersalinity experienced in large parts of the system during the previous decade (Whitfield et al. 2013). The second change is related to management and human-induced transformation of the system, involving among others the relinkage of the St Lucia and Mfolozi mouths to form a combined inlet from the ocean (Whitfield et al. 2013). This change is also expected to reduce desiccation and hypersalinity around the lake, as well as create optimal conditions for a predominantly open mouth state (Lawrie and Stretch 2011; Stretch et al. 2013), leading to increased connectivity between the St Lucia estuarine system and the oceanic environment.

The lake hosts a wide range of habitat types, both around (mangrove forests, freshwater dune seepage points, salt marsh, sand forests – Taylor et al. 2006; Adams et al. 2013) and within the lake (open water, intertidal shoreline, dry shoreline, groundwater dependent shoreline – Taylor et al. 2006). This habitat diversity in turn promotes a high level of biodiversity with various freshwater, estuarine and marine species having been recorded in the system over time (Millard and Broekhuysen 1970; Whitfield et al. 2006; Nel et al. 2012; Perissinotto et al. 2014). Accordingly, brachyurans have been recorded around the lake in a variety of habitats, both terrestrial and aquatic (Millard and Broekhuysen 1970; MacKay et al. 2010). Despite environmental changes and habitat shifts around the system, the drivers of movement and survival of these key ecosystem components have not been investigated. Many factors are known to influence the distribution and ecology of crabs, i.e. connection to the ocean, salinity, water availability, predators, food availability, space and competitors (Barnwell 1966; Hodgson 1987; Owen 2003; Lee 2008). Due to the mobile nature of these

crustaceans, species may migrate out of the system in response to a stimulus in search of a more suitable habitat. However, as crabs are also known to be highly adaptable and opportunistic (Fusi et al. 2014), it is possible that they may persist despite environmental changes and overcome certain challenges, e.g. by using dietary shifts with changes in available food sources or by burrowing to avoid desiccation.

With the current changes occurring in the St Lucia Estuary, i.e. the natural movement from a drought to a flood phase and back to drought, and the anthropogenic reconnection of the St Lucia and Mfolozi mouths, two associated events are expected regarding the distribution and ecology of brachyurans within the St Lucia system. The first is the movement of freshwater crabs (Genus *Potamonautes* MacLeay, 1838) out of the system during the drought phase and their subsequent spread through the system at the onset of the freshwater phase. The most apparent threats to diversity of freshwater crabs are loss of habitat and habitat degradation with sedimentation, increased nutrient loading and reduced water quality (Yeo et al. 2008; Marijnissen et al. 2009). Some recent work has been done on the taxonomy and genetics of the genus leading to the discovery and description of a few new species (Gouws et al., 2000; Daniels et al., 2001; Gouws et al., 2001; Daniels 2006; Daniels and Bayliss 2012; Daniels et al. 2014; Phiri and Daniels 2014; Daniels et al. 2015). Within the iSimangaliso Wetland Park itself, systematics of the genus have not been examined in recent years. A range of specialised habitats creates various niches and drives speciation. This means that the park has a high potential for endemism.

The most dominant freshwater crab species around the St Lucia Lake is *Potamonautes sidneyi* Rathbun, 1904. However, the trophic role of this species in the system has not been investigated and is poorly understood. Reports suggest that members of the genus may occur in high densities (Hill & O’Keeffe, 1992), usually around shallow streams, swamps and lake edges (Reavell & Cyrus, 1989). The latter authors have also suggested that *Potamonautes* spp. play an integral role in trophic functioning of ecosystems, by utilising energy from various trophic levels and making it available to a wide variety of organisms, either directly through predation or indirectly by facilitating the decomposition of organic matter through feeding. In addition to this, freshwater crabs form a spatial link between aquatic and terrestrial habitats as a result of their amphibious lifestyle (Morris & van Aardt, 1998).

The second expected observation is the recolonisation of the St Lucia mangroves by fiddler crabs (Genus *Uca* Leach, 1814) with increased marine connectivity. Fiddler crabs are cosmopolitan flagship species, occurring in tropical and subtropical habitats, particularly

mangrove swamps which are currently declining worldwide. Over 100 species of *Uca* have been described, five of which occur in South Africa at their southernmost distribution range. Little is known about the ecology of fiddler crabs in this region, despite the wide array of studies conducted on this genus globally.

Fiddler crabs are key species in mangroves where they can occur in high densities (Cannicci et al. 2009). Their primary food source is microphytobenthos and their feeding rhythms are known to be influenced by tidal and diel rhythms (Barnwell 1966). However, in the St Lucia mangroves, fiddler crabs currently exist in a non-tidal habitat. The St Lucia fiddler crabs thus present an opportunity to examine ecological dynamics of a tidally-influenced taxon in a non-tidal environment.

A possible driver of *Uca* survival in the St Lucia estuarine system includes reduced marine connectivity affecting zoeal development through retention in the St Lucia estuarine system. Here zoeae would be subjected to increased predation, salinity fluctuations and silt loading. All African fiddler crab species are known to undergo a marine-dependent larval phase during development. It is expected that with the closure of the St Lucia Estuary mouth to the sea, fiddler crabs would migrate out of the unfavourable St Lucia environment. They could form refuge populations in the nearby Mfolozi mangroves and recolonize the St Lucia mangroves once marine connectivity has been restored.

In summary, the ecological role of brachyurans in the St Lucia system has been largely unexplored. It is critical to understand the diversity, distribution and role of these organisms in the face of natural and anthropogenic environmental change. Due to their resilient, wide-spread, and adaptable nature, the biodiversity and ecology of crabs would be a key aspect in decision-making within an already degraded World Heritage Site. Understanding the factors that structure crab diversity and ecology is also crucial for management of the system and the following hypotheses were formed to address this.

1. The diversity of brachyurans in Lake St Lucia has changed in response to environmental change around the lake.
2. Speciation could be facilitated by the unique suite of habitats within and around the St Lucia estuarine lake leading to the presence of potentially endemic species.
3. The diet of resilient organisms such as brachyurans would change with a shift in habitat and associated food availability.
4. Environmental stress affects species already at their southern boundary.

5. Mangrove crabs adapt to a lack of tidal influence, by adjusting their feeding ecology, for instance.
6. Not all stages of fiddler crabs survive the effects of natural and anthropogenic change when retained in a closed estuary.

Hence the main objectives of this study were:

1. To examine the change in the diversity of true crabs (Crustacea: Brachyura) in the St Lucia Estuary over time.
2. To examine the morphology of potentially endemic and undescribed species that were highlighted in the earlier biodiversity survey.
3. To investigate the change in diet of *Potamonautes sidneyi* associated with an environmental change or ontogenetic shift.
4. To review the ecology of fiddler crabs in South Africa with emphasis on the history of their distribution within the St Lucia Estuary.
5. To determine the feeding dynamics of *Uca annulipes* in the non-tidal St Lucia mangrove habitat.
6. To investigate the impacts of silt loading and salinity fluctuations in the St Lucia Estuary on the survival of first stage fiddler crab zoeae.

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Chapter 1

Lake St Lucia hosts a wide range of habitat diversity, which in turn promotes a rich biodiversity. Various freshwater, estuarine and marine species have been recorded in the system over time. Brachyuran species have been recorded around the lake in a variety of aquatic habitats, from hypersaline to freshwater dominated, with some persisting despite drastic environmental disturbances. Species are regarded as building blocks of ecosystems and should be monitored in areas granted special conservation status. However, the true crabs of St Lucia remain poorly investigated with the last dedicated biodiversity survey conducted by Millard and Broekhuysen in the late 1940's. A biodiversity census was necessary to determine the present diversity of true crabs in and around the St Lucia estuarine lake complex as well as to determine the change in diversity over time as a response to physical-chemical changes within the system.

Note: Part of this chapter has been submitted in partial fulfilment of a Honours degree. However, the diversity census was continued and completed during the PhD, in order to provide the foundations and rationale for the other chapters. Substantial changes were made to the original Honours report, both in the text and the checklist prior to submission for publication and inclusion in this thesis.

Temporal variations in the diversity of true crabs (Crustacea: Brachyura) in the St Lucia Estuary, South Africa

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ABSTRACT

The St Lucia Estuary is part of the iSimangaliso Wetland Park, which is a UNESCO World Heritage Site. It is characterised by instability and experiences ongoing anthropomorphic change, both of which have a significant impact on the biodiversity of the estuary and surrounding area. Brachyurans (true crabs) play an integral role in the functioning and maintenance of this ecosystem. They are a food source for organisms at higher trophic levels, maintain nutrient balance, regulate trophic flow and aerate dense mud through the construction of burrows. However, since the early survey of Millard and Broekhuysen (1970), no study has focussed on this taxon, the identification of which is confounded by the existence of cryptic and pseudocryptic species. This study provides a census of the brachyuran species inhabiting the St Lucia estuarine lake, highlighting the changes in diversity that have occurred in this region between 1948 and 2012. A total of thirty species were found in the area during this period, five of which have not been recorded in previous literature. The extent to which regional endemic species, such as *Paratyrodiplox blephariskios*, have been affected by the dynamics of the system is discussed. The distribution and abundance of three key species, namely *P. blephariskios*, *Neosarmatium africanum* and *Hymenosoma projectum*, are outlined; and possible reasons for observed changes are discussed. Future scenarios regarding the state of the estuary mouth and the stability of physico-chemical variables are also considered. Lastly, an annotated checklist illustrated by photographs is included to aid in identification of species for research and management purposes.

KEY WORDS: Crustacea, Brachyura, South Africa, iSimangaliso Wetland Park, St Lucia estuarine system, true crabs, diversity, estuarine variability, illustrated checklist.

INTRODUCTION

The St Lucia Estuary is a crucial component of the iSimangaliso Wetland Park, which is a UNESCO World Heritage Site. It is the largest estuarine lake system in Africa and covers approximately 80% of the total estuarine area of KwaZulu-Natal, South Africa (Begg 1978). The estuary is characterised by prolonged mouth closure and experiences large-scale periodic fluctuations in physico-chemical characteristics due to stochastic flood and drought events (Begg 1978; Owen & Forbes 1997; Pillay & Perissinotto 2008). The shallow nature of the lake, combined with its large surface area, results in high evaporative loss. The system experiences additional stress from increased human numbers, forestry and agricultural developments in the catchment area around the lake (MacKay *et al.* 2010; Cyrus *et al.* 2011). These activities include manipulation of the St Lucia Estuary mouth, freshwater abstractions from surrounding rivers (Fig. 1a) and the increase in sugar cane farming and number of tree plantations in adjacent areas (Whitfield & Taylor 2009), all of which lead to an intensification of drought conditions. As a result, the St Lucia Estuary experiences regional hypersalinity at times, especially in the northern part of the lake where salinities occasionally exceed 200 ppt (Whitfield & Taylor 2009; Cyrus *et al.* 2011). In drought conditions, however, the Back Channel (Fig. 1b) may provide a connection to the Mfolozi River and the ocean, thereby supply-

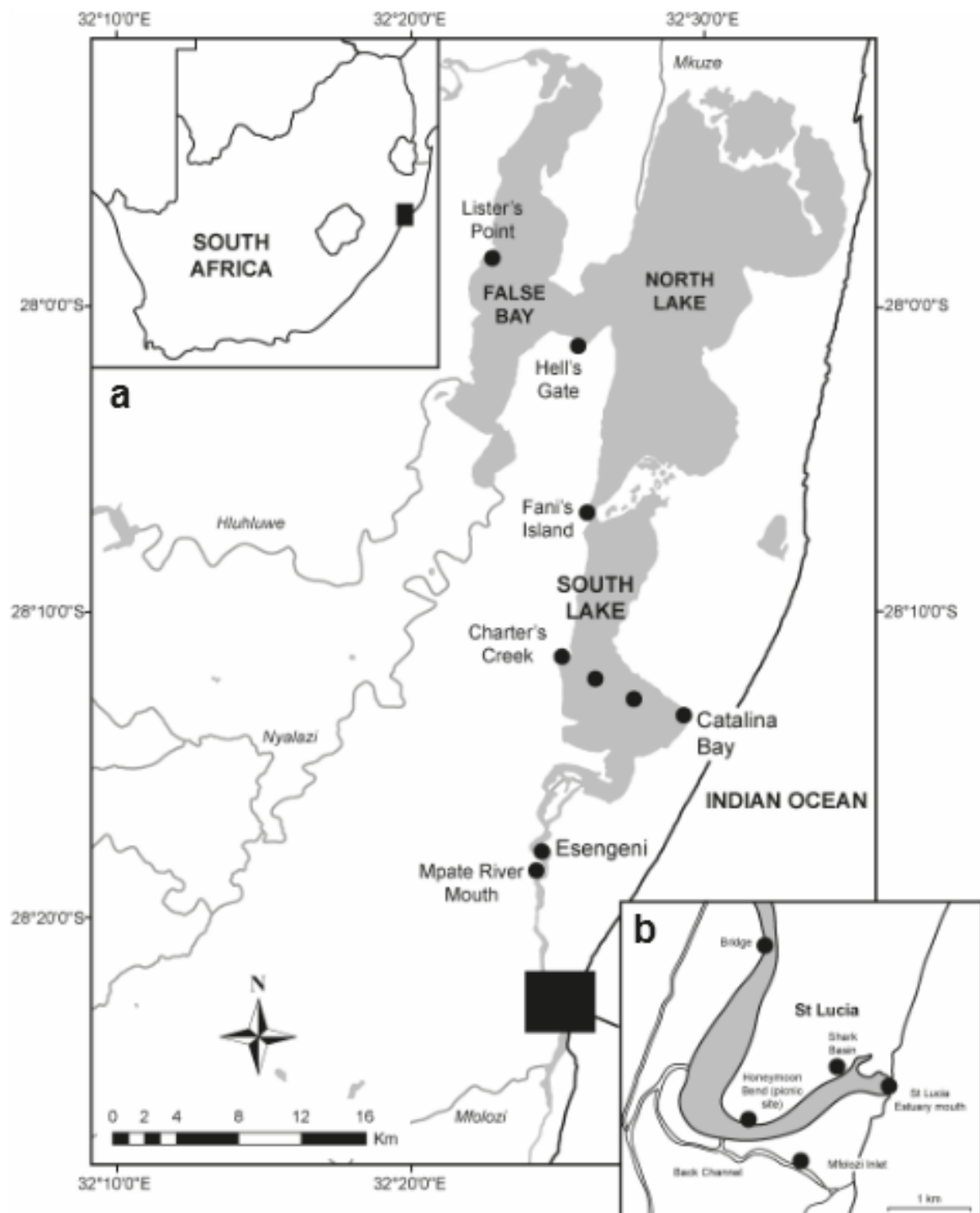


Fig. 1. Maps of the St Lucia Estuary: (a) expansion of the estuary and mouth region (adapted from Carrasco *et al.* 2010); (b) highlighting sampling sites and sources of freshwater inflow via tributary rivers.

ing water to the system, allowing limited biological migrations into St Lucia from the sea, and decreasing the overall salinity of the Narrows and estuary mouth (Whitfield & Taylor 2009). Most of the recent research on the system has been carried out during drought events (Cyrus *et al.* 2011).

The instability and ongoing degradation of the estuarine lake both have a significant impact on associated biodiversity (Schlacher & Wooldridge 1996; MacKay *et al.* 2010).

Hypersaline conditions lead to movement of stenohaline species out of the area and extinction of less mobile organisms, resulting in changes in community structure and species richness (Schlacher & Wooldridge 1996; Owen & Forbes 1997). The decrease in salinity caused by freshwater run-off from the Mfolozi promotes biodiversity (Whitfield & Taylor 2009). Persistent mouth closure (since June 2002) has resulted in limited juvenile recruitment from the ocean and no tidal exchange, which has led to desiccation of the extensive mangrove swamps that occur in the regions of the mouth and Narrows (Adams *et al.* unpubl. data).

Brachyurans (true crabs) play an integral role in the functioning and maintenance of the mangrove ecosystem (Day 1981). Herbivorous and detritivorous species are important components of mangroves as they feed on leaf-litter and decaying organic matter present on the forest floor (Dahdouh-Guebas *et al.* 1997). They facilitate the decomposition process by breaking down organic matter and exposing it to microbes, thus playing an important role in nutrient cycling and energy flow in these ecosystems (Steinke *et al.* 1993; Cumberlidge *et al.* 2009). In addition, burrowing species are important for aeration and oxygenation of the dense mangrove mud. The creation of burrows further allows for movement of nutrients and water through the soil, which in turn is beneficial for the growth and development of mangrove seedlings (Steinke *et al.* 1993). Brachyurans also modify sediment topography and associated microfloral structure (Skov *et al.* 2002).

The biological survey conducted by Millard and Broekhuysen (1970) in the St Lucia Estuary revealed the presence of twenty-six brachyuran species, all located mainly within the Narrows and estuary basin. However, the same areas are currently dominated by only a few brachyuran species, such as *Paratyloidiplax blephariskios* (Stebbing, 1924), *Hymenosoma projectum* Dawson & Griffiths, 2012 together with the mangrove crabs *Neosarmatium africanum* Ragionieri, Fratini & Schubart, 2012 and *Chiromantes eulimene* (De Man in Weber, 1897) (Owen & Forbes 1997; MacKay *et al.* 2010). Moreover, the mangroves along the Narrows have been separated from the ocean for virtually the past 10 years (Whitfield & Taylor 2009). Thus, the unstable salinity levels in many parts of the lake are believed to impact on brachyuran diversity negatively (Owen & Forbes 1997). Land use, mostly in the form of agriculture and forestry, is also a major contributor to the decreased diversity within the system, as it leads to deterioration in water quality, reduction in freshwater inflow, and urbanisation of the natural habitat (Darwall *et al.* 2009). Brachyurans endemic to the north-east region of KwaZulu-Natal are especially vulnerable to environmental degradation, given their restricted distribution range.

Considering that the last thorough survey of brachyuran diversity in St Lucia was conducted by Millard and Broekhuysen in 1970, the primary aim of this study was to investigate current brachyuran diversity within the estuarine system, with particular emphasis on the Narrows, estuary basin and estuary mouth. The extent to which the brachyuran community has been altered was determined by comparing the distribution and abundance of three key species and examining records of past and present surveys. An additional aim of this study was to provide an illustrated, annotated checklist of all brachyuran species recorded historically in the area, in order to update the current database of brachyurans known from the system and to provide an identification guide for future research and management purposes.

MATERIAL AND METHODS

Sampling sites

The study was conducted at the St Lucia estuarine lake, located between 27°52'S to 28°24'S and 32°21'E to 32°34'E. The estuary consists of three lakes, viz. False Bay, South Lake and North Lake, all connected to the mouth via a 20 km channel called the Narrows. Sampling was undertaken in both the wet season (17–19 March 2012) and the dry season (10–13 July 2012) at various representative sites around the lake including Charter's Creek, Lister's Point, the St Lucia mouth, the boardwalk mangroves near the mouth, the Bridge, Hell's Gate, Makakatana, Fani's Island, Honeymoon Bend (picnic site), Shark Basin (near the dredge outlet pipe) and the Back Channel (Fig. 1).

Physico-chemical parameters

Salinity (ppt), temperature (°C) and turbidity (NTU) were recorded through the use of a YSI® 6600 data-logger. Further data on salinity, temperature and turbidity were obtained from past records at the Iziko South African Museum (Cape Town) and from published literature.

Published literature and museum records

All literature relevant to the abundance and diversity of brachyurans in St Lucia was perused and necessary data extracted. Preserved specimens were examined at the Iziko South African Museum, which houses the largest collection of brachyurans in the country, along with records of historical surveys undertaken at St Lucia and dating back to 1948. No brachyuran collections or records pertaining to St Lucia were found at the Durban Natural Science Museum or the KwaZulu-Natal Museum (Pietermaritzburg).

Collection methods

During the current survey of 2012, various methods were employed for the collection of specimens, the most useful being active search and capture. A shovel was used to dig up burrows, while a Zabalocki-type Ekman grab and modified D-net were used in softer sediments and vegetation patches. Baited pitfall traps were set at the bridge and monitored over 2 days. In the case of D-net tows, quantitative samples were taken and quadrats were counted for selected species to determine their abundance.

Measuring distribution and abundance for selected species and sites

Distribution and abundance data were collected for certain species so as to compare past and present conditions. Included were *P. blephariskios*, a species endemic to the region, *H. projectum*, a species once distributed throughout the lake, and *N. africanum*, currently the dominant species in the system. Abundance was represented using the density code system of Owen & Forbes (1997) for *H. projectum* and *P. blephariskios*, where a density (ind.m⁻²) of 1–10 is very rare (V), 11–100 is rare (R), 101–1000 is common (C), 1001–10000 is abundant (A) and > 10001 is super-abundant (S). Estimates of *N. africanum* abundance were obtained using a crab:burrow ratio of 0.81 (Skov *et al.* 2002).

Compilation of a photographic database

Dorsal and ventral images of a representative specimen of each species were obtained using a Canon Powershot G11 digital camera. Either female or male specimens were

used for this purpose on the basis of availability, but when species exhibited a marked sexual dimorphism (e.g. *Uca* spp.), only males were used. Photographs were taken using only fresh specimens with full colours, immersed in a shallow layer of distilled water in a white tray. Photographs were edited using Corel Photo-Paint X3 for Windows, Picasa 5, Paint and Microsoft Office Picture Manager.

RESULTS

In total, thirty brachyuran species were recorded at St Lucia from 1948 to 2012. In 1948/49, twenty species were found in the system (Millard & Broekhuysen 1970). These are listed in Table 1 and include four of the five sesarmid species, two fiddlers and the freshwater crab *Potamonautes sidneyi* (Rathbun, 1904). Six additional species were collected in 1964/65 (Millard & Broekhuysen 1970) (Table 1). In 2012, seventeen species were found in and immediately around the St Lucia estuarine system (this study), including the mangroves near the Mfolozi inlet. Four of these crabs were previously unrecorded from the system, viz. *Ocypode madagascariensis* Crosnier, 1965, *Ocypode ryderi* Kingsley, 1880, *Neosarmatium smithi* (H. Milne Edwards, 1853) and *Potamonautes* cf. *lividus*, which may represent a new species.

As regards sesarmids, the following inhabitants of mangrove forests were recorded from 1948 to 2012: *N. africanum*, *Parasesarma catenatum* (Ortmann, 1897) and *C. eulimene*. *Perisesarma guttatum* (A. Milne-Edwards, 1869) has been known from the system since 1964 and *Neosarmatium inerme* (De Man, 1887), which was present in 1948, has not since been seen in the system. *Varuna litterata* (Fabricius, 1798) was found near Charter's Creek and on the mudbanks of the Mfolozi in 1948, but currently has been located alive only at the mouth. Dead specimens were also collected after a flood event at False Bay in March 2012, along the shore just south of Lister's Point.

Of the total of thirty species recorded in the system, nine are known only from single records. Aside from *N. inerme*, *Acanthonyx quadridentatus* (Krauss, 1843) and *Acanthonyx scutellatus* MacLeay, 1838 were both recorded only in 1948, in the channel connecting the Mfolozi to St Lucia. *Ptychognathus onyx* Alcock, 1900 was found in the mud, also at the mouth, in 1949. *Macrophthalmus (Mareotis) depressus* Rüppell, 1830 and *Uca (Gelasimus) vocans* (Linnaeus, 1758) were both collected at the Mfolozi inlet, while *Uca (Tubuca) urvillei* (H. Milne Edwards, 1852) was found at Shark Basin in 1964. *Uca (Paraleptuca) chlorophthalmus* (H. Milne Edwards, 1852) was recorded at the Mpate River mouth in 1949. *Metopograpsus thukuhar* (Owen, 1839) was collected in the South Lake at Catalina Bay and at Shark Basin in 1948. To complete the illustrated checklist, specimens of *Ashtoret lunaris* (Forskål, 1775), *P. sidneyi*, *Cardisoma carnifex* (Herbst, 1796), *M. thukuhar*, *Portunus pelagicus* (Linnaeus, 1758), *U. (P.) chlorophthalmus* and *U. (T.) urvillei*, none of which currently occur in the system, were obtained from a variety of locations along the KwaZulu-Natal coast.

The range of *Hymenosoma projectum* (Fig. 2) appears to have contracted since the survey conducted in 1948 (Day *et al.* 1954; Millard & Broekhuysen 1970), when the species occurred throughout the system. In 2012, it was found only at Fani's Island, Charter's Creek and Catalina Bay, all stations within the South Lake. The distribution of *H. projectum* probably fluctuates with the state of the lake and this current, more restricted distribution is possibly due to the drought conditions that have prevailed in the region until recently. *P. blephariskios* was recorded throughout the Narrows and at the estuary

TABLE 1
Brachyuran species (with previously used names and describing author) collected from St Lucia since 1948. * – As recorded by Millard & Broekhuysen (1970).

Accepted name	Author	Previous name*	Years collected in St Lucia					
			1948/49	1964/65	2007	2011	2012	
<i>Acanthonyx quadridentatus</i>	(Krauss, 1843)	<i>Dehaanius quadridentatus</i>	x					
<i>Acanthonyx scutellatus</i>	McLeay, 1838	<i>Dehaanius scutellatus</i>	x					
<i>Ashtoret lunaris</i>	(Forskål, 1775)	<i>Matuta lunaris</i>	x					x
<i>Cardisoma carnifex</i>	(Herbst, 1796)	<i>Secarma eulimense</i>		x				x
<i>Chiromantes eulimense</i>	de Man in Weber, 1897		x					x
<i>Cyclograpsus punctatus</i>	H. Milne Edwards, 1837		x					
<i>Donilla fenestrata</i>	Hilgendorf, 1869		x					x
<i>Hymenosoma projectum</i>	Dawson & Griffiths, 2012	<i>Hymenosoma orbiculare</i>	x		x			x
<i>Macrophthalmus depressus</i>	Rüppell, 1830			x				
<i>Metopograpsus thukuhar</i>	(Owen, 1839)		x					
<i>Neorhynchoplax bovis</i>	(Barnard, 1946)	<i>Rhynchoplax bovis</i>	x		x			x
<i>Neosarmatum inerme</i>	(De Man, 1887)	<i>Sarmatum inerme</i>	x					
<i>Neosarmatum africanum</i>	Ragionieri, Fratini & Schubart, 2012	<i>Secarma meinerti</i>	x				x	x
<i>Neosarmatum smithi</i>	(H. Milne Edwards, 1853)	<i>Secarma smithii</i>						x
<i>Ocypode ceratophthalmus</i>	(Pallas, 1772)		x				x	x

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TABLE 1 (continued)
 Brachyuran species (with previously used names and describing author) collected from St Lucia since 1948. * – As recorded by Millard & Broekhuysen (1970).

Accepted name	Author	Previous name*	Years collected in St Lucia					
			1948/49	1964/65	2007	2011	2012	
<i>Ocypode madagascariensis</i>	Crosnier, 1965							x
<i>Ocypode ryderi</i>	Kingsley, 1880						x	x
<i>Parasesarma catenatum</i>	(Ortmann, 1897)	<i>Sesarma catenata</i>	x					x
<i>Paratyloplitax blephariskios</i>	(Stebbing, 1924)	<i>Tyloplitax blephariskios</i>	x		x			x
<i>Perisesarma guttatum</i>	(A. Milne-Edwards, 1869)	<i>Sesarma guttata</i>				x		x
<i>Portunus pelagicus</i>	(Linnaeus, 1758)	<i>Lupa pelagica</i>				x		
<i>Potamonautes sidneyi</i>	(Rathbun, 1904)		x					
<i>Potamonautes cf. sidneyi</i>	-							x
<i>Psychognathus onyx</i>	Alcock, 1900		x					
<i>Scylla serrata</i>	(Forskål, 1775)		x					x
<i>Uca annulipes</i>	(H. Milne Edwards, 1837)		x					x
<i>Uca chlorophthalmus</i>	(H. Milne Edwards, 1837)		x					
<i>Uca urvillei</i>	(H. Milne Edwards, 1852)					x		
<i>Uca vocans</i>	(Linnaeus, 1758)	<i>Uca marionis</i>				x		
<i>Varuna litterata</i>	(Fabricius, 1798)		x				x	x

TABLE 2

Density codes indicating the maximum density of brachyuran species at each sampling period in St Lucia Estuary. A = abundant (1001–10000 m⁻²), C = common (101–1000 m⁻²), R = rare (11–100 m⁻²) and V = very rare (1–10 m⁻²). Figures in brackets denote average abundance over the entire estuary (m⁻²), except for *P. blephariskios*, found at the Back Channel in 2012.

Date (and reference)	<i>Paralydoplax blephariskios</i>		<i>Hymenosoma cf. orbiculare</i>		<i>Neosarmatium africanum</i>	
	Abundance	Location	Abundance	Location	Abundance	Location
1983 (Owen & Forbes 1997)	A	Narrows	-	-	-	-
1984 (Owen & Forbes 1997)	C	Narrows	R	Narrows	-	-
1987 (Owen & Forbes 1997)	A	Narrows	V	Narrows	-	-
1988 (Owen & Forbes 1997)	C	Narrows	V	Narrows	-	-
1989 (Owen & Forbes 1997)	A	Narrows	R	Narrows	-	-
1990 (Owen & Forbes 1997)	C	Narrows	-	-	-	-
1993 (Owen & Forbes 1997)	C	Narrows	-	-	V (3.7 ± 0.7 SD)	Mouth and Narrows
1994 (Owen & Forbes 1997)	C	Narrows	-	-	-	-
2005 (Pillay & Perissinotto 2008)	R (20.4)	Mouth, Narrows and South Lake	-	-	-	-
2012	R (88.8)	Back Channel	V (5.0)	Fani's Island	V (5.7 ± 1.1 SD)	Mouth and Narrows

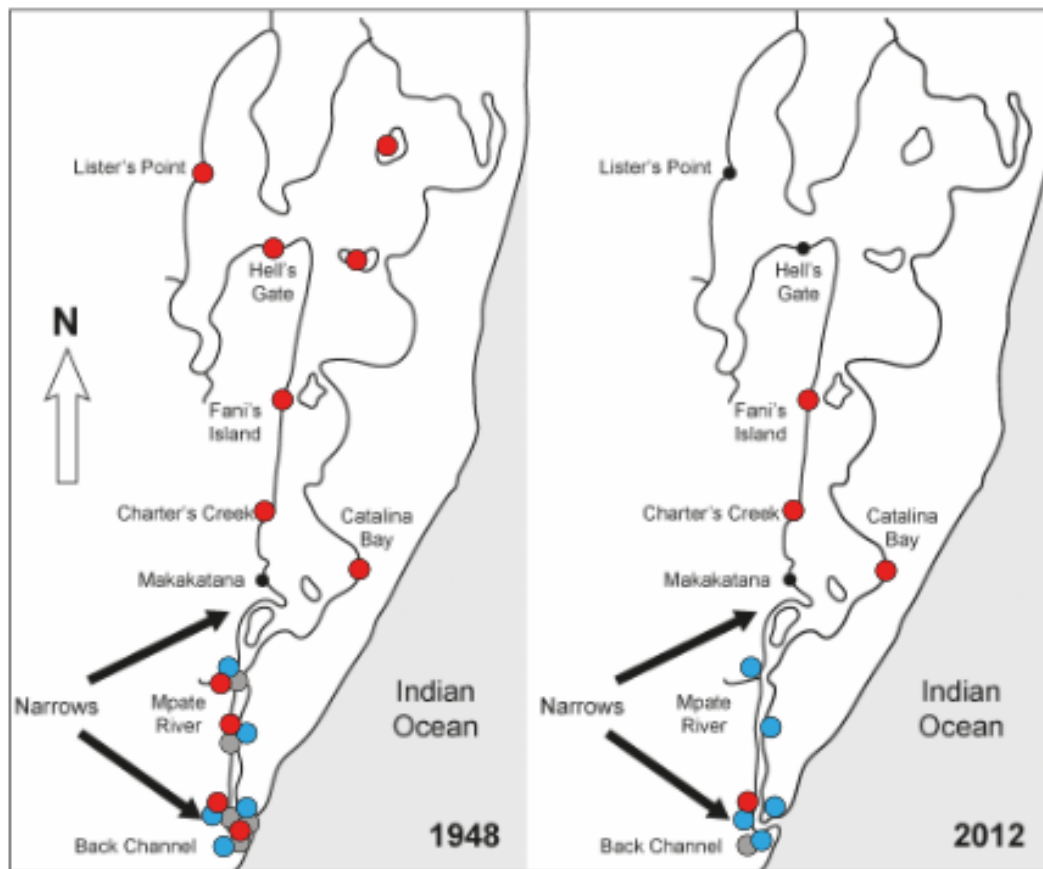


Fig. 2. Distribution of *Hymenosoma projectum* (red), *Paratyloidiplax blephariskios* (grey) and *Neosarmatium africanum* (blue) in 1948 and 2012.

mouth in 1948 (Day *et al.* 1954) (Fig. 2). However, during the 2012 survey, the species was not encountered in the system. It was only found along the banks of the Mfolozi and the Back Channel which leads into St Lucia. The mangrove crab, *N. africanum*, is the only species which has maintained its original distribution (Fig. 2). It still occurs where it was previously found in 1948, from the estuary mouth up to the Mpaté River mouth in the Narrows (Millard & Broekhuysen 1970; Owen & Forbes 1997).

In terms of abundance (Table 2), *P. blephariskios* was regarded as common to abundant in the Narrows during 1994 (Owen & Forbes 1997). In 2005, it was recorded as rare in this region (Pillay & Perissinotto 2008) and in 2012, its status was rare in the Mfolozi Back Channel. *H. projectum* has been designated as either rare or very rare in the Narrows and South Lake and its abundance appears to fluctuate erratically. *N. africanum* has always been very rare at all locations (Pillay & Perissinotto 2008).

DISCUSSION

Only 13 of the originally recorded brachyuran species appear to be in the St Lucia system at present, with 5 additional species having been found. As most of these species occur naturally in mangroves or on the beach berm, they are the least affected by the extreme salinity fluctuations of the system, which at times experiences a reverse salinity gradient. The exceptions were all at the mouth or the Mfolozi inlet. *P. blephariskios* individuals were seen burrowing in the muddy banks of the Mfolozi near the inlet;

Scylla serrata (Forskål, 1775) was found dead at the mouth and alive on the banks of the Mfolozi; and *V. litterata* occurred regularly at the mouth.

Therefore, the distribution range of brachyurans around the estuarine lake has changed compared to earlier surveys (Millard & Broekhuysen 1970). In the late 1940s, *H. projectum* specimens were netted as far north as the North Lake, while *V. litterata* was found at False Bay (Fig. 1). In the 1960s, *P. pelagicus* occurred as far north as Catalina Bay. In 2012, Fani's Island was the northernmost point of collection of live specimens previously recorded in the system and only *H. projectum* was found here in high abundance, while only dead *V. litterata* were collected at False Bay. However, *P. sidneyi* was present in a freshwater stream flowing into the lake just north of Lister's Point and *P. cf. lividus* was netted from ephemeral pans between Dukandlovu and Lister's Point. This species is yet to be conclusively identified and appears to occupy only ephemeral pans, as it has not yet been found in any other habitat. These pans represent a harsh but unique habitat niche for specialised species, as they are often waterless for long periods during the dry season. It has been suggested by Millard and Broekhuysen (1970) that salinity levels affect crab distribution. They reported an "excessively high" salinity of 89 ppt at False Bay. In recent years, salinity has been much higher in this region, even exceeding 200 ppt at times during 2010–2011 (Carrasco & Perissinotto 2012).

Brachyurans play a prominent role in maintaining mangrove forests, as they facilitate a process known as tidal flushing. The construction of burrows allows for oxygenation of the dense mangrove mud (Vopel & Hancock 2005). Tidal fluctuations or, in the case of St Lucia, wind-driven fluctuations in water levels transport nutrients through the mud and burrows, allowing for the removal of ammonium and other forms of nitrogen by the outgoing flow. Even in systems where tidal movement is negligible or completely absent, the feeding and burrowing behaviour of the inhabitant brachyurans is vital to preservation of the mangrove system. In a study conducted by Smith *et al.* (1991) in Queensland, Australia, mangrove crabs were removed over a 12-month period to determine whether or not burrowing activity influenced nutrient concentrations, soil sulphide concentration, forest productivity and growth. It was determined that burrowing affects soil aeration, which in turn affects reproduction and growth of mangrove forests. Furthermore, feeding and selectivity of feeding allows for recycling of nutrients and shaping of the mangrove community structure, respectively (Lee 1998).

The genus *Uca* and the family Sesarmidae are the two most important taxa in South African mangroves in terms of abundance (Skov *et al.* 2002). *Uca* maintains an important flow of nutrients by feeding on microphytobenthos, making this source of production available to higher trophic levels (Nagelkerken *et al.* 2008). By feeding largely on benthic micro-organisms, they alter both the sediment topography and composition of the mangrove forest floor (Skov *et al.* 2002). However, as this genus has an obligate marine phase for its larvae, it is unable to colonise when there is no sea-estuary connection (Papadopoulos *et al.* 2002). The current loss of *Uca* from the St Lucia mangroves is detrimental. There is a similar problem in respect of the swimming crab *S. serrata*. The only two specimens of this species collected from the system during 2012 were both dead. Hill (1975) reported a similar phenomenon: large numbers of dead and dying *S. serrata* were found following heavy rainfall in Eastern Cape estuaries. This indicates that the species is drastically affected by a sudden change in physico-chemical parameters, despite its euryhaline nature (Forbes & Hay 1988). The negative impact on the St Lucia

S. serrata population could be exacerbated by the need for females to move out to sea with their fertilised eggs in order to release their larvae (Hill 1975). The closure of the mouth means that females have difficulty reaching the sea and larvae have limited access to the estuary once they are released.

In terms of abundance, the brachyurans belonging to the family Sesarmidae are dominant in St Lucia, currently occurring at all mangrove sites around the estuarine lake. Sesarmids feed predominantly on leaf litter in the mangroves (Dahdouh-Guebas *et al.* 1997) and have been found to remove up to 67% of all leaf litter produced in a day (Ólafsson *et al.* 2002). *N. africanum* is the largest and most common mangrove sesarmid (Skov *et al.* 2002) in South Africa. Individuals are mainly herbivorous, with mangrove leaf litter forming approximately 75% of the diet of this species (Steinke *et al.* 1993). Individuals compete for fallen leaves and drag them back to their burrows where they are left to senesce for the removal of unpalatable tannins. They are then consumed. In this way, mangrove production is retained within the ecosystem, while detritus is broken down, leading to a faster rate of decomposition and facilitating the biogeochemical cycle within the mangrove ecosystem (Steinke *et al.* 1993; Dahdouh-Guebas *et al.* 1997). Additionally, the floor remains relatively free from leaf litter and this is especially important in areas lacking tidal influence. *N. africanum* usually inhabits the landward side of mangrove forests and can survive in fairly dry areas (Dahdouh-Guebas *et al.* 1997), largely due to its semi-terrestrial, air-breathing habits (Lee 1998). This could be the main reason for their success and dominance around the St Lucia Estuary and lake system (Fig. 2).

In all surveys, the mouth and the Mfolozi inlet have appeared to exhibit the highest diversity in terms of brachyuran species. A Mfolozi-St Lucia link can be considered a particularly valuable feature of the system. Because of its fairly stable physico-chemical properties, the Mfolozi could serve as a refuge when hypersalinity prevails in the St Lucia estuarine lake. This possibility is evident when the diversity of the Mfolozi mangroves is compared to those fringing St Lucia. In 2012, the mangroves around St Lucia were mostly inhabited by only one brachyuran species, with the exception of the boardwalk mangroves and the Bridge, which had two and three inhabitant species, respectively. On the other hand, six species were found at the Mfolozi mangroves, including *Uca annulipes* (H. Milne Edwards, 1837). The Mfolozi is also currently the only habitat of *P. blephariskios* in the entire system (Fig. 2). A species endemic to the southeast coast of Africa (Owen 2003), it occurs abundantly in muddy substrata where it plays an important role as a deposit- and filter-feeder (De Villiers *et al.* 1999). Until recently, the Mhlathuze and St Lucia estuaries both supported the largest populations of *P. blephariskios* and in 1997, its average density in St Lucia was calculated at 1500 ind.m⁻² (Owen & Forbes 1997). Owen and Forbes (2002) stated that the species is euryhaline and able to survive in the St Lucia Narrows at a maximum salinity of 55 ppt. This salinity tolerance was, however, affected by food availability and temperature and a marked decline in abundance was observed at a salinity of 38 ppt, whereas torpor was induced at 50 ppt. Moreover, the primary method of dispersal for the species is tidal and the lack of tidal fluctuation in the Narrows and the estuary in general means that *P. blephariskios* has a limited means of dispersal (Owen & Forbes 2002). As the system experiences highly fluctuating salinity levels, it is unlikely that *P. blephariskios* would be able to survive the current conditions. Owen *et al.* (2010) have suggested that during periods of crisis,

TABLE 3 (continued)

Distribution of brachyuran species sampled from 1948 to 2012, where: BM – boardwalk mangroves, BP – black pipe, BR – bridge, CB – Catalina Bay, CC – Charter’s Creek, EM – estuary mouth, FB – False Bay, FI – Fani’s Island, HB – Honeymoon Bend, MI – Mfolozi inlet, MR – Mpate River mouth, MT – Makakatana, NA – Narrows and NL – North Lake.

Identification	EM	BM	BP	MI	HB	BR	MR	NA	MT	CB	CC	FI	FB	NL
<i>Ocypode ceratophthalmus</i>	1948 2012													
<i>Ocypode madagascariensis</i>	2012													
<i>Ocypode ryderi</i>	2012													
<i>Parasarcma catenatum</i>		1949		1949 2012										
<i>Paratyloplax blephariskios</i>	1948			2012		1964								
<i>Perisesarma guttatum</i>	2012					1964 2012								
<i>Portunus pelagicus</i>						1964	1964	1964	1964	1964				
<i>Potamonautes cf. invidus</i>													2012	
<i>Potamonautes sidneyi</i>										1948				
<i>Pychognathus oryx</i>	1949													
<i>Scylla serrata</i>	2012			2012							1948			
<i>Uca annulipes</i>				2012			1949							
<i>Uca chlorophthalmus</i>							1949							
<i>Uca urvillei</i>	2013	1948												
<i>Uca vocans</i>				1965										
<i>Varuna litterata</i>	2012			1949							1948		1948	2012

the Mfolozi-Msunduzi system may provide a refuge to organisms that normally occur in the St Lucia estuarine lake. Indeed, *P. blephariskios* is found at the Back Channel and, should favourable conditions be restored, dispersal and recolonisation from this “refuge population” could occur via a newly restored Mfolozi- St Lucia link (Owen *et al.* 2010). This is an important consideration and supports the recently implemented reconnection of the St Lucia Estuary to the Mfolozi.

The North Lake and False Bay are the least diverse areas, inhabited by the lowest number of species found in the various regions. In 1948, there were two species present at each of these two locations (Day *et al.* 1954; Millard & Broekhuysen 1970) (Table 3), while in 2012, only *V. litterata*, was found (dead) in False Bay and had probably been washed downstream from a nearby river. The reverse salinity gradient that persists in the system best explains the lack of brachyurans in the northern reaches of the estuarine lake, as even the most euryhaline species would be unable to tolerate the salinity levels currently prevailing in these areas (Carrasco & Perissinotto 2012). *H. projectum* was once recorded as *Hymenosoma orbiculare* Desmarest, 1823 until recent genetic studies proposed splitting of the South African *H. orbiculare* population into five distinct species (Edkins *et al.* 2007; Teske *et al.* 2009). These have subsequently been described by Dawson and Griffiths (2012). The species once occurred throughout False Bay and the North Lake (Fig. 2). It is endemic to the east coast of southern Africa, and is known from as far south as Port St Johns (Branch *et al.* 2010; Teske *et al.* 2009).

Lawrie and Stretch (2011) proposed three possible scenarios for the future state of the St Lucia estuarine system. In scenario 1, the St Lucia Estuary is separated from the Mfolozi and an open mouth is artificially maintained. Scenario 2 provides for separation from the Mfolozi with no mouth manipulation (closed), while in scenario 3, the St Lucia Estuary and the Mfolozi have a combined inlet with no further manipulation. In the recent past, Scenario 2 has prevailed, although the mouth has now been linked to the Mfolozi (Scenario 3). Scenario 2 is largely associated with high salinity levels and low water levels for prolonged periods, leading to the predominant closure of the mouth. Salinity would be expected to fluctuate between extremely high and extremely low levels. This would negatively affect the diversity and distribution of brachyurans, as large salinity fluctuations and lack of ocean influence in the estuarine lake and surrounding mangroves create conditions that are unfavourable for them. This is problematic when an affected species depends largely on the St Lucia Estuary and is endemic to the region, as is the case with *P. blephariskios*. Additionally, scenario 2 would prevent recruitment of new species and juveniles from the ocean, leading to a temporary loss of species such as *S. serrata* and those belonging to the genus *Uca*. However, species capable of surviving these conditions, such as *N. africanum* and *C. eulimene*, would dominate in the system and possibly spread due to lack of competition. When the mouth does open briefly, as it did in March 2007, diversity would probably increase, although unsustainably so because of reversion to the closed mouth state soon afterwards. MacKay *et al.* (2010) reported an increase in the diversity of brachyurans following the overtopping/breaching event of March 2007, which could possibly indicate that larval recruitment had taken place. However, whereas four species were recorded after the storm, only one was found six months later.

In scenario 1, medium to high water levels would persist, although hypersalinity would be experienced about 30% of the time. This would allow for a much higher diversity

and abundance of species, as well as faster recovery after hypersaline events, due to greater stability in salinity. Scenario 3 would have the least extreme conditions, with no anthropogenic intervention subsequent to the linking of the Mfolozi and St Lucia systems. The chances of hypersalinity occurring and desiccation taking place are the lowest in this scenario, while abundance and diversity would be highest (Lawrie & Stretch 2011). Bolt (1974) reported rapid re-colonisation of the system by benthic fauna following a period of high salinity. As there are refuge populations of some species around the Mfolozi River, this could be a future possibility and the presence of *U. (T.) urvillei* has already been noted near the mouth, in March 2013 (R.H. Taylor pers. obs.) (Table 3). The open mouth in scenarios 1 and 3 would allow for the recruitment of juveniles and possibly new species, although the threat of alien invasion would also increase. A good example of a non-indigenous species is the crab *Carcinus maenas* (Linnaeus, 1758) which, however, has yet to successfully invade the east coast of South Africa, having been found to prefer sheltered bays as opposed to the high-energy coastline of KwaZulu-Natal (Hampton & Griffiths 2007).

There is no well-defined arrangement for the identification of brachyurans within the system and this is partly due to the recent discoveries of pseudocryptic (identifiable through careful morphological analysis, but easily misidentified) and cryptic (morphologically similar but genetically different) species (Sarno *et al.* 2005), particularly amongst the sesarmids and within the genera *Uca* and *Hymenosoma* (Edkins *et al.* 2007; Teske *et al.* 2009; Ragionieri *et al.* 2012). The aim of the illustrated and annotated checklist in the Appendix is to provide interested parties with an updated and definitive means of identification. This will hopefully reduce identification error and facilitate both research and management.

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APPENDIX

An annotated and illustrated checklist of all brachyuran crustaceans identified from St Lucia Estuary during this study and that of Millard and Broekhuysen (1970). Abbreviations: CWW – Carapace width at widest point. Scale bars = 10 mm.

FAMILY CAMPTANDRIIDAE

Paratylodiplax blephariskios (Stebbing, 1924)

Synonyms: *Cleistostoma blephariskios* Stebbing, 1924.

Common name: Eastern oval crab.

Size: 10 mm CWW.

Distinguishing features: Carapace almost oval in shape, with highly setose legs and eye stalks.

Distribution: Mngazana to Moçambique.^[13]

St Lucia records:

1948 – Collected in sandy mud at the mouth and the bridge; abundant in the lower Narrows.^[7]

2012 – Collected at the Mfolozi Back Channel.

Fig. 3. Mfolozi River, October 2012, N.A.F. Miranda, 10 mm.



3

FAMILY DOTILLIDAE

Dotilla fenestrata Hilgendorf, 1869

Synonyms: None.

Common name: Army crab.

Size: 10 mm CWW.^[13]

Distinguishing features: Small and pea-shaped with a grooved carapace.^[1]

Distribution: Breede River to Moçambique.^[13]

St Lucia records:

1965 – Recorded at the Mfolozi inlet.^[7]

2012 – Recorded at the St Lucia Bridge and the Mfolozi Back Channel.

Fig. 4. Mlalazi Estuary, June 2012, N. Peer, 8 mm.



4

FAMILY EPIALTIDAE

Acanthonyx quadridentatus (Krauss, 1843)

Synonyms: *Dehaanius quadridentatus* Krauss, 1843.

Common name: 4-toothed decorator crab.

Maximum size: 20 mm CWW.

Distinguishing features: Bears hooked hairs and three or four pairs of marginal teeth on the carapace; usually covered in algal fragments (decorations), as displayed here.^[1]

Distribution: East London to Moçambique.^[13]

St Lucia records:

1948 – Netted with seaweed fragments from the channel between St Lucia and Mfolozi.^[7]

Fig. 5. Rocky Bay, October 2012, N. Peer, 11 mm.



5

***Acanthonyx scutellatus* MacLeay, 1838**Synonyms: *Acanthonyx macleayi* Krauss, 1843.

Common name: Shield decorator crab.

Maximum size: 20 mm CWW.

Distinguishing features: Bears hooked hairs on the carapace. Usually covered in algal fragments (decorations).^[1]Distribution: East London to Moçambique.^[1]

St Lucia records:

1948 – Netted with seaweed fragments from the channel between St Lucia and Mfolozi.^[7]

Fig. 6. Treasure Beach, October 2012, N.A.F. Miranda, 12 mm.



6

FAMILY GECARCINIDAE***Cardisoma carnifex* (Herbst, 1796)**Synonyms: *Cancer carnifex* Herbst, 1796; *Cancer urvillei* H. Milne Edwards, 1853; *Cardisoma obesum* Dana, 1851; *Perigrapsus excelsus* Heller, 1862.

Common name: Mangrove butcher crab.

Maximum size: 10 mm CWW.^[1, 10]Distinguishing features: Body dark red to brown, rounded carapace and smooth.^[1, 10]Distribution: Durban Bay to Moçambique.^[6, 10]

St Lucia records:

1965 – Recorded at the Mfolozi inlet.^[7]

2012 – Recorded at the St Lucia Bridge and the Mfolozi Back Channel.

Fig. 7. Mlalazi Estuary mangroves, May 2012, N.A.F. Miranda, 95 mm.



7

FAMILY GRAPSIDAE***Metopograpsus thukuhar* (Owen, 1839)**Synonyms: *Grapsus thukuhar* Owen, 1839; *Metopograpsus eydouxi* H. Milne Edwards, 1853; *Metopograpsus intermedius* H. Milne Edwards, 1853; *Pachygrapsus parallelus* Randall, 1840.

Common name: Estuarine rock crab.

Size: 35 mm CWW.^[1]Distinguishing features: External face of palm and dactylus often violet in colour, with carapace and legs mottled.^[1]Distribution: East London to Moçambique.^[1, 4]

St Lucia records:

1948 – Juveniles were collected on the northern shore of the SAAF station at Shark Basin and on Catalina Bay.^[7]

Fig. 8. Durban Bay Harbour, March 2012, N. Peer, 21 mm.



8

FAMILY HYMENOSOMATIDAE***Hymenosoma projectum* Dawson & Griffiths, 2012**

Synonyms: None.

Common name: Eastern crown crab.

Size: 15 mm CWW.^[1]Distinguishing features: Lighter in colour compared to other species of this genus and described as the least setose. Length ratio of first leg : second leg = 1.3 – 1.5:1, a smaller ratio compared to the other species.^[2]Distribution: Port St Johns to Moçambique.^[3]

St Lucia records:

1948 – Found throughout the system.^[7]

2012 – Collected at Fani's Island and Catalina Bay.

Fig. 9. Fani's Island, St Lucia, July 2012, N. Peer, 9 mm.

***Neorhynchoplax bovis* (Barnard, 1946)**Synonyms: *Rhynchoplax bovis* Barnard, 1946.

Common name: Furry crown crab.

Size: 5 mm CWW.^[1]Distinguishing features: Brown to dark green in colour. Fur-lined chelae are prominent in both sexes.^[1]Distribution: Restricted to tropical and subtropical estuaries along the KwaZulu-Natal coast, to Moçambique.^[4]

St Lucia records:

1948 – Found throughout the system.^[7]

2012 – Collected in the Narrows.

Fig. 10. Mpate Mouth, July 2012, R. Perissinotto, 5 mm.

**FAMILY MACROPHTHALMIDAE*****Macrophthalmus (Macrophthalmus) grandidieri* A. Milne-Edwards, 1867**Synonyms: *Macrophthalmus hilgendorfi* Tesch, 1915.

Common name: Long-eyed crab.

Size: 25 mm CWW.^[1]Distinguishing features: Carapace wider than long, with two pairs of antero-lateral teeth and two shallow grooves running from the midline to the sides of the carapace.^[1]Distribution: Durban Bay to Moçambique.^[1, 2]

St Lucia records:

The species recorded in St Lucia by Millard & Broekhuysen (1970) was *M. depressus* (1965 – Mfolozi inlet), a species currently thought to occur only as far south as Moçambique^[1]. Thus, *M. grandidieri* is reported here instead, as it is possible that misidentification had occurred.

Fig. 11. Durban Bay, May 2012, N. Peer, 19 mm.



FAMILY MATUTIDAE***Ashtoret lunaris* (Forskål, 1775)**

Synonyms: *Cancer lunaris* Forskål, 1775; *Matuta banksii* Leach, 1817; *Matuta lunaris* (Forskål, 1775).

Common name: Lunar box crab.

Size: 40 mm CWW. (excluding spines).^[1]

Distinguishing features: Cream, round carapace with red dots and two lateral spines. Spiny chelae.^[1]

Distribution: East London to Moçambique.^[1]

St Lucia records:

1948 – Seine-netted at the mouth.^[7]

2012 – Found dead on the beach berm in front of the closed St Lucia Mouth.

Fig. 12. Vetch's Beach, August 2012, N. Peer, 35 mm.



12

FAMILY OCYPODIDAE***Uca (Austruca) annulipes* (H. Milne Edwards, 1837)**

Synonyms: *Gelasimus annulipes* H. Milne Edwards, 1837.

Common name: Pink-clawed fiddler crab.

Size: 20 mm CWW.^[1]

Distinguishing features: Broad frontal margin, mottled light-coloured carapace and long, light pink chela in males.^[1]

Distribution: Port St Johns to Moçambique.^[1]

St Lucia records:

1949 – Collected from the Mpate River mangroves.^[7]

2012 – Collected at the Mfolozi Back Channel.

Fig. 13. Mlalazi Estuary, N.A.F Miranda, 13 mm.



13

***Uca (Paraleptuca) chlorophthalmus* (H. Milne Edwards, 1837)**

Synonyms: *Gelasimus chlorophthalmus* H. Milne Edwards, 1837; *Uca amazonensis* Doflein, 1899.

Common name: Green-eyed fiddler crab.

Size: 20 mm CWW.^[1]

Distinguishing features: Broad frontal margin. Bright green/blue and black mottled carapace with red legs and chelae.^[1]

Distribution: Port St Johns to Moçambique.^[1]

St Lucia records:

1948 – Collected in Mpate River mangroves.^[7]

Fig. 14. Mlalazi Estuary, N.A.F Miranda, 18 mm.



14

***Uca (Tubuca) urvillei* (H. Milne Edwards, 1852)**

Synonyms: *Gelasimus urvillei* H. Milne Edwards, 1852.

Common name: Urville's fiddler crab.

Size: 25 mm CWW.^[4]

Distinguishing features: Narrow frontal margin with black/brown mottled legs and carapace, red granulated chelae and cheliped.^[11]

Distribution: Port St Johns to Moçambique.^[4]

St Lucia records:

1949 – Found at Shark Basin.^[7]

2013 – Observed in the Back Channel for the first time after a long absence from the system.

Fig. 15. Mlalazi Estuary, November 2012, R.H. Taylor, 30 mm.



15

***Uca (Gelasimus) vocans* (Linnaeus, 1758)**

Synonyms: *Cancer vocans* Linnaeus, 1758; *Gelasimus cultrimanus* White, 1847; *Gelasimus marionis* Desmarest, 1823; *Gelasimus nitidus* Dana, 1851; *Ocypode cetharosedicus* Say, 1817; *Uca marionis* (Desmarest, 1823); *Uca marionis cultrimana* (Adams & White, 1848); *Uca marionis excisa* Nobili, 1906; *Uca vocans excisa* (Nobili, 1906); *Uca (Thalassuca) vocans hesperiae* Crane, 1975.

Common name: Brown fiddler crab.

Size: 25 mm CWW.^[4]

Distinguishing features: Narrow frontal margin with black/brown mottled legs and carapace, red granulated chelae and cheliped.^[11]

Distribution: Port St Johns to Moçambique.^[4]

St Lucia records:

1948 – Collected in Mplate River mangroves.^[7]

Fig. 16. Mlalazi Estuary, August 2012, R. Perissinotto, 19 mm.



16

***Ocypode ceratophthalmus* (Pallas, 1772)**

Synonyms: *Cancer caninus* Herbst, 1782; *Cancer ceratophthalmus* Pallas, 1772; *Ocypoda macleayana* Hess, 1865; *Ocypode brevicornis* var. *longicornuta* Dana, 1852; *Ocypode urvillei* Guérin, 1829.

Common name: Horn-eyed ghost crab.

Size: 40 mm CWW.^[4]

Distinguishing features: Has horned eyestalks and a green-coloured carapace. One chela usually noticeably larger than the other.^[4]

Distribution: Knysna to Moçambique.^[4]

St Lucia records:

1948 – Found on the beach near the Mfolozi inlet.^[7]

2012 – Found on the berm at the St Lucia Estuary mouth.

Fig. 17. St Lucia Beach, November 2011, N. Peer, 32 mm.



17

***Ocypode madagascariensis* Crosnier, 1965**Synonyms: *Ocypode madagascariensis* Crosnier, 1965.

Common name: Madagascan ghost crab.

Size: 35 mm CWW.^[1]Distinguishing features: Sandy in colour. Similar in appearance to *O. ryderi* but unlike this species, *O. madagascariensis* has orange/brown joints.^[1]Distribution: Durban to Moçambique.^[1]

St Lucia records:

2012 – Found on the berm at the St Lucia Estuary mouth.

Fig. 18. St Lucia Beach, July 2012, R. Perissinotto, 28 mm.



18

***Ocypode ryderi* Kingsley, 1880**

Synonyms: None.

Common name: Pink ghost crab.

Size: 35 mm CWW.^[1]Distinguishing features: Dull pink in colour and similar in appearance to *O. madagascariensis*.Unlike this species, *O. ryderi* has mauve joints.^[1]Distribution: Port Elizabeth to Moçambique.^[1]

St Lucia records:

2012 – Found on the berm at the St Lucia Estuary mouth.

Fig. 19. St Lucia Beach, December 2011, N. Peer, 30 mm.



19

FAMILY PORTUNIDAE***Scylla serrata* (Forskål, 1775)**Synonyms: *Achelous crassimanus* MacLeay, 1838;*Cancer serrata* Forskål, 1775; *Lupa lobifrons* H.Milne Edwards, 1834; *Scylla tranquebarica* var.*oceanica* Dana, 1852.

Common names: Giant mud crab, Serrated swimming crab.

Size: 300 mm CWW.^[1]

Distinguishing features: Carapace bears nine pairs of marginal teeth on an oval-shaped carapace.

Usually green/brown in colour with orange-tipped chelae and walking legs.^[1]Distribution: Indo-Pacific; in southern Africa, occurs between Knysna to Moçambique.^[1]

St Lucia records:

1948 – Found at the St Lucia Estuary mouth and near islands, located in the Narrows.^[7]

2011 – Observed at Charter's Creek.

2012 – Found dead at the St Lucia Mouth.

Fig. 20. Mfolozi River, March 2012, N. Peer, 121 mm.



20

***Portunus (Portunus) pelagicus* (Linnaeus, 1758)**

Synonyms: *Cancer pelagicus* Linnaeus, 1758; *Cancer cedonulli* Herbst, 1794; *Lupa pelagica* (Linnaeus, 1758); *Portunus denticulatus* Marion de Procé, 1822; *Portunus (Portunus) pelagicus* var. *sinensis* Shen, 1932.

Common name: Blue swimming crab.

Size: 120 mm CWW.^[1]

Distinguishing features: Carapace is mottled brown and pink with a toothed, fur-lined anterolateral margin. A lateral spine is present on each side of the carapace and chelae and walking legs are usually blue.^[1]

Distribution: Durban to Moçambique.^[1]

St Lucia records:

1964 – Seine-netted between Catalina Bay and Brodie's Shallows, below the M pate River mouth and at the St Lucia Bridge.^[7]

Fig. 21. Durban Bay Harbour, September 2012, Durban Seine-Netters, 90 mm.



21

FAMILY POTAMONAUTIDAE***Potamonautes* cf. *lividus* (Gouws, Stewart & Reavell, 2001)**

Synonyms: None.

Common name: St Lucia river crab.

Size: 15 mm CWW.

Distinguishing features: This could be an undescribed species (molecular and morphological study currently in progress). Very similar in appearance to *P. lividus* except for the larger size and colouration.

Distribution: Currently known only from ephemeral pans around False Bay, Lake St Lucia.

St Lucia records:

2012 – Netted from ephemeral pans adjacent to False Bay.

Fig. 22. Dukandlovu Pan, south of Lister's Point, July 2012, R. Perissinotto, 14 mm.



22

***Potamonautes sidneyi* (Rathbun, 1904)**

Synonyms: *Potamon sidneyi* Rathbun, 1904.

Common names: Natal river crab, Sidney's river crab.

Size: 50 mm CWW.^[12]

Distinguishing features: Carapace strongly granulated, forming sharp angle between postfrontal crest and epibranchial region. Usually brown in colour.^[12]

Distribution: Mozambique, South Africa (Eastern Cape Province, Free State, Gauteng, KwaZulu-Natal, Mpumalanga, Northern Cape Province, North-West Province) and Swaziland.^[12]

St Lucia records:

1949 – Collected on the bank opposite the Catalina Jetty.^[7]

2012 – Found at a freshwater stream north of Lister's Point.

Fig. 23. Cobham, Drakensberg, February 2012, R. Perissinotto, 48 mm.



23

FAMILY SESARMIDAE***Neosarmatium smithi* (H. Milne Edwards, 1853)**Synonyms: *Sesarma smithi* H. Milne-Edwards, 1853; *Sesarma smithii* H. Milne-Edwards 1853.

Common name: Marsh crab.

Size: 50 mm CWW.^[43]Distinguishing features: Has uniformly bright red chelae and a black carapace. Very similar in appearance to *P. guttatum* but unlike *P. guttatum* this species bears at least two spines on the upper margin of its dactylus.^[44]Distribution: Mngazana to Moçambique.^[42, 41]

St Lucia records:

2012 – Found amongst the mangroves around the St Lucia Mouth, the Narrows and the Mfolozi inlet.

Fig. 24. St Lucia Estuary mouth, February 2012, R. Perissinotto, 50 mm.



24

***Neosarmatium africanum* Ragionieri, Fratini & Schubart, 2012**Synonyms: Previously regarded as *Neosarmatium meineri* (De Man, 1887).

Common name: Red mangrove crab.

Size: 50 mm CWW.^[13]Distinguishing features: Square-like carapace with red and yellow/orange granulated chelae. Chest strongly granulated and ridged upper margin of chelae.^[13, 21]Distribution: Port Elizabeth to Moçambique.^[11]

St Lucia records:

1948 - Collected from Charter's Creek and mangroves around the Narrows and the St Lucia Mouth.^[17]

2012 – Found amongst the mangroves at the mouth, the Narrows and the Mfolozi inlet.

Fig. 25. St Lucia Estuary mouth, March 2012, N.A.F Miranda, 48 mm.



25

***Parasesarma catenatum* (Ortmann, 1897)**Synonyms: *Sesarma catenata* Ortmann, 1897.

Common name: Furry marsh crab.

Size: 25 mm CWW.^[13]Distinguishing features: Chelae are orange/yellow in colour, similar to *S. eulimense*. *P. catenatum* is distinguished by the fur-lined chelae present in males and the oblique-shaped ridge on the upper margin of the dactylus.^[13, 111]Distribution: Cape Agulhas to Moçambique.^[43]

St Lucia records:

1948 – Collected from mangroves in the lower Narrows and St Lucia Mouth region.^[17]

2012 – Found at the Mfolozi inlet.

Fig. 26. Mfolozi River, March 2012, N. Peer, 13 mm.



26

***Chiromantes eulimene* (De Man in Weber, 1897)**Synonyms: *Sesarma eulimene* De Man, 1895;*Holomestopus eulimene* (De Man, 1898).

Common name: Common marsh crab.

Size: 25 mm CWW.^[1]Distinguishing features: Chelae are similar in colour as those of *P. catenatum* but without the fur-lined chelae in males and with more rounded granulation of the dactyl's upper margin.^[1, 11]Distribution: Bashee to Moçambique.^[1]

St Lucia records:

1949 – Found north of the Mfolozi inlet, on the islands near Charter's Creek, at the Mpate River mouth, near the pond at the mouth and at Honeymoon Bend Picnic Site.^[7]

2012 – Found at the St Lucia Bridge, Honeymoon Bend, near the Mfolozi inlet and in Shark Basin.

Fig. 27. Honeymoon Bend, St Lucia, March 2012, N. Peer, 18 mm.



27

***Perisesarma guttatum* (A. Milne-Edwards, 1869)**Synonyms: *Sesarma guttata* A. Milne-Edwards, 1869.

Common name: Red-clawed marsh crab.

Size: 50 mm CWW.^[1]Distinguishing features: Carapace is black and chelae are uniformly red, similar to *N. smithi*.Distinguished from *N. smithi* by the granulation on the upper margin of the chelae.^[1, 4]Distribution: Port St Johns to Moçambique.^[1]

St Lucia records:

1964 – Found at the St Lucia Bridge.^[7]

2012 – Collected at the St Lucia Mouth and Bridge.

Fig. 28. Mlalazi Estuary, May 2012, N. Peer, 26 mm.



28

FAMILY VARUNIDAE***Cyclograpsus punctatus* (H. Milne Edwards, 1837)**Synonyms: *Cyclograpsus reynaudi* H. Milne Edwards, 1837; *Gnathochasmus barbatus* MacLeay, 1838.

Common name: Brown shore crab.

Size: 30 mm CWW.^[1]Distinguishing features: Smooth carapace, which is almost square in appearance. Usually dark brown to dark green in colour, with orange/brown legs.^[1]Distribution: Entire South African coastline.^[1]

St Lucia records:

1948 – Collected from Shark Basin and islands located within the Narrows.^[7]

Fig. 29. Mission Rocks, October 2012. N. Peer, 14 mm.



29

***Psychognathus onyx* Alcock, 1900**

Synonyms: None.

Common name: Hairy swimming crab.

Size: 14 mm CWW.^[14]Distinguishing features: Similar in appearance to *Varuna litterata* but differs because of the presence of fur-lined outer palms of chelae and toothed margins of carapace.^[14]Distribution: In Africa, this species has only been recorded in St Lucia^[7] and in Tanzania.^[15]

St Lucia records:

1949 – Rarely found in mud banks of estuary. As the species is very similar to *V. litterata*, this record may represent an erroneous identification.^[7]

Fig. 30. St Lucia, Estuary mouth, July 1949, K.H. Barnard, 10 mm. [Note – These photographs depict the 1949 specimen from the collection at the Iziko South African Museum. Photographs were highly manipulated due to the poor condition and colouration of the actual specimen.]

***Varuna litterata* (Fabricius, 1798)**Synonyms: *Alpheus litteratus* Weber, 1795; *Cancer litterata* Fabricius, 1798; *Varuna tomentosa* Pfeffer, 1889.

Common name: River swimming crab.

Size: 70 mm.^[12]Distinguishing features: Carapace almost square in appearance. Dorso-ventrally flattened and mottled brown/green. Highly setose walking legs.^[12]Distribution: Indo-Pacific; in southern Africa, reaching as far south as Port St Johns.^[11]

St Lucia records:

1948 – Recorded at a freshwater stream near Charter's Creek and at False Bay.^[7]

2012 – Found at the mouth (alive) and at False Bay (dead).

Fig. 31. St. Lucia Estuary mouth, February 2012, R. Perissinotto, 45 mm.



Chapter 2

One expected observation in the St Lucia estuarine lake was the spread of freshwater crabs (*Potamonautes* spp.) through the system with the onset of the freshwater phase, between 2011 and 2013. As a result of the biodiversity census (Chapter 1), a morphologically-distinct form of the freshwater crab *Potamonautes lividus* was discovered in the ephemeral pans around False Bay. The genus *Potamonautes* has been subject to ongoing genetic and morphological analyses with several undescribed species being discovered recently. Within the iSimangaliso Wetland Park itself, the systematics of the genus have not recently been examined, even though a high potential for endemism is created by a range of specialised niches in the park. A new species is described in this chapter following genetic and morphological analyses.

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RESEARCH ARTICLE

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Description of a new species of *Potamonautes* MacLeay, 1838, from the iSimangaliso Wetland Park, South Africa

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Abstract

A new species of freshwater crab, *Potamonautes isimangaliso* **sp. n.**, is described from the western shores of False Bay, Hluhluwe, within the iSimangaliso Wetland Park, South Africa. While bearing a superficial resemblance to *P. lividus*, the new species has been found to be genetically distinct, diverging from the former by 7.4–7.8% in mtDNA. *Potamonautes isimangaliso* most closely resembles *P. lividus*, but is distinguished by a unique suite of carapace characters, colouration, and size. The new species also lives in close association with oxygen-poor, fresh ephemeral pans, while the habitat of *P. lividus* is well above the surface water line of the closest water body. An updated identification key for the *Potamonautes* species of South Africa is provided.

Keywords

Brachyura, freshwater, *Potamonautes*, taxonomy, ephemeral pans, sand forest, iSimangaliso Wetland Park

Introduction

Freshwater crabs play a key role in ecosystems by serving as an important food source for larger taxa, and recycling nutrients through detritivorous feeding habits (Cumberlidge 2009). They link terrestrial and aquatic habitats by moving between the two systems, and are considered bioindicator species of environmental change in some habitats (Schuwerack et al. 2001). *Potamonautes* is the only genus of primary freshwater crab (Yeo et al. 2014) in South Africa, with 16 described species occurring in the country, two having been described in recent years (Daniels and Bayliss 2012; Phiri and Daniels 2014).

The iSimangaliso Wetland Park forms the southernmost region of the Maputaland centre of endemism and constitutes the focus of biodiversity conservation in the region (Smith et al. 2008). Recent ecological and biodiversity surveys of Lake St Lucia have been conducted in an attempt to update local taxonomic records, identify undescribed species, highlight the change in diversity over time, and provide illustrated and annotated checklists to use as identification tools (Nel et al. 2012; Peer et al. 2014; Perissinotto et al. 2014). Surveys have revealed the existence of an undescribed species of *Potamonautes* along the western shores of False Bay (Fig. 1) that most closely resembles *P. lividus* Gouws, Stewart & Reavell, 2001 in morphological appearance, exhibiting a rounded vaulted carapace and the potential ability to spend a large amount of time out of water. However, genetic analysis showing a 7.4–7.8% difference across the combined 16S rDNA and COI gene fragments in comparison to *P. lividus* (G. Gouws unpubl.) and morphological analysis (present study) indicate that the two species are indeed distinct.

In this paper we describe *Potamonautes isimangaliso* sp. n. from the sand forests of the iSimangaliso Wetland Park. NP and GG wrote the taxonomic part of this study, including the description of the new species, while the contribution of the other authors dealt with natural history and ecological observations.

Materials and methods

Collection of crabs

Crabs were collected from four localities (Fig. 1) using a sweep net in pans or by active hand capture. The unidentified species was found in 2012–2013 during routine surveys in the area as part of an ongoing project on the biodiversity of Lake St Lucia, supported by the iSimangaliso Park Authority and the provincial conservation authority, Ezemvelo KZN Wildlife, and subsequently during a dedicated survey undertaken in February 2015. Specimens were preserved in 10% formalin or 70% ethanol, once photographs were taken using a Canon Powershot G12.

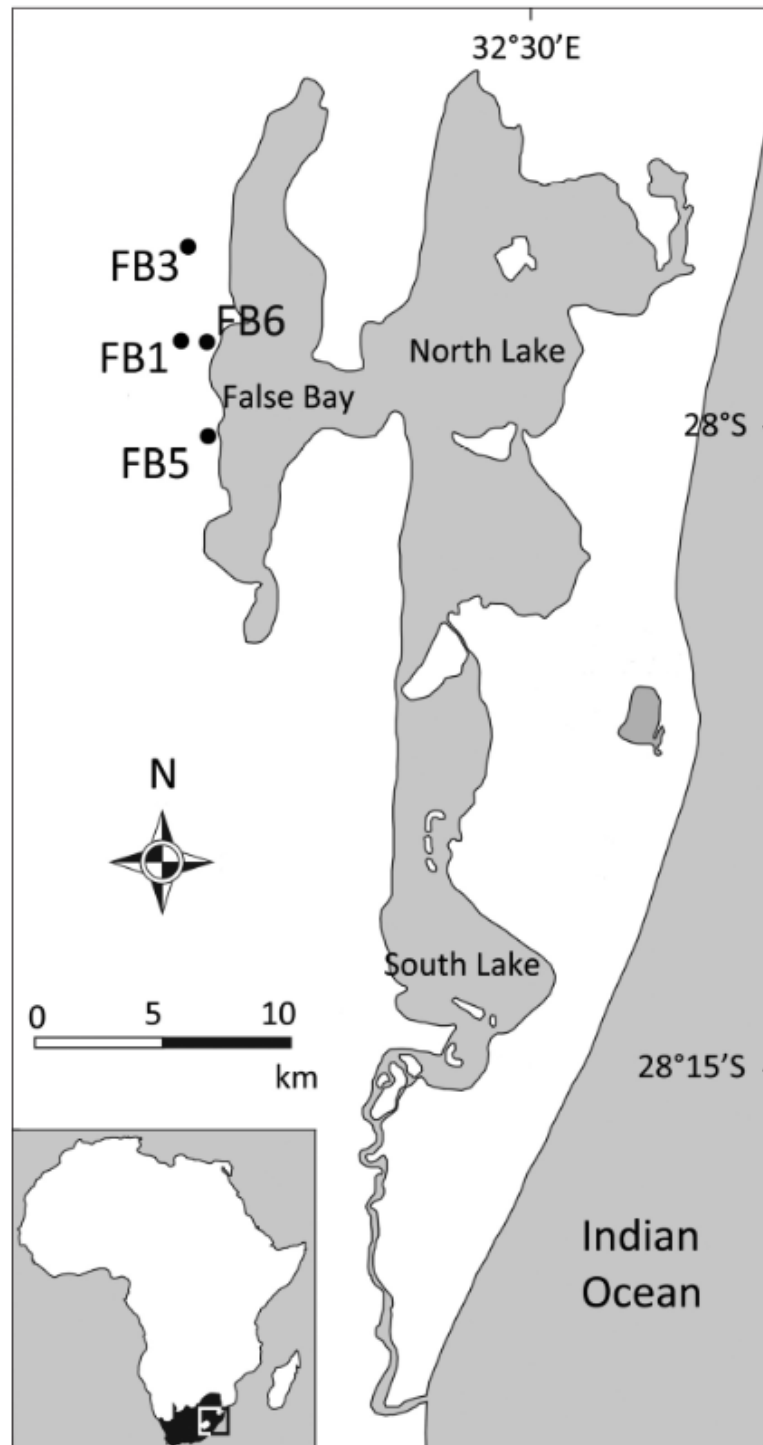


Figure 1. Map of Lake St Lucia on the east coast of South Africa. Collection localities, indicated by black dots and labelled with codes, are all restricted to the western shore of False Bay, within the False Bay Park. FB1 - Main Road Pan; FB3 - Mpophomeni Pan; FB5 - Dukandlovu Pan; FB6 - Sandy Point Pan.

Morphological and morphometric analyses

In the laboratory, a pair of Vernier callipers was used to measure morphological variables. A Nikon SMZ25 microscope fitted with a Nikon Digital Sight DS-Fi2 camera was used for macro-examination and to take photos of gonopods and mouthparts.

Abbreviations for depositories and provinces:

ISAM	Iziko South African Museum, Cape Town, South Africa
NMMU	Nelson Mandela Metropolitan University Collection.
EC	Eastern Cape
WC	Western Cape
KZN	KwaZulu–Natal

Abbreviations for all morphological and morphometric characters (Gouws et al. 2001)

CL	Carapace length
CWW	Carapace widest width
CWP	Carapace posterior width
PFC	Distance between postfrontal crest and anterior margin
ED	Distance between orbits
CWA	Distance between exorbital teeth
CH	Carapace height
AW6	Width of sixth abdominal segment
MCPL	Major cheliped propodus length
MCPH	Major cheliped propodus height
P2ML	Pereopod 2, merus length
P2MH	Pereopod 2, merus height
s2/s3	First sternal groove (suture between the second and third sulci)
s3/s4	Second sternal groove (suture between the third and fourth sulci)
CRDL	Right cheliped, dactyl length
CLDL	Left cheliped, dactyl length
CRPL	Right cheliped, propodus length
CLPL	Left cheliped, propodus length
CRPW	Right cheliped, propodus width
CLPW	Left cheliped, propodus width
ML	Merus length
MW	Merus width

For the morphometric analyses, eight variables (CL, PFC, CWP, ED, CH, AW6, CRPL and CRPW) were log transformed and used to run a stepwise discriminant function analysis in STATISTICA v 12.5 (Statsoft 2004). Data for *Potamonautes lividus* were obtained from G. Gouws and represent the specimens used for the de-

scription of *P. lividus* (Gouws et al. 2001). Classification functions were calculated and individuals were then reassigned to groups based on a priori probabilities. Canonical scores were plotted for both species on a frequency histogram to support distinction between the two forms. Lastly, a linear regression analysis was used to examine variation for specific variables.

Genetic analysis

DNA was extracted from each specimen and amplification of the mitochondrial cytochrome c oxidase subunit I (COI) and 16S ribosomal DNA genes were carried out following protocols outlined by G. Gouws (unpubl.). Amplifications were confirmed by electrophoresis in 1% agarose gels with an ethidium bromide stain. The product was then viewed on an ultraviolet transilluminator. Sequences were generated from a representative of the new species, using approaches described elsewhere (Daniels et al. 2002; Phiri and Daniels 2014; G. Gouws (unpubl.)).

Results

Morphometric analysis

The new species (*Potamonautes isimangaliso* sp. n.) was distinguished from *P. lividus* by its larger size, flatter carapace and more rounded posterior. The carapace variables CL, CH and CWP contributed the most to distinguishing between the two forms in the discriminant analysis. Fig. 2 highlights the morphometric distinction between the two species.

The classification function was calculated for both species as follows:

$$Y(P. isimangaliso) = 926.798(\text{LogCL}) - 602.076(\text{LogCH}) - 7.966(\text{LogCWP}) - 178.319$$

and

$$Y(P. lividus) = 1428.33(\text{LogCL}) - 743.234(\text{LogCH}) - 321.805(\text{LogCWP}) - 296.179$$

Individuals were reassigned to groups based on a priori probabilities using these classification functions. 100% of both forms were correctly classified with no individuals being reassigned. Three variables (CWP, PFCD and CH) were regressed over CL and a significant difference was seen between the two species as follows: CWP/CL – SS = 0.1, df = 2, F = 2.29, p < 0.001; PFCD/CL – SS = 0.1, df = 2, F = 2.29, p < 0.001; CH/CL – SS = 0.1, df = 2, F = 5.99, p < 0.001 (Fig. 3a, b, c)

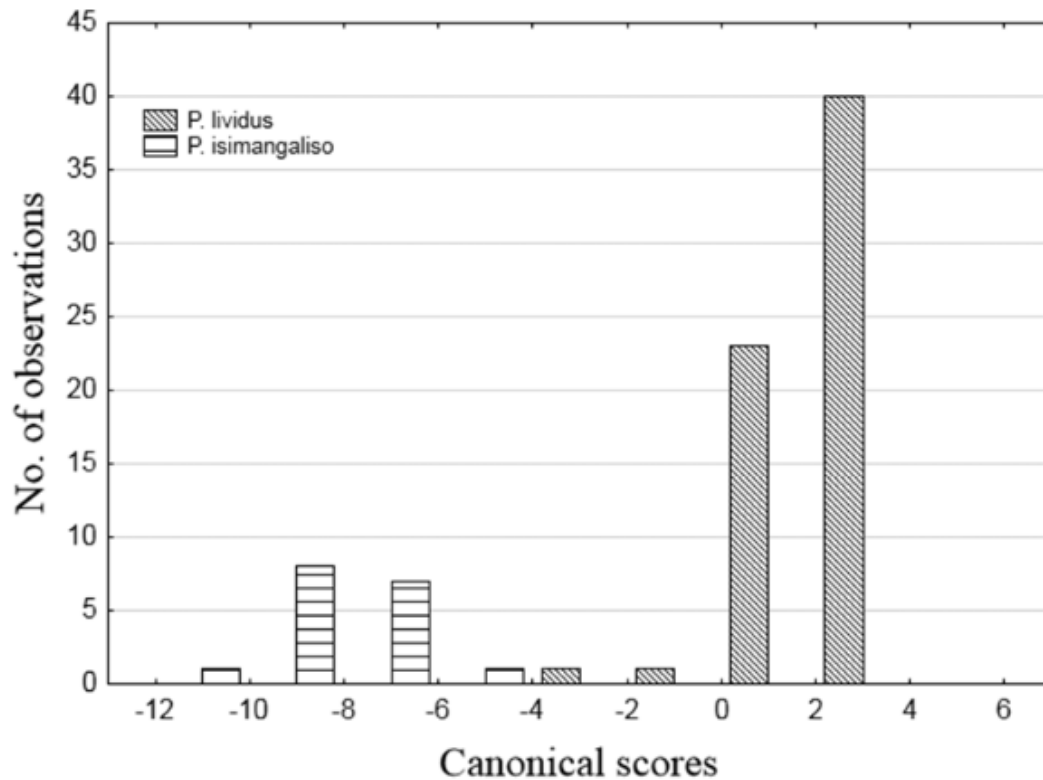


Figure 2. Histogram of canonical scores for *P. isimangaliso* and *P. lividus* calculated from a discriminant function analysis.

Taxonomic description

Potamonautes isimangaliso Peer & Gouws, sp. n.

<http://zoobank.org/4D5E76D6-BFEB-41CE-BF3D-EBD2AA3820D7>

Type series. Holotype: male, CL = 37 mm, ephemeral pan 200 m away from the western fence of False Bay Park (FB3), iSimangaliso Wetland Park (27°57'31.33"S, 32°21'42.15"E; elevation 62 m), 2 February 2015, R. Perissinotto, R.H. Taylor, D. Bilton, M.S. Bird, S.J. du Plooy and L. Clennell legit (ISAM A78908).

Allotype: female, CL = 27 mm, ephemeral pan, next to road leading from Dukandlovu campsite to False Bay Park entrance gate (FB5), 5 km south of Lister's Point, iSimangaliso Wetland Park (28°0'51.70"S, 32°21'55.36"E; elevation 10 m), 1 February 2015, R. Perissinotto, R.H. Taylor, D. Bilton, M.S. Bird, S.J. du Plooy and L. Clennell legit (ISAM A78909).

Paratypes: one male, one female, collection data same as per holotype (NMMU); one male, ephemeral pan along the main road of False Bay Park (FB1), iSimangaliso Wetland Park (27°58'32.02"S, 32°21'51.62"E; elevation 42 m), 1 February 2015, R. Perissinotto, R.H. Taylor, D. Bilton, M.S. Bird, S.J. du Plooy, and L. Clennell

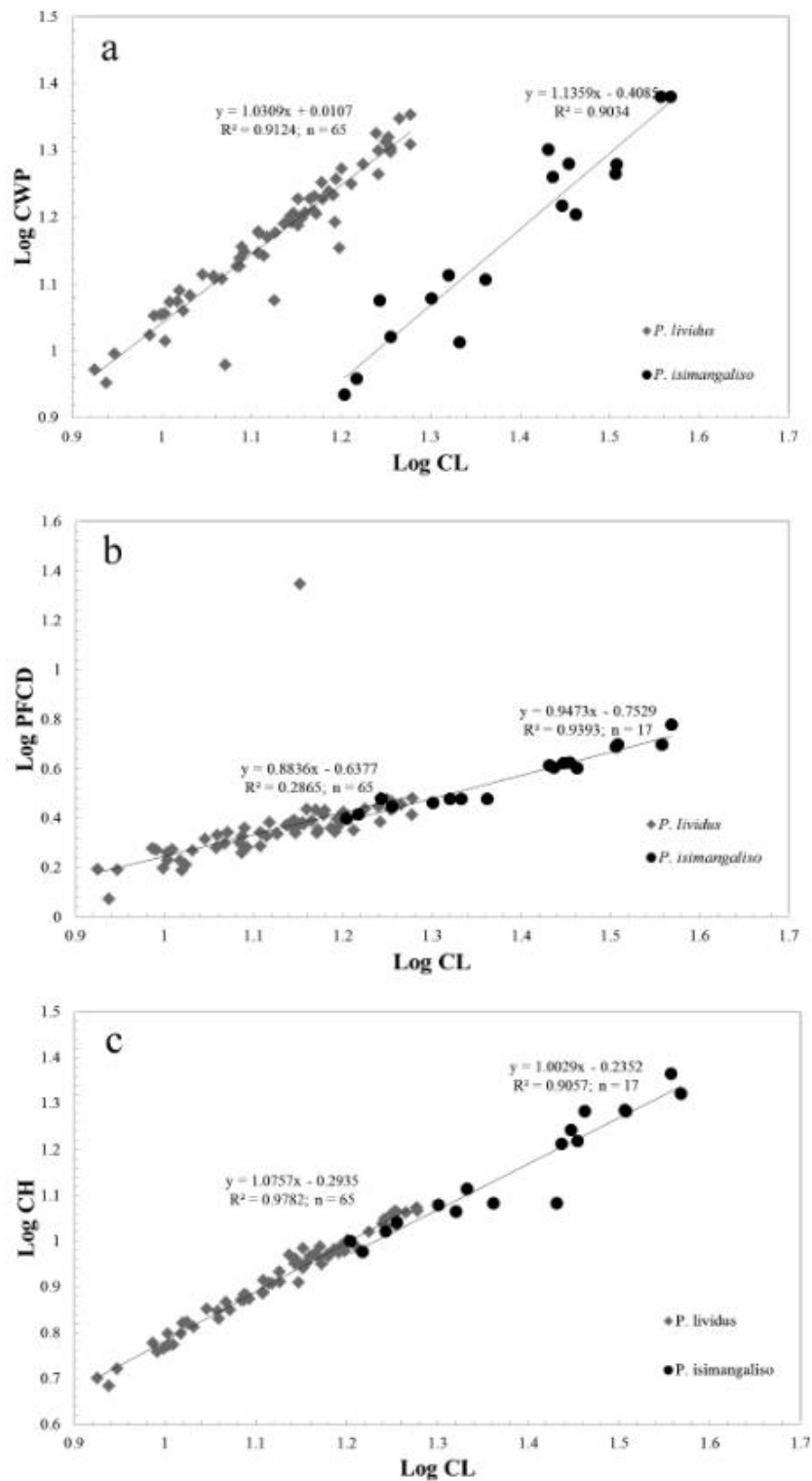


Figure 3. Regressions of **a** LogCWP over LogCL **b** LogPFCD over LogCL and **c** LogCH over LogCL between the two species *P. isimangaliso* and *P. lividus*. All differences between regressions were statistically significant ($p < 0.001$).

Table 1. Morphometric variables (mm) of *Potamonautes isimangaliso* sp. n. holotype and paratype specimens.

Variable	Holotype	Males (n=8)	Females (n=7)
CL	37	13.2–36.1	18–27
CWW	55.1	18–53	26–40.1
CPW	24	9–24	10.5–20
PFGD	6	2–5	2.8–4.1
ED	15.6	5–16	8.5–12.8
CWA	34	14.1–40.5	21.5–32
CH	21	7–23.2	11–12.1
AW6	12	3.1–11	7–23.4
MCPL	49.3	11.5–44.5	17.2–29.2
MCPH	21.9	4.1–20.1	7–13.7
P2ML	21.3	6.5–18.9	8.9–13.8
P2MH	6.5	2–6.1	3–5

legit (ISAM A78910); one male, ephemeral pan, collection data same as per allotype (ISAM A78911); two males, two females, ephemeral pan along the main road of False Bay Park (FB1), iSimangaliso Wetland Park (27°58'32.02"S, 32°21'51.62"E; elevation 42 m), 31 January 2015, R. Perissinotto, R.H. Taylor, D. Bilton, M.S. Bird, S.J. du Plooy, and L. Clennell legit (ISAM A78912); two females, collection data same as per holotype, 26 November 2013, R. Perissinotto, R.H. Taylor, N. Peer, N.A.F. Miranda, M.S. Bird, J.L. Raw and L. Clennell legit (NMMU); one male, one female, ephemeral pan near Sandy Point in False Bay Park (FB 6), iSimangaliso Wetland Park (27°58'36.0"S, 32°22'17.0"E; elevation 12 m), 25 November 2013, R. Perissinotto, R.H. Taylor, N. Peer, N.A.F. Miranda, M.S. Bird, J.L. Raw and L. Clennell legit (ISAM A78913); two males, ephemeral pan, collection data same as per allotype, 5 December 2012, R. Perissinotto, N.A.F. Miranda, N. Peer, J.L. Raw legit (ISAM A78914).

Diagnosis. Main distinguishing features of *P. isimangaliso* from *P. lividus* Gouws, Stewart & Reavell, 2001 as follows: slightly granulated, horizontal anterolateral margin more rounded than in *P. lividus*; downward projection of postfrontal crest at exorbital edges; uniform colouration of dark purplish brown with lighter or orange coloured joints, cheliped tips and pereopods tips. *Potamonautes isimangaliso* is larger than *P. lividus*, with a maximum size of 37 mm CL recorded in males.

Description. Carapace (Fig. 4a, c). Cephalothorax somewhat vaulted (CH/CL = 0.57), wide (CWW/CL = 1.49) and ovoid in general. Branchial region extremely rounded, forming a quarter of a circle with anterolateral margin. Anterior margin straight, lying on same horizontal plane as anterolateral margin; anterolateral margin slightly granulated. Urogastric grooves well-defined; cardiac and cervical grooves well-defined where attached to the urogastric groove, but then becoming poorly defined and shallow towards edge of carapace. Epigastric lobes well-defined above postfrontal crest by two indentations forked from midpoint of postfrontal crest. Postfrontal crest slightly granulated, curving forward medially. Postfrontal crest indistinct medi-



Figure 4. *Potamonautes ismangaliso* sp. n. male holotype CWW 55.1 mm (ISAM A78908). **a** dorsal view **b** ventral view and **c** cephalothorax, frontal aspect. Scale bar: 10 mm. Photos: Nasreen Peer.

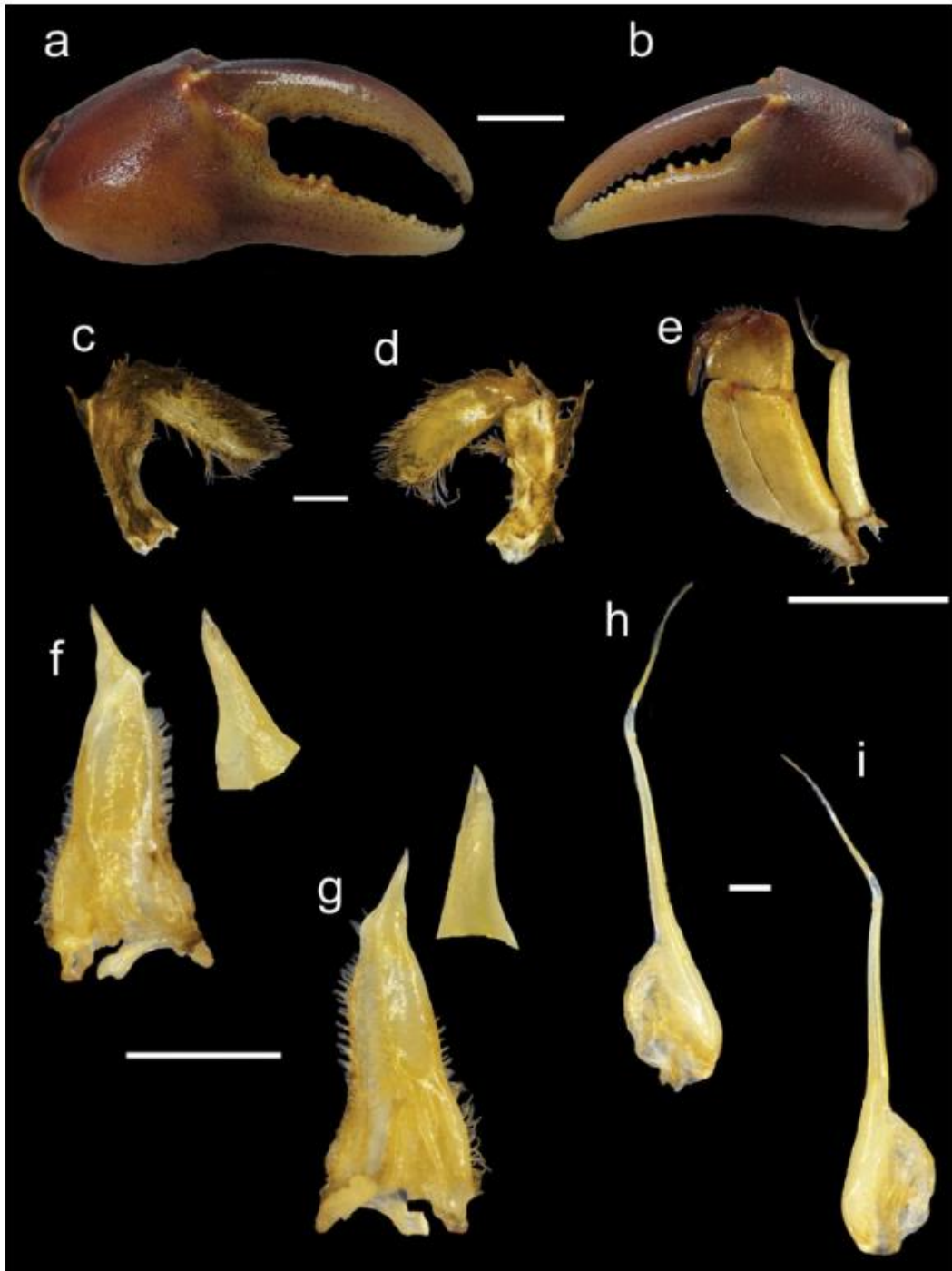


Figure 5. *Potamonautes isimangalis* sp. n. male holotype CWW 55.1 mm (ISAM A78908). **a** major cheliped **b** minor cheliped **c** right mandibular palp posterior view **d** right mandibular palp anterior view **e** 3rd maxilliped **f** left gonopod 1 anterior view with enlarged terminal segment **g** left gonopod 1 posterior view with enlarged terminal segment **h** left gonopod 2 anterior view and **i** left gonopod 2 posterior view. Scale bars: 10 mm (**a**, **b**), 1 mm (**c**, **d**), 10 mm (**e**), 5 mm (**f**, **g**), 1 mm (**h**, **i**). Photos: Nasreen Peer.

ally but pronounced posterior to orbital margins, curving prominently downwards at epibranchial region. Moderate presence of small exorbital teeth, but complete absence of epibranchial teeth. Flank of carapace smooth, with clear horizontal (epimeral) suture separating pterygostomial region from subhepatic and suborbital regions; vertical (pleural) groove dividing subhepatic region from suborbital region.

Sternites (Fig. 4b). Sternites 1 and 2 fused; first sulcus absent as a result; second sulcus s2/s3 prominent, running completely across sternum; third sulcus s3/s4 projecting downwards medially towards abdominopelvic region. Sulci and episternal sulci thereafter well-defined but shallow.

Third maxillipeds (Figs 4c, 5e). Filling entire buccal frame except transversely oval respiratory openings at top lateral corners. Ischium slightly scabrous, with pronounced groove running vertically. Flagellum on exopod of third maxilliped fairly long, curving upward at distal ends.

Mandibular palp (Fig. 5c, d). Consisting of two segments; terminal segment undivided and smooth, with dense tuft of setae protruding from base; hirsute margins; light covering of setae on posterior surface; subterminal segment enlarged distally where it joins with terminal segment.

Pereopods (Figs 4a, b, 5a, b). General right-handedness and prominent inequality of chelae where $CRDL/CLDL = 1.32$. Dactyl of major chela moderately arched; large interspace formed in major cheliped when fingers are closed, long slim interspace formed by closing of fingers in minor cheliped. Twenty four cutting teeth present on the dactyl of major cheliped and 29 on dactyl of minor cheliped; 3 larger and more prominent than the rest. Propodus fairly inflated; right propodus larger ($CRPL/CLPL = 1.41$) and wider ($CRPW/CLPW = 1.75$) than left. Left pollex with 25 cutting teeth and right propodus with 18. Carpus on either side containing one prominent tooth followed by one smaller tooth. Meri strongly granulated around margins; slender pereopods (pereopod 2: $ML/MW = 3.28$; pereopods 5: $ML/MW = 2.17$), pereopod 3 is longest and pereopod 5 shortest; ventral margins of meri smooth; ventral margins of propodi slightly serrated; dorsal margins of meri and propodi bearing fine sharp bristles; dactyli serrated and ending in sharp points.

Pleon (Fig. 4b). First five segments broad and short, with segments 6 and 7 longer; segments 1–6 four sided, with triangular distally-rounded terminal segment (telson).

Pleopods (Fig. 5f, g, h, i). Gonopod 1 bearing short terminal segment only 0.23 times the length of the subterminal segment. Terminal segment curving slightly away from midline when viewed posteriorly. Gonopod widest at base, with both subterminal and terminal segments tapering and ending in sharp point. Inner lateral margin of subterminal segment irregular; outer lateral margin curving in a concave manner towards middle of gonopod; both margins hirsute. Groove extending almost through entire length of gonopod, visible on posterior surface, lined with setae. Distal margin of subterminal segment irregularly curved. Gonopod 2 consisting of two segments; terminal segment relatively long (0.47 times length of subterminal segment), very slim; subterminal segment wide at base, sharply becoming very narrow around 0.4 of length at which point narrow process forms, leading up to terminal segment. Small tuft of

setae present on outer margin of base of subterminal segment. Gonopod 2 curved, moving outwards away from medial line of gonopod proximally, curving back towards medial line distally.

Variation. The major cheliped does not always display a pronounced interspace when fingers are closed. In juveniles and in the female allotype this was less prominent. The arching of chelipeds varies too, with some (particularly the minor chelipeds) bearing straight dactyli while others are fairly rounded. All collected specimens display a pronounced heterochely and all appear to be right-handed.

Live colouration. Colouration of carapace may vary between light brown, maroon, purplish-brown and almost black. Similarly, tips of dactyli may be either orange, bright yellow or a dull yellow.

Distribution. Currently only known from the False Bay region of the iSimangaliso Wetland Park on the north-east coast of South Africa.

Type locality. South Africa, KwaZulu-Natal, iSimangaliso Wetland Park, False Bay - Western Shores: Mpophomeni Pan (27°57'31.33"S, 32°21'42.15"E); Dukandlovu Pan (28°0'51.70"S, 32°21'55.36"E); Main Road Pan (27°58'32.02"S, 32°21'51.62"E); Sandy Point Pan (27°58'36.0"S, 32°22'17.0"E).

Etymology. The species is named after the iSimangaliso Wetland Park, located in northern KwaZulu-Natal, where it is currently thought to be micro-endemic. This is significant as the iSimangaliso Wetland Park falls within the Maputaland centre of endemism (Smith et al. 2008), highlighting the importance of this park as a global biodiversity hotspot. The Park is a UNESCO World Heritage Site and contains three Ramsar Wetlands of International Importance.

Remarks. *Potamonautes isimangaliso* sp. n. is easily distinguishable from most other *Potamonautes* spp. found in South Africa. *Potamonautes dentatus* Stewart, Coke & Cook, 1995, *P. parvispina* Stewart, 1997, *P. unispinus* Stewart & Cook, 1998, *P. warreni* Calman, 1918 and *P. calcaratus* (Gordon, 1929) all bear dentate anterolateral margins or epibranchial corners, while *P. isimangaliso* has a rounded epibranchial corner and mildly granular anterolateral margin.

Potamonautes perlatus (H. Milne Edwards, 1837), *P. granularis* Daniels, Stewart & Gibbons, 1998, *P. sidneyi* Rathbun, 1904, *P. barbarai* Phiri & Daniels, 2014 and *P. barnardi* Phiri & Daniels, 2014 all have sharply-defined scabrous or granular epibranchial corners and prominent postfrontal crest, while *P. isimangaliso* has a heavily rounded smooth epibranchial corner and poorly-defined postfrontal crest. *Potamonautes parvicorpus* Daniels, Stewart & Burmeister, 2001 also displays a finely granulated anterolateral margin and rounded epibranchial corners, but the resemblance to *P. isimangaliso* is superficial, as it differs in the indentation of its anterior margin where *P. parvicorpus* bears a slightly indented anterior margin while that of *P. isimangaliso* lies straight. Further differences are seen in locality as the habitat of *P. parvicorpus* is restricted to high mountain streams in the Western Cape (Daniels et al. 2001).

Potamonautes clarus Gouws, Stewart & Coke, 2000, *P. depressus* (Krauss, 1843), *P. brincki* (Bott, 1960), *P. flavusjo* Daniels, Phiri & Bayliss, 2014 and *P. lividus* Gouws, Stewart & Reavell, 2001 all have smooth anterolateral margins and rounded smooth

epibranchial corners but bear differences compared to *P. isimangaliso*. One of the diagnostic characters of *P. depressus* is the dorsally flattened carapace, where CL/CH = 2.3–2.6. *Potamonautes isimangaliso* has a more vaulted carapace with a CL/CH ratio of 1.6–1.8. *Potamonautes brincki* and *P. clarus* are smaller crabs (max CL = 27 mm in males for both species), preferring fast-flowing mountain stream habitats. *Potamonautes flavusjo* is ecologically distinct from *P. isimangaliso* and can be found in the Mpumalanga Highveld. In addition to this, the species is smaller and has flattened chelipeds, not adapted for burrowing (Daniels et al. 2014). Light yellow chelipeds and ventral surfaces of pereopods characterise *P. flavusjo*.

Potamonautes lividus shares a similar distribution, outward appearance and preference for air-breathing with *P. isimangaliso*. However various differences exist between the two species. The level and angle of anterolateral margin differ, where *P. isimangaliso* bears an anterolateral margin lying on the same horizontal plane as the anterior margin. Conversely, *P. lividus* has an anterolateral margin which angles downward to join the anterior margin and thus sits higher than the anterior margin. The downward angle of postfrontal crest at exorbital edges is seen in *P. isimangaliso* but not in *P. lividus*. Carapace flatness is indicated by the CL/CH ratio which equates to 1.5 for *P. lividus* and 1.8 for *P. isimangaliso* holotypes. The maximum size (37 mm CL in *P. isimangaliso* and 25.5 mm CL in *P. lividus*), colouration (dark blue carapace with bright orange chelipeds in *P. lividus* and dark brown/purple carapace with brown or dull yellow cheliped in *P. isimangaliso*), inflation of chela with gap between propodus and dactyl (dactyl of *P. lividus* is more arched than that of *P. isimangaliso*) and the number of poorly-developed teeth on carpus (*P. lividus* containing one prominent and three rudimentary teeth; *P. isimangaliso* containing one prominent and one rudimentary tooth) further distinguish the two species. Gonopods of both species are very similar with the only difference being the tuft of setae found at the base of pleopod 2 in *P. isimangaliso*. Specimens resembling *P. lividus* were found in the Dwesa Forest, Eastern Cape and appear to be genetically nearly identical to *P. lividus* (Daniels et al. 2014). This further substantiates the genetic distinctiveness of *P. isimangaliso*. The smallest mature male of *P. isimangaliso* recorded had a CL of 13.2 mm whilst all females recorded were mature (min CL = 18 mm).

Preliminary sequence data for two mitochondrial gene regions (16S: GenBank accession number KR137640; COI: KR137642) generated from a representative of the new species, using approaches described elsewhere (Daniels et al. 2002; Phiri and Daniels 2014; G. Gouws unpubl.), were notably divergent (7.3% and 7.9%, respectively) from published 16S (AY042248; Daniels et al. 2002) and COI (AF510879; Daniels et al. 2002) sequences of *Potamonautes lividus* from KwaZulu-Natal.

Habitat and ecology. *Potamonautes isimangaliso* sp. n. inhabits freshwater ephemeral pans (maximum salinity recorded: 0.75) which fill up with fresh, oxygen-deprived water after rainfall events, mainly during the summer wet season. These pans are located along the western shores of False Bay, Lake St Lucia (Fig. 6a–d) in clearings of the sand forest biome of False Bay and are generally partially shaded. *Potamonautes isimangaliso* and *P. lividus* are found in close proximity although *P. lividus* has not



Figure 6. Sampling localities of *Potamonautes isimangalis* sp. n.: **a** Main Road Pan (FB1) **b** Mpopophmeni Pan (FB3) **c** Dukandlovu Pan (FB5) and **d** Sandy Point Pan (FB6), completely dry during Feb 2015. Photos: **a–c** Lynette Clennell; **d** Nasreen Peer.

been found in False Bay Park and *P. isimangalis* has not been found outside of the park. Furthermore, a difference in habitat type between *P. isimangalis* and *P. lividus* Gouws, Stewart & Reavell, 2001 is seen, where the latter is known to inhabit burrows well above the surface water line in *Ficus* and *Barringtonia* swamps (Gouws et al. 2001), while the new species was found in close association with ephemeral pans in sand forest habitat with burrows extending below the surface waterline. Vegetation types include the dominant canopy species *Cleistanthus schlechteri*, *Hymenocardia ulmoides*, *Psydrax fragrantissima*, *Croton pseudopulchellus* and *Drypetes arguta* (Kirkwood & Midgley, 1999), as well as various *Acacia* spp. (Moll 1980). Grass species such as *Paspalum vaginatum* and *Eleocharis* sp. are also closely associated with this environment (Moll 1980). Aquatic plants associated with the ephemeral pans include the reed *Typha capensis*, the sedge *Juncus kraussii*, the mangrove fern *Acrostichum aureum* and the duckweed *Lemna* sp. (Howard-Williams 1980).

Potamonautes isimangalis adults form burrows on the banks of these pans (Fig. 7a), while juveniles are found either in burrows or free-crawling in shallow water (2–50 cm). The species lives sympatrically with *P. sidneyi* but is separated by habitat

Table 2. Physico-chemical parameters of sampling localities †.

	Main Road Pan (FB1)	Mpophomeni Stream (FB2)	Mpophomeni Pan (FB3)	Dukandlovu Pan (FB5)
Temperature (°C)	26.1	20.4	22.03	26.73
Salinity	0.15	8.36	0.29	0.75
Maximum depth (mm)	80	500	700	250
pH	7.2	7.03	7.42	6.9
Turbidity (NTU)	1310.5	14	151	306.3
Dissolved oxygen (% sat.)	19.8	90.1	22.4	69.6

† No data is included for Sandy Point Pan (FB6) as the site was dry at the time of sampling.

type, with *P. sidneyi* inhabiting flowing streams and able to withstand higher salinities of up to 9 (18 May 2013, Mpophomeni Stream, 27°57'7.17"S, 32°22'37.21"E). Oxygen levels in the pans inhabited by *P. isimangaliso* are quite low compared to flowing streams (Table 2).

Although the species appears to be more closely associated with water than its morphologically closest congener, *P. lividus* (Gouws et al. 2001), the low levels of oxygen characteristic of the pans along with the ephemeral nature of the waterbodies indicate a greater affinity for a terrestrial lifestyle, as it may be more effective to obtain oxygen through air-breathing. This has been recorded previously in various African freshwater brachyuran genera and a high-vaulted carapace may be indicative of this change, where periods of dryness favour the evolution of burrowing semi-terrestrial, air-breathing tendencies (Cumberlidge 1999; Cumberlidge 2009). Specimens of *P. isimangaliso* have been observed in deep burrows (30–50 cm) around desiccated pools. Because the rainy season in this area is generally restricted to the period November–April (late Austral spring to early Autumn), much of the population hibernates deep in the mud, where traces of moisture persist throughout the dry season. Crabs return to the surface only after major rainfall events have filled up the ephemeral pools. The summer of 2014–2015 had been particularly dry in the area, with substantial rain falling in the False Bay area starting only in the middle of January (69 mm during 15–17 Jan, 54 mm during 28–30 Jan 2015; False Bay Park Meteo Station). Numerous adult and sub-adult crabs were observed from 31 Jan to 3 Feb in the newly filled ephemeral pools but hardly any young juvenile, indicating that the previous drought conditions had not allowed spawning to happen yet.

The feeding ecology of the species is largely unknown, although *Potamonautes* crabs are generally thought to shift from a diet of aquatic invertebrates to a more herbivorous or opportunistic diet with age (Hill and O’Keeffe 1992). The chelar dentition is serrate and the larger crusher chela lacks rounded or molariform occlusive geometry in the proximal region, probably due to wearing down over time. The dentition of the chela is indicative of an opportunistic omnivorous diet (Yamada and Boulding 1998).



Figure 7. **A** Burrows of *Potamonautes isingalis* sp. n. are typically found on the banks of ephemeral pans and are even maintained when pans are completely dry **B** *Potamonautes isingalis* sp. n. in its natural habitat. Photos: Lynette Clennell.

Updated key for the identification of the *Potamonautes* species of South Africa

Based on Day et al. (2001)

- 1 Anterolateral margin bearing one tooth or many distinct teeth 2
- Anterolateral margin smooth tooth, sometimes serrated or granulated 6
- 2 Anterolateral margin bearing two or more distinct teeth 3
- Anterolateral margin bearing one distinct tooth at epibranchial corner 4
- 3 Postfrontal crest complete to anterolateral margin; epibranchial sinus absent..
..... *Potamonautes warreni* Calman, 1918
- Postfrontal crest interrupted at exorbital teeth; epibranchial sinus present
..... *P. dentatus* Stewart, Coke & Cook, 1995
- 4 Postfrontal crest not continuous posterior to exorbital teeth; merus of chelipeds bearing a spine on both antero- and posterior-inferior granulate margins..... *P. calcaratus* (Gordon, 1992)
- Postfrontal crest complete; no spine on merus of cheliped 5
- 5 Postfrontal crest not sloping backwards towards anterolateral margin; epibranchial sinus absent *P. unispinus* Stewart & Cook, 1998
- Postfrontal crest sloping backwards to meet anterolateral margin; epibranchial sinus present..... *P. parvispina* Stewart, 1997
- 6 Anterolateral margin granulated, forming distinct angle with postfrontal crest at epibranchial corner; epibranchial region usually scabrous or granulated....7
- Anterolateral margin rounded and smooth, meeting postfrontal crest at rounded epibranchial corner; epibranchial region usually without scabrosity or granulation 10
- 7 Carapace and postfrontal crest strongly granulated, with pronounced scabrosity in epibranchial region..... 8
- Carapace and postfrontal crest moderately granulated, with relatively smooth epibranchial region 9
- 8 Carapace anterior relatively narrow and curved moderately over the branchial region; inward-extending lobe absent from short terminal segment of gonopod 2; confined to the Olifants River system in the Cape Fold Mountains below the Bulshoek dam wall (WC)
..... *P. granularis* Daniels, Stewart & Gibbons, 1998
- Carapace anterior relatively wide and curved slightly over the branchial region; long slender S-shaped terminal segment of gonopod 2 is formed by inward extending lobe; not occurring in the Western Cape..... *P. sidneyi* Rathbun, 1904
- 9 Occurring largely in the Western Cape, also extending further north and east; found in western flowing drainage systems including the Olifants River, where it occurs above the Bulshoek dam wall.....
..... *P. perlatus* (H. Milne Edwards, 1837)
- Restricted to southern flowing drainages in the Western Cape (Gamtoos River and Gourits River)..... *P. barbarai* Phiri & Daniels, 2014

- Restricted to the Berg River and tributaries of the Breede River (WC).....
..... *P. barnardi* Phiri & Daniels, 2014
- 10 Carapace depressed and dorso-ventrally flattened; ratio of carapace length to height between 2.1 and 2.6..... 11
- Carapace vaulted and arched; ratio of carapace length to height between 1.5 and 2.2 12
- 11 Carapace flatter, with a ratio of carapace length to carapace height between 2.3 and 2.6; postfrontal crest often directed forward near anterolateral margin; dark yellow-brown or green-brown in colour *P. depressus* (Krauss, 1843)
- Carapace more vaulted, with ratio of carapace length to carapace height between 2.1 and 2.3; postfrontal crest straight near the anterolateral margin; orange in colour..... *P. clarus* Gouws, Stewart & Coke, 1995
- 12 Dactyli of chelipeds flattened; postfrontal crest, pereopods and chelipeds bright yellow; occurring in the Mpumalanga Highveld.....
..... *P. flavusjo* Daniels, Phiri & Bayliss, 2014
- Dactyl of chelipeds moderately or highly arched..... 13
- 13 Anterolateral margin curving inward over carapace surface in the branchial region; occurring in KZN 14
- Anterolateral margin not curving inward over carapace surface in the branchial region; occurring in the WC 15
- 14 Bearing one prominent tooth and three rudimentary teeth on carpus of cheliped; tuft of setae absent from base of pleopod 2; carapace dark with distinctive blue sheen; chelipeds and pereopods bright orange
..... *P. lividus* Gouws, Stewart & Reavell, 2001
- Bearing one prominent tooth and one rudimentary tooth on carpus of cheliped; tuft of setae present at base of pleopod 2; carapace uniformly purplish brown with similar coloured or slightly brighter chelipeds and pereopods.....
..... *P. isimangaliso* sp. n.
- 15 Flange present on terminal segment of mandibular palp... *P. brincki* (Bott, 1960)
- Flange absent from terminal segment of mandibular palp
..... *P. parvicorpus* Daniels, Stewart & Burmeister, 2001

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Chapter 3

The dominant freshwater crab species around the St Lucia Lake is *Potamonautes sidneyi* Rathbun, 1904. However, the trophic role of this species in the system has not been investigated and is poorly understood. Reports suggest that members of the genus may occur in high densities, usually around shallow streams, swamps and lake edges. It has also been suggested that *Potamonautes* species play an integral role in the trophic functioning of ecosystems, by utilising energy from various trophic levels and making it available to a wide variety of organisms, either directly through predation or indirectly by facilitating the decomposition of organic matter through feeding. In addition to this, freshwater crabs form a spatial link between aquatic and terrestrial habitats as a result of their amphibious lifestyle. A stable isotope approach was used here to investigate the trophic role of the species in St Lucia. Comparisons in diet were made between two discrete habitat types and two seasons, to examine the influence of habitat change and season on its trophic role.

A stable isotopic study of the diet of *Potamonautes sidneyi* (Brachyura: Potamonautidae) in two coastal lakes of the iSimangaliso Wetland Park, South Africa

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ABSTRACT

Potamonautes sidneyi Rathbun 1904, is a dominant freshwater crab in KwaZulu-Natal, South Africa. Recent flood events in the iSimangaliso Wetland Park have allowed a substantial range expansion of this species, including previously hypersaline and desiccated areas. A stable isotope study was conducted to examine the feeding habits of the populations from Lake Sibaya and Mpophomeni Stream, two contrasting sites in the iSimangaliso Wetland Park. Juveniles from Mpophomeni Stream were more depleted in $\delta^{13}\text{C}$ and more enriched in $\delta^{15}\text{N}$ compared to adults, indicating a more carnivorous diet and higher trophic position. A general shift in diet was observed at both sites, with consumption of aquatic invertebrates and sedimentary organic matter more prevalent in the wet summer months, while greater proportions of detritus and microphytobenthos were consumed in autumn/winter. No significant difference was observed between adults from the two sites despite the abiotic variations. The species appears to play a complex role in the trophic web, by acting as an intermediate consumer facilitating the flow of nutrients across levels and by breaking down decomposing organic matter, allowing for rapid recycling of nutrients within its ecosystem.

Keywords: diet, trophic role, stable isotopes, freshwater, brachyurans, opportunistic feeders

INTRODUCTION

Freshwater crabs comprise approximately one fifth of all brachyuran species (Yeo et al., 2008, Cumberlidge et al., 2009). They are widely consumed by humans and act as an intermediate host for food-borne diseases such as paragonimiasis (Appleton, 2012). These crabs are ecologically important, as their role in decomposition of detrital matter, combined with their large abundance and biomass (Dobson et al., 2007; Klaus and Plath, 2011), makes them a critical component of nutrient recycling in their ecosystems and ideal for use as bio-indicators (Steenkamp et al., 1994; Reinecke et al., 2003). In addition to this, crabs form a spatial link between aquatic and terrestrial habitats as a result of their amphibious lifestyle (Morris and Van Aardt, 1998).

The Natal River Crab, *Potamonautes sidneyi* Rathbun, 1904, is widespread throughout southern Africa occurring mainly in the lower and middle reaches of streams and rivers (Barnard, 1950). *Potamonautes sidneyi* has been described as having a stable population trend by the IUCN. It is a species of 'Least Concern' (LC) based on its wide habitat distribution and high degree of tolerance, especially to pollutants and habitat modification (Cumberlidge, 2008; Cumberlidge et al., 2009).

Despite the ecological importance of *P. sidneyi* (Purves, 1991; Dyer et al., 2013), no work has been done on the species in terms of population studies, diet, trophic position and tolerance to anthropogenic and natural disturbances or habitat modification. While Reavell and Cyrus (1989) classified the species as a 'benthic scavenger', Dobson (2004), in a statement referring to all African freshwater crabs, suggested that in addition to this they had a preference for plant-based detritus. Hill and O'Keefe

(1992) examined the diet of *P. perlatus* H. Milne Edwards 1837, a related species from the Eastern Cape (South Africa), using gut content analysis. They found that smaller individuals, i.e. < 40 mm carapace widest width (CWW), were herbivorous, also feeding on aquatic invertebrates, while larger individuals of the species (> 40 mm CWW) were detritivorous, feeding mainly on leaf litter, detritus and algae.

The iSimangaliso Wetland Park is a UNESCO World Heritage Site in northern KwaZulu-Natal on the east coast of South Africa. It contains three Ramsar Wetlands of International Importance, two of which are considered in this study. These are Lake St Lucia, Africa's largest estuarine system (Whitfield et al., 2013), and Lake Sibaya, southern Africa's largest natural freshwater lake (Allanson, 1979). The region is characterised by wet summer months with high rainfall between October and March and dry winter months between May and August with minimal rainfall (Whitfield and Taylor, 2009). Rainfall in the iSimangaliso Wetland Park has increased dramatically since the end of 2011, with above-average precipitation causing floods in the summers of both 2012 and 2013. This, together with the Mfolozi re-connection (Whitfield et al., 2013), has resulted in substantially decreased salinity levels and increased water depths throughout Lake St Lucia. Throughout the region, the increased freshwater supply has led to the introduction of a number of freshwater taxa into previously saline systems (Lake St Lucia) and a range expansion in their distribution elsewhere (Nel et al., 2015). *Potamonautes sidneyi* is expected to spread through the St Lucia estuarine lake as the system shifts towards freshwater-dominated phases from hypersaline states (Whitfield et al., 2013). The species is one of three recorded freshwater brachyuran species found around the lake, the others being the potamonautid *Potamonautes isimangaliso* Peer and Gouws, 2015 and the varunid *Varuna litterata* (Fabricius, 1798). *Potamonautes sidneyi* could become dominant at many sites, affecting the associated ecosystems, both terrestrial and aquatic.

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The aim of this study was to compare the diet of adult and juvenile *P. sidneyi* occupying different habitats in two coastal lakes of the iSimangaliso Wetland Park, Lake Sibaya and Lake St Lucia (Fig. 1). By relating the carbon and nitrogen signatures of *P. sidneyi* individuals to those of potential food items, it is possible to determine food sources and trophic position, respectively (Post, 2002). Stable isotope analysis (SIA) is used to examine the diet of an organism on a long-term basis, as the unique carbon and nitrogen values of food items are incorporated into the tissue of the target species. Gut content analysis (GCA) was also used to provide insight into the most recent dietary behaviour of individuals. It was hypothesized that *P. sidneyi* displays an ontogenetic diet shift indicated by different isotope values and trophic positions, most likely due to changes in dietary requirements and also variation in habitat occupation by juveniles and adults. It was further hypothesized that seasonal shifts in diet and trophic position would be found as a consequence of variation in available food items.

MATERIALS AND METHODS

Two sites were selected: the Mpophomeni Stream (27°57'7.17"S 32°22'37.21"E) located on the western shore of False Bay (Lake St Lucia); and the eastern shore of Lake Sibaya (27°23'49.28"S 32°42'42.17"E) (Fig.1).

These systems vary in physico-chemical properties such as salinity, hydrodynamics and substrate characteristics (Table 1). Lake Sibaya hosts a number of originally marine and estuarine species as a result of its past connection to the marine environment. These species are now uniquely adapted to freshwater conditions (Bruton, 1975). The lake has an average depth of 13 m with a steep profile through the littoral zone (Bruton, 1980). At the time of the study, the level of the lake was low according to previous records (Allanson, 1979). While there was no overhanging vegetation at the sampling sites, fringing vegetation at the water's edge included *Phragmites* sp., *Typha latifolia* and *Cyperus* sp. Submerged macrophytes, such as *Stuckenia* spp. were dominant close to shore. The Mpophomeni Stream is a small brackish forest stream that persists even during the dry season. It is connected to the saline waters of False Bay via a *Phragmites mauritianus* marsh. The stream is shaded by sand forest trees, many of which belong to the Fabaceae family, and some are unique to this habitat (Kirkwood and Midgley, 1999). Fringing vegetation included unidentified grasses and *Phragmites*. Specimens were collected both in the wet summer and dry autumn/winter months, i.e., December 2012 – January 2013 and May – June 2013, respectively. Physico-chemical variables, including conductivity, temperature, dissolved

oxygen, turbidity and pH, were recorded using a YSI 6600-V2 multiprobe system. Samples collected included crabs and potential food items, such as juvenile fish, bivalves, gastropods, particulate organic matter (POM), microphytobenthos (MPB), sedimentary organic matter (SOM), detritus, macroalgae and fringing vegetation. All samples were frozen immediately upon collection until they were processed in the lab.

Sample collection and processing

Crabs collected ranged in carapace widest width (CWW) between 9 and 57 mm and were dug out of burrows using a shovel or netted out of the sediment-water interface. Specimens with a CWW < 30 mm were classified as juveniles, while individuals with a CWW > 30 mm were recorded as adults. No

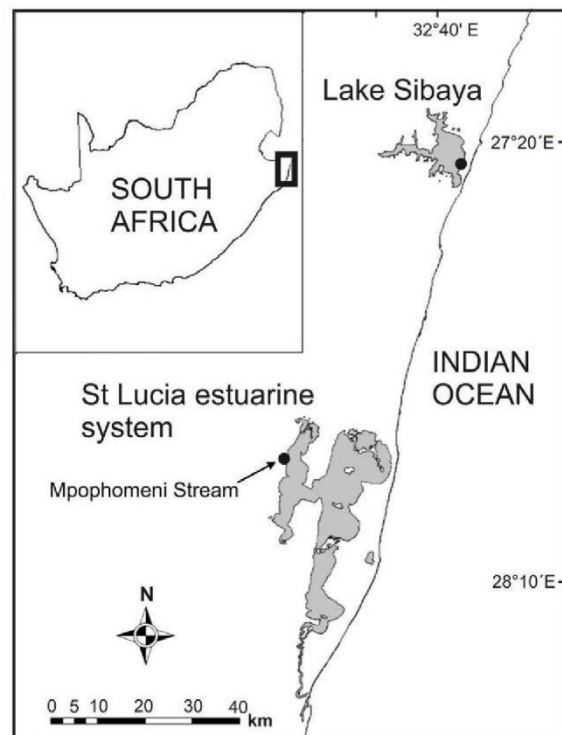


Figure 1

Map showing Lake Sibaya and Lake St Lucia, with black dots indicating sampling locations (adapted from Miranda and Perissinotto, 2012)

	Mpophomeni Stream		Lake Sibaya	
	27°57'7.17"S 32°22'37.21"E		27°23'49.28"S 32°42'42.17"E	
	Wet	Dry	Wet	Dry
Temperature (°C)	26.3	19.7	27.2	22.8
Salinity	7.6	9.1	0.4	0.4
Turbidity (NTU)	26.8	2.7	5.7	0.0
Dissolved oxygen (mg/l)	8.5	10.0	8.0	8.7
pH	8.5	7.4	8.8	7.6

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juveniles were found at Lake Sibaya. Juvenile fish were collected using an epibenthic sled (100 µm mesh size). Tissue samples were collected from the chelae of each crab, and from the dorsal muscle of juvenile fish to prevent the inclusion of lipid content.

Bivalve and gastropod samples were extracted by cracking open the shell and removing the muscle tissue. The samples were then washed in a solution of methanol:chloroform: distilled water (2:1:0.8) for approximately 3 h to remove any lipid content. As the entire organism was used, samples were further rinsed in 2% HCl to remove biogenic compounds.

POM was collected by filtering triplicate 20 l buckets of water onto pre-combusted Whatman GF/F filters (0.7 µm mesh size). Sediment containing MPB was suspended in filtered water, which was then filtered onto pre-combusted GF/Fs once the sediment had settled out of the water column. The POM and MPB filters were washed with 2% HCl to remove any sediment and biogenic compounds. Sediment collected from both sites was also rinsed in 2% HCl before further processing.

Macrophytes and algae were rinsed thoroughly in distilled water to remove any sediment, epiphytes or epifauna.

The brachyuran, gastropod, bivalve, fish, plant and algae samples were dried in an oven at 50°C for 48 h before being crushed into a fine powder using a mortar and pestle. Between 0.6 and 0.7 mg of animal matter and 1 mg of plant and algal matter was extracted and placed into 5x8 mm tin capsules.

Isotope analysis

Samples consisting of 3–10 replicates were analysed at the Stable Light Isotope Unit (Department of Archaeology, University of Cape Town). They were combusted in a Flash EA 1112 series elemental analyser (Thermo Finnigan, Italy). Gases were passed through a ConFlo III gas control unit (Thermo Finnigan, Germany) to the isotope ratio mass spectrometer (Delta Plus XP IRMS, Thermo Electron, Germany) to obtain isotope ratios, which were standardised using the equation of Peterson and Fry (1987):

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where: δX represents variation from a standard in ‰ (per mille) and X represents the heavier isotope. R_{sample} is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ of the sample and R_{standard} is $^{13}\text{C}/^{12}\text{C}$ of Vienna PDB or $^{15}\text{N}/^{14}\text{N}$ of atmospheric nitrogen. A more positive value is thus 'isotopically enriched' and contains a higher proportion of the heavier isotope (Vander Zanden and Rasmussen, 1999).

Gut content analysis

The foreguts of 10–20 individual crabs from each site were excised for GCA on each sampling occasion. These were frozen to prevent further digestion and preserved for laboratory analysis, where they were examined using a dissecting microscope. All contents were identified and quantified using a counting grid (Hynes, 1950) under 30x magnification and the volumetric proportion of each food item was recorded.

Data analysis and determination of trophic position

To determine if isotope values were significantly different between seasons, juvenile and adult crabs as well as the various food sources, MANOVAs were run in Statistica 11. All

assumptions of randomly-selected data, normally distributed data and equal variances were met.

Mixed models were constructed using the Stable Isotope Analysis in R (SIAR) v4.0 package of Parnell et al. (2010), in order to determine the proportion of different items in the diet of each population. Gut content analysis results were used to eliminate some potential but unlikely food sources to improve the accuracy and precision of the mixing models. The trophic position of sampled brachyurans was estimated on the basis that consumer $\delta^{15}\text{N}$ levels are enriched by 3.4‰ (± 0.2 SD) (Minagawa and Wada, 1984; Post, 2002) and $\delta^{13}\text{C}$ levels are enriched by 1‰ (± 0.5 SD), due to metabolic processes, such as respiration (Minagawa and Wada, 1984; Hobson et al., 2002). There is great variability in enrichment factors, particularly the shift in nitrogen, between consumers and their diet where the enrichment factor ranges from -0.8 to 5.9‰ (McCutchan et al., 2003).

The trophic position of organisms can be compared between sites using the standardising equations of Vander Zanden and Rasmussen (1999):

$$\text{TP} = \lambda + (\delta^{15}\text{N}_c - \delta^{15}\text{N}_{\text{base}})/\Delta_n$$

where: $\delta^{15}\text{N}_c$ is the consumer nitrogen isotopic composition, $\delta^{15}\text{N}_{\text{base}}$ is that of the food base, estimated from the carbon ratios of all primary consumers in the system (Vander Zanden and Rasmussen, 1999), λ is the trophic position of the base ($\lambda = 2$ for primary consumers) and Δ_n is the estimate of the average increase in $\Delta^{15}\text{N}$ per trophic position. A value of 3.4 was assigned to $\Delta^{15}\text{N}$, following Minagawa and Wada (1984), as it is not habitat-specific and is widely applied to isotope studies of crustaceans and other invertebrate taxa.

RESULTS

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of sources

There was a significant difference between isotope values of food sources, both at the Mpophomeni Stream (wet: Pillai's Trace = 1.999, $F = 2190.3$, $p < 0.05$; dry: Pillai's Trace = 1.98, $F = 145.1$, $p < 0.05$) and Lake Sibaya (wet: Pillai's Trace = 1.991, $F = 181.8$, $p < 0.05$; dry: Pillai's Trace = 1.954, $F = 42.7$, $p < 0.05$), allowing for high source discrimination by the mixing model used.

At Mpophomeni Stream (Fig. 2, Table 2), $\delta^{13}\text{C}$ values ranged from -29.07 (± 0.32) for *Melanoides tuberculata* (Müller, 1774) to -6.48 (± 0.76) for MPB in the wet season, while more depleted $\delta^{13}\text{C}$ values prevailed in the dry season. In terms of $\delta^{15}\text{N}$, fringing vegetation collected from around the stream had the most depleted value of -0.34 (± 0.03), while the Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852), had the most enriched value of 18.12 (± 0.08). The same was true for the dry season, with *O. mossambicus* displaying the most enriched nitrogen value of 17.93 (± 0.91), while detritus was the least nitrogen-enriched source with a value of -3.47 (± 2.86).

Unlike in the Mpophomeni Stream, the range of $\delta^{13}\text{C}$ values at Lake Sibaya was relatively low in both wet and dry seasons (Fig. 2, Table 3). *Cladophora* sp. algae had the most enriched $\delta^{13}\text{C}$ signature in both seasons, with values of -9.50 (± 0.29) and -8.35 (± 0.11), respectively. The bivalve *Corbicula fluminalis* (Müller 1774) had the most depleted carbon signature, with a value of -24.13 (± 0.09) in the wet season, but was not found at the site in the dry season. Instead, POM displayed the most depleted carbon signature with a value of -24.62 (± 0.17). *Cladophora* sp. algae had the most depleted $\delta^{15}\text{N}$ in both seasons, with a value of 1.62 (± 0.29) in the wet

and 0.12 (± 0.22) in the dry part of the year. In the wet season, MPB had the highest δ¹⁵N value of 10.95 (± 0.00). The fish larvae had a similar signature, with a value of 10.06 (± 0.06), while in the dry season adult *O. mossambicus* were the most enriched in nitrogen, with a value of 9.78 (± 0.12).

δ¹³C and δ¹⁵N values of *Potamonautes sidneyi*

At Mpopphomeni, there was a significant difference between values of juveniles and adults in both wet (Pillai's Trace = 0.998, *F* = 659.4, *p* < 0.05) and dry seasons (Pillai's Trace = 0.980,

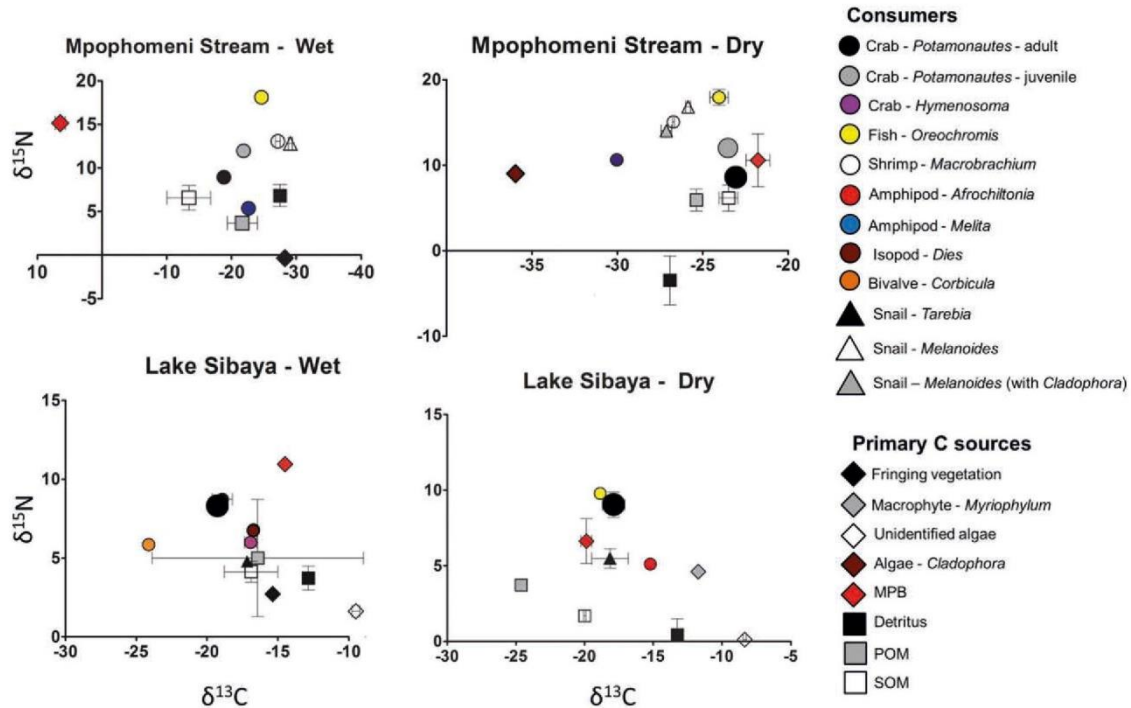


Figure 2

δ¹⁵N and δ¹³C biplots of dietary items and *Potamonautes sidneyi* from Mpopphomeni Stream and Lake Sibaya in both the wet and dry seasons. Error bars denote SD; POM = particulate organic matter, SOM = sedimentary organic matter, MPB = microphytobenthos

Sources	Wet		Dry	
	δ ¹⁵ N	δ ¹³ C	δ ¹⁵ N	δ ¹³ C
<i>Oreochromis mossambicus</i>	18.12 (± 0.08)	-24.60 (± 0.06)	17.93 (± 0.91)	-24.05 (± 0.53)
<i>Melanoides tuberculata</i>	12.80 (± 0.09)	-29.07 (± 0.32)	16.83 (± 0.11)	-25.85 (± 0.14)
<i>M. tuberculata</i> with algae	-	-	14.02 (± 0.44)	-27.12 (± 0.31)
<i>Macrobrachium equidens</i>	13.07 (± 0.65)	-27.15 (± 0.37)	15.05 (± 0.08)	-26.71 (± 0.05)
<i>Melita zeylanica</i>	5.38 (± 0.13)	-22.61 (± 0.04)	10.62 (± 0.14)	-30.03 (± 0.12)
Fringing vegetation	-0.34 (± 0.03)	-28.24 (± 0.05)	-0.35 (± 0.00)	-28.29 (± 0.00)
<i>Cladophora</i> sp.	-	-	9.08 (± 0.10)	-36.00 (± 0.18)
MPB	15.16 (± 0.00)	-6.48 (± 0.76)	10.57 (± 3.09)	-21.78 (± 0.70)
Detritus	6.84 (± 1.26)	-27.47 (± 0.61)	-3.47 (± 2.86)	-26.91 (± 0.13)
POM	3.69 (± 0.11)	-21.66 (± 2.33)	5.92 (± 1.27)	-25.36 (± 0.07)
SOM	6.57 (± 1.40)	-13.40 (± 3.37)	6.16 (± 1.53)	-23.49 (± 0.55)
Targets				
<i>P. sidneyi</i> adults	8.95 (± 0.14)	-18.8 (± 0.04)	8.76 (± 0.04)	-22.39 (± 0.64)
<i>P. sidneyi</i> juveniles	11.87 (± 0.15)	-21.93 (± 0.12)	12.03 (± 0.28)	-23.57 (± 0.07)

TABLE 3
 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (with standard deviation in brackets) of all potential food items and the target species
***Potamonautes sidneyi* from Lake Sibaya in the wet and dry season ($n = 5$ for each source and target)**

Sources	Wet		Dry	
	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<i>Oreochromis mossambicus</i>	–	–	9.78 (± 0.12)	–18.86 (± 0.04)
<i>Corbicula fluminalis</i>	5.85 (± 0.01)	–24.13 (± 0.09)	–	–
<i>Tarebia granifera</i>	4.79 (± 0.00)	–17.17 (± 0.00)	5.48 (± 0.64)	–18.15 (± 1.33)
<i>Afrochiltonia capensis</i>	–	–	5.11 (± 0.32)	–15.21 (± 0.04)
<i>Hymenosoma projectum</i>	5.99 (± 0.20)	–16.93 (± 0.43)	–	–
<i>Dies monodi</i>	6.77 (± 0.12)	–16.71 (± 0.09)	–	–
Fish larvae	10.06 (± 0.06)	–22.49 (± 0.00)	–	–
Egg mass	–	–	3.57 (± 0.17)	–14.45 (± 0.06)
<i>Cladophora</i> sp.	1.62 (± 0.29)	–9.50 (± 0.29)	0.12 (± 0.22)	–8.35 (± 0.11)
<i>Juncus kraussii</i>	3.69 (± 0.09)	–12.66 (± 0.02)	0.09 (± 1.67)	–11.68 (± 0.03)
<i>Myriophyllum</i> sp.	2.71 (± 0.11)	–15.36 (± 0.14)	4.61 (± 0.32)	–11.71 (± 0.09)
MPB	10.95 (± 0.00)	–14.49 (± 0.00)	6.63 (± 1.48)	–19.87 (± 0.40)
Detritus	3.72 (± 0.77)	–12.84 (± 0.23)	0.44 (± 1.06)	–13.24 (± 0.31)
POM	5.00 (± 3.72)	–16.43 (± 7.47)	3.72 (± 0.03)	–24.62 (± 0.17)
SOM	4.13 (± 0.67)	–16.88 (± 1.88)	1.69 (± 0.01)	–19.99 (± 0.08)
Target				
<i>P. sidneyi</i> adults	8.71 (± 0.32)	–18.92 (± 0.69)	9.02 (± 0.84)	–17.88 (± 0.81)

$F = 49.3$, $p = 0.02$), with juveniles exhibiting a more enriched $\delta^{15}\text{N}$ and more depleted $\delta^{13}\text{C}$ signature (Table 2). Juvenile carbon values ranged from $-21.93 (\pm 0.12)$ in the wet to $-23.57 (\pm 0.07)$ in the dry season, while adults displayed a shift from a carbon value of $-18.8 (\pm 0.04)$ in the wet to $-22.39 (\pm 0.64)$ in the dry season (Fig. 2). Regarding nitrogen, juvenile values did not increase significantly from the wet to the dry season ($F = 0.562$, $p = 0.508$), exhibiting values of $11.97 (\pm 0.00)$ and $12.03 (\pm 0.28)$, respectively. The same was observed for adults, where values ranged from $8.95 (\pm 0.14)$ in the wet to $8.79 (\pm 0.00)$ in the dry season and were not significantly different ($F = 3.101$, $p = 0.153$) (Fig. 2).

At Lake Sibaya (Fig. 2, Table 3), no juveniles were found during either sampling period. Adults had statistically similar isotope values to those from Mpophomeni Stream in the wet season (Pillai's Trace = 0.264, $F = 0.894$, $p = 0.465$), while dry season values (-17.88 ± 0.81) differed significantly from those of the Mpophomeni Stream counterparts (Pillai's Trace = 0.938, $F = 22.504$, $p = 0.02$).

Mixing models

At the Mpophomeni site (Fig. 3), during the wet season juveniles predominantly ingested and assimilated the amphipod *Melita zeylanica* Stebbing, 1904, the penaeid shrimp *Macrobrachium equidens* (Dana, 1852) and SOM. Adults had elevated proportions of *Afrochiltonia capensis* (Barnard, 1916) amphipods and SOM, together contributing up to 55% (50% C.I.) of adult assimilated diet. Detritus appeared to contribute minimally to the assimilated diet of adults. In the dry season, both adults and juveniles largely assimilated amphipods and

Cladophora sp. algae, which together constituted approximately 50% (50% C.I.) of the total assimilated diets. However, while adults assimilated large amounts of detritus, the opposite was seen in juvenile individuals, which had greater proportions of MPB and lower detrital isotope values.

The bivalve *C. fluminalis* contributed 40 to 50% (50% C.I.) of the diet of adult *P. sidneyi* collected from Lake Sibaya in the wet season, while elevated isotopic values of SOM and *Cladophora* sp. were also recorded (Fig. 4). In the dry season, however, MPB and gastropods together contributed roughly up to 70% (50% C.I.) of adult assimilated diet.

Gut content analysis

The guts of Mpophomeni juveniles had a greater percentage of animal tissue in the wet season compared to the dry season (Fig. 5A), ranging from 47% to 15%, respectively. Percentage of sediment increased from 11% in the wet season to 32% in the dry season, while both algal filaments and MPB increased by approximately 10% from the wet to the dry season.

Adults (Fig. 5B) contained mostly sedimentary and animal matter, including fatty tissue and exoskeletal remains. Animal matter comprised 17% of the total diet in the wet season and increased to 27% of the total diet in the dry season. Detritus was also prevalent and constituted 15% (dry) to 22% (wet) of the total gut contents, showing a decrease from the wet to the dry season.

Adults from Lake Sibaya (Fig. 6) consumed mostly detritus (31%), animal tissue (29%) and sediment (33%) during the wet season. The contribution of both detritus and sediment to gut content decreased by 18% and 6%, respectively, from the wet to

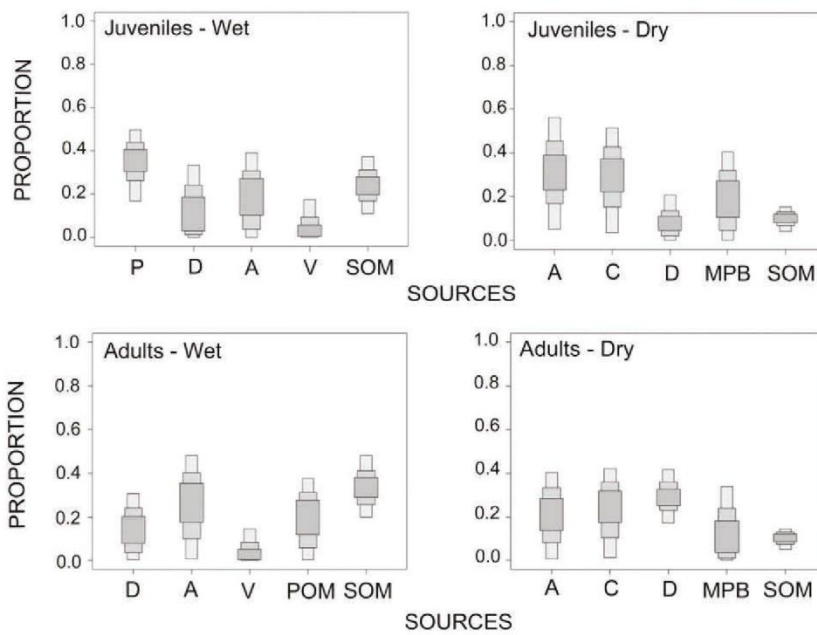


Figure 3

Mixed models based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures for adults (CWW > 30 mm) and juveniles (CWW < 30 mm) *P. sidneyi* from the Mpophomeni Stream in the wet and dry season. The proportions are plotted at 95%, 75% and 50% credibility intervals. P – *Macrobrachium equidens penaeid shrimp*, D – detritus, A – *Melita zeylanica amphipod*, V – fringing vegetation, C – *Cladophora sp. algae*, POM – particulate organic matter, SOM – sedimentary organic matter, MPB – microphytobenthos.

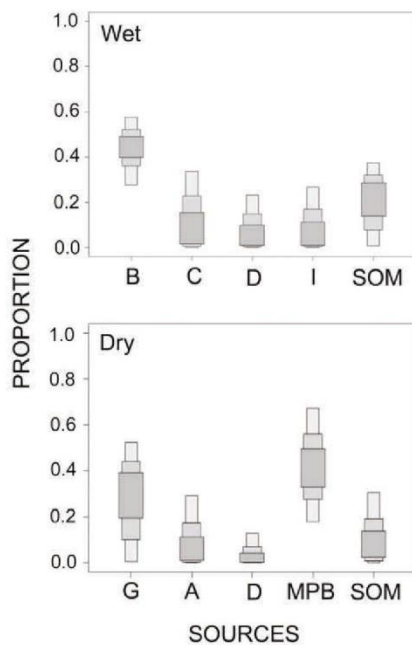


Figure 4

Mixed models based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures for adult *P. sidneyi* from Lake Sibaya in wet and dry seasons. The proportions are plotted at 95%, 75% and 50% credibility intervals. B – *Corbicula fluminalis bivalve*, C – *Cladophora sp. algae*, D – detritus, I – *Dies monodi isopod*, G – *Tarebia granifera gastropod*, A – *Afrochiltonia capensis amphipod*, SOM – sedimentary organic matter, MPB – microphytobenthos.

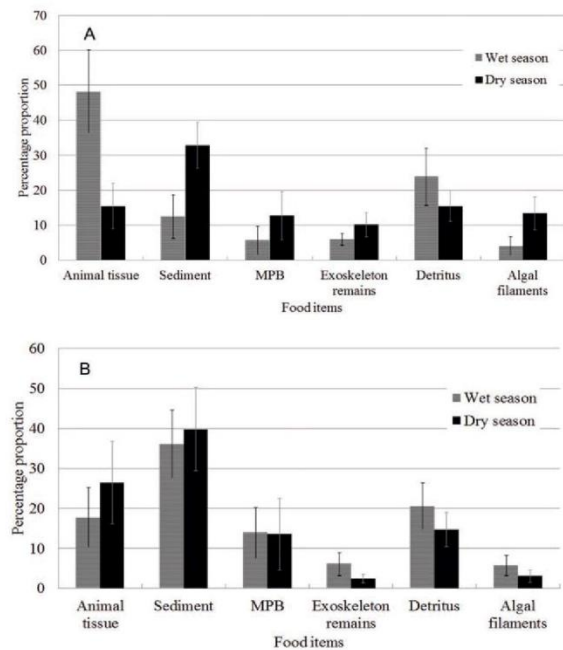


Figure 5

Percentage composition of gut contents for (A) juveniles and (B) adults *P. sidneyi* in the wet and dry season at the Mpophomeni Stream. Error bars represent standard error

the dry season. An increase of 15% and 9% was observed in the presence of MPB and algal filaments, respectively, from the wet to the dry season.

Trophic position

Juveniles at Mpophomeni Stream had a higher trophic position (Table 4) than adults, which were located approximately one trophic level below juveniles. Trophic positions of adults at Lake Sibaya (Table 4) were higher than those of adults at Mpophomeni Stream. The trophic position of adults from Lake Sibaya did not change with season.

DISCUSSION

Although tropical freshwater crabs are traditionally characterised as being largely herbivorous and detritivorous (Hill and O’Keeffe, 1992; Burrell et al., 2013), they have been shown to feed opportunistically and even display cannibalistic tendencies (Dobson, 2004; Marijnissen et al., 2009; Burrell et al., 2013). The dynamic dietary composition of *P. sidneyi* between sites and seasons indicates plasticity in feeding behaviour and the opportunistic tendencies of these populations. This is in partial agreement with the idea that the species has a scavenging nature (Reavell and Cyrus, 1989; Dobson, 2004). However, the extent to which aquatic invertebrates form part of the diet of this species emphasises its multidimensional role and importance in the trophic food web. Primarily considered to be largely herbivorous and detritivorous, *P. sidneyi* has so far been regarded as a recycling component of these trophic webs, where leaf litter and detritus are broken down during the feeding process, thus facilitating decomposition and nutrient recycling. While the presence of detritus and algal matter in the guts of *P. sidneyi* individuals bears testament to this, the significant consumption of aquatic invertebrates implies an additional consumer role for the species. Considering the nitrogen isotopic ratios obtained in this study, the *P. sidneyi* populations sampled

are not the apex consumers of their respective food webs. The fish *O. mossambicus* and various other macrobenthic organisms display the most enriched nitrogen values, while *P. sidneyi* displays $\delta^{15}\text{N}$ ratios intermediate to these higher consumers and the producers. The transitional role of the genus in many food and trophic webs is discussed by Dobson (2004).

St Lucia is currently inhabited by at least 14 other brachyuran species (Peer et al., 2014). With the predicted spread of *P. sidneyi* through the lake, it is expected that they will interact with other species, possibly competing for space and food. It is therefore essential to understand the ecological role that the species plays. Within Lake Sibaya, *P. sidneyi* co-exists with *Hymenosoma projectum* (Dawson and Griffiths, 2012), another brachyuran species with freshwater tolerance (Forbes and Hill, 1969). However, the two species occupy separate niches, with *H. projectum* found predominantly below the water level burrowed in sandy patches, while *P. sidneyi* occurs beneath clumps of detritus and algae or in burrows along the sandy banks. They do not appear to interact directly. The absence of *P. sidneyi* juveniles from the site throughout the year is unusual. However, bearing in mind the apparent preference of juveniles for the profundal zone, it is possible that they occur at greater depths in the lake due to its low turbidity (Table 1).

In Lake St Lucia, juvenile *P. sidneyi* of the Mpophomeni Stream population had a high $\delta^{15}\text{N}$ signature, indicating that they occupy a higher trophic position than adults. In support of the first hypothesis, this implies that there is an ontogenetic diet shift and highlights the occupation of two different trophic roles by one species at different stages of its life cycle. A more enriched $\delta^{15}\text{N}$ often indicates a greater carnivorous tendency (Post, 2003). The ^{13}C depletion of juvenile crabs relative to adults seen in the wet season can be attributed to the greater dependence of juveniles on pelagic penaeid shrimps, which have been feeding on $\delta^{13}\text{C}$ -depleted food sources such as detritus (Table 2). Ontogenetic shifts in the diet of aquatic organisms are widely documented in the literature, with the most apparent reason for such shifts being a change in dietary requirement of adults from the juvenile life stage (Werner and Gilliam, 1984). Williams (1965) suggested that larger animals (adults) move slower than smaller animals (juveniles) and are thus less likely to actively pursue animal prey. This author also showed that differentially-sized individuals of a population display variation in resource-utilisation abilities. However, habitat differences between adults and juveniles may further explain a dietary shift between ontogenetic phases. A study by France (1995) showed that pelagic algae are generally more $\delta^{13}\text{C}$ -depleted in relation to benthic algae and that this difference was significant enough to be transmitted to consumers in these aquatic environments. Additionally, adult crabs tend to remain along the edges of the stream where they feed heavily upon the substratum and associated biota, while juveniles are usually found in the dark water column under detrital patches, most likely employing a predator-avoidance strategy common in juvenile aquatic organisms (Werner and Gilliam, 1984). Vander Zanden and

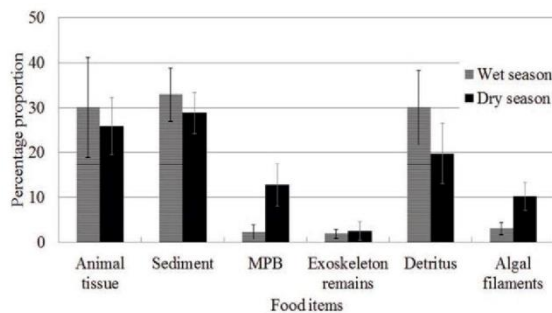


Figure 6

Percentage composition of adults *P. sidneyi* in a) the wet and b) dry season at Lake Sibaya. Error bars represent standard error.

	Wet	Dry
Mpophomeni Stream – Juveniles	2.97 (± 0.06)	2.08 (± 0.22)
Mpophomeni Stream – Adults	2.18 (± 0.06)	1.02 (± 0.04)
Lake Sibaya – Adults	2.95 (± 0.11)	3.09 (± 0.26)

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Rasmussen (1999) described the progressive $\delta^{13}\text{C}$ depletion as one moves from the littoral zone to the pelagic zone, to the profundal zone. There are various mechanisms to explain the $\delta^{13}\text{C}$ variation along this gradient. The algal uptake of respired CO_2 , which increases in abundance from the littoral to the profundal zone, is reflected in the carbon isotope values of consumers at higher trophic levels (Rau, 1978). France (1995) showed an enrichment of benthic algae compared to phytoplankton due to the effects of a CO_2 boundary layer which limits CO_2 diffusion in benthic algae compared to pelagic algae, allowing for greater assimilation of $\delta^{13}\text{C}$. The location of juveniles relative to adults within the shallow turbid stream means that juvenile crabs gain easier access to pelagic invertebrates, as they are also located within the $\delta^{13}\text{C}$ -depleted 'profundal zone' of the system. This may explain the difference in $\delta^{13}\text{C}$ between adults and juveniles, while the access to a wider range of invertebrates would account for the greater trophic position and $\delta^{15}\text{N}$ signature of juveniles relative to adults.

In this study, support for the second hypothesis was obtained with a slight shift in diet observed between seasons and consumption of MPB and detritus generally more prevalent in the dry season. Variation in isotopic values is expected between seasons due to changes in rainfall, freshwater input and deposition of organic matter from allochthonous sources. Changes in dissolved inorganic carbon are influenced by the supply of $\delta^{13}\text{C}$ -depleted soil from surrounding areas, which increases during the wet season with a higher flow of freshwater throughout the system leading to greater soil movement (Lawrie and Stretch, 2011). Reduced photosynthetic activity during the dry season may also contribute to depletion of $\delta^{13}\text{C}$ at this time (Farquhar et al., 1989; Anandraj et al., 2008). The increased freshwater inflow during the rainy season (summer, in this case) (Whitfield and Taylor, 2009; Lawrie and Stretch, 2011) results in an increased biomass of primary producers (Van der Molen and Perissinotto, 2011) and, subsequently, consumers (MacKay et al., 2010). Aquatic invertebrates, such as amphipods, gastropods, penaeid shrimps and bivalves, are found in the Mpophomeni Stream and Lake Sibaya habitats. Considering that *P. sidneyi* is an opportunistic feeder, it may feed more upon these aquatic invertebrates during the wet summer months. In the dry autumn/winter period, MPB and detritus are probably more pronounced in the crab diet due to the reduced numbers of aquatic invertebrates available during this time (MacKay et al., 2010). During the autumn/winter months productivity is low due to lack of rainfall, freshwater inflow, low temperatures and light availability (Anandraj et al., 2008; Whitfield and Taylor, 2009; Lawrie and Stretch, 2011). Nutritious food (e.g. MPB and aquatic invertebrates) is scarce and too energetically costly to find, while nutrient-poor detritus (Mann, 1988) is abundant and a better food choice in accordance with the optimal foraging theory (MacArthur and Pianka, 1966).

Both food webs appear to be largely based on allochthonous rather than autochthonous input. In the wet season, this is more pronounced at the Mpophomeni Stream, as $\delta^{13}\text{C}$ values of consumers and detritus more closely match those of fringing and overhanging vegetation, while in Lake Sibaya detrital $\delta^{13}\text{C}$ values incorporate those of both fringing vegetation and submerged macrophytes. This effect is reduced in the dry season, when MPB plays a more significant role in the diet of crabs and both allochthonous and autochthonous food sources are incorporated into the diet of *P. sidneyi*.

The consumption of the alien invasive gastropod *Tarebia granifera* (Lamarck, 1816) by *P. sidneyi* at Lake Sibaya is particularly noteworthy. Here, *P. sidneyi* may have previously fed

on *Melanooides tuberculata*, a native gastropod that previously occurred around the lake (Hart, 1979). The absence of *M. tuberculata* is possibly due to competitive displacement by the invasive *T. granifera* (Raw et al., 2013) and crabs may now feed on *T. granifera* instead. However, preliminary studies indicate that this snail is tougher to crack compared to *M. tuberculata* (Miranda, unpubl. data). It is unlikely that the predator-prey interaction of the two species is a result of co-evolution as found in similar African ecosystems (West and Cohen, 1994; Marijnissen et al., 2009), due to the fairly recent introduction of *T. granifera* into the system. Coevolution between ancestors of the two species at a mutual site is also unlikely, as the evolution of Potamonautidae freshwater crabs (Klaus et al., 2011) most likely occurred on a separate continent to that of *T. granifera* (Genner et al. 2007). The proficiency with which *P. sidneyi* feeds on the bivalve *C. fluminalis*, also bearing a tough shell, indicates an adept handling ability that may be suitable for its predation upon *T. granifera*. Alternatively, the crab may opportunistically feed upon freshly dead molluscs (detritus), as *T. granifera* often become stranded at this site and die due to desiccation when the water level recedes. *Potamonautes sidneyi* may also feed on native gastropods such as *Bulinus natalensis* which have an isotope signature similar to that of *T. granifera* (Miranda and Perissinotto, 2012).

A large variation in the carbon isotope signature is expected for mixed carbon sources, such as POM and SOM, and has been observed in other studies (Richoux and Froneman, 2007). Carbon values of mixed sources also vary significantly between seasons with SOM, POM, MPB and detritus usually showing a great degree of $\delta^{13}\text{C}$ depletion in the dry relative to the wet season at both sites. The elevated nitrogen signature of MPB at both sites (Tables 2 and 3) is unusual, as MPB is a primary producer. This has been recorded previously in the literature (Hobson et al., 1995; Lapointe et al., 2004; Richoux and Froneman, 2007), where nitrogen enrichment occurs in algal communities with an increase in land-based nitrogen run-off. This includes agricultural and sewage run-off from nearby sources. The Mpophomeni Stream is potentially subject to various sources of nitrogen pollution, including agricultural and domestic run-off from nearby farms and developmental plots, as well as the possible release of nutrients from deforested surrounding areas. This nitrogen pollution is then reflected in consumers (Xu and Zhang, 2012) and may explain elevated $\delta^{15}\text{N}$ values in MPB. The results of the GCA were used to eliminate some potential but unlikely food values from the stable isotope mixing models, indicating that SOM, detritus, animal and algal remains are part of the diet of *P. sidneyi*. GCA provides an insight into the most recent consumption by an organism. However, variations in digestion rates of different material, a phenomenon well-recorded in fish (Olson and Boggs, 1986; Olson and Mullen, 1986) and applicable to all organisms, may constitute a serious bias when attempting to quantitatively examine dietary intake using this method. For this reason, GCA is generally used in conjunction with SIA, as neither is without caveats (Hyslop, 1980; Gannes et al., 1997). Combined use of the two methods does provide a more accurate representation of diet over a relatively long-term period and also offers some idea regarding what portion of the ingested matter is actually assimilated.

The present study has shown that *P. sidneyi* adults and juveniles are associated with different trophic positions and habitats. These crabs are affected by changes in a wide variety of ecosystem processes and can, thus, provide general indications about ecosystem status. Globally, urbanisation and changes in

land-use are occurring quite rapidly and subsequent pollution of aquatic systems is anticipated (Grimm et al., 2008). Several tributary rivers and streams around the iSimangaliso Wetland Park have recently become polluted with nutrients, agricultural toxicants and excess silt loading (Perissinotto et al., 2013). However, potamonautids appear to be fairly resistant to environmental change including heavy metal and organic pollution (Schuwerack et al., 2001; Darwall et al., 2009). Further changes include the effects of salinity on the distribution of freshwater crabs. While the Lake Sibaya population experiences a fairly stable freshwater environment, the St Lucia estuarine system is prone to extended flood and drought phases. During drought phases the increase in salinity causes a decrease in distribution of *P. sidneyi* around the lake. The ecological role of the species during a drought phase has not been investigated, although it can be expected that these crabs do not fulfil the same role under these conditions.

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Chapter 4

A major observation made during the biodiversity census (Chapter 1) was the potential recolonisation of the St Lucia mangroves by fiddler crabs (Genus *Uca* Leach, 1814). This is expected with increased marine connectivity. Fiddler crabs are cosmopolitan flagship species, occurring in tropical and subtropical habitats, particularly mangrove swamps which are currently declining worldwide. Over 100 species of *Uca* have been described, five of which occur in South Africa at their southernmost distribution range. Little is known about the ecology of fiddler crabs in this region, despite the wide array of studies conducted on this genus globally. The aim of this chapter was to review the ecology and distribution of fiddler crabs in South Africa with emphasis on the St Lucia population. St Lucia is a unique habitat due to the current lack of tidal influence in the associated mangrove swamps. This is significant, as it provides a unique model for global change, as many aquatic habitats are expected to undergo decreased marine connectivity with habitat transformation and fragmentation.

Review Paper

A review of fiddler crabs (genus *Uca* Leach, 1814) in South Africa

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Fiddler crabs occur globally across tropical and subtropical coastal habitats including mangrove swamps, which are in decline worldwide. The genus has been well-studied in the Americas, Australia and Asia, whereas information on African species is scarce. This review summarises the existing literature on fiddler crabs and highlights gaps in research for species at their southernmost distribution ranges in South Africa. Biological and ecological aspects including life cycle and reproduction, feeding ecology, biotic interactions and tolerance to environmental fluctuations and pollution are discussed. The systematics and distribution of the five fiddler crab species that occur in South Africa is provided. The St Lucia estuarine lake is presented as a case study for the effects of environmental change on *Uca* populations. Future research should focus on less-studied *Uca* populations, such as those found in the Indo-Pacific region. The effects of climate change and habitat modification on *Uca* populations should also be more widely investigated.

Keywords: connectivity, distribution limits, larval development, life cycle, mangrove ecology

Introduction

Fiddler crabs (Ocypodidae: genus *Uca*) often occur in dense populations in coastal habitats within tropical, subtropical and even some temperate coastlines (Hodgson 1987; Mouton and Felder 1995). They are therefore regarded as flagship species in mangrove, marsh, salt marsh and sandy beach intertidal habitats globally. The latitudinal distribution of fiddler crabs extends from Uruguay (35° S) in the south to Cape Cod, Massachusetts, USA (42° N), in the north (Crane 1975; Rosenberg 2001). This distribution may change in response to climate change effects, such as shifting temperatures (Edney 1961; Vernberg and Vernberg 1967; Sanford et al. 2006) and habitat transformation (Macnae 1963; Crane 1975; Vermeiren and Sheaves 2015). There are more than 100 described species within this cosmopolitan genus (Crane 1975; Naderloo et al. 2010; Rosenberg 2013).

The genus is characterised by its sexual dimorphism. Males are asymmetrical and bear one enlarged and one minor cheliped, whereas females possess two equally sized chelipeds. The enlarged cheliped of male individuals is used for combat as well as displays of aggression, species recognition and mate attraction. In the past century there have been numerous descriptive and comparative studies of *Uca* spp. taxonomy, genetics and ecology from across the world (e.g. Hyman 1920, 1922; Brown and Sandeen 1948; Vernberg and Vernberg 1967; Bott 1973; Crane 1975; Rabalais and Cameron 1983; Salmon 1987; von Hagen and Jones 1989; O'Connor 1993; Levinton et al. 1996; Sturmbauer et al. 1996; Backwell et al. 1999; Rosenberg 2001; Yamaguchi 2001; Takeda et al. 2004;

Beinlich and von Hagen 2006; Naderloo et al. 2010; Shih et al. 2013).

Five species of *Uca* are known to currently occur at the southernmost limit of their distribution range on the east coast of South Africa (Figure 1, Table 1). These are *U. (Austruca) annulipes* (H. Milne Edwards, 1837), *U. (Paraleptuca) chlorophthalmus* (H. Milne Edwards, 1837), *U. (Tubuca) urvillei* (H. Milne Edwards, 1852), *U. (Gelasimus) hesperiae* (Linnaeus, 1758) and *U. (Cranuca) inversa* Hoffmann, 1874. Until recently, the Kariega Estuary (33.6° S) was thought to represent the southernmost point of distribution for *Uca* in Africa. However, the recent discovery of *U. annulipes* in the Knysna Lagoon (34° S) (RSK Barnes pers. comm.) presents a new southernmost limit for the genus in Africa (Table 1). The purpose of this review is therefore to assess what is known, whilst highlighting knowledge gaps and potential pathways for further research on these five *Uca* species in South Africa. The history of the genus *Uca* in the St Lucia estuarine lake (Figure 2) is comprehensively reviewed since the site has been known to host at least four of these species in large abundance until the closure of its mouth in July 2002. The lake is a crucial component of a World Heritage Site (iSimangaliso Wetland Park) and a Ramsar Wetland of International Importance. The system has experienced drastic changes since the artificial separation of its mouth from the Mfolozi Estuary in the early 1950s, with prolonged mouth closure since 2002 (Whitfield et al. 2013). As a result, the St Lucia Estuary has undergone major degradation with the

deleterious consequence of biodiversity loss (Cyrus and Vivier 2006). *Uca* spp. were last recorded in abundance within St Lucia in 1949 (Millard and Broekhuysen 1970; Peer et al. 2014), although potential for the recolonisation of these species is high.



Figure 1: Map of South Africa with major mangrove sites and former southern distribution limit of fiddler crabs, i.e. Kariega Estuary. Southernmost distribution point of fiddler crabs is currently recorded at Knysna Lagoon

Systematics and distribution along the South African coast

The unique nature of the genus *Uca* (Leach, 1814) has allowed for its unequivocal identification, especially in males. The first observations and descriptions of these species were initiated over 300 years ago when the German naturalist Marcgrave described the colour and habitat of two Brazilian forms in 1648. He highlighted their important role as a food source for the local human population (Crane 1975). The history of *Uca* taxonomy is outlined in detail by Crane (1975) and Rosenberg (2001), both of whom remark upon the complicated systematics and classification of this genus over the last few hundred years. Crane (1975) argued that early systematists from across the world would have struggled to compare their work with the various collections of others. As the genus is widespread, collections would have been situated in disparate locations. The arduous nature of travel therefore made inter-collection loans difficult to conduct over a global scale. As a result, early collections were most likely meagre and descriptions were fraught with synonymies. It was only in 1918 that Rathbun clarified the issue of which characteristics would be most diagnostic to distinguish between species. To this day the classification and systematics of the genus remains complex and ever-changing. It is beyond the scope of this review to explain in detail the various delineations formed over the last three centuries. Instead we have presented here a summary of this taxonomic progression.

The classification of the genus *Uca* has been proposed by various authors based on different analyses. Bott (1973) did not make use of numerical analyses and based his divisions on the two main geographic groups, i.e. American and Indo-West Pacific. He proposed 10 genera instead of one and, as a result, constructed a highly disputed phylogenetic scheme. Crane (1975) did not base her phylogeny on numerical analyses either, but rather used her extensive knowledge of the species and their geographic distribution, dividing the genus

Table 1: Density estimates of *Uca* spp. along the east coast of southern Africa. Letters represent records from Macnae (1963) where p = present, c = common, a = abundant. Square brackets indicate recent records as per communication and details are indicated below. Where values are presented (individuals m⁻²), references are indicated by a superscript numeral and presented in the footnote. *, unknown presence; +, known presence but unknown density; -, known absence

Species	Density											
	Knysna Lagoon	Kariega ¹	Mngazana	Durban Bay	Mlalazi ²	Richard's Bay	Mfolozi ²	St Lucia ²	Kosi Bay	Inhaca Island (Mozambique) ³	Maruhubi (Tanzania) ^{4,5}	Mikindani/Gazi Bay (Kenya) ^{5,6}
<i>Uca annulipes</i>	[p]	1–20	a	a	10–23; c	c	9–44	11–41	p	16–24; a	47–61	20–70
<i>Uca chlorophthalmus</i>	-	p	a	p	c	c	6–19	-; c†	p	a	+	0–3
<i>Uca urvillei</i>	-	3–100	c	p	c	c	5–10	-	-	0–6; a	+	1–86
<i>Uca hesperiae</i>	-	-	p	p	[p]	*	*	-	-	c	+	+
<i>Uca inversa</i>	-	-	-	-	-	-	-	-	[p]	3–11; a	+	18–43

¹ Hodgson (1987); ² Unpublished data property of the authors; ³ Cannicci et al. (2009); ⁴ Hartnoll (1975); ⁵ Skov and Hartnoll (2001); ⁶ Kochev (2013)

[p] Knysna Lagoon = RSK Barnes pers. comm.; Mlalazi = RH Taylor pers. comm.; Kosi Bay = G Branch pers. comm.

† Recorded as common by Macnae (1963), now known to be absent

primarily according to the width of the front gills on the third maxilliped, as well as gonopod and orbit structures. This proposed phylogeny included nine subgenera and many subspecies. She also observed an evolutionary trend of species inhabiting niches further from the high water mark and exhibiting more complex mating behaviour. The phylogenies of Crane (1975) and Bott

(1973) were contradictory in many regards. Sturmbauer et al. (1996) and Levinton et al. (1996) conducted the first genetic analyses on 28 species and all nine subgenera included in Crane's phylogeny. Rosenberg (2001) used 236 morphological characteristics to revise these phylogenies and proposed clades. He constructed two possible dendrograms (Figure 3), denoting biogeographic history based on either a narrow-fronted ancestor or a broad-fronted ancestor. He found most of Crane's (1975) subgeneric divisions to hold true with a few deviant species, but refuted her suggestion of a narrow-fronted ancestor. The genus was thus split into seven subgenera.

Beinlich and von Hagen (2006) combined the work of Crane, Bott and Rosenberg in an attempt to remove all uncertainties regarding the taxonomy of *Uca*. Their system is based largely on the differential weighting of a few characters. Although this classification system is subject to imperfection, it is the most widely used to date (Ng et al. 2008) (Table 2). These authors also proposed a hypothetical reconstruction of dispersal for the genus during the Miocene period. Using fossil records and morphology, the epicentre of *Uca* dispersal is situated in present-day Australia. This hypothesis suggests that the genus migrated west, although two separate migrations are envisaged. The broad-fronted species would have crossed Wegener's Indo-Atlantic Ocean, passing southern Africa then moving to America. The narrow-fronted species would have migrated north along the east African coastline and towards India until they reached North Africa. At that stage the Tethys Ocean above Africa served as a passage before the narrow-fronted taxa moved west to America.

The five species occurring in South Africa all fall under the Indo-West Pacific clade (Figure 3) (Rosenberg 2001; Beinlich and von Hagen 2006; Naderloo et al. 2010; Shih et al. 2013). This is the southernmost point of global distribution for these five species (Crane 1975). The taxonomic status of each of the five species is reviewed below.

***Uca (Austruca) annulipes* (H. Milne Edwards, 1837) (Figure 4a)**

The subgenus *Austruca* was revived by Naderloo et al. (2010) with further support from Shih et al. (2013), after Beinlich and von Hagen (2006) placed the genus *Celuca*

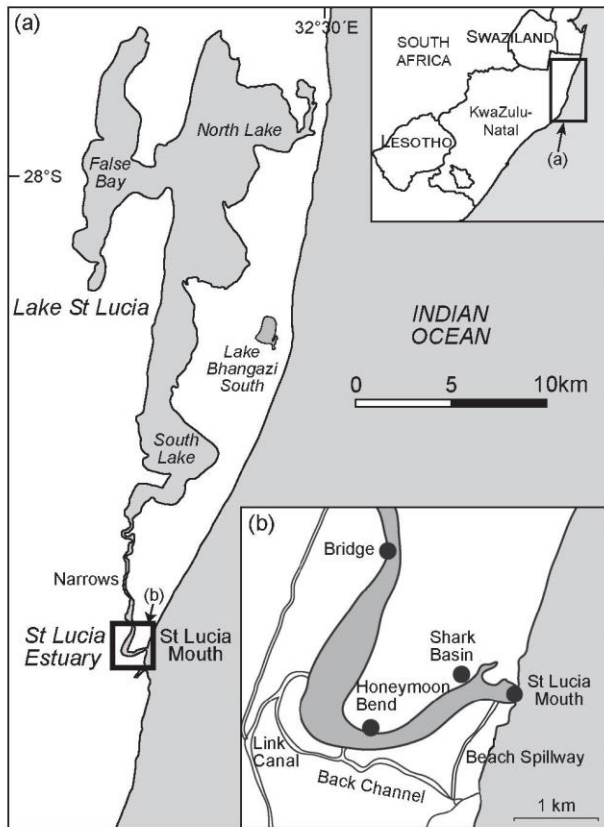


Figure 2: Map of the St Lucia estuarine lake on the east coast of South Africa. The black dot indicates passage of fiddler crabs from the Mfolozi to St Lucia. Figure adapted from Miranda et al. (2010)

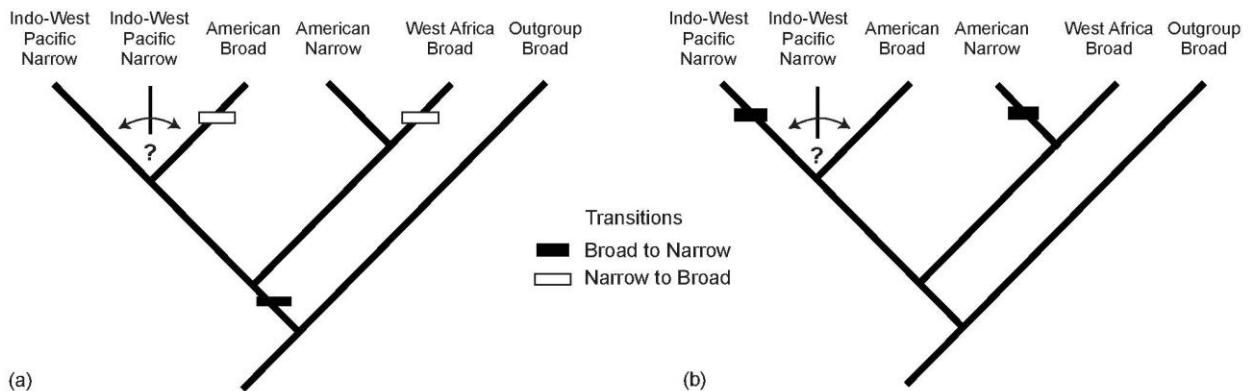


Figure 3: Rosenberg's proposed biogeographic history of *Uca* based on either (a) a narrow-fronted *Uca* ancestor or (b) a broad-fronted *Uca* ancestor. Figure from Rosenberg (2001)

Table 2: Revised classification of *Uca* subgenera as noted in the following literature: Rosenberg (2001), Beinlich and von Hagen (2006), Ng et al. (2008) and Shih et al. (2013)

Subgenus	Authority
<i>Austruca</i>	Bott, 1973
<i>Australuca</i>	Crane, 1975
<i>Cranuca</i>	Beinlich and von Hagen, 2006
<i>Gelasimus</i>	Latreille, 1817
<i>Leptuca</i>	Bott, 1973
<i>Minuca</i>	Bott, 1954
<i>Paraleptuca</i>	Bott, 1973
<i>Tubuca</i>	Bott, 1973
<i>Uca</i>	Leach, 1814

(see Crane 1975) within *Paraleptuca*. Based on preliminary genetic work, the East African *Uca annulipes* populations were classified with uncertainty (Beinlich and von Hagen 2006; Naderloo et al. 2010; Shih et al. 2013). Shih et al. (2013) suggested that further genetic analyses be conducted to determine whether or not this taxon is a different species altogether. Within Africa, however, gene flow among populations of the species appears to be fairly high. In an attempt to define the geographic structure of *U. annulipes* along the East African coastline, Silva et al. (2010) found a lack of genetic variation between populations and no significant morphological differences between geographic populations. Along the East African coastline marine larvae are transported by major currents between disparate locations. Larval settlement is then guided across a smaller scale by chemical cues to areas where populations are established (Lutjeharms 2006). This supports enhanced gene flow among populations of the species. This mechanism could easily apply to the other South African species of *Uca*, as the larvae of all five species are carried out to the open ocean (Figure 5). *Uca annulipes* can inhabit a wide range of sandy to muddy substrata, but appears to opt for sandy habitats in South African mangroves (Macnae 1963). The species is broad-fronted with light to bright pink chelipeds. Female patterning varies (see Figure 6).

***Uca (Paraleptuca) chlorophthalmus* (H. Milne Edwards, 1837) (Figure 4b)**

Uca chlorophthalmus, along with all other species of the subgenus *Paraleptuca*, is thought to have originated in the Indo-West Pacific region (Shih et al. 2009). Species belonging to this subgenus occur in the tropics and subtropics, with South Africa representing their southern limit (Crane 1975). *Uca chlorophthalmus* inhabits the spring high tidal region of mangroves and muddy banks. Typically, *U. chlorophthalmus* does not occur too close to the open ocean. This species is often sympatric with *U. urvillei*. Colouration of this broad-fronted species is variable. In males, the carapace is black with a blue to green marbled patterning (Branch et al. 2010), whereas in females it can be marbled, uniformly red or black. The limbs are typically bright red.

***Uca (Tubuca) urvillei* (H. Milne Edwards, 1852) (Figure 4c)**

The subgenus *Tubuca* is closely related to *Australuca* and

both genera were considered by Crane (1975) to be less evolutionarily advanced. These species exhibit primitive waving displays, devote only a short amount of time to social behaviour and reproduce by simple surface mating. The close relationship between these subgenera is further substantiated through genetic analyses (Sturmbauer et al. 1996; Rosenberg 2001). The species *U. urvillei* lives relatively far upstream, but close to the low-tide level (Crane 1975), preferring shaded, muddy substrata in South African mangroves (Macnae 1963). Its niche occasionally overlaps with those of *U. chlorophthalmus* and *U. annulipes*. This species is narrow-fronted with a black, purple or blue carapace. It is the largest of the South African *Uca* (maximum size recorded at 30 mm CWW) and males have a heavily-granulated orange cheliped (Branch et al. 2010).

***Uca (Gelasimus) hesperiae* (Linnaeus, 1758) (Figure 4d)**

The South African populations of *U. hesperiae* (previously recorded as *U. vocans*) represent not only the southern limit of the species distribution, but also its western boundary as was once indicated by its subspecific name, i.e. *Uca vocans hesperiae* (Crane 1975). The species requires a firm sandy substratum (Macnae 1963) and prefers unshaded habitat along the low tidal levels of protected bays (Crane 1975). They are often sympatric with *U. annulipes*. *Uca hesperiae* is narrow-fronted and typically has a light yellow, orange or brown carapace with a white and yellow/orange enlarged cheliped in males. The cheliped bears a characteristic subterminal tooth on the inner margin of the propodus (Branch et al. 2010).

***Uca (Cranuca) inversa* Hoffmann, 1874 (Figure 4e)**

The fifth species of *Uca* mentioned here, *U. (Cranuca) inversa*, has only been occasionally recorded in South African mangroves. It is the only representative of the broad-fronted African subgenus *Cranuca*, which was erected by Beinlich and von Hagen (2006) to separate the species from other broad-fronted Indo-West Pacific species. This separation was based on morphological differences between *U. inversa* and other 'proper' broad-fronted subgenera. *Cranuca* has been considered to be monophyletic with the narrow-fronted subgenus *Gelasimus* (Shih et al. 2009). *Uca inversa* was recorded in KwaZulu-Natal by Kingsley (1880) but was not reported from the area thereafter. Subsequently, it has long been regarded as occurring only as far south as Mozambique (Branch et al. 1994). However, the species was included by Branch et al. (2010) in the latest revision of *Two Oceans*. *Uca inversa* was recorded as extending southward to Kosi Bay, which is near the Mozambican border. Aside from the record of Branch et al. (2010), *U. inversa* has not been found in South Africa since Kingsley's single record in 1880 (see also Hoffmann 1874; Hilgendorf 1878; Macnae 1963). A recent survey undertaken by the authors between July 2014 and February 2015 in Kosi Bay failed to produce any evidence of its current presence in the area described by Branch et al. (2010). It seems likely that its occurrence in South Africa may be sporadic and transient. *Uca inversa* is not covered extensively in this review due to the rarity of the species over time, its fragmented distribution in this region and the limited information available regarding

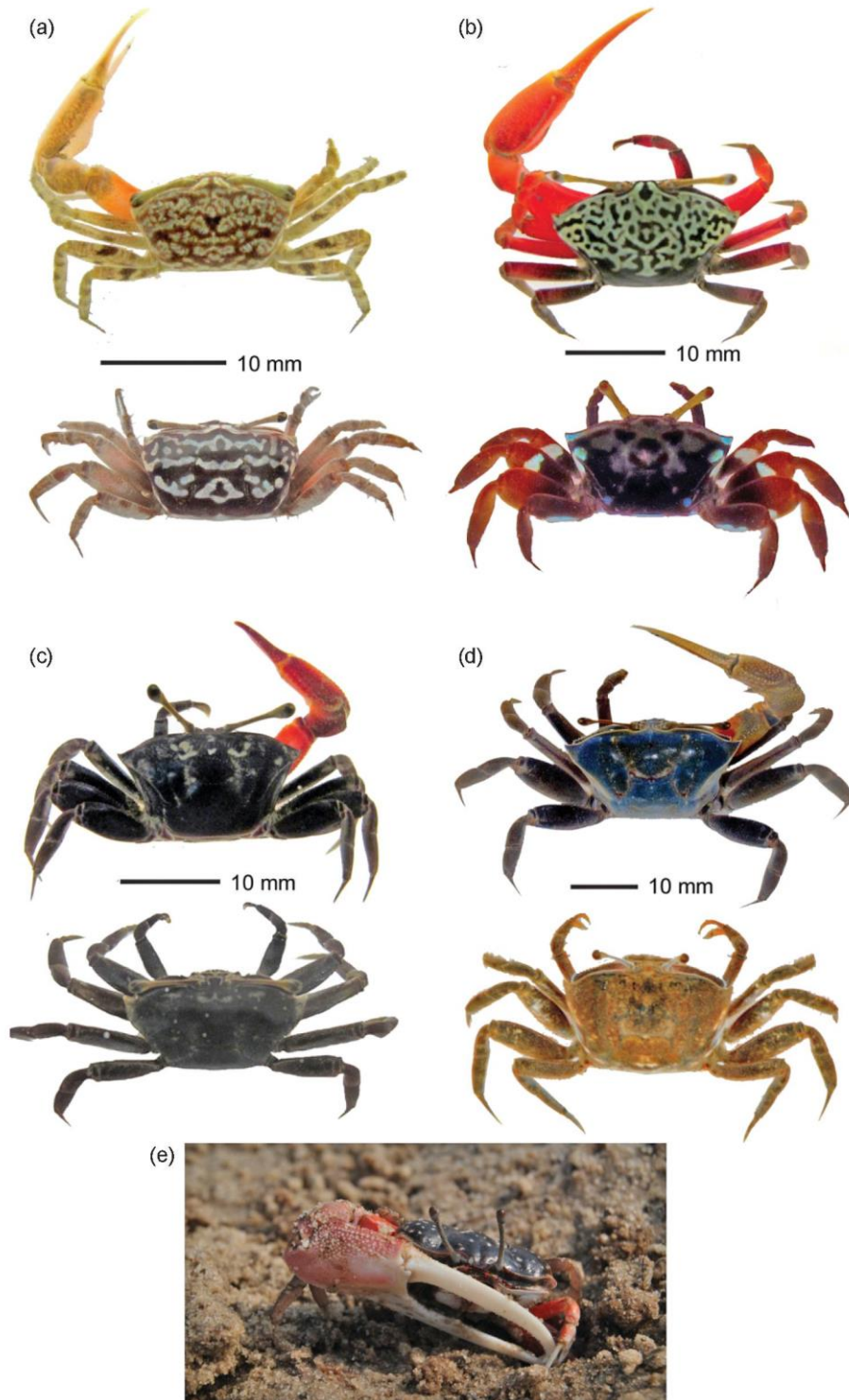


Figure 4: Male and female dorsal habitus of the five *Uca* species occurring in South Africa. (a) *Uca annulipes* male and female, (b) *Uca chlorophthalmus* male and female, (c) *Uca hesperiae* male and female, (d) *Uca urvillei* male and female, (e) *Uca inversa* male (courtesy of George Branch)

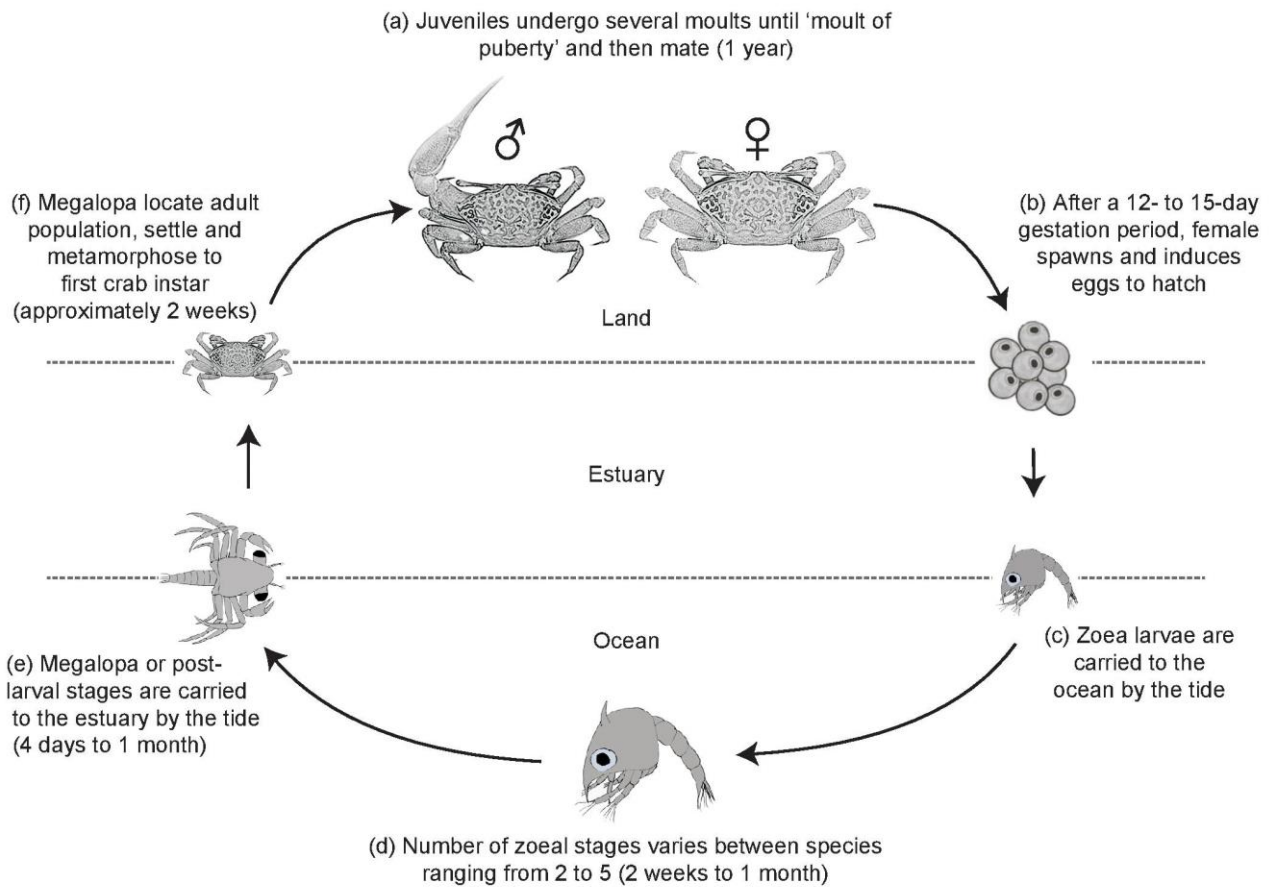


Figure 5: Representation of the life cycle of *Uca* spp. depicting the location of individuals at each stage of development. The time in parentheses indicates the approximate duration for a particular life stage (adapted from Hyman 1920 and Hemminkind 1968)

its biology. Morphologically, this species most closely resembles *U. annulipes*, although the shape of the cheliped differs in having a prominent tooth on the inner margin of the cheliped (Branch et al. 2010).

Confusion over systematics has most likely been exacerbated by the extreme polymorphism and colour changing abilities of fiddler crabs. The patterns and colours of the carapace vary greatly between and even within populations (Crane 1975). For example, *U. lactea* var. *annulipes* (= *U. annulipes*) from Africa have been described to display 'fine marbling' of black and white on the carapace (Crane 1975). Figure 6 shows the variation in colour and patterns of *U. annulipes* females from the mangrove habitat of the Mlalazi Estuary (28°57'20" S, 31°46'48" E) in northern KwaZulu-Natal. Here the typical black and white fine marble pattern is observed, as well as a uniform red coloured carapace. Colour change has been previously recorded for *Uca*. It is usually associated with moulting, stress, mating or temperature variations (Abramowitz 1937; Brown and Sandeen 1948; Detto et al. 2008). Dull patterned individuals sampled from the same population were most likely brown as a result of stress due to capture (Hemmi et al. 2006). A rapid decrease in luminance in just 60 min after capture has been recorded for *U. vomeris*

McNeill, 1920 (Hemmi et al. 2006). This stress response may be related to predator avoidance (Hemmi et al. 2006). However, aside from colour changes due to stress or environmental variability, the existence of polymorphism is noteworthy and has not been adequately addressed in studies concerning species of *Uca*. Bright colouration of the carapace is important for social signalling, territorial behaviour and individual recognition (Hemmi et al. 2006). However, dull or uniformly coloured individuals face a lower predation risk. Therefore, polymorphism in *Uca* populations could be considered a trade-off strategy between reproductive success and predator avoidance.

Occurrence and density records for *Uca* reveal changes in diversity and abundance of the genus along the East African coastline (Table 1). For *U. annulipes*, abundance increases towards the northerly locations. The lowest abundance (one individual) was recorded at the Knysna Lagoon (34°02' S), whereas the highest abundance (maximum 70 individuals m⁻²) was recorded from Kenya (4°31' S).

Four of the five *Uca* species that are recorded from South Africa are found in the mangroves of the Mlalazi Estuary, Durban Bay and the Mngazana Estuary. In contrast, only *U. annulipes* occurs at Knysna Lagoon and St Lucia. As the Knysna Lagoon is the southernmost locality with the



Figure 6: Polymorphic individuals of *Uca annulipes* females collected from the Mlalazi mangroves at the same site and on the same day (1 June 2013)

lowest temperature and St Lucia experiences large salinity fluctuations, this distribution pattern may attest to the wide tolerance of *U. annulipes* for both temperature and salinity. It is worthwhile noting that the majority of these studies were conducted over 10 years ago and there have been no published updates for these populations. Populations that exist at the limits of their species distribution range, such as fiddler crabs in South Africa, are sensitive to environmental disturbances. As tropical ectotherms they are expected to have a narrow thermal tolerance (Sunday et al. 2011). Furthermore, as temperatures are expected to rise with global climate change, these populations are most likely to exhibit a poleward shift. The discovery of *U. annulipes* in the Knysna Lagoon (Table 1) may be an early indication of this expected trend.

Life cycle and reproductive behaviour

A general annotated life cycle of fiddler crabs is presented in Figure 5. According to Hartnoll (1969), a crab reaches sexual maturity once it has reached the intermolt that allows for copulation, approximately one year after settlement (Vernberg and Vernberg 1975; Mokhtari et al. 2008). In males, this is when large numbers of spermatozoa are present in spermatophores within the vasa deferentia. This often correlates with changes in chelae morphometrics occurring during the 'moult of puberty'. In *Uca* spp. this has been recorded to coincide with the growth of the enlarged cheliped in males. In contrast, with females, maturity is not characterised by development of internal reproductive organs, but rather by the 'moult of puberty'. As

ovulation may only occur after mating, the ovaries can still be immature at the time of copulation (Yamaguchi 2001). However, successful copulation cannot occur prior to the moult of puberty largely due to physical constraints.

Semilunar courtship rhythms are prevalent in many marine invertebrate taxa and have been widely recorded in the genus *Uca* (Yamaguchi 1971; Crane 1975; Christy and Salmon 1984). Courtship and mating behaviour increases either close to or at spring tide in most populations (Crane 1975; Christy and Salmon 1984). The reason for this general trend in semilunar courtship is not clear, but the most favoured hypothesis is that it may minimise predation risk in both adults and larvae (Christy 1978; Christy and Salmon 1984; Christy 1987; Koga et al. 1998). Kim and Choe (2003) have also indicated that food availability influences the timing of courtship, by affecting either male courtship behaviour or female receptivity (Kim et al. 2004).

The type of courtship behaviour between species of *Uca* also varies and this is discussed extensively in the literature (Crane 1975; Christy 1987; Salmon 1987; Croll and McClintock 2000; Araujo et al. 2013). Reproductive behaviour has been roughly grouped into two general types based on the narrow-front vs broad-front division of species (Salmon 1987). The broad-fronted males generally provide a complex visual display and synchronised claw-waving to attract females through honest signalling. They defend breeding burrows and are visited by wandering females. Breeding occurs underground within these burrows. The females then remain underground for incubation and ovulation. In this case, mate selection is based on resource-provision and honest signalling. Claw-waving is less common in narrow-fronted species. Burrows are generally constructed by females while males move around looking for a receptive mate. Copulation then occurs briefly above-ground near the female burrow, after which the male leaves and the female uses her burrow as a breeding site. The receptivity of females regarding their choice of a suitable partner may be influenced by a suite of factors (Backwell et al. 1999; Detto et al. 2008; Detto and Backwell 2009).

Uca spp. breed like most crabs, where the female holds onto a clutch of eggs and hatches them rhythmically. Individuals exposed to constant light regimes were found to have a running cycle of approximately 25 h. However, on days lacking a night-time high tide, hatching delay was reported to increase with exposure to experimental conditions (de Vries and Forward 1991). This indicates that *Uca* adult females, rather than embryos, stimulate hatching by signalling release of the enzyme responsible for egg membrane-degradation. In this way females compensate

for effects of temperature at different sites and times by adjusting the time of breeding (Christy 2011). This allows eggs to hatch at a suitable time when the environmental conditions are most favourable. Endogenous timers and hatch cycles of different species vary according to the tides and temperatures they experience, so that most hatchings occur during a night-time high tide. Emmerson (1994) examined the breeding seasonality of four South African species of *Uca* by counting the number of ovigerous females. The results indicated that the peak of breeding activity occurs in March, when temperatures are higher than during the rest of the year. The study was conducted in the temperate Mngazana Estuary, where four species of *Uca* co-existed with four other brachyuran species. It is therefore likely that temperature as well as competition-avoidance influenced the seasonality of breeding (see also Table 3 for peak mating season).

Fecundity, sex ratios and the size at sexual maturity have also been reported for four species of *Uca* from this site (Emmerson 1994, 1999). Although regarded as the most abundant *Uca* species in South Africa, *U. annulipes* appears to have the lowest fecundity with females carrying a maximum of 3 951 eggs. In comparison *U. urvillei* is the most fecund and has been reported to carry a maximum of 22 980 eggs (Table 4). However, *U. annulipes* reaches 'puberty' at the smallest size, whereas *U. urvillei* matures at a much larger size (Table 4). Furthermore, sex ratios seem largely skewed for all species and indicate up to 4.5 times more males than females for *U. annulipes*. It is important to note here that ovigerous females remain inconspicuous in their burrows and are scarcely seen at the surface until larval release.

Release of larvae into the water (Figure 5) is governed by tidal and lunar cycles. Papadopoulos et al. (2002) examined the release of larvae into the Mngazana Estuary by sampling the water column with a zooplankton net. The authors found that maximal larval release of *Uca* spp. occurred when the high tide was crepuscular (around twilight). This occurs 2–3 d after a new and full moon when the nocturnal ebb tide is strongest. During the hours of 20:00 and 21:30, abundance of larvae in the water column reached a peak of approximately 500 individuals m⁻³. The strong tidal flow experienced at these times is most effective for larval transportation to the marine environment. It is widely thought that nocturnal release of larvae is a predator-avoidance strategy. The predictable nature of hatching and larval release can make females easy targets for alert predators. To reduce the risk of predation by larger terrestrial animals females move down to the open water mark under the cover of

Table 3: Variation in courtship behaviour (Crane 1975; Yamaguchi 2001) and dome construction (Crane 1975) among the South African species of *Uca* with peak mating season of the Mngazana populations (Emmerson 1994)

Species	Wave type	Dome construction	Copulation location	Peak mating season
<i>Uca annulipes</i>	Circular	Males / semi-domes	Above- or below-ground	March–April
<i>Uca chlorophthalmus</i>	Vertical	Large females / semi to full domes	Above- or below-ground	December–April
<i>Uca urvillei</i>	Side-to-side	Males / semi-domes	Above-ground	January–May
<i>Uca hesperiae</i>	Vertical	Males / semi-domes	Above-ground	October–May
<i>Uca inversa</i>	Obliquely vertical	Unknown	Unknown	Unknown

darkness. The larvae are less endangered at nocturnal high tides, as planktivorous fish feed during the day and the high tide ensures maximal dispersal (Papadopoulos et al. 2002) preventing the larvae from being trapped in the shallow mangrove habitat that is home to many juvenile fish. Larvae are carried by the ebb tide into the adjacent marine environment (Figure 5), where they are less likely to encounter planktivorous predators. As a result of this reduced predation, and also to aid with buoyancy, larvae are smaller with fewer spines for protection.

The larval development of relatively few *Uca* species has been described (Hyman 1920, 1922; Herrnkind 1968; Feest 1969; Rabalais and Cameron 1983; Christy 1989; Rodriguez and Jones 1993; Armendariz 2005; Spivak and Cuesta 2009). The number of zoeal stages varies between species and ranges from two to five (Rabalais and Cameron 1983). This most likely depends on the environment experienced by each population. Once the first zoeal stage is released into the water, movement of larvae into the ocean is quite rapid. It is thought that *Uca* larvae develop to the megalopa stage in the ocean before returning to the estuary to find a suitable place for recruitment. However, some species have evolved specialised and rapid development strategies. These serve to minimise predation and to allow adaptation to terrestrial life styles, or to constrained and unfavourable environmental conditions (Rabalais and Cameron 1983; Christy 1989). Rabalais and Cameron (1983) discussed the development of *U. subcylindrica* (Stimpson, 1859), a species endemic to southern Texas and northern Mexico where it is found in semi-arid habitats. Here, larval development occurs in temporary puddles and ponds and must therefore be rapid. In *U. subcylindrica* larvae develop to the megalopa stage in as little as 2.5 d as opposed to the 2–4 weeks observed in other species (Hyman 1920; Herrnkind 1968; Feest 1969). Litulo (2005) suggested that the Mozambique population of *U. annulipes* undergoes rapid larval development and settlement, although this was not shown conclusively. The first zoeal stages of *U. annulipes* and *U. urvillei* were illustrated and compared by Ghory and Siddiqui (2006) from Pakistani mangroves, although the total duration of development was not noted and remains unknown. In fact, information on the developmental period and morphology of *Uca* larvae is notably absent for all five South African species.

Once individuals have reached the megalopa or post-larval stage, they re-enter estuaries or brackish environments through tidal transport (Figure 5) (Tankersley and Forward 1994). *Uca* megalopae are known to undergo

vertical migration within the water column during tidal rhythms. This is to facilitate up-stream migration towards adult habitats. During high tide, megalopae are found in surface waters. When the tide changes they settle on benthic substrata during the ebb phase to avoid being carried back to the ocean (Tankersley and Forward 1994). The megalopae appear to locate their adult populations either through the use of chemical cues or appropriate salinity levels, or a combination of both (Brodie et al. 2005). Other environmental cues also affect timing and distribution of settlement, such as time of day (night-time activity is preferential), habitat suitability and population density (O'Connor 1993). The location of settlement has, however, been found to be less of a priority in taxa with a motile adult stage, such as fiddler crabs (O'Connor 1993). The megalopae then metamorphose to the first crab instar. Just like the timing of settlement, correct timing of this metamorphosis can be accelerated or delayed through environmental cues (O'Connor 1991; Tankersley and Forward 1994; Brodie et al. 2005). In addition, O'Connor (1991) indicated that metamorphosis of the megalopa was delayed until at least two stimuli were present, i.e. an adult crab and sediment.

Feeding ecology

The general consensus among ecologists is that fiddler crabs are deposit feeders. Adult individuals consume microphytobenthos (MPB), microheterotrophs and plant detrital matter from the surface of the substrate (Crane 1975; Montague 1980; Dye and Lasiak 1986; France 1998; Takeda et al. 2004). Diet determination of *Uca* has mostly been conducted through gut content analysis. Griffen and Mosblack (2011) reported that MPB occupies the most volume within the gut of the species investigated. Fiddler crabs have relatively small stomachs compared with those of other herbivorous brachyurans, and their guts usually contain conspicuous amounts of indigestible sand. These characteristics support the assimilation of bacteria, which form a significant part of fiddler crab diet (Dye and Lasiak 1986). This has been supported by a stable isotope study by France (1998). By measuring ^{13}C and ^{15}N isotopes in *Uca vocator* (Herbst, 1804) it was estimated that cyanobacteria were the main food source assimilated by fiddler crabs, whereas detritus was hardly assimilated.

The feeding apparatus of each species is adapted to its habitat (Miller 1961), more specifically the substratum off which it feeds. For example, species of *Uca* inhabiting muddy flats and marshes bear fine feathery setae on the second maxillipeds, whereas species inhabiting sandy or rocky shores exhibit more stiff spoon-shaped setae for scraping bacteria off indigestible sediment (Maitland 1990). Lim (2004) also reported on *U. annulipes* and *U. vocans* in Singapore, where the former inhabits a sandy beach habitat and the latter a muddy flat. *Uca annulipes* bears a significantly greater number of setae on the second maxillipeds, compared with *U. vocans*. The author concluded that a greater number of setae are required for processing sandy sediments. The rate of feeding has also been determined for various species (Table 5) and it has been found that in some cases females feed faster

Table 4: Fecundity (number of eggs per individual), sex ratio and size at sexual maturity (carapace width of smallest ovigerous female in mm) of *Uca* spp. from the Mngazana Estuary

Species	Fecundity ¹		Sex ratio ² M:F	Size at sexual maturity ¹
	Min.	Max.		
<i>Uca annulipes</i>	451	3 951	4.508	8.3
<i>Uca chlorophthalmus</i>	1 674	11 200	1.871	10.3
<i>Uca urvillei</i>	2 205	22 590	2.964	14.4
<i>Uca hesperiae</i>	2 494	19 980	1.938	13.1

¹ Emmerson (1994); ² Emmerson (1999)

than males. This is most likely due to their use of both minor chelipeds, whereas the male only has one with which to feed. To compensate for this, males spend more time feeding. Feeding studies globally involve a variety of methods (Table 5), which makes feeding rates between species difficult to compare. This is further confounded by interspecific size variation as body size affects feeding rate (Mokhlesi et al. 2011). The most common method used to estimate feeding rate is the count of faecal pellets produced (Valiela et al. 1974; Dye and Lasiak 1986; Mokhlesi et al. 2011). This information has not been confirmed for South African species and represents a further gap in basic knowledge, where feeding rates are important when considering the impact that a species has on its biotic and abiotic environment. Feeding involves selectively filtering through sediment for micro-organisms, and the disturbance has been shown to alter associated benthic microbial community structures (Dye and Lasiak 1986; Kristensen 2008). Fiddler crabs can also affect benthic communities through direct competition for resources (Ólafsson and Ndaro 1997; Weis and Weis 2004; Kristensen 2008).

Although *Uca* spp. generally possess specialised feeding traits, there is evidence for opportunistic generalist feeding and even cannibalism. Crabs can be successfully fed a variety of food items including fish, brine shrimp and *Arbacia* (sea urchin) eggs (Wilkins and Fingerman 1965; Vernberg 1969). Koga et al. (1995) observed that *U. tetragonon* males in Phuket, Thailand, often attack conspecific females as well as other sympatric *Uca* species. Similarly, Milner et al. (2010) observed *U. annulipes* actively hunting juvenile shrimp and conspecifics, attempting to subdue an insect and scavenging on the army crab *Dotilla fenestrata* on Inhaca Island, Mozambique.

Fiddler crabs thus play an important role in the movement of energy through trophic levels by feeding on microalgae and, in turn, being preyed upon by a wide variety of higher organisms that would not likely have consumed microalgae. Furthermore, these species facilitate nutrient recycling by breaking down organic matter and increasing the rate

of decomposition. Fiddler crabs are partly responsible for the retention of nutrients in tidal ecosystems as systems that are regularly flushed easily lose nutrients to adjacent aquatic habitats.

Predation on fiddler crabs

Fiddler crabs are preyed upon by a variety of animals. The larvae are eaten by fish and birds as well as benthic and pelagic macro-invertebrates (Morgan 1992; Morgan and Christy 1996). Adults are consumed mainly by birds (Backwell et al. 1998), small mammals (Carlton and Hodder 2003), other brachyuran species (Steinke et al. 1993) and even cannibalised (Koga et al. 1995). A number of researchers have suggested that predation is male-biased, due to their greater conspicuousness (Koga et al. 2001) and slower movement (Jordão and Oliveira 2001).

Anti-predation mechanisms are divided into avoidance and evasion strategies. Avoidance of predators plays a huge role in the ecology and various physiological cycles of fiddler crabs. Timing is essential when it comes to feeding, mating and larval release, as these activities usually render *Uca* individuals more vulnerable to predators (Christy 1978; Christy and Salmon 1984; Koga et al. 1998; Papadopoulos et al. 2002). The use of visual and chemical cues to avoid predators has been well-documented in fiddler crab species (Leyne 1998; Chiussi and Diaz 2002; Hazlett 2011).

Thanatosis (also known as 'apparent death' and characterised by immobility) has been observed in other taxa, such as lobsters and crickets, when pressure is applied to certain parts of the body. Bergey and Weis (2006) showed that *Uca* individuals sometimes became catatonic when turned upside down. This is thought to be linked to antipredator behaviour, as avian predators often use motion to detect prey. Some individuals remained in this state for up to 2 h. As an escape strategy, autotomy is most common among all brachyurans. Male fiddler crabs shed the enlarged cheliped more than 50% of the time when caught (Mace and Curran 2011). Usually, the limb being

Table 5: Feeding rates (\pm SD) of *Uca* spp. around the world measured using a variety of methods as outlined below. In the case of Dye and Lasiak (1986) no significant difference was found between feeding rates of males and females and data is thus reported as one consolidated value

Species	Technique used	Unit of measurement	Feeding rate		Country of study	Reference
			Males	Females		
<i>Uca annulipes</i>	<i>In situ</i> gut fluorescence	Gut evacuation rate (per hour)	0.212–0.795	0.322–0.410	South Africa	Peer et al. (in press)
<i>Uca pugnax</i>	Volume of mud weighed before and after feeding	Amount of sediment ingested (g)	0.40 \pm 0.04	0.39 \pm 0.10	USA	Valiela et al. (1974)
<i>Uca pugnax</i>	Faecal pellet count over 24 h	No. of pellets produced per day	177.5 \pm 3.5	176	USA	Valiela et al. (1974)
<i>Uca lactea</i>	Telescope observations of food transfer	Scoops per minute	66.8 \pm 3.6	105.8 \pm 5.8	Indonesia	Retraubun et al. (1998)
<i>Uca vocans</i>	Telescope observations of food transfer	Scoops per minute	66.8 \pm 4.3	91.7 \pm 7.3	Indonesia	Retraubun et al. (1998)
<i>Uca sindensis</i>	Faecal pellet count over 24 h – average	Dry mass (g) of produced pellets per day	49.1 \pm 24.5	31.1 \pm 11.1	Iran	Mokhlesi et al. (2011)
<i>Uca vocans</i>	Faecal pellet count per minute – maximum	Dry mass (g) of produced pellets per minute	322.5 \pm 51.6		Australia	Dye and Lasiak (1986)
<i>Uca polita</i>	Faecal pellet count per minute – maximum	Dry mass (g) of produced pellets per minute	144.8 \pm 9.65		Australia	Dye and Lasiak (1986)

attacked is the limb shed (Hoadley 1937) and crabs are subsequently more likely to escape.

The most obvious method of predator evasion is through the use of burrows, either their own or a neighbouring one (Christy 1987; Koga et al. 2001). Once a crab enters a burrow, it is difficult to remove by both avian and terrestrial predators (Backwell et al. 1998).

Interaction with biotic and abiotic environment

Fiddler crabs are ecosystem engineers because they interact with and influence their environment and are responsible for bioturbation of the sediment as they rework the substrate through feeding and burrowing behaviour. Feeding involves selectively filtering through sediment for micro-organisms and results in the alteration of benthic microbial community structure (Dye and Lasiak 1986; Kristensen 2008). Burrowing activities of *Uca* populations bring sediment from greater depths to the surface, leading to turnover of surface sediment by up to 20% (Retraubun et al. 1998). Sediment surface area is increased, although this appears to vary depending on the species and population density (Retraubun et al. 1998). An increase in surface area changes the nutrient and chemical exchange rates of soil (Nielsen et al. 2003). Katz (1980) reported that burrows allow for faster removal of toxic compounds out of the soil. Burrows affect the nitrogen processes occurring within the substratum (Wolfrath 1992). The impacts of *Uca* may also extend to larger spatial scales. In Florida, *Uca* were shown to have a positive effect on the growth and success of mangroves (Smith et al. 2009). Sites containing burrows had larger mangrove trees, more controlled salinities and increased redox potential compared with uninhabited sites. In areas where fiddler crab density is high, excreted ammonium provides a source of reduced nitrogen, which is promptly utilised by both benthic microalgae and mangrove plants to substantially improve their growth rates (Smith et al. 2009).

It is generally stated that fiddler crab burrowing facilitates aeration and oxygenation of the associated substratum (Bertness 1985; Nielsen et al. 2003; Araújo et al. 2012). However, Michaels and Ziemann (2013) showed that this is dependent on substrate type and therefore cannot be generally applied to all species in all habitats, as the positive effect may be very minor. Furthermore, the detrimental effects of *Uca* activity include destabilisation of sediment through the formation of easily erodible pellets (Botto and Iribarne 2000) and retardation of seedling success in densely populated areas (Smith and Tyrrell 2012).

Fiddler crabs also affect benthic communities, either through disturbance of the benthic habitat or through direct competition for resources (Ólafsson and Ndaró 1997; Weis and Weis 2004; Kristensen 2008). The presence of fiddler crabs is also known to reduce the presence of meiobenthic species (Hoffman et al. 1984). Ólafsson and Ndaró (1997) showed that fiddler crabs in Tanzania inhibit the settlement of meiobenthic organisms that are not accustomed to the erodible nature of reworked sediment. The crabs were also found to feed directly on meiobenthic species. However, the interference and competitive effects of fiddler crabs on the environment and associated biota is poorly understood

in the South African context. As these species play an integral role in various ecosystem processes, their impacts should be examined more closely in the future to better understand ecosystem dynamics in associated habitats.

Tolerance to abiotic fluctuations, extremes and pollution

Temperature and salinity affect the metabolic processes and distribution of *Uca* spp. (Dame and Vernberg 1978) by influencing growth, regeneration and moulting, modulating hormonal and biochemical activities, and governing reproductive periodicity (Miller and Vernberg 1968; Mouton and Felder 1995; Litulo 2004). Responses to environmental factors depend on evolutionary history and are specific to a species and its different life stages (Miller and Maurer 1973). Vernberg (1969) differentiated between larval and adult responses and showed that temperate (cold-acclimated) *Uca* species have a greater adaptive ability to thermal variation than tropical (warm-acclimated) species, probably as a result of genotypic response (Vernberg and Vernberg 1967) (Table 6). Larvae of tropical species, unlike their adult counterparts, are cold-resistant. Lethal temperatures, both upper and lower, differ significantly between temperate and tropical species. Although crabs are ectotherms, they can regulate body temperature to a certain extent. This can be done through photoregulation (Brown and Sandeen 1948; Palmer 1962), transpiration and burrowing (Edney 1961). Abramowitz (1937) recorded a daily colour change pattern in *U. pugnator*. Brown and Sandeen (1948) went on to describe how, during the day, black pigments were more concentrated while white pigments were dispersed. It is believed that the function of such colour change is partly thermoregulatory in nature, as concentrated black pigments would allow for minimal light absorption. Thurman (2003) examined osmoregulatory capabilities in American fiddler crab species and discovered that freshwater species had the lowest haemolymph osmolality, with limited osmoregulatory capabilities. Euryhaline species occurring in saltwater and brackish environments were more capable of osmoregulation at higher salinities.

Thermal and salinity tolerance studies conducted on southern African *Uca* were performed on specimens from Inhaca Island, Mozambique (Table 6). Here, Edney (1961) examined the osmotic tolerance of *U. annulipes* and showed that individuals were less likely to acclimatise to, and survive, immersion in seawater (i.e. 35‰) than they were to survive immersion in freshwater. Although mostly hypotonic, the osmotic nature of the water around Inhaca Island is highly variable (Macnae and Kalk 1958) and it appears that the ability to osmoregulate is invaluable in such a dynamic environment. Recently, Khanyile (2012) examined the salinity tolerance of four South African *Uca* spp. and showed that *U. annulipes* was the most tolerant of high salinities (Table 6), whereas all species were able to survive in freshwater conditions.

Uca crabs are thought to be suitable bioindicators of ecosystem health, as extreme natural abiotic conditions lead to changes in their physiology, distribution and development (Wilkins and Fingerma 1965; Brandt et

Table 6: Salinity and temperature limit data for fiddler crabs from South Africa, South America and North America. Temperate zone species are indicated with an asterisk, while the unmarked species are considered tropical zone species

Species	Country	Salinity (ppt)		Temperature (°C)		Reference
		Lower	Upper	Lower	Upper	
<i>Uca annulipes</i>	Salinity: South Africa; Temperature: Mozambique	0	65	7	42.1	Salinity: Khanyile (2012); Temperature: Edney (1961)
<i>Uca chlorophthalmus</i>	Salinity: South Africa; Temperature: Mozambique	0	55	7	40.8	Salinity: Khanyile (2012); Temperature: Edney (1961)
<i>Uca hesperiae</i>	Salinity: South Africa; Temperature: Mozambique	0	55	7	41.4	Salinity: Khanyile (2012); Temperature: Edney (1961)
<i>Uca inversa</i>	Salinity: South Africa; Temperature: Mozambique	0	Unknown	7	43.3	Salinity: Khanyile (2012); Temperature: Edney (1961)
<i>Uca urvillei</i>	Salinity: South Africa; Temperature: Mozambique	0	55	7	40.0	Salinity: Khanyile (2012); Temperature: Edney (1961)
<i>Uca minax*</i>	USA	0	>58	Unknown	39.9	Teal (1958)
<i>Uca pugilator*</i>	USA	0	>58	Unknown	39.5	Teal (1958)
<i>Uca pugnax*</i>	USA	7	>58	Unknown	40.0	Teal (1958)
<i>Uca rapax</i>	Salinity: Venezuela; Temperature: Brazil	<4	>125	<7	42	Salinity: Zanders and Rojas (1996); Temperature: Vernberg and Vernberg (1967)
<i>Uca uruguayensis*</i>	Brazil	Unknown	Unknown	7	39	Temperature: Vernberg and Vernberg (1967)

al. 2010). The recent PUMPSEA (Peri-Urban Mangrove Forests as Filters and Potential Phytoremediators of Domestic Sewage in East Africa) initiative undertaken by a consortium of nine European and African countries was conducted in Kenya, Tanzania and Mozambique. The aim was to examine the role of mangroves in reducing sewage pollution to the marine environment, paying close attention to environmental, ecological and sociopolitical impacts (PUMPSEA 2007). A number of studies examined the effect of increased sewage load on *Uca* populations within controlled experimental plots. The impact of increased sewage load on *Uca* in these East African mangroves was found to be significant. In sites with a high sewage load, males had higher survival rates than females. Furthermore, bioturbation of sediment increased during feeding, although less sediment was processed (Penha-Lopes et al. 2009). It was found that peri-urban sites could host a larger biomass of fiddler crabs with less surface sediment being reworked (Cannicci et al. 2009; Bartolini et al. 2011). Although this could have potential benefits for mangrove growth and development, the increase in biomass and density was found to be unsustainable and could possibly lead to a collapse of the entire mangrove ecosystem (Cannicci et al. 2009). The implications of the study point to the usefulness of fiddler crabs as bioindicators and highlight the potential impact of using mangroves and wetlands to filter urban wastewater.

The St Lucia Estuary: a case study of environmental change and *Uca* persistence

The St Lucia Estuary has historically been connected to the Mfolozi Estuary, where a combined inlet was formed from the sea and the Mfolozi provided a large supply of water to the St Lucia system (Whitfield et al. 2013). In the 1920s agriculture and the canalisation of water from the Mfolozi River led to St Lucia experiencing degradation

in water quality and increase in silt loading. The two estuaries were separated to minimise the degradation of the St Lucia Estuary but, as a result, St Lucia experienced a decrease in freshwater input especially during drought conditions. It is now closed to the ocean more frequently and subject to limited marine connectivity. In 2012 the St Lucia and Mfolozi estuaries were partially reconnected in the hope that the system could be restored and experience less severe consequences during periods of prolonged drought.

Four species of fiddler crabs were recorded in the St Lucia mangroves in 1949 by Millard and Broekhuysen (1970). These were *U. annulipes*, *U. chlorophthalmus*, *U. urvillei* and *U. hesperiae*. Subsequent surveys undertaken during closed mouth conditions revealed the complete absence of all four species within these St Lucia mangrove habitats (Peer et al. 2014). In 2014, however, three species, namely *U. annulipes*, *U. chlorophthalmus* and *U. urvillei*, were recorded in the Back Channel between the St Lucia and Mfolozi estuarine systems (Figure 2), while *U. annulipes* was found in the St Lucia mangroves. One reason for the absence of the fiddler crabs is attributed to the closure of the mouth. From the life cycle denoted in Figure 5, it is evident that *Uca* larvae require a great degree of marine connectivity to metamorphose successfully. While the mouth remained closed, megalopae could have possibly reached the mangroves through small Mfolozi River flood events, as this has been documented for other aquatic species (Vivier et al. 2010), including freshwater penaeid shrimps (Bickerton 2011). The recently connected tidal link through the beach spillway could also play an important role in recruitment. However, the perched nature (the Back Channel is more elevated than the St Lucia Estuary) of the link between St Lucia and Mfolozi favours the inflow of water from Mfolozi to St Lucia during high tide and high Mfolozi riverine flow, but limits outflow from St Lucia through the same link at any other time. In this way, a

number of adults and larvae can be introduced into St Lucia during floods and high tides, but these small populations then become practically isolated from the ocean. Larvae are certainly unable to swim against the inflowing current at times when the connection to the ocean is established. During a recent survey, fiddler crabs were found in low densities at sites around the Mfolozi back channel (Table 1), providing a good indication of the importance of connectivity with the ocean for recruitment. Resettlement of adults in the St Lucia mangroves could easily occur from refuge populations around the Mfolozi mangroves, due to the close proximity of the two mangrove systems and the connection of the two systems via the Link Canal and the Back Channel operating tidally (Figure 2).

The closure of the St Lucia Estuary mouth could have further affected the life cycle of fiddler crabs by severely reducing propagule pressure. In St Lucia, all fiddler crab species were found within the mangroves, a fairly shaded and sheltered habitat compared with the open mouth area, where avian predation is more prevalent. However, fish are a significant source of predation on larvae and megalopae (Morgan and Christy 1995). The current closed mouth condition of the estuary inhibits movement of larvae to the open ocean, a migration generally thought to minimise predatory impact on the population. As mentioned above, fish and larvae are able to enter the estuary via the tide-dependent Back Channel (Whitfield and Taylor 2009), but are largely unable to leave on the outgoing tide because of the perched nature of the inlet. Aside from disrupting the marine-dependent life cycle, larvae would essentially be trapped in the estuary with an increased risk of predation, which negatively affects recruitment.

In St Lucia, land-use change has resulted in increased sedimentation and decreased water quality (Whitfield et al. 2013). Similarly, the Beachwood Mangroves (29°47'46.68" S, 31°2'33.72" E) and the Bayhead Mangroves (29°53'17" S, 31°00'49" E) in Durban Bay are subject to industrial pollution, alien vegetation encroachment, heavy urban run-off and deposition of litter. Yet four species of *Uca* still persist along the Mgeni River banks and four *Uca* species have been noted in the Durban Bay Mangroves (NP pers. obs.). Research into the environmental tolerance of fiddler crabs in South Africa is useful for management and conservation, especially in degraded and developed habitats such as the Beachwood, Sipingo, Durban Bay, Mlalazi, St Lucia and Richards Bay mangrove forests (Moll et al. 1971; Rajkaran et al. 2009; Hoppe-Speer et al. 2013). It is yet unknown how the fluctuations in salinity and silt loading may have affected the St Lucia populations. However, if connectivity, water quality and the abundance of predators are considered, it is unlikely that fiddler crabs would have been able to sustain their populations under closed mouth conditions.

The story of the St Lucia fiddlers provides opportunities for studies related to habitat transformation, which affects the survival and recruitment of *Uca* at various stages of its ontogenetic development. The recent management decision to combine the St Lucia and Mfolozi inlets could possibly restore favourable conditions in terms of tidal influence, stable salinity and temperature levels and connectivity to the ocean. The degree of connectivity required by fiddler

crabs to colonise or persist in an area has not been well studied. It is known that larvae are carried out to the ocean and have high levels of dispersal (Wieman et al. 2014). However, there are many influential factors determining these levels, including developmental rates, ocean currents and, in the case of St Lucia, physical barriers. Further studies may address connectivity between different populations through genetic pool identification (Silva et al. 2010; Wieman et al. 2014). The recolonisation of fiddler crabs into the St Lucia mangroves before the mouth breaches offers a rare opportunity to investigate aspects such as breeding, feeding dynamics and the effects of *Uca* on their habitat in a non-tidally influenced environment.

The dynamic salinity levels of the St Lucia mangroves undoubtedly influence the distribution of fiddler crabs in that system. The effects of the most recent severe drought, combined with anthropogenic changes, led to high levels of desiccation in the system. This decreased the available habitat and drastically affected physicochemical parameters, such as salinity and temperature (Whitfield and Taylor 2009). Although desiccation is prevalent in a number of South African estuaries (Rajkaran et al. 2009), its effects on *Uca* populations is virtually unknown. The primary method employed by brachyurans to avoid desiccation is burrowing (Macnae 1968). The sesarmids currently dominating the St Lucia mangroves may be more tolerant in this regard due to the greater depth of their burrows. These crabs are also able to inhabit a drier, tougher substratum in comparison to *Uca*. The species native to the area might not be adapted to these conditions and are thus unlikely to survive long periods of desiccation. While adults may find refuge in freshwater seepage areas and are able to survive by feeding opportunistically as mentioned above, they would not be able to successfully reproduce. Response to desiccation, turbidity, and change in soil and water quality should be examined to better understand how the fiddler crab populations may have been affected within the estuary during this time. Globally, rising temperatures may result in temporarily open/closed estuaries remaining closed for longer periods, similar to the St Lucia Estuary. Thus the St Lucia Estuary is a suitable model to predict the response of similar species to climate change in other such aquatic systems.

Conclusion

Nabout et al. (2010) noted that future work should be more focused to gain a better understanding of the macro-ecological and macro-evolutionary aspects of the genus *Uca* on a global scale. This cannot be achieved by simply studying individual populations. However, even though fiddler crabs have been extensively studied and observed over the last few centuries, both the cosmopolitan and speciose nature of this genus bring about large degrees of inter- and intraspecific variation between populations. These variations have been recorded in all aspects of the ecology of *Uca*; from courtship, mating and breeding to development, tolerance and feeding. Predictably, there is great sexual variation, a large amount of which is related to the sexual dimorphism of fiddler crabs. It is thus difficult to draw macro-ecological

conclusions, especially due to the plastic responses to climate change. Thus there is a continuous research need at the species level and within each biogeographic region, as many studies are outdated and have not accounted for recent shifts in distribution. These shifts have been associated with a variety of factors including population success, changes in behaviour and the impact of fiddler crabs on the newly invaded habitat.

While most of the work done on fiddler crabs has focused on North American species, focus is shifting towards the Indo-Pacific species. Australian species have been used in particular to examine behaviour (Booksmythe et al. 2008; Detto and Backwell 2009; Milner et al. 2010, 2012; Callander et al. 2013). Various African species have been used to describe the effects of environmental change on the genus (Amaral et al. 2009; Cannicci et al. 2009; Penha-Lopes et al. 2009; Bartolini et al. 2011) and South American species are the focus of physiological studies (Benetti et al. 2008; Simith et al. 2010; Colpo and Negreiros-Fransozo 2011; Martins and Masunari 2013).

Research surrounding climate change impacts is still lacking. Species at distribution limits are the most affected by climate change, when temperature shifts and habitat changes are experienced at these boundary regions. In South Africa, the opportunity to study five such *Uca* species presents itself, as these species all occur here at their southernmost boundary. Mangroves are drastically declining worldwide, due to land-use and climate change (Duke et al. 2007; Polidoro et al. 2010). Anthropogenic modification of habitats is also prominent yet the fiddler crabs occurring in South African mangroves persist despite the extreme conditions they encounter at this boundary. Fiddler crab persistence in modified habitats has previously been linked to a favourable increase in nutrients at these sites (Cannicci et al. 2009) and this may explain the presence of South African fiddler crabs in modified habitats. Furthermore, observations regarding their ecology may provide insight into the effects of climatic extremes on other species operating under similar or less extreme conditions.

Fiddler crabs are known as ecosystem engineers through their burrowing and foraging behaviour. It is not yet known what impact the removal of these key species would have on associated habitats. Thus, aside from investigating the basic biology of fiddler crabs in South Africa, research should focus on the effects of habitat modification and climate change on the persistence and ecology of fiddler crabs at their southern limits. Interactions of fiddler crabs with the associated environment and sympatric species need to be further examined to better understand the complex nature of mangrove communities in which these species play a large role. Lastly, South African research should focus on the impact that fiddler crabs have on their habitat. This would provide an understanding of the importance of fiddler crabs in coastal habitats and how these habitats would respond to the loss of these species.

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Chapter 5

The lack of tidal influence in mangrove systems is a rare phenomenon but one that is expected to increase with global environmental change. The response of ecosystems to such a prominent environmental rhythm is virtually unexplored. The feeding rhythms of fiddler crabs are known to be influenced by tidal and diel rhythms (Barnwell 1966). However, in the St Lucia mangroves, fiddler crabs currently exist in a non-tidal habitat. The St Lucia fiddler crabs thus present an opportunity to examine ecological dynamics of a tidally-influenced taxon in a non-tidal environment. An *in situ* gut fluorescence technique was used in this case, as the primary food source of fiddler crabs is microphytobenthos.

Feeding dynamics of the fiddler crab (*Uca annulipes*) in a non-tidal mangrove forest

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Abstract. To investigate the lack of tidal influence on the feeding dynamics of fiddler crabs, we used an *in situ* gut fluorescence technique to measure gut pigment content of *Uca annulipes* in the non-tidal mangrove habitat of the St Lucia Estuary. Measurements were taken over a 24-h cycle and in the two extreme seasons, austral summer and winter, to examine any diel and seasonal shifts in feeding. Three hour gut evacuation experiments were conducted to determine the gut evacuation rate and potential sexual differences in feeding. It was found that under lack of tidal fluctuations, *U. annulipes* feeding is influenced by diel rhythms. In summer, males displayed a bimodal pattern of feeding, becoming more active in the morning and late afternoon with a gut evacuation rate of 0.795 h^{-1} , whereas females remained generally inactive and displayed short bouts of feeding during the day with a gut evacuation rate of 0.322 h^{-1} . The summer grazing impact of *U. annulipes* on microphytobenthos was higher compared with winter. In winter both sexes were fairly inactive, but displayed a greater consumption efficiency (65% compared with 45% in summer). *U. annulipes* feeding dynamics in a non-tidal habitat are shown to vary seasonally, daily and among sexes.

Additional keywords: consumption efficiency, feeding impacts, gut fluorescence, ingestion rate, St Lucia Estuary.

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Introduction

Fiddler crabs, like most brachyurans are opportunistic feeders (Milner *et al.* 2010). However, as deposit-feeders they mainly obtain nutrition through consumption of microphytobenthos, microheterotrophs and plant detrital matter (Crane 1975; Dye and Lasiak 1986; France 1998; Ribeiro and Iribarne 2011). The feeding rate and the subsequent impact of fiddler crabs on the associated substratum have been estimated with a variety of methods, including feeding pellet counts (Ribeiro and Iribarne 2011), gut removal and microscopic analysis (Dye and Lasiak 1986; Griffen and Mosblack 2011), stable isotopes (France 1998), amount of food scooped up (Weis and Weis 2004; Mokheles *et al.* 2011) and digital photography (di Virgilio and Ribeiro 2013).

Various physical factors affect foraging and feeding dynamics in fiddler crabs, with tidal influence playing a key role among them (Reinsel 2004; Nordhaus *et al.* 2009; Kim 2010; Griffen and Mosblack 2011). Griffen and Mosblack (2011) highlighted a strategy in which crabs display bouts of foraging behaviour during a daytime low tide and night-time high tide, whereas Reinsel and Rittschof (1995) brought to attention the sediment water content of the immediate supratidal band (fully saturated with an organic content of 1.0%), which is most favourable for fiddler crab foraging. However, in the absence of tidal fluctuations an alternative feeding strategy must be employed. Barnwell (1966, 1968) discussed the adaptation of fiddler crabs

to two cycles, i.e. day–night and tidal. It is most likely that in the absence of one, the other will dominate the rhythmic activities of fiddler crabs.

Fiddler crabs have been shown to significantly affect the benthic microalgal stocks upon which they graze. Reinsel (2004) showed that fiddler crabs in a North American sandflat reduced the organic content of sediment by over 40%, photosynthetic content by 20% and meiofaunal abundance by 60% in a single tidal cycle. Tidal inundation allows for the replenishment of nutrients and a cessation in fiddler crab grazing (Ribeiro and Iribarne 2011) and in this way is thought to alleviate the grazing pressure on microphytobenthic standing stocks. A lack of tidal inundation may thus exacerbate the effects of grazing on these photosynthetic communities.

St Lucia is the largest estuarine lake in Africa (Begg 1978) and forms a crucial component of the iSimangaliso Wetland Park, a UNESCO World Heritage Site on the east coast of South Africa. The system is characterised by prolonged mouth closure and large-scale periodic fluctuations in physico-chemical characteristics, as a result of stochastic flood and drought events (Begg 1978; Owen and Forbes 1997; Pillay and Perissinotto 2008). Currently, despite intermittent links with the nearby tidal Mfolozi River system, the St Lucia mouth remains closed and the mangrove habitat is largely non-tidal (Hoppe-Speer *et al.* 2013). Four species of fiddler crabs were once present in mangroves and sandflats around the estuary mouth but have

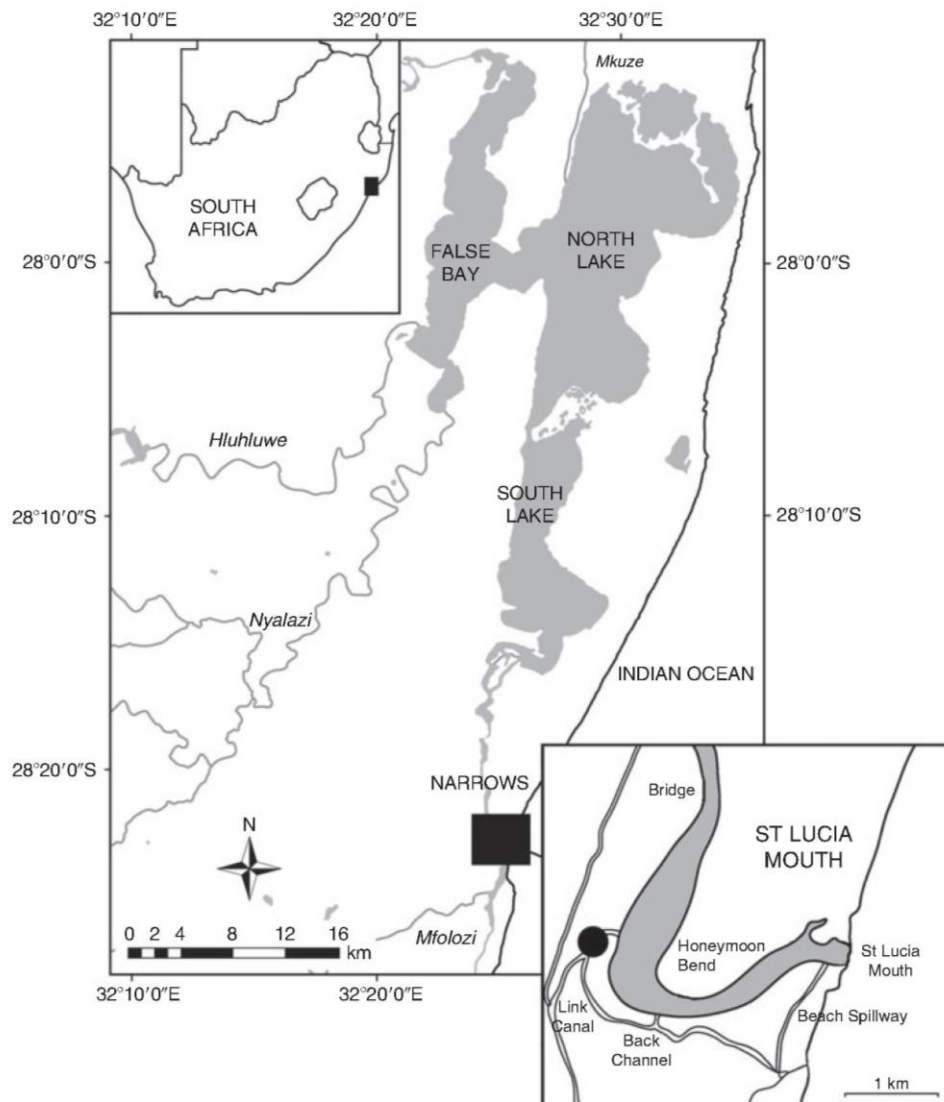


Fig. 1. Map of the St Lucia estuarine lake on the east coast of South Africa. The location of the sampled *Uca annulipes* population is indicated by a black dot.

subsequently ceased to inhabit these areas because of mouth closure and unfavourable habitat conditions (Peer *et al.* 2014). They have, however, persisted in the nearby Mfolozi mangrove habitat which is linked to St Lucia and is more suitable because of its physico-chemical stability. With the recently reconstructed beach spillway serving as a partial connection to the ocean, and allowing an inflow of freshwater from the Mfolozi, the St Lucia system is currently moving towards a wet phase (Perissinotto *et al.* 2013; Whitfield *et al.* 2013). Fiddler crabs are currently recolonising the mangrove habitat in the channel region (Fig. 1) and *Uca annulipes* appears to be the dominant species at present. The re-establishment of *U. annulipes* in the St Lucia mangrove system presents an ideal opportunity to examine the feeding dynamics of fiddler crabs in a non-tidal mangrove habitat.

Here we present a novel approach to examine feeding dynamics in fiddler crabs, using an *in situ* gut fluorescence

technique. The amount of chlorophyll-*a* present in the gut of individual crabs at the time of extraction is measured to provide an estimate of photosynthetic biomass that has been consumed. This method has been successfully applied to a range of invertebrate organisms including zooplankton (Perissinotto 1991; Perissinotto and Pakhomov 1996; Kibirige and Perissinotto 2003; Carrasco and Perissinotto 2010), bivalves (Nel 2014) and gastropods (Miranda *et al.* 2011; Díaz *et al.* 2012). As *Uca* spp. are mainly herbivorous species, consuming predominantly benthic microalgae (Wolfrath 1992; France 1998; Griffen and Mosblack 2011; Ribeiro and Iribarne 2011; di Virgilio and Ribeiro 2013), this method allows for the estimation of fiddler crab feeding impact on the standing stocks of a microphytobenthic community previously unaffected by their grazing. The method further allows for the quantification of gut passage time in fiddler crabs, by estimating the gut turnover rate of photosynthetic material.

The aim of the current study was to examine sexual, seasonal and diel differences in the feeding rate and feeding impact of *U. annulipes* on the newly occupied mangrove area of St Lucia, where the absence of tidal fluctuations influences foraging. The current study also provided an opportunity to utilise a novel approach of *in situ* gut fluorescence to examine ingestion rate and feeding cycles in *U. annulipes*. By determining the amount of chlorophyll present within the guts of individuals at the time of capture, both the 24-h feeding cycle and the gut turnover rate of *U. annulipes* can be determined with periodic sampling. The combination of density estimates and feeding rates allows the assessment of feeding impact on the microphytobenthic communities within the natural habitat of *U. annulipes*. It was hypothesised that feeding would vary with time of day, season and sex. Accordingly, the following was predicted: (1) diel differences in feeding under non-tidal conditions would be more pronounced than under normal tidal influence; (2) seasonal differences in feeding would occur; (3) the consumption–destruction efficiency of *U. annulipes* would be greatest in winter, because of limited dietary intake during this season; and (4) males and females would display differential gut turnover rates. A further aim of the present study was to describe the extent of *U. annulipes* grazing impact on the associated microphytobenthic biomass.

Materials and methods

Study site

Uca annulipes were collected from the Back Channel connecting the Mfolozi River to the St Lucia Estuary (28°23'30''S 32°24'32''E) in KwaZulu–Natal, South Africa (Fig. 1). The St Lucia Estuary is classified as an estuarine lake and *U. annulipes* occurs in bare dry areas or clearings in mangrove forests, often in association with patches of the rush, *Juncus kraussii*.

'Summer', the wet season on the east coast of southern Africa, is characterised by high levels of rainfall and spans from September to April, whereas 'winter', the dry season, occurs between May and August. Summer sampling was conducted in February 2014 (sunrise: 0536 hours; sunset: 1836 hours) whereas winter sampling was carried out in June 2014 (sunrise: 0642 hours; sunset: 1702 hours). Physico-chemical variables, including water temperature, pH and salinity were recorded using a YSI 6600-V2 multiprobe system (YSI Inc., Yellow Springs, OH, USA). The density of *U. annulipes* (individuals per square meter) was estimated through burrow counts. According to Skov and Hartnoll (2001), counting burrows is least invasive and provides a fairly accurate method for the estimation of *U. annulipes* density. Five 1 × 1-m quadrats were sampled at the study site and burrows within these quadrats were counted. Using a Bushnell Trophy Cam HD Wireless video camera (Bushnell Outdoor Products, Overland Park, KS, USA), quadrats were filmed over 24-h periods to establish activity patterns and time spent feeding by the crabs. Feeding activity, involving the movement of chelipeds from the sediment to mouthparts, was easily distinguishable from other activities including resting on the surface, burrow maintenance and fighting or interaction. Between five to seven replicates of filmed quadrats were used per season.

Gut pigment content over a 24-h cycle

To examine the gut pigment content (gut fullness) of *U. annulipes* over a 24-h period, between three to five male and female individual crabs were collected at 3-h intervals and processed immediately. A 3-h interval was chosen as the most fitting compromise to both minimise the destructive impact on the crab colony and to obtain sufficient resolution for the time series data. Crabs were rinsed in distilled water and wiped to remove any surface algae. Individuals were killed through immersion in a magnesium chloride anaesthetic solution followed by freezing as an adjunctive method. The carapace widest width (CWW) was measured using a pair of Vernier callipers. The full gut (including the foregut and hindgut) was excised from each individual and placed into a centrifuge tube containing 10 mL of 90% acetone solution for the extraction of chlorophyll-*a* and phaeopigments. After a 48-h period of dark storage and refrigeration at 4°C, pigment concentrations were measured using a 10-AU fluorometer (Turner Designs, Sunnyvale, CA), fitted with a narrow band, non-acidification system (Welschmeyer 1994). Chlorophyll-*a* and phaeopigment values were added and reported as chlorophyll-*a* equivalents (pigment). These values were size-standardised to account for any differences in animal size that may confound the gut pigment value in a method adapted from Nel (2014). To do this, the mean CWW was used in the following equation:

$$\text{Gut pigment content} = (\text{chlorophyll-}a + \text{phaeopigments}) \\ \times (\text{Average CWW} \div \text{Individual CWW})$$

Gut pigment content ($\mu\text{g pigment individual}^{-1}$) was used here as a proxy for feeding activity and differences between seasons, day–night and sexes were investigated using these data. To assess the significance of feeding peaks and inactivity, we used the mesor (midline estimating statistic of rhythm) method, where the average gut pigment content was calculated for male and female data and pooled over 24 h (Aguzzi *et al.* 2005). A significant peak is indicated by a data point above the line, whereas low activity or inactivity is represented by data points below the line.

Gut evacuation rate

Gut evacuation rate was measured over a period of 4 h. Approximately 110 crabs were pre-fed and acclimatised to filtered estuarine water, buckets and mesh for a period of 1 h in a stress-free environment (natural lighting, noise-free, ambient temperature) before they were rinsed and wiped to remove any associated algal matter. Individuals were placed in two litre buckets and submerged in filtered estuarine water (Whatman GF/F, 0.7 μm). Cornstarch was provided as a non-fluorescent food substance that would displace previously ingested food in the gut while promoting continuous feeding over time. A slightly elevated mesh was used to separate animals from faecal pellets produced, thereby preventing re-ingestion. Initial gut pigment was determined by removing 10 individuals at time zero after feeding and processing immediately. During the first 2 h, between three to five male and female individuals were identified, removed and immediately processed as described

above every 15 min. From that point onwards, individuals were only removed every hour. Treatment buckets were interspersed, where males and females as well as different samples were alternated in 20 rows of five. As above, pigments were measured and values were size-standardised using the average CWW measurement. The gut evacuation rate (k) was estimated using the slope of a linear regression fitted to log-transformed data over time (see Perissinotto and Pakhomov 1996).

Consumption–destruction efficiency

A two-compartment (water and grazer) pigment budget approach (Lopez *et al.* 1988) was used to estimate consumption–destruction efficiency. Ten individuals were placed separately in buckets filled with filtered estuarine water and cornstarch for a period of 24–48 h, thus starving the crabs of photosynthetic food substances. As described above, a mesh barrier was used to prevent ingestion of faecal pellets. The filtered water and cornstarch solution was changed every six hours to prevent unfavourable conditions arising from the build-up of metabolic wastes. Five individuals were then processed to determine background fluorescence. The remaining five were used as the ‘grazer’ component of the pigment budget approach. Estuarine water containing resuspended microbenthic algae was filtered through a 20- μm mesh to exclude grazers. The control treatment contained 300 mL of estuarine water only. Five replicates were prepared for the treatment and each individual was placed in a bucket containing 300 mL of filtered estuarine water. Treatments were placed alternatingly with a bucket containing a crab next to a bucket without a crab. Buckets were placed in two rows of five. After an incubation period of 1 h, the water was filtered (Whatman GF/F filter 0.7 μm) and filters were placed in 8 mL of 90% acetone for pigment extraction and subsequent measurement. Individuals were processed and the pigment content of their guts was measured accordingly. Any significant losses of pigment in the budget of the experimental treatment were attributed to consumption–destruction, as no faecal pellets were produced.

Microphytobenthic biomass and feeding impact

Triplicate cores were removed from the substrate using a 20-mm internal diameter corer and placed in 30 mL of 90% acetone to measure chlorophyll-*a* and phaeopigments fluorometrically as described above. Cores were selected by splitting the sample site into three and a representative core from each sub-site was removed. Microphytobenthos (MPB) biomass was then calculated as milligrams of pigment per square metre and feeding

impact determined by multiplying the average fiddler crab density by the ingestion rate, calculated for both sexes as follows:

$$I = kG/(1 - b^1)$$

where I represents ingestion rate, k is the gut evacuation rate constant (h^{-1}), G is average gut pigment concentration and b^1 is the consumption–destruction efficiency (%) (Mackas and Bohrer 1976; Perissinotto 1991).

The feeding impact (FI) was calculated using an equation adapted from (Perissinotto 1991):

$$FI = (D \times I) \times \text{time spent feeding}$$

where D represents density, I is the average ingestion rate (μg pigment individual $^{-1}$ day $^{-1}$) calculated from both sexes and time spent feeding refers to the percentage of time spent feeding within a 24-h period which was estimated from the filmed quadrats as described above.

Data analysis

Data were size-standardised to account for size variation between individuals and gut pigment content is reported as micrograms of pigment per individual. Independent sample t -tests were performed in SPSS version 21 for Windows (IBM Corp., Armonk, NY, USA), to investigate diel, seasonal and sexual differences in gut pigment contents once statistical assumptions of normality and equality of variance had been met. t -tests were also used to test for differences between the gut evacuation slopes of males and females and between seasons (Zar 1984). P -values were used to indicate statistical significance at a level of 0.05.

Results

Physico-chemical environment

Mean water temperature was 28.18°C in summer and 20.71°C in winter whereas salinity varied from 7.31 ± 1.90 (s.d.) in summer to 9.33 ± 0.13 (s.d.) in winter. Average microphytobenthic biomass in summer was estimated to be 44.11 ± 22.85 mg pigment m^{-2} whereas the average winter biomass was 41.17 ± 7.79 mg pigment m^{-2} (Table 1). Values ranged from 20.94 mg pigment m^{-2} to 76.56 mg pigment m^{-2} in summer and from 33.52 mg pigment m^{-2} to 55.17 mg pigment m^{-2} in winter.

Table 1. Estimated gut evacuation rate (k) (expressed as a range) of *Uca annulipes* males and females in summer and winter

I represents the ingestion rate (μg pigment individual $^{-1}$ day $^{-1}$) and b is the consumption–destruction efficiency (%). The feeding impact (FI , mg pigment m^{-2} day $^{-1}$), microphytobenthos (MPB) biomass (mg pigment m^{-2}) and percentage consumption are also expressed

Season	Density (individual m^{-2})	Males		Females		I	b (%)	Biomass		
		k (h^{-1})	R^2 (%)	k (h^{-1})	R^2 (%)			FI	MPB biomass	Consumption (%)
Summer	20 ± 7	0.270–0.795	59.79	0.182–0.322	56.61	182–658	45	1.75–4.73	44.11 ± 22.85	3.98–10.73
Winter	33 ± 8	0.127–0.212	58.73	0.187–0.410	53.99	116–153	65	1.42–2.65	41.17 ± 7.79	3.42–6.44

24-hour feeding cycle

Analysis of video footage showed that the period of darkness coincided with a period of inactivity, with no *Uca annulipes* observed at the surface during this time. At dusk, crabs retreated into their burrows and remained there for the duration of the night. During daylight hours, crabs were most active in the morning and late afternoon, when all crabs within plots surfaced to feed, interact or maintain their burrows (Fig. 2). At approximately midday, reduced activity was observed, with most crabs retreating into their burrows or simply resting on the surface. The average percentage of time that crabs were observed feeding within a 24-h period was 54% in summer and 46% in winter.

The sex ratio (M : F) was lower in summer (1 : 0.32) compared with winter (1 : 0.96).

The average CWW of crabs collected in summer was 16.68 mm ± 3.38 s.d., whereas crabs caught in winter were on average 16.42 mm ± 1.96 s.d. The average gut pigment content calculated over a 24-h period for males was significantly higher ($t = -2.262$; $P = 0.028$) in summer compared with winter (Table 2). There was, however, no significant difference ($t = 1.006$; $P = 0.323$) in female gut pigment content between summer and winter (Table 2). In summer, diel gut pigment values (average ± s.d.) for males ranged from 529.6 ± 397.0 µg pigment individual⁻¹ during the day to 163.7 ± 114.1 µg

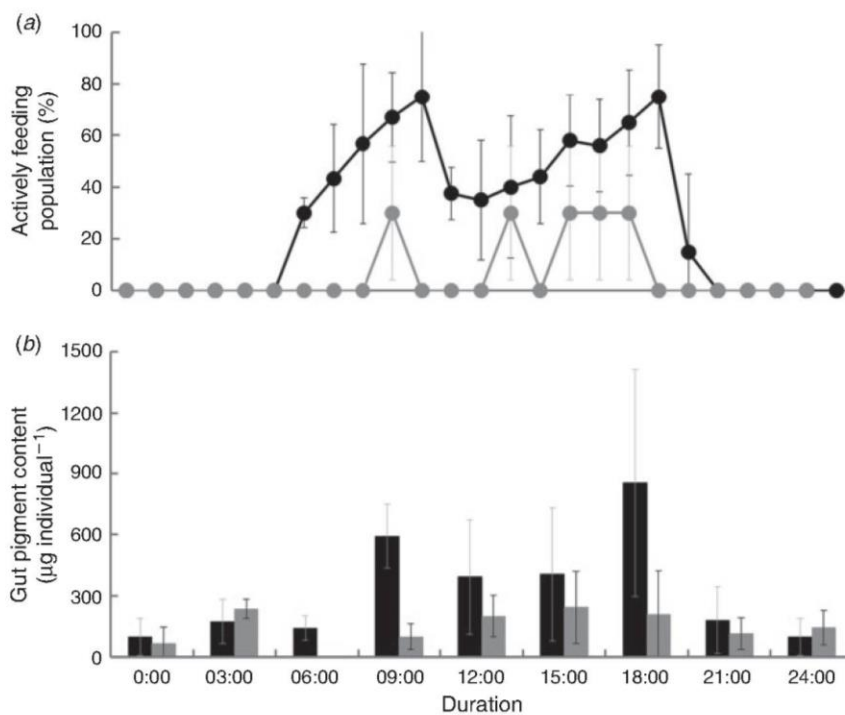


Fig. 2. Video footage data showing (a) the percentage of the *Uca annulipes* population actively feeding throughout the day in summer and (b) the corresponding gut pigment content. Males are represented by black and females by grey dots.

Table 2. Seasonal and diel variation in gut pigment content (G) of *Uca annulipes* males and females
Gut pigment content is represented as mean ± s.d. (µg pigment individual⁻¹)

	Male		Female	
	Summer	Winter	Summer	Winter
G (day)	529.6 ± 397.0	127.6 ± 82.00	192.9 ± 159.5	210.6 ± 67.66
G (night)	167.7 ± 114.1	213.2 ± 114.0	163.7 ± 79.6	224.9 ± 165.9
G (average)	359.7 ± 349.3	175.6 ± 108.3	181.2 ± 130.5	217.8 ± 123.9
diel variation				
<i>t</i>	3.203	-1.747	0.412	0.246
<i>P</i>	0.004	0.093	0.687	0.794
d.f.	26	24	13	20
seasonal variation				
<i>t</i>		-2.262		1.006
<i>P</i>		0.028		0.323
d.f.		52		26

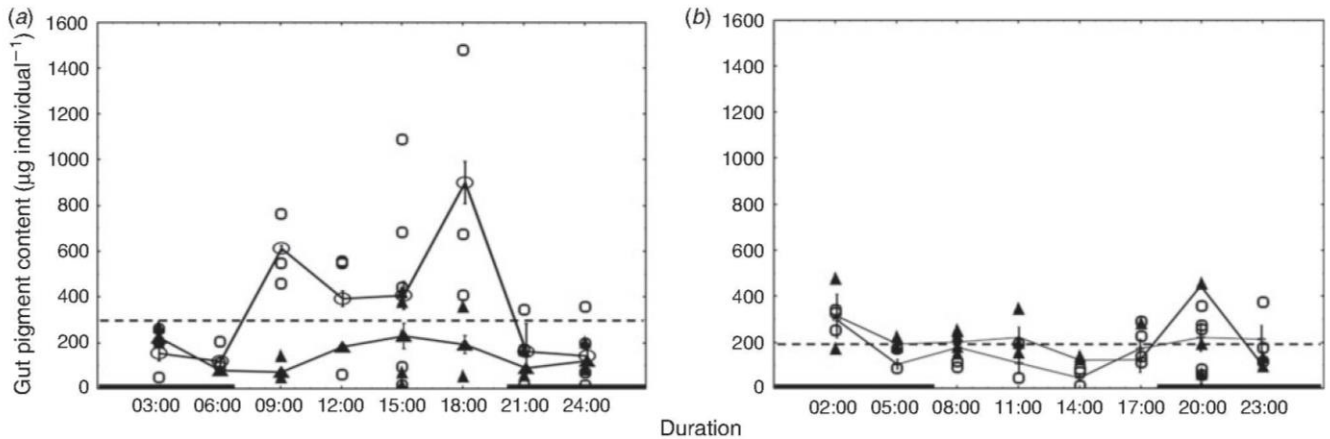


Fig. 3. Gut pigment content ($\mu\text{g pigment individual}^{-1}$) of *Uca annulipes* over a 24-h period in (a) summer and (b) winter. The black line on the x-axis indicates the period of darkness between sunset and sunrise, whereas the dotted line represents the calculated mesor. Males are represented by open dots and females by black triangles. Moving averages are indicated by solid lines.

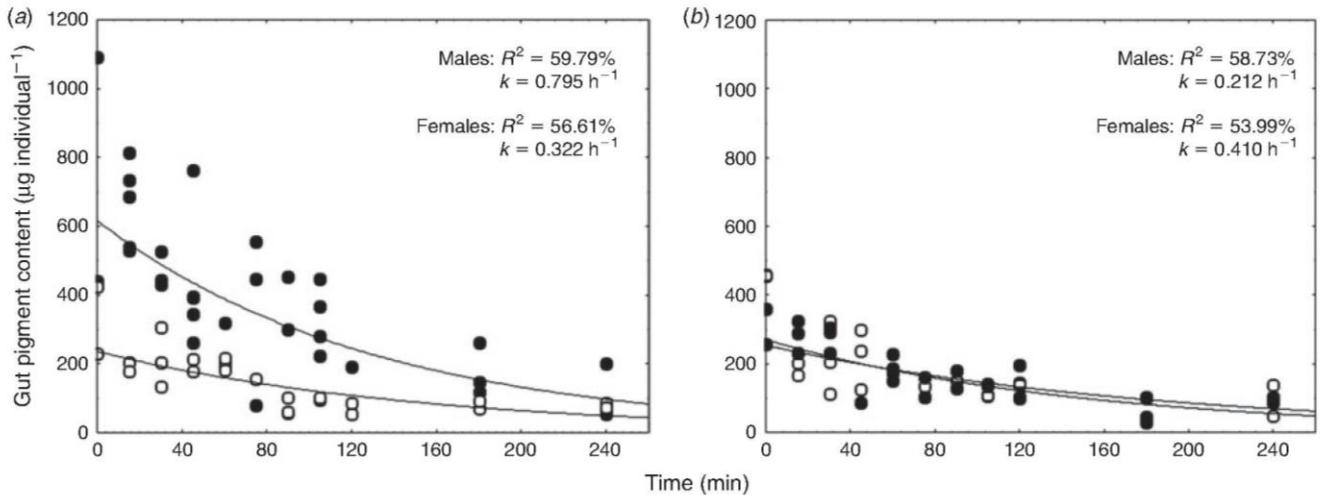


Fig. 4. Gut evacuation rate of *Uca annulipes* in (a) summer and (b) winter. Males are represented by black dots whereas females are represented by open dots. The maximum gut evacuation rate (h^{-1}) and coefficient of determination are represented for both sexes.

pigment individual⁻¹ at night, exhibiting a significant difference ($t = 3.203$; $P = 0.004$) (Table 2, Fig. 3). Gut pigment content over a 24-h period coincided with feeding activity observed from video footage (Fig. 2). Females, however, displayed no significant difference between day and night gut pigment content ($t = 0.412$; $P = 0.687$). In winter, there was no significant difference between day and night gut pigment values for either males or females (Table 2).

Gut evacuation rate

The gut evacuation rate (k) for males was significantly faster in summer, ranging from 0.507 to 0.795 h^{-1} , and much slower in winter, ranging from 0.001 to 0.211 h^{-1} ($t = 79.62$; $P < 0.05$). Females displayed a lower k compared to males (summer: $t = -35.92$; $P < 0.05$; winter: $t = -13.58$; $P < 0.05$), with values ranging from 0.011 to 0.322 h^{-1} in summer and significantly higher in winter (0.086 to 0.410 h^{-1} ; $t = -3.60$; $P = 0.001$). Negative exponential curves represented the best fit

to relate the evacuation of pigments by individuals over the 4-h period in which they were deprived of photosynthetic food substances (Fig. 4, Table 1).

Consumption–destruction efficiency, ingestion rate and feeding impact

In summer, the consumption–destruction efficiency (b) was estimated at 45% of total autotrophic food matter ingested, whereas in winter b was estimated at 65% (Table 1). Ingestion rates calculated using these values were higher in summer compared with winter, with values ranging between 182 and 658 $\mu\text{g pigment individual}^{-1}$ and between 116 and 153 $\mu\text{g pigment individual}^{-1}$ respectively (Table 1).

The feeding impact was estimated by accounting for the average proportion of the day that crabs were observed engaging in feeding activity (13 h in summer and 11 h in winter). Density was higher in winter compared with summer (Table 1). Despite the lower density of the population in summer compared with

winter (Table 2), a higher potential feeding impact was found in summer, when the local *U. annulipes* population graze between 1.754 and 4.732 mg pigment m⁻² day⁻¹. In winter, the potential feeding impact was lower ranging between 1.419 and 2.652 mg pigment m⁻² day⁻¹. The overall percentage of MPB consumed by the *U. annulipes* population appears to be fairly low, with only 3.98–10.73% of the total MPB biomass consumed daily in summer, whereas 3.42–6.44% was consumed in winter (Table 1).

Discussion

Currently, the St Lucia population of *Uca annulipes* does not experience any tidal influence, so foraging appears to be driven by diel rhythms. This is clearly the case in summer when feeding activity by males and females is prevalent only during daylight hours (Fig. 2). Males further display a bimodal pattern of feeding, being most active in the morning and late afternoon, and spending the midday hours in their burrows or simply resting on the surface. The habit of feeding during daylight hours has previously been attributed to visual localisation of food (Nordhaus *et al.* 2009). The bimodal pattern of feeding, however, has not been sufficiently examined in fiddler crabs and, although it has been observed in other fiddler crab species including *U. pugilator* and *U. princeps* (Barnwell 1966; Stillman and Barnwell 2004), both species were under the influence of tidal and diel rhythms. In a study conducted by Gianuca and Vooren (2007) on the rock crab *Grapsus grapsus*, the authors found a similar pattern of surface presence, where midday surface activity is greatly reduced. The authors suggested that avoidance of insolation plays a role in this, as crabs seek shelter during the midday high temperatures. It is possible that the same applies to fiddler crabs in St Lucia during summer, because of more extreme temperature peaks during the day.

Barnwell (1966, 1968) highlighted the entwined nature of tidal and diel influence on fiddler crab activity. Whereas foraging times are primarily influenced by tidal patterns, a diel rhythm is superimposed over this influence leading to a complex optimal foraging strategy which varies between species and habitats. The influence of tide on fiddler crab feeding activity may be related to the optimal sediment water content being found just above the water mark (Reinsel and Rittschof 1995), where the more saturated the sediment is, the easier it is to scoop it up. Thus in the absence of tidal fluctuations, foraging of *U. annulipes* appears to be governed by diel rhythms, including those of light and temperature. It is important to note, however, that a complex plethora of external abiotic and biotic factors along with an endogenous circadian cycle influence locomotor rhythms in crustaceans (Kronfeld-Schor and Dayan 2003; Chiesa *et al.* 2010). During our study, as the experiment was carried out under natural conditions, these influential factors were not controlled for. Although the light and temperature associated with diel rhythms are known to influence feeding of fiddler crabs, this can only be determined under laboratory conditions where all influential cues are controlled for.

Feeding activity decreased in the winter, with *U. annulipes* displaying lower gut pigment content and evacuation rates during this period (Fig. 3). Metabolism is known to decrease with temperature in poikilotherms (Gillooly *et al.* 2001) and

therefore the reduction in activity of *U. annulipes* means that there is less time spent feeding during winter months. Energy requirements are also lower during this period, as crabs exhibit prolonged periods of surface inactivity and lower rates of reproduction (Emmerson 1994). However, it is thought that feeding rate or gut evacuation rate is inversely proportional to food extraction from the sediment (Mokhlesi *et al.* 2011). In the current study ~45% of all ingested MPB was consumed in 1 h during summer, whereas the winter consumption–destruction efficiency was estimated at ~65%, lending support to the prediction that consumption–destruction efficiency would be greater in winter. This could be because of a seasonal difference in metabolic requirements. The metabolic rate of crabs decreases with decreasing temperature in winter, and there is a lower intake of food which is digested at a slower rate. This is indicated by the slower gut evacuation rate observed in *U. annulipes* during winter compared with summer (Table 1; Fig. 4). However, although energy requirements are comparatively lower in winter, consumption–destruction efficiency appears to increase so that sufficient energy is still obtained despite the lower food intake. Higher consumption–destruction efficiency can be most beneficial in winter, in order to maximise nutrition intake from the limited amount of food ingested (Giguere 1981; Navarro and Winter 1982).

Aside from the influence of temperature, feeding activity and gut evacuation rate vary between sexes (Figs 3, 4). Differential feeding rate between sexes has been well documented (Weissburg 1993; Weis and Weis 2004; Mokhlesi *et al.* 2011) and is generally attributed to the sexual dimorphism of fiddler crabs. Although the current study did not directly account for the use of chelipeds in determining the feeding rate, the time spent feeding by each sex and the pigment content observed in their gut both support this explanation of sexual difference in fiddler crab feeding. The method of feeding in fiddler crabs has been extensively described, whereby the minor cheliped is used to scoop up grains of sand and pass these to the mouth (Miller 1961; Icely and Jones 1978; Mokhlesi *et al.* 2011). Lim (2004) showed that *Uca annulipes* in Singapore has a greater number of spoon-tipped setae, compared with *Uca vocans* which inhabits muddy sediment, as opposed to *Uca annulipes*' preference for more coarse sandy habitats. Crane (1975) provided similar anecdotal evidence for the incidence of a greater number of spoon-tipped setae in species inhabiting sandy substrata as opposed to those inhabiting muddier substrata. Although males feed at a lower rate compared to females, because of their inability to feed with their enlarged cheliped, they compensate for this by spending more time feeding than females and as a result process the same amount of sediment on a daily basis (Mokhlesi *et al.* 2011). The current study is in agreement with Mokhlesi *et al.* (2011). Males spend a larger portion of time feeding compared with females (Fig. 2). However, males exhibited a higher gut evacuation rate in summer, compared with females (Fig. 4). This may be explained by the continuous feeding activity of males during the day, which leads to a higher gut turnover rate, as food is constantly being ingested and subsequently displaced. Conversely, females spend a large amount of time in their burrows and display short erratic bouts of feeding behaviour throughout the day. While *U. annulipes* are in their burrows and feeding activity ceases, previously ingested

food is not displaced and thus a slower rate of evacuation is detected. Increased gut retention may present advantages in terms of more effective consumption for both sexes as discussed above. Females in general seem to be less active than males and display less seasonal variation, whereas males spend more time feeding in summer and display a markedly less efficient consumption rate than in winter.

Fiddler crabs can occur in large populations, with densities of up to 200 individuals per square meter (Bertness 1985; di Virgilio and Ribeiro 2013). At high densities, fiddler crab communities could have a significant effect on the MPB biomass upon which they feed. In St Lucia, the feeding impact of this population is not sufficient to reduce the MPB biomass significantly over a single day, with a maximum of 10.73% of total MPB biomass potentially being consumed per day in summer and only 6.44% in winter. In this case, food availability far exceeds the feeding impact of the *U. annulipes* population. Reinsel (2004) highlighted the increase in organics and patches of chlorophyll-*a* in winter, when fiddler crabs are minimally active, indicating that they may play a significant role in structuring the associated environment. Ribeiro and Iribarne (2011) also indicated the low feeding impact of fiddler crabs on microphytobenthic productivity. In the St Lucia mangroves MPB growth appears to be governed by favourable physico-chemical growth conditions, as opposed to *Uca annulipes* feeding activity. However, there are currently three *Uca* species co-occurring in nearby mangroves along with various sesamids (Peer *et al.* 2014), as well as six species of gastropods (Perissinotto *et al.* 2014). Therefore, the cumulative impact on MPB biomass and its availability remain unknown. Furthermore, the current study only measures the impact of feeding on MPB biomass and does not account for the effects of disturbance through burrowing or movement across the ground (i.e. bioturbation). Reinsel (2004) indicated that cumulatively, the disturbance and feeding impact of fiddler crabs on associated benthic habitats is significant, especially in summer when crabs are highly active. These secondary impacts of *U. annulipes* on MPB communities were not dealt with in the present study.

Time spent feeding also affects the estimated feeding impact. The potential impact of *U. annulipes* on the MPB community was calculated based on the amount of daylight hours in each season. Assuming that *U. annulipes* are only active on the surface during the day and thus only feed during this time, they could potentially spend 13 h feeding in summer and 11 h in winter, per day. The observed feeding impact was higher in summer compared with winter, even though *U. annulipes* density was higher in winter and MPB biomass was slightly higher in summer. The high ingestion rate, combined with two hours more spent for feeding on higher MPB biomass in summer compared with winter, can be attributed to optimal growth conditions of MPB in summer, i.e. high levels of rainfall, increased humidity and warmer temperatures (Jury 1998; Whitfield and Taylor 2009). In tidal systems, MPB communities are subjected to regular inundation, which leads to a cessation in feeding activity and resupply of nutrients, thereby allowing for the regeneration of photosynthetic material (Reinsel 2004; Ribeiro and Iribarne 2011). In St Lucia, the lack of tidal inundation means that feeding can occur continuously throughout the day. Any cessation in feeding activity would be brought

about by endogenous rhythms or external factors including light, temperature or predation as mentioned above.

The *in situ* gut fluorescence technique appears to be well suited to the study of fiddler crab feeding ecology owing to several factors. First, fiddler crabs are largely primary consumers and MPB forms a significant portion of their diet (Wolfrath 1992). As this method relies primarily on the ingestion and consumption of autotrophic pigmented dietary matter, it works well with most primary consumers. However, although MPB forms a significant proportion of the diet of *U. annulipes*, other food sources may also be present in the diet, including detritus and microheterotrophs (Crane 1975; France 1998; Reinsel 2004; Ribeiro and Iribarne 2011). The contribution of these food items to the diet of *U. annulipes*, was not considered in the current study. Second, the immediate cessation of the digestive process and extraction of pigments allows for accurate instantaneous measurements of gut content at any time. Therefore the method is suitable for examining small-scale feeding cycles and elucidating diel differences in feeding. Lastly, this method can be applied at community and population scales to determine more accurately the impact of macrobenthos on MPB communities and to compare the impact between various populations while investigating localised environmental effects. Methods employing stable isotope analysis (France 1998) and gut content analysis (Dye and Lasiak 1986; Griffen and Mosblack 2011) are better suited to the quantification of heterotrophic material in the diet. France (1998), however, showed that fiddler crabs prefer cyanobacteria over vascular plant detritus in mangrove ecosystems. A further advantage of stable isotope analysis is that it measures assimilation as opposed to ingestion. The combination of both gut fluorescence techniques as well as stable isotope analysis to consider all possible food sources and the proportion of each food item assimilated as well as the impact and fine-scale dynamics of feeding behaviour could be considered an ideal way forward for future studies.

Lastly, it is noteworthy to mention that the prolonged mouth closure and subsequent lack of tidal fluctuation in the St Lucia Estuary is not the natural state of the system and has been brought about by a combination of anthropogenic manipulation and severe drought conditions experienced over the last 13 years (Whitfield and Taylor 2009; Taylor 2013). The interruption and alteration of tidal influences in mangrove habitats is a potentially detrimental phenomenon (Hoppe-Speer *et al.* 2013), which has received very little attention yet. However, in the face of climate change and an increase in anthropogenic developments worldwide, this phenomenon will most likely become more common globally (Polidoro *et al.* 2010). It is thus important to understand and consider the ecological changes brought about by such events.

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Chapter 6

A lack of tidal influence is brought about by reduced marine connectivity. This is often the case in coastal systems that have been subjected to anthropogenic modifications. A possible driver of *Uca* survival in the St Lucia estuarine system includes reduced marine connectivity affecting zoeal development through retention within the St Lucia system. Here zoeae would be subjected to increased predation, salinity fluctuations and silt loading. All African fiddler crab species are known to undergo a marine-dependent larval phase during development. It is expected that with the closure of the St Lucia Estuary mouth to the sea, fiddler crabs would migrate out of the unfavourable St Lucia environment. They could form refuge populations in the nearby Mfolozi mangroves and recolonize the St Lucia mangroves once marine connectivity has been restored.

This chapter is currently in press in *African Journal of Marine Science*.

Suspended silt and salinity tolerances of the first zoeal stage of the fiddler crab *Uca annulipes* (Decapoda: Brachyura) and why marine connectivity is essential to the survival of this species.

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ABSTRACT

Fiddler crabs (*Uca* spp.) undergo the zoeal stage of development in open ocean waters experiencing stable salinity levels, low turbidity and reduced predation. The St Lucia Estuary has undergone many geomorphological changes, both natural and anthropogenic, and the estuary mouth has been closed since the early 2000s. Marine connectivity therefore is limited, occurring only on the flood tide through channels connected to the adjacent Mfolozi River. Larval export from the St Lucia Estuary is thus virtually non-existent. A study was undertaken to examine the silt and salinity tolerance of *Uca annulipes* first stage zoeae, to determine whether survival in the closed estuary conditions would be possible. Salinity tolerance was narrow, with zoeae displaying 100% mortality at salinities <20 ppt and >35 ppt after five days. Zoeae were widely tolerant to silt loading and did not display a significant decrease in survival over a range of 0 NTU to 1000 NTU. A limited salinity tolerance is in accordance with the life history strategy of this species, while a high tolerance to turbid waters can be advantageous to small-bodied merozooplankton. Marine connectivity is thus essential for the persistence of *Uca annulipes* in this estuarine habitat.

RUNNING TITLE: Effects of silt and salinity on fiddler crab zoeae

KEYWORDS: Larval export; salinity tolerance; turbidity; St Lucia Estuary; closed mouth conditions; global change

INTRODUCTION

With the global advance of a changing climate and increasing anthropogenic activity around aquatic systems, changes in the hydrodynamics of estuaries, lagoons and coastal lakes are inevitable. It is predicted that as climate change progresses, an increase will be seen in the frequency of extreme climatic events such as droughts and floods (Easterling et al. 2000). Such events alter the freshwater inflow to estuaries and affect the formation of sand berms at the ocean/estuary interface (Gillanders et al. 2011). Regarding anthropogenic change, the redirection of water flow and change in land use are predicted to cause habitat destruction and a decrease in riverine inputs to estuaries across the globe (Kennish 2002). This will further influence the degree of marine connectivity experienced by these estuaries, lagoons and coastal lakes and impact the physico-chemical conditions of these systems. Naturally, associated ecosystems are affected by these changes along with migratory species. Although studies have previously addressed the salinity tolerance and estuarine retention of fiddler crab zoeae (O'Connor & Epifanio 1985; Spivak & Cuesta 2009), to our knowledge, no studies have directly examined the effect of reduced marine connectivity on the development and survival of species with a marine-dependant life stage.

The St Lucia Lake is part of a UNESCO World Heritage site and is a Ramsar Wetland of International Importance. It consists of three connected lakes all joined to the estuary mouth via a channel called the Narrows. Historically the lake was connected to the adjacent Mfolozi River via a back channel, link canal and both systems formed a combined inlet open to the sea. With the advent of agriculture, canalisation of the Mfolozi River in 1927 allowed for the inflow of large amounts of silt into both systems. As a result, the two mouths were separated in the 1950s and the St Lucia Estuary mouth was artificially maintained open until 2002 when it closed off to the sea (Whitfield et al. 2013). While the two systems were still linked via the back channel and link canal, marine connectivity in St Lucia was minimal and salinity levels were not tidally influenced (Whitfield et al. 2013). Episodic flooding may have further rapidly decreased the salinity within the system (Cyrus 1988), while drought conditions and habitat deterioration prevailed with water levels becoming very low.

Under closed mouth conditions, a reverse salinity gradient formed within the system, where fresh to brackish waters were recorded near the mouth while the upper reaches of the estuary became hypersaline (Carrasco & Perissinotto 2012). Furthermore, turbidity levels throughout the lake increased under closed mouth conditions. The ecology of the lake was affected by the subsequent change in the system due to the adverse effects of elevated turbidity and drastic salinity fluctuations (Cyrus et al. 2011; Carrasco & Perissinotto 2012). Species that were less mobile or sedentary were trapped in the system and died out (Nel et al. 2012; Perissinotto et al. 2014), while species that were highly mobile and able to leave the system formed small refuge populations elsewhere (Peer et al. 2014). A recent management decision was taken to reconnect the beach spillway between the Mfolozi and St Lucia estuaries in an attempt to manage the problem of sporadic changes in physico-chemical parameters and drought-like conditions (Whitfield et al. 2013).

Fiddler crabs (Genus *Uca*) are flagship species of mangrove swamps, sand flats, mud flats and other intertidal habitats. This is largely due to their cosmopolitan distribution, pronounced heterochely in males (characteristic of the genus) and sometimes brightly patterned and coloured carapaces and appendages. The life cycle of fiddler crabs has been extensively outlined (Crane 1975; Brodie et al. 2005), with females undergoing a two week gestation period and releasing larvae on a crepuscular high tide, so that they can be carried out to the open ocean with the nocturnal ebb flow (Christy 1989; Forward Jr et al. 2001). Zoeae undergo multiple moults in open water until the megalopa stage is reached. At this point they re-enter the estuary using a flood-tide transport mechanism (Borgianini et al. 2012) and settle once they reach the first crab instar stage (O'Connor 1991; Tankersley & Forward Jr 1994). Settlement cues include chemical cues from adults as well as physico-chemical parameters, the time of day and habitat suitability (O'Connor 1993; Brodie et al. 2005).

Four species of *Uca* once inhabited the mangrove swamps around the St Lucia mouth area (Millard & Broekhuysen 1970) i.e. *Uca annulipes* (H. Milne Edwards, 1837), *Uca chlorophthalmus* (H. Milne Edwards, 1837), *Uca hesperiae* Crane, 1975 and *Uca urvillei* (H. Milne Edwards, 1852). However, in recent surveys all four species were recorded as absent (Peer et al. 2014). The closure of the estuary mouth was suggested as responsible for the disappearance of *Uca* spp. from the system. The reduced marine connectivity would have rendered the system unsuitable for the development of *Uca* larvae and maintenance of the community. Whilst megalopae would be carried into the system via the back channels during the flow tide, it is unlikely zoeae would have been carried out to sea. Aside from the increased predation experienced by the zoeae trapped in the estuary within this period (Morgan & Christy 1996), low salinity and silt loading would have also affected survival and recruitment (Cyrus et al. 2011). Recently small populations of *Uca* spp. have been observed in mangrove habitats near the mouth. Recolonisation is fostered by the presence of refuge populations in the mangrove swamps around the Mfolozi River. However, as more extreme flood and drought events are predicted for the future, it is imperative to determine more accurately the factors affecting survival and recruitment of these flagship species in the mangrove swamps of St Lucia.

Larvae are typically stenohaline, able to tolerate stable marine environments (Morgan 1987), however a few exceptions have a wider range similar to their adult counterparts (Epifanio et al. 1988). The aim of this study was to determine whether *Uca annulipes* zoeae could possibly survive under closed mouth conditions by examining the tolerance of first stage larvae to salinity and silt loading. Zoeae were subjected to a range of salinities and turbidity levels in the laboratory. It is hypothesised that at low salinity and high turbidity levels zoeae would experience increased mortality due to osmotic stress (Anger 2003) and physical abrasion (McCabe and O'Brien 1983) respectively. Currently two of the four *Uca* species have recolonized the mangroves i.e. *U. annulipes* and *U. chlorophthalmus*. *Uca annulipes* is currently the most abundant and widespread species of fiddler crabs within the system and was thus used as test species in this study.

MATERIALS AND METHODS

Study site and physico-chemical parameters.

The St Lucia Estuary is located between longitudes 32°20' and 32°35'E and latitudes 27°50' and 28°25'S on the north east coast of South Africa. It is the largest estuarine system in Africa, spanning an area of approximately 300 km² (Begg 1978). The lake is characterised by prolonged flood and drought events and naturally experiences large scale salinity fluctuations. Despite recent increased marine connectivity, St Lucia is still considered a non-tidal habitat. Zoeae were collected from an island in the Narrows region of the estuary close to the mouth (Fig. 1).

Physico-chemical parameters were measured using a YSI 6600-V2 multiprobe system. Turbidity was measured in Nephelometric Turbidity Units (NTU) and salinity was measured in practical salinity units. Historical data were also obtained from published literature (Fielding et al. 1991; Cyrus 1992).

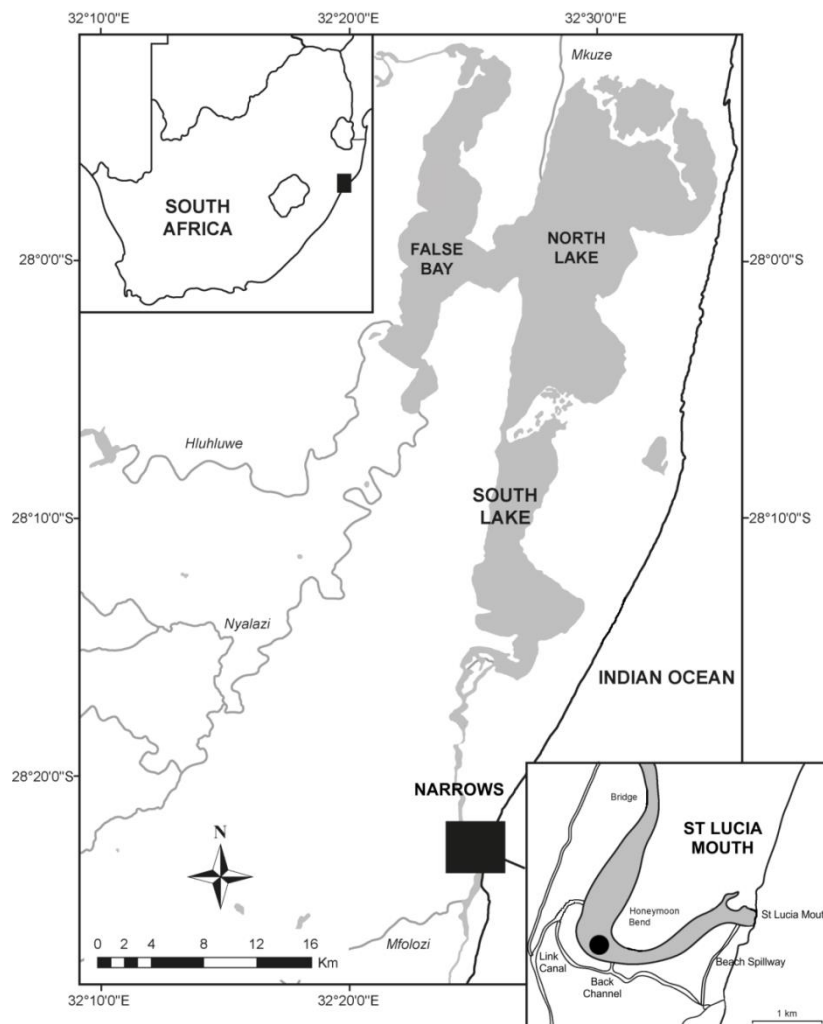


Fig. 1: Map of the St Lucia estuarine lake on the east coast of South Africa. The sampling location is indicated by a black dot.

Larval collection and maintenance

Zoeae were collected on the 7th of January 2015, 2 days after the full moon as this is known to be the ideal time for spawning. A 100µm zooplankton tow-net was used and, once identified using a field microscope, zoeae were placed in buckets of water collected at the site. Once in the lab, buckets were aerated and zoeae were acclimated for a period of 16 hours. The larvae were subject to a 12:12 h light:dark regime using artificial light in the laboratory and maintained at a constant temperature (25°C) and salinity (35) in the holding buckets. A stable marine salinity of 35 was maintained as this is the optimal temperature for the survival of *Uca* larvae. No molting occurred during the experimental period so it is safe to assume that the length of time taken for stage I zoeae to molt to stage II is at least five days.

Salinity tolerance

Estuarine water was filtered through a Whatman Glass Fibre Filter (0.7 µm mesh size) to remove any unwanted grazers. For the shock treatment, salinity solutions of 0, 10, 20, 35 and 50 were pre-made using 'Instant Marine' artificial aquarium salt and larvae were placed directly in the test salinity. For the acclimation experiment, zoeae were placed in treatments and the desired salinity was reached over a period of 24 hours at which point the experiment began. During this time, the rate of change of salinity was no greater than 3 units.hr⁻¹. In both experiments, salinity was monitored daily throughout the experimental process using a handheld refractometer and a stable salinity was maintained throughout the experiment. Each treatment contained five replicates, with ten individuals per replicate placed in a 100ml polyethylene vial and mortality monitored at hours 2, 4, 8, 16, 24, 48, 72, 96, and 120 hours. Water in each treatment was changed every two days and zoeae were fed 1 ml per treatment of a phytoplankton stock solution daily. Larvae were maintained under the 12:12 LD cycle at 25°C at a turbidity of <3 NTU.

Silt tolerance

Silt was collected from the site using a shovel and combusted at 450°C for 4 hours to remove any organic matter. Once more, estuarine water was filtered through a Whatman Glass Fibre Filter (0.7 µm mesh size) to remove any unwanted grazers from the experimental medium. For the shock experiment, filtered estuarine water was used to make turbidity treatments of 0, 50, 100, 500 and 1000 NTU and zoeae were then placed directly into each treatment. Turbidity in the mouth and Narrows region has never been recorded to exceed 300 NTU (Carrasco et al. 2013; Jones et al. 2015). However, Jones et al. (2015) point out that the excessive turbidity (2500 NTU) of the nearby Mfolozi system could potentially increase the turbidity of the St Lucia itself if the two systems are reconnected as they have been in the past. For this reason, a maximum turbidity level of 1000 NTU was considered to be a more than sufficient experimental limit. For the acclimation experiment, the desired turbidity was reached over a 24 hour period with a maximum rate of change of 30 NTU.hr⁻¹ and the same turbidity values were used. Each treatment contained five replicates, with ten individuals per replicate placed in a 100ml polyethylene vial and mortality monitored at hours 2, 4, 8, 16, 24, 48, 72, 96, and 120 hours. Turbidity was monitored regularly throughout the five day

experiment using a HANNA HI 93703 portable turbidity meter. Silt was kept in suspension by placing all treatments on a plankton wheel rotating at a speed of 4 revolutions per minute. Water in each treatment was changed every two days and zoeae were fed 1 ml per treatment of a phytoplankton stock solution daily. Larvae were maintained under the 12:12 LD cycle at 25°C at a salinity of 35.

Data analysis

All data were analysed and graphs constructed using STATISTICA v 12 (Statsoft 2013). Data were not normally distributed even after transformation. However, it has been noted that ANOVA is robust enough to perform statistical analyses on data, even if they are not normally distributed (Zar 1996; Carrasco & Perissinotto 2011). So a two-way repeated measures ANOVA was used to examine the effects of salinity, turbidity and time as well as the interaction effects of salinity/time and turbidity/time on the survival of zoeae in both the shock and acclimation treatments. Each bottle containing ten individuals was considered as one replicate. Time was used as the within-subject factor, while silt and salinity were used as between-subject factors. Ten levels were used for each test. An independent samples t-test was used to determine whether survival varied between acclimation and shock treatments of salinity and turbidity.

RESULTS

Physico-chemical parameters

Historical salinity data show the changes in salinity near the estuary mouth since 1964 (Fig. 2A). A trend of low salinities (8.2 ± 1.9 SD) over the last ten years is seen with two intermittent spikes indicating the breach following Cyclone Gamede (March 2007) and the excavation of the beach spillway connecting the Mfolozi and St Lucia estuary mouths (July 2012). Turbidity levels in the Narrows region and near the mouth have seldom exceeded 300 NTU (Fig. 2B). There is a substantial lack of turbidity data prior to 1981 and from 1983 to 2004.

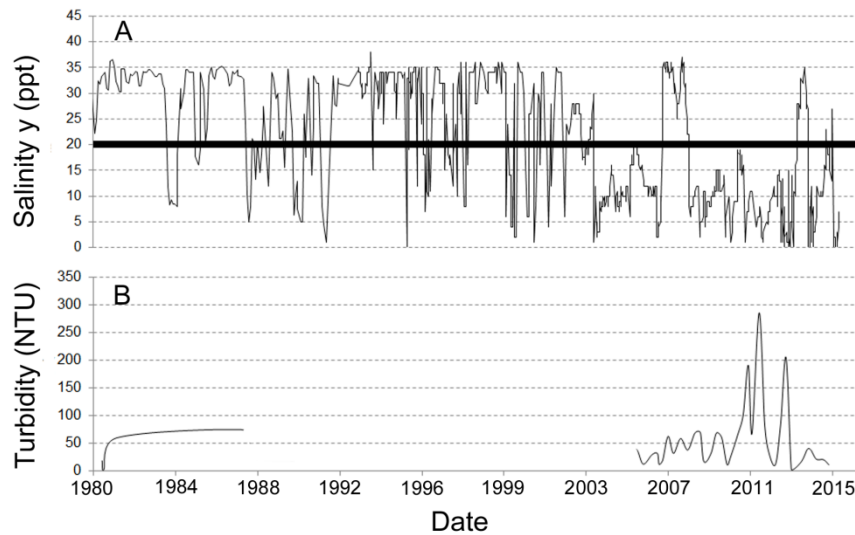


Fig. 2: Changes in (A) Salinity (ppt) and (B) turbidity (NTU) levels in the St Lucia mouth and Narrows region between 1980 and 2015. The thick line in A indicates the minimum value at which > 50% of first stage larvae survived under experimental conditions. Turbidity data for the period 1980 – 1983 were obtained from Cyrus (1992) and Fielding et al. (1991). No turbidity data are available for the period between the 1983 and 2004.

Response to salinity

Salinity was found to significantly affect the survival of first stage zoeae after five days (Table 1; Fig. 3). In the shock experiment (Fig. 3A), 54% survival was recorded for animals exposed to 35 salinity treatments. Survival of animals at a salinity of 20 was 34% after five days, while no animals survived the 0, 10 and 50 salinity treatments. Animals in the 0 and 50 salinity treatments died within the first four hours exhibiting lack of motion, pulse or response to a stimulus. Zoeae maintained at a salinity of 10 reached 100% mortality after 48 hours.

Table 1: Repeated-measures ANOVA comparing the effects of salinity, turbidity and time on the survival of *Uca annulipes* first stage zoeae over a period of five days.

Treatment	Variable	Sum of squares	df	F	p-value	
Salinity	Shock	Salinity	202150	4	252.7	< 0.001
		Time	149300	9	365.9	< 0.001
		Salinity x Time	50170	36	30.74	< 0.001
	Acclimation	Salinity	227746	4	128.9	< 0.001
		Time	97000	9	146.4	< 0.001
		Salinity x Time	38982	36	14.71	< 0.001

Turbidity	Shock	Turbidity	7100	4	1.932	0.145
		Time	165362	9	139.6	< 0.001
		Turbidity x Time	7508	36	1.584	0.027
	Acclimation	Turbidity	6180	4	1.929	0.145
		Time	86360	9	103.2	< 0.001
		Turbidity x Time	4660	36	1.392	0.084

Although zoeae appeared to display a wider tolerance to salinity when gradually exposed to a treatment (Fig. 3B), this difference was not significant when compared to the results obtained in the shock treatments ($t = -1.563$, $df = 46$, $p = 0.12$). In the acclimation experiments, zoeae in both the 20 and 35 salinity treatments displayed a survival rate over 50% at the end of the experiment, with values of 58% and 62% respectively. Zoeae maintained at a salinity of 10 displayed a 28% survival rate after five days, while animals at a salinity of 0 died within the first hour and those at 50 died after 24 hours.

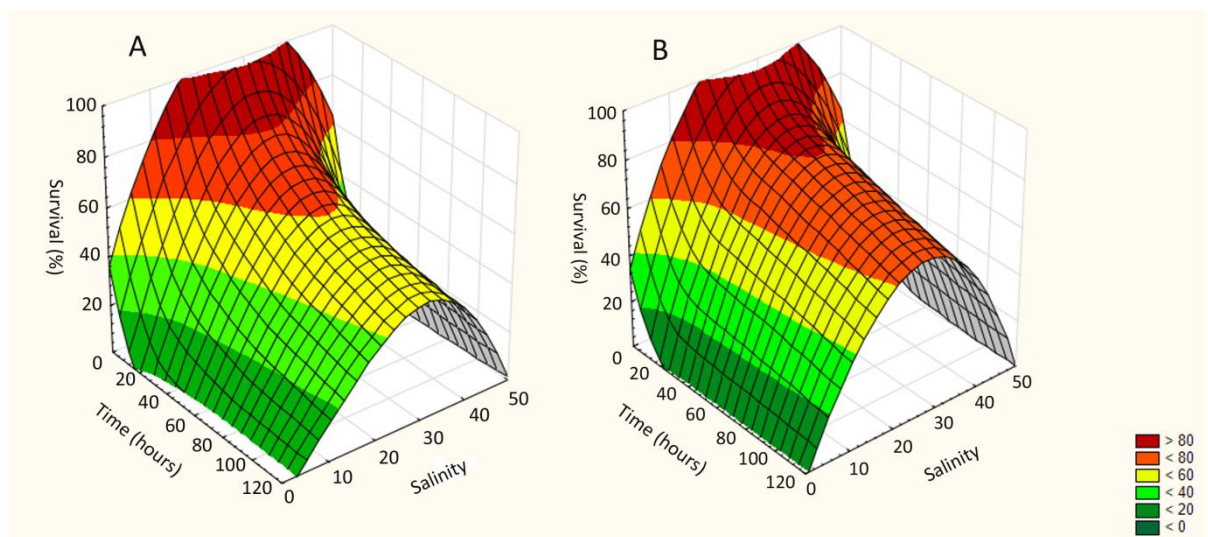


Fig. 3: Percentage survival of *Uca annulipes* first stage zoeae exposed to salinity treatments ranging from 0 to 50 over a period of 120 hours. Zoeae were (A) exposed to a shock salinity treatment, or (B) allowed to acclimatise gradually to a salinity treatment.

Response to turbidity

A change in turbidity did not appear to affect the survival rate of zoeae, except under the interactive influence of a sudden change in turbidity and prolonged time (Table 1). In the shock treatment, survival was < 20% for the 100 and 500 NTU treatments and 26 % for the 1000 NTU treatment (Fig. 4A). A 40% survival was recorded for zoeae at 50 NTU and a 38% survival for zoeae at 0 NTU after five days.

Survival was significantly higher for zoeae in the acclimation experiment compared to the shock experiment ($t = -3.588$; $df = 46$; $p < 0.001$), although in this case no significant change in survival was observed with an increase in turbidity (Table 1). Survival of zoeae maintained at 500 and 1000 NTU was the lowest, with values of 38% and 36% respectively (Fig. 4B). Zoeae in the 100 NTU treatment displayed a survival rate of 44%, while zoeae in both the 0 and 50 NTU treatments displayed a survival of over 50% with values of 64% and 58% respectively.

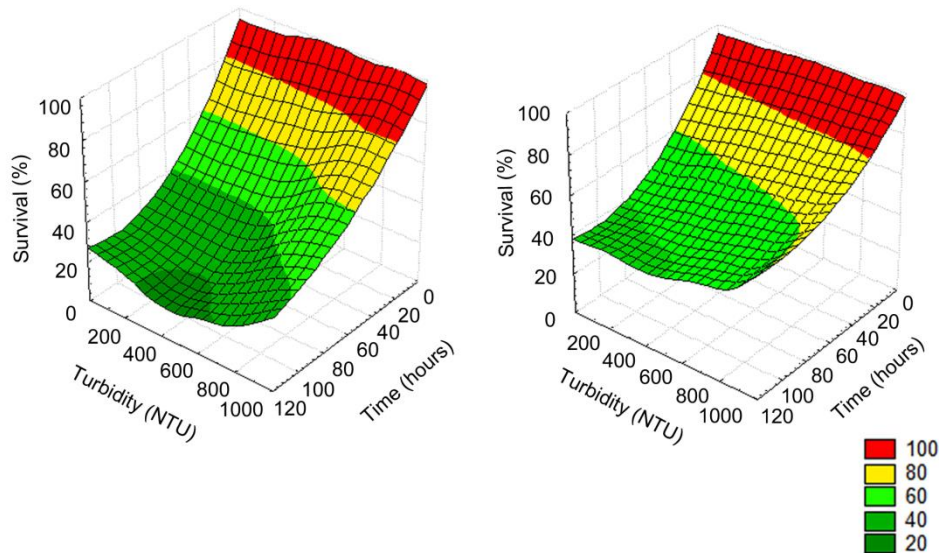


Fig. 4: Percentage survival of *Uca annulipes* first stage zoeae exposed to turbidity treatments ranging from 0 to 1000 NTU over a period of 120 hours. Zoeae were (a) exposed to a shock turbidity treatment or (b) allowed to acclimatise gradually to a turbidity treatment.

DISCUSSION

The optimal survival of *U. annulipes* first stage zoeae was recorded at a salinity of 35, with a very narrow tolerance to variation (Fig. 3). Turbidity, however, only significantly affect the survival of zoeae over the experimental period. These results indicate that, unlike *U. annulipes* adults which are able to tolerate salinities from 0 to 65 (Khanyile 2012), larvae are unable to survive under unstable salinity conditions in a closed estuarine environment. Marine connectivity is thus crucial for the successful development of *U. annulipes*, due to the optimal salinity experienced in the marine environment.

A few reasons have been proposed for the necessity of a marine larval phase in some brachyuran species. Even though the high fecundity of *Uca* species (Litulo 2004) allows them to withstand greater advective loss, Epifanio et al. (1988) suggested that it is still selectively advantageous for these species to release larvae into an ebb flow, so that development occurs in the ocean under favourable biological conditions. The authors go on to deduce that due to

the limited salinity tolerance of *Uca* zoeae, they potentially exhibit low osmoregulatory capabilities (Epifanio et al. 1988).

The predator avoidance hypothesis (Christy 2003) suggests that reproduction is timed so larvae are carried out on a nocturnal ebb tide to avoid predation, as offshore predators are encountered less frequently than estuarine predators (Morgan 1990). In the case of *Uca*, this is further supported by the morphology of larvae, which bear small protective spines compared to other taxa (Morgan 1990). Gene flow, dispersal to adjacent habitats and the subsequent preservation of species despite the degradation of associated coastal habitats are further advantages of having a marine larval stage (Bilton et al. 2002). This occurs when larvae are transported between estuaries during development. Movement from one system to another allows for a high level of gene flow between various populations. This has been recorded for *U. annulipes*, where genetic and morphometric analyses indicated that the species undergoes extensive gene flow along the East African coast (Silva et al. 2010). These authors have suggested that the marine larval dispersal strategy is the most probable cause for the lack of geographic population structure of the species in Africa.

Despite the newly-constructed beach spillway (Whitfield et al. 2013), marine connectivity is currently limited in the St Lucia Estuary. Van Elden et al. (2014) reported high abundance of crab zoeae in the spillway linking the St Lucia to the Mfolozi Estuary in both flood and ebb tides, indicating that recruitment from the sea has subsequently improved considerably. However, as the Mfolozi-St Lucia spillway is regularly obliterated due to siltation and geomorphological shifts of the Mfolozi system (van Elden et al. 2014), this resurgence in larval export is unlikely to be effective. Recruitment of megalopae from adjacent habitats is still possible through the back channel and link canal (Fig. 1), although larval export is unlikely to occur through these channels either, due to their perched nature.

Aside from lack of connectivity, physico-chemical variables within the estuary may not be ideal for larval development if they are retained within the system. The narrow tolerance of zoeae to salinity fluctuations could be a major driver of their unsuccessful persistence in the system. Within the last ten years, salinity levels in the Narrows have been consistently low, regularly reaching levels close to virtual freshwater (Fig. 2A). This has created a limnetic to oligohaline habitat during the drought phase and under closed mouth conditions. As larval transport would not occur under closed mouth conditions, zoeae would essentially have been trapped in the estuary, under conditions of low salinity and increased predation pressure. As larvae are intolerant of salinities < 20, they would not be able to successfully survive past the first stage in this habitat which rarely exhibits a salinity level above 10. A shortcoming of this study is that no data were collected for survival of larvae between 0-10 and 35-50. However, as lethal tolerance levels are estimated at 50% mortality, a survival rate of greater than or equal to 50% was considered to indicate successful survival of zoeae.

Zoeae of *U. annulipes* are stenohaline compared to adults (Khanyile 2012). This has been recorded for other species (Simith et al. 2012), but is not always the case. Capaldo (1993) reported that zoeae of three American fiddler crab species had a salinity preference similar to that of the adults. Epifanio et al. (1988) found similar results and attributed this to

the salinity at which the eggs are incubated. It is known that adults of *U. annulipes* are widely euryhaline and are also proficient osmoregulators (Khanyile 2012). This is likely advantageous, as they are the most terrestrial of all South African fiddler crab species occupying the areas furthest away from the water mark. At these higher elevations they are subject to greater evaporation rates and thus higher salinities (Khanyile 2012). However, the larvae of many crab species do not display the same osmoregulatory proficiency (Charmantier 1998) and a limited osmoregulation capability is certainly seen in the stenohaline response of *U. annulipes* zoeae to salinity fluctuations. It is suggested that in open marine waters osmoregulation may not be necessary, with osmoconforming behaviour observed in many species that typically undergo larval export or ontogenetic shifts in habitat (Charmantier 1998). Instead larvae develop osmoregulatory capabilities between the last zoeal stage and the megalopa, as seen with the related species, *Uca subcylindrica*, in the Gulf of Mexico (Rabalais & Cameron 1985). This correlates to the period in which individuals re-enter the estuary and are subjected to unstable salinity levels.

The effect of turbidity on zoeal mortality was significantly higher in for the shock treatment compared to the acclimation treatment (Fig 4). While the negative effects of turbidity on zooplankton filter feeding has been well-documented (Hart 1988; Carrasco et al. 2013), survival under high turbidity levels is not always adversely affected (Lougheed & Chow-Fraser 1998; Carrasco et al. 2013). It is possible that turbidity may protect zooplankton from predators (Gardner 1981) and provide an additional source of nutrition in the form of organic matter adsorbed to suspended particulates (Arruda et al. 1983). A study by Ferrari et al. (2014) showed that turbidity favoured the survival of juveniles of an open water fish species in the Sacramento-San Joaquin Delta. The authors suggested that a decrease in turbidity may be detrimental to open water species. Although fiddler crab larvae can be considered to be open water organisms at this stage of development, they did not display any significant change in mortality in response to turbidity changes except under the combined influence of the shock treatment and time (Table 1). Furthermore, Lougheed and Chow-Fraser (1998) found that larger filter-feeding zooplankton species were adversely affected by high turbidity levels and a subsequent decrease in abundance of these species created a niche for smaller zooplankton species in Lake Ontario, Canada. Carrasco et al. (2013) also suggest that while high silt loads may interfere with the feeding physiology of some zooplankton species, sediment may be advantageous as a supplementary source of nutrition. Even though these studies were specific to fish and other zooplankters aside from crab zoeae, a combination of these ideas suggests that *Uca* larvae may not react adversely to silt loading and may even benefit to some degree. Jones et al. (2015) showed that the copepod *Pseudodiaptomus stuhlmanni* experiences deleterious effects above a turbidity level of 1500 NTU. However, larvae retained within the St Lucia Estuary would experience a maximum turbidity of ≈ 1200 NTU (Carrasco et al. 2013; Jones et al. 2015) and would not be subjected to such detrimental silt loads near the estuary mouth. Cyrus (1992) measured turbidity in the St Lucia Estuary and estimated that the maximum turbidity attained in the Mouth and Narrows region was approximately 280 NTU while recent data shows that turbidity in this region has obtained a maximum value of 286 NTU (Fig. 2B).

Although the population structure of *U. annulipes* from the St Lucia Estuary is not yet known, adults occur in densities of up to 20 individuals.m⁻² and release larvae into the water. While the population appears to be healthy, persistence is unlikely. These results strongly suggest that the inability of *Uca* larvae to osmoregulate plays a significant role in their mass mortality within the St Lucia Estuary. Larvae wouldn't survive past the first zoeal stage under the current conditions in the system. However, although persistence of the population is highly reduced if larvae are unable to successfully develop or undergo export from the system, survival of *Uca* populations under closed mouth conditions would be possible as long as marine connectivity is maintained through the connection of St Lucia with the Mfolozi. While not allowing the export of newly-hatched first stage larvae from the system, this would secure recruitment of megalopae and crab instars into the system. These recruits would settle in suitable habitats following the required chemical cues (Brodie et al. 2005).

Globally, the dynamics of intermittently open estuaries and lakes are expected to change with the changing climate and anthropogenic modifications (Whitfield et al. 2008; Gillanders et al. 2011). Many of these systems are expected to remain closed for longer periods following the reduced freshwater inflow and increased wave action associated with the predicted change (Turpie et al. 2002). If this is the case, then the St Lucia Estuary is a perfect model to predict the response of similar species to climate change in aquatic systems worldwide, as it typifies a system experiencing prolonged mouth closure in response to the alternation of dry and wet phases. The persistence of estuarine populations with marine-dependent life stages should be investigated more thoroughly. Preservation of such communities then relies on the resilience and adaptability of these species.

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General conclusions and suggestions for future research

The traditional approach to conservation relies on the use of ‘biodiversity hotspots’, a term created by Myers (1989; 1990) to initially describe relatively small areas with high endemism that were under the threat of habitat loss. These hotspots were used to identify areas of high priority for conservation. However, researchers are beginning to realise that conservation may be more complex than simply trying to protect the highest number of species in the smallest possible geographical region (Cincotta et al. 2000; Margules and Pressey 2000; Mittermeier et al. 2003; Fisher and Christopher 2007; Durant et al. 2014). Côté and Darling (2010) explored the diversity-resilience paradigm in the face of climate change. The authors highlighted the fact that an increase in biodiversity does not simply increase the resilience or stability of an ecosystem. Instead, it is the tolerance of the species found within the ecosystem that determines the resilience of the ecosystem. A highly diverse ecosystem may contain many species with a limited tolerance to environmental change. As a result, the ecosystem would be more susceptible to the adverse effects of anthropogenic interference, climate change and alien invasive species.

Since environmental change is inevitable, one way of preserving ecosystem function maybe by focussing on the conservation of organisms that create resilience and stability within an ecosystem. True crabs appear to be an example of organisms that lend to both the resistance and the recovery of ecosystems. The St Lucia estuarine lake experiences a host of environmental changes due to anthropogenic and natural environmental change. As a result of these pressures, the system is now largely closed off to the ocean. This creates a non-tidal environment with reduced marine connectivity. The shallow nature of the lake facilitates a fast rate of evaporation, which drastically alters water levels and promotes hypersalinity in some parts of the system. The anthropogenic modification of hydrodynamics along with the past drought phase have both reduced the inflow of freshwater into the system (Whitfield et al. 2013). This exacerbates the hypersalinity and low-lake levels of the system. When the St Lucia Estuary is connected to the adjacent Mfolozi River, it is subject to silt loading due to anthropogenic activity in the nearby floodplains. Furthermore, the system is subject to the introduction and spread of alien invasive species due to both anthropogenic and natural causes (Miranda and Perissinotto 2014). Although the St Lucia environment is constantly changing, a few organisms are able to persist here while some even thrive under the harsh

conditions (Carrasco and Perissinotto 2012). As seen in Chapter 1, the range of diversity of true crabs changes over time in response to environmental fluctuations experienced in the system. The location of similar habitats nearby means that species are able to migrate or form refugia. Once conditions are favourable, recolonisation by crabs could occur. They are also important because they link various habitats, i.e. terrestrial and aquatic, pelagic and benthic, different systems. In this way they are important promoters of ecosystem stability (Lundberg and Moberg 2003).

Furthermore, new habitats in a changing landscape provide unoccupied niches and promote diversity through ecological speciation (Seehausen et al. 2008), especially where dispersal barriers create isolation. Lake St Lucia contains many different habitat types and spatially a large variety of niches is present. However, temporal landscape variation should also be considered here. Geological records show that the system has evolved over the last 2.6 million years (the last glacial cycle) in response to marine and groundwater level change, sediment influx from surrounding catchments, evaporation and the littoral adjacent marine environment (Botha et al. 2013). During this time, the system alternated between an open marine embayment, a partially exposed shallow valley lowland and a dry terrestrial ecosystem. The current form of the lake is thought to only have been achieved during the last 1000 years. This drastic landscape evolution is partially responsible for the resilience of the St Lucia environment and its biota. Perhaps just as importantly, it would have been fundamental in driving the speciation of many invertebrate organisms. Today the region is globally recognised as a biodiversity hotspot with a high number of endemic species (Smith et al. 2008). In Chapter 2, a new species of freshwater crab found in ephemeral pans along the western shore of False Bay is described. It is most likely that its burrowing and air-breathing nature facilitates its ability to successfully avoid desiccation during times of drought. The species appears to be micro-endemic to the False Bay region in St Lucia, where it fills an important trophic role in a unique ecosystem. Endemism has traditionally been regarded as an important factor to consider during conservation planning as the degree of endemism in an ecosystem is thought to provide some idea of its biodiversity (Myers et al. 2000). Although it is currently understood that various factors are crucial in the planning of conservation, endemics are still held in high regard due to their rarity (Mason et al. 2015). Furthermore, it is believed that narrow endemics are more susceptible to environmental change as they are generally unable to relocate due to dispersal barriers (Thomas 2011).

The survival and persistence of a population has been correlated with its feeding success since Alfred Russel Wallace (1859) first mentioned this in his essay entitled ‘*On the tendency of varieties to depart indefinitely from the original type*’. Here he used the example of forest birds and seabirds, claiming that forest birds were so few in number partly due to their food limitations, while seabirds were abundant due to their diet of marine invertebrates, which are always plentiful. If this is true, the ability to feed on many food types is surely advantageous. It is thus a useful ability of many true crab species to switch their diet based on what is available, as shown in Chapter 3. Here, the diet of the dominant freshwater crab *Potamonautes sidneyi* was discussed from two contrasting habitats with subsequent differences in food availability. A change in diet was recorded in accordance with seasonal, food availability and ontogenetic shifts and highlights the role of the species as a trophic and spatial link between habitats. The opportunistic feeding habits of crabs ensure that they are able to shift their diet with a shift in food availability, or shift their feeding patterns when circadian rhythms are disrupted. They maintain the integral trophic link between producers, decomposers and consumers, facilitating the flow of energy through a food web even when the ecosystem undergoes a disturbance event. This opportunistic, adaptable feature facilitates recovery of the system to its previous ecological state and adds to the stability of an ecosystem. The role of prominent crab species as decomposers allows for the rapid recycling of nutrients within the ecosystem. The rate of recycling has been shown to correlate negatively with the resilience of a system, i.e. the more rapid the recycling rate, the greater the resilience (DeAngelis 1980). Although the ecology of *P. sidneyi* is poorly understood, evidence seems to favour the role of freshwater crabs in general as ecosystem stabilisers (Hill and O’Keeffe 1992; Marijnissen et al. 2009; Burress et al. 2013; Williner and Collins 2013).

Even species at their latitudinal distribution limits are important in fulfilling this role. In South Africa, five species of fiddler crabs occur here at their latitudinal limit (Chapter 4). It is thought that populations occupy the least favourable and most fragmented habitat at their latitudinal limits (Travis and Dytham 2004). For this reason population dynamics and behaviour at latitudinal limits are critical in determining the response of the species to climate change (Thomas et al. 2001; Travis and Dytham 2004; Hampe and Petit 2005). It was also determined that the St Lucia fiddler crab community is important in a particular scientific context. The fiddler crabs in St Lucia persist here despite a constantly-changing environment and could provide useful insights into the behaviour of the genus under stressful conditions. During unfavourable conditions, populations retreat to nearby suitable habitats and recolonise

the area once conditions become suitable again. This is particularly relevant in the face of global increasing habitat degradation in mangrove ecosystems (Polidoro et al. 2010). Fiddler crab persistence in a modified habitat has been previously recorded in an east African mangrove (Cannicci et al. 2009). In this case, the authors linked this persistence to the favourability of increased nutrients at the site, which contributes to the evidence of feeding adaptability in crabs.

It is important to note that food availability is only one of many factors affecting feeding success. Complex intertwined circadian rhythms and the risk of predation control when vulnerable organisms are able to feed (Barnwell 1966; Palmer 1990). In the case of the St Lucia fiddler crab population, food is easily available in the form of microphytobenthos. However, it is also known that a combination of diel and tidal patterns governs feeding. The effects of tidal absence have resulted in a dietary shift although diurnal, seasonal and sexual differences in feeding patterns are still present. With St Lucia experiencing both natural and anthropogenic shifts in freshwater and marine inflow, adaptability as seen in the feeding dynamics of *Uca annulipes* (Chapter 5) is advantageous, possibly contributing to the survival of this genus at the southernmost limit of its geographic distribution. The potentially high density of fiddler crabs along with the high rate of feeding means they have a significant impact on the microphytobenthic and microbial communities of the mangrove substratum.

Although true crabs have a huge influence on the associated environment, they are in turn affected by changes in the environment. Management decisions do not always consider the various life stages of invertebrates and as a result, conservation may be superficial or non-existent. Chapter 6 highlights this by showing that fiddler crab larvae, unlike their adaptable adult counterparts, exhibit a marine phase, partly so that they can develop at a suitable salinity level. The reduced connectivity of the St Lucia Estuary due to drought conditions and human intervention disrupts the life cycle of these key mangrove species.

Due to their ambulatory, swimming and burrowing nature (Lundberg and Moberg 2003), true crabs are efficient in linking freshwater and marine habitats, terrestrial and aquatic habitats, benthic and pelagic habitats and even similar adjacent habitats. Furthermore, the opportunistic character of true crabs makes them ideal colonisers, as range expansion increases with habitat availability (Thomas et al. 2001). Their ability to survive under a wide range of environmental change means that a wider variety of habitats is available for range expansion or colonisation. True crabs thus form an integral part of conservation largely due

to their movement. However, it is still unclear what exactly drives this movement. This research shows that both natural and anthropogenic changes drive brachyuran distribution but whether these factors stem from physico-chemical changes, interspecific interactions or resource availability has yet to be determined. One of the biggest challenges encountered by carcinology in South Africa is the lack of distribution records in both prominent and unique aquatic systems.

Future research of brachyuran diversity and ecology in South Africa is important because: 1) brachyurans are highly resilient to environmental change and may be key in the preservation of ecosystem functioning; 2) many brachyuran species occur in South Africa at the southernmost limit of their distribution and populations at their poleward limits are useful in determining the behaviour and dynamics of the species in the face of climate change; 3) brachyurans link various environments and thus potentially transmit environmental impacts from one region to another; and 4) invertebrates in unique aquatic systems which are subject to natural fluctuations and human intervention are crucial in determining the fate of organisms all over the world, under the influence of recent climate change and anthropogenic regimes. St Lucia is an example of such an aquatic system and is ideal in that it hosts a wide variety of habitat types. Specifically, further research could be structured as follows.

1. Ongoing biodiversity studies are necessary on a larger spatial and temporal scale. While Chapter 1 looked at the change in biodiversity of true crabs in St Lucia, many aquatic habitats around South Africa lack this sort of information, particularly in marine and brackish environments. Long-term monitoring of population biodiversity can provide a more accurate insight into the effects of environmental change on benthic invertebrates.
2. Investigating the drivers of true crab distribution, particularly in specialised habitats (i.e. mangrove forests) or unique environments (non-tidal mangrove forests) could provide useful information to determine which species are the most resilient and useful to the ecosystem. This can be done through the use of distribution models incorporating various environmental parameters and field observations of abundance. It is important to incorporate potential biotic drivers in these models as biotic interactions are often overlooked in such studies.
3. Tolerance mechanisms and reactions to various environmental changes are partially understood for some species. Ecological behaviours such as feeding, reproduction and social interactions will all change in response to an environmental stimulus. The question

is how? And to what extent will key species tolerate environmental change before they migrate to more favourable habitats? The physiological and behavioural response of key species to a range of environmental stressors can be monitored in order to answer these questions.

4. Investigation into the drivers of survival is also required at different stages of the life cycle. Chapter 6 shows that while adults of a population may be widely tolerant to environmental fluctuations, juveniles may have a narrower tolerance for change. This could adversely affect population dynamics and, in turn, conservation of key resilient species. Survival lab-based experiments could be conducted at a range of environmental parameters such as temperature, pH, salinity and turbidity.
5. In order to examine the ecology of a species at various stages of development, the life cycles of these species need to be accurately described and documented. This has not yet been done for several South African brachyuran species. Laboratory-based hatching and rearing of these species is required to do so.
6. In South Africa, research surrounding the impacts of key brachyuran assemblages on their habitats and associated biota are poorly understood. Crabs are well-known as ecosystem engineers due to their burrowing and foraging effects on the substratum, especially in mangrove habitats. Through the use of field exclusion experiments, it will be possible to examine the presence/absence impacts of fiddler crabs and other key mangrove species on associated biota such as microphytobenthic communities, meiofaunal communities and other macrofauna species. The interaction of crabs with alien invasive species is also significant. The results in Chapter 3 show that true crabs can potentially feed on alien gastropods and play some role in the effects of mitigation. These predator-prey interactions with alien species should be further investigated.
7. In order to look at the extent to which crabs link various environments, a combination of genetics and isotope analysis could be used. Genetics could provide an insight into the large-scale movements of a species between various regions (Silva et al. 2010), while stable isotope analysis could be used to determine the small-scale movement of brachyurans within a region (Marguillier et al. 1997).
8. The biogeography of many species as well as speciation events are still debated today (Chapter 4). Jackson and Blois (2015) discuss how palaeoecology and community ecology can complement each other by incorporating ecological and environmental processes on a

larger time scale into community ecology to better understand ecological change in a changing climate. Such a multidisciplinary approach to understanding the drivers of distribution and even speciation has the potential to greatly enhance the field of ecology.

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