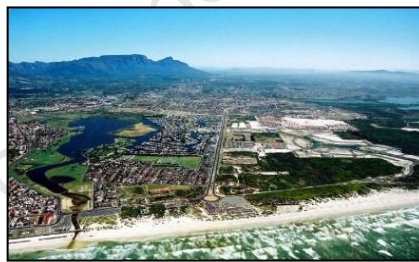


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Long-term change in the invertebrates of Zandvlei Estuary, with focus on the invasive reef worm *Ficopomatus enigmaticus*.



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Dissertation submitted in partial fulfilment of the degree of Masters in Applied Marine Science, University of Cape Town

Date: 6 May 2013

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Plagiarism Declaration

I know the meaning of plagiarism and declare that all of the work in this dissertation, save for that which is properly acknowledged, is my own. I have not allowed, and will not allow, anyone to copy my work.

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Acknowledgments

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Abstract

Zandvlei is a small, seasonally closed, urban estuary situated 20 km south of Cape Town, and been subjected to many physical changes, including the construction of a rubble weir, canalisation of the Estuary mouth, construction of a marina and hardening of the banks with concrete. These changes have facilitated the expansion of an invasive reef-building polychaete, *Ficopomatus enigmaticus*. This study quantifies long term changes in the abundance of *F. enigmaticus* in Zandvlei and investigates historical changes in the salinity and invertebrate community. The standing stock of *F. enigmaticus* in the Marina da Gama has increased from 11.80 t in 1989 to 50.03 t in 2012 due both to an increase in the total area colonised by *F. enigmaticus*, and the dry mass of worm per m². There has also been a general trend of increased salinity in the system since 1989, with an increase of 4‰ recorded at the head of the Estuary in 2011. This study provides the first record of the infauna associated with *F. enigmaticus* in Zandvlei, which comprises 16 species. One of these is the hitherto unrecorded alien bryozoan, *Conopeum seurati*. Further research is required to understand the effects of long-term salinity change on the growth of *F. enigmaticus* and the role of *F. enigmaticus* as an ecosystem engineer.

Keywords: Zandvlei Estuary, *Ficopomatus enigmaticus*, human activities, invasive species, infauna, historical change.

CHAPTER 1.

A review of the Zandvlei Estuary

1.1 Estuaries in South Africa

Estuaries form the interface between oceans and land and are the point where freshwater from land drainage is mixed with inflowing sea water (Allanson & Baird 1999). Day (1980) describes an estuary as “a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity”. The input from the ocean is driven by the tides, while the freshwater input is determined by rainfall in the catchment area (Allanson & Baird 1999). Estuaries are highly dynamic systems (Grange et al. 2000; Elsdon & Gillanders 2006). The climate of the region in which an estuary is found as well as the physical environment affects the characteristics of the estuary (Allanson & Baird 1999). Conditions vary over a range of spatial and temporal scales. For example, seasonal changes in freshwater runoff, winds, wave action and insolation affect circulation and water column structure, while episodic events, such as strong winds, high waves, extreme rain or drought, can also severely alter estuarine systems (Allanson & Baird 1999). Each estuary is therefore different and the mix of different conditions and processes ultimately determines its characteristics.

Estuaries are some of the most extensively modified aquatic environments through anthropogenic activities (Blaber et al. 2000). Activities in the drainage basin, estuary itself or in the coastal seas nearby have varying effects on estuarine environments (Day & Grindley 1981). Some of the principle activities are water abstraction, soil erosion and pollution, exploitation of resources and construction and habitat modification (Day & Grindley 1989; Baird et al. 1996; Schlacher & Wooldridge 1996; Allanson & Baird 1999; Blaber et al. 2000;

Grange et al. 2000; Danovaro et al. 2002; Jerling 2005). The effects of these activities include changes in salinity, sedimentation, turbidity, tidal action, water quality and oxygen concentration (Day & Grindley 1981). In South Africa, there is a wide range of estuaries, nearly all of which have been impacted through human activity (Allanson & Baird 1999). The modifications to these systems have a great impact in determining their characteristics.

1.2 Zandvlei Estuary

1.2.1 Physical characteristics

One such highly modified estuary is the Zandvlei Estuary. The Zandvlei is a temporarily open/closed system situated 20 km south of Cape Town. It is the largest estuary in False Bay and forms approximately 80% of the estuarine area in the Bay (Brown & Magoba 2009). The Estuary is divided into three parts: a shallow main section, the Westlake wetland and the Marina da Gama, as seen in Figure 1 (Morant & Grindley 1982; Davies et al. 1989; Brown & Magoba 2009). The main section of the Estuary is 2.5 km long and 0.5 km wide, at its widest point, with water levels fluctuating between a mean of 0.7-1.3 m (Morant & Grindley 1982). The Marina da Gama consists of a network of canals, which reach up to 2 m deep in places (Morant & Grindley 1982).

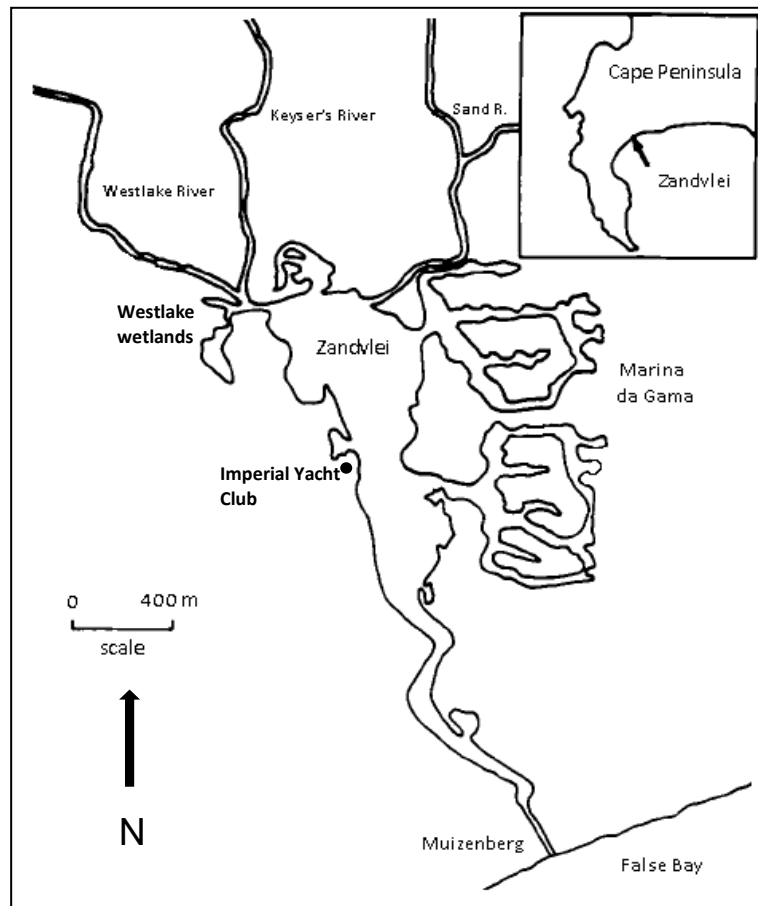


Figure 1. Zandvlei Estuary, showing the Marina da Gama and inflowing rivers. Inset shows position of Zandvlei on the Cape Peninsula. Map adapted from Davies & Stewart (1984).

Three main rivers feed into Zandvlei – the Westlake, Keyser's and Sand Rivers (Burman 1962; Day 1981b; Brown & Magoba 2009) (Figure 2). The Westlake River rises on Steenberg Mountain and flows into Zandvlei near Lakeside. The Sand River starts as Diep River, but after the Little Princessvlei it is called the Sand River. It collects water from the southern end of Table Mountain and south of Wynberg Hill. The Sand River flows freely through Constantia, but is restricted further downstream, where it once spread out into a series of small estuaries. This is the most important river feeding the Zandvlei (Burman 1962). Finally, the Keyser's River drains Constantiaberg and flows into the Zandvlei in the north-western corner.

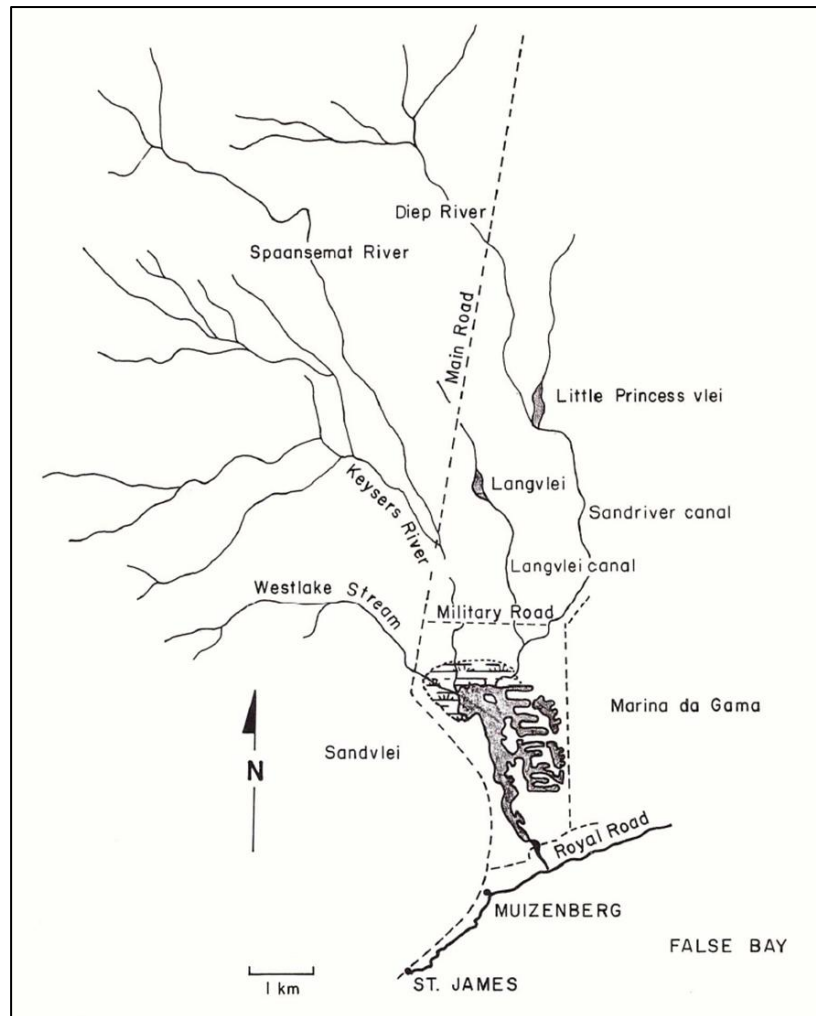


Figure 2. The catchment area of Zandvlei Estuary, showing the Westlake, Keyser's and Sand Rivers. Map adapted from Begg (1976).

The catchment area of Zandvlei covers approximately 8 500 ha on the southern slopes of Table Mountain and has been highly built-up and modified through human activity (Morant & Grindley 1982; Davies et al. 1989; Brown & Magoba 2009). Land-use in the catchment area includes light industry, housing, agriculture, forestry, conservation and commerce (C.A.P.E. 2010b). All of the rivers have been impacted by human activity and development since World War II and therefore carry many urban, agricultural and industrial wastes (Morant & Grindley 2009). This results in low quality, high nutrient water in the Estuary.

Rainfall in the catchment is restricted mainly to the winter months, from May to September, and summer is hot and dry (Morant & Grindley 1982). During summer months a sand bar forms, closing the mouth of the Estuary to the sea. In winter, when the mouth is open, it is a partially mixed system and this allows sea water to flow into the Estuary. In its disturbed state, the physico-chemical characteristics of the Estuary show homogenous temperature patterns, neutral to slightly alkaline pH and fresh to saline water, with stratification occurring mainly in winter, when the mouth is open (Morant & Grindley 1982). The Estuary is eutrophic, with homogenous surface dissolved oxygen conditions and anoxic conditions at some places in bottom waters (Morant & Grindley 1982).

1.2.2 History

Development of Muizenberg and Zandvlei

False Bay is rich in estuaries when compared to the western shore of Table Bay and Hout Bay. It boasts a total of eight estuaries, the largest of which is the Zandvlei Estuary (Brown & Magoba 2009). The Zandvlei Estuary is depicted on charts dating as far back as 1700 and is suspected to have been named by van Riebeeck in the late 1650s (Morant & Grindley 1982; Walker 2009). The name has undergone several changes in spelling over the years, including Sand Vlei (Burman 1962), de Zand Valei (Burman 1977) and Zand Vlei (Burman 1977). In 1981 the Cape Town City Council officially established the name as Zandvlei (Morant & Grindley 1982).

In 1672 the Dutch East India Company built an outpost on the banks of the Zandvlei and this marked the beginning of the development of the Muizenberg area and Zandvlei Estuary (Burman 1962; Morant & Grindley 1982; Walker 2009). Over the next 70 years this outpost became increasingly important and in 1743 a military post was established by Sergeant Wynand Willem Muys, after whom the seaside resort of Muizenberg was named.

This served as a stop-off point on the route from Cape Town to Simon's Town (Morant & Grindley 1982).

In 1795 the Dutch were defeated by British troops in the battle of Muizenberg and South Africa became a British Colony (Burman 1962; Burman 1977). With this came a great increase in the number of immigrants and visitors to Cape Town, leading in turn to an upgrade in the infrastructure of the region (Walker 2009). Where there was only a sandy track running from Cape Town to Simon's Town, a military road was constructed in 1814. However, it was not until the rail line was established from Cape Town to Muizenberg and Kalk Bay in 1882 that a great surge in the number of houses and holiday houses occurred (Walker 2009). Over the years the popularity of Muizenberg grew so much that a direct railway line from Johannesburg Park Station to Muizenberg was built.

The arrival of the train involved not only development of the north-western edges of the Estuary for the railway embankments, but also increased use of the Estuary for recreational purposes (Morant & Grindley 1982). Sailing on the Zandvlei became an extremely popular recreational activity and in 1907 the Imperial Yacht Club was established (Burman 1977; Morant & Grindley 1982). However, siltation and weed infestation in the Estuary forced the disbandment of the club in 1946 (Brown & Magoba 2009). Muizenberg's popularity as a holiday destination meant it was often at the fore-front of development in the country. The first electric telegraph line in South Africa passed through this sea-side town in 1860 and it also boasted the country's first bus service in 1902, cinema in 1910 and airmail in 1911. The popularity of Muizenberg as a holiday destination dwindled somewhat after World War II (Burman 1977). However, the development of the Marina da Gama on Zandvlei in the 1970s played a role in increasing the popularity of the area once more (Burman 1977).

Physical manipulations

The Zandvlei has been subjected to much manipulation and change over the years, all of which was brought about through human activities. This has occurred in both the Estuary and catchment areas and has involved physical modifications, as well as changes to water quality and drainage patterns (C.A.P.E. 2010). The major physical changes to the Estuary were the canalisation of the mouth, the development of the rubble weir, the stabilisation of the shores into steep concrete banks, the development of the Marina da Gama and the construction of the railway, which cut the wetlands off from the rest of the Estuary (Davies et al. 1989; C.A.P.E. 2010a).

The earliest plans for interventions to the functioning of the Estuary were in 1866, when it was to be drained following a long period of drought (C.A.P.E. 2010a). The Zandvlei has dried out completely at times when severe drought conditions persist for long periods of time (Brown & Magoba 2009). For example, Stephens (1929) stated that the Zandvlei would sometimes dry up by the end of the summer. If drought conditions were coupled with the natural closure of the Estuary mouth, evaporation would cause the entire system to dry up. In January 1866 a severe drought greatly reduced the water levels in the Estuary (Morant & Grindley 1982; Brown & Magoba 2009; Walker 2009). This led to considerations of draining the system and reclaiming the land. However, the inflowing river water was not accounted for and when the winter rainfall increased riverine inflow, the project was abandoned.

The construction of the railway in the 1880s cut the Westlake wetlands off from the Estuary. These are now connected by only a narrow causeway and this has had major impacts on the flora of the wetlands (C.A.P.E. 2010a). In the 1930s weirs were built where the rivers flowed into Zandvlei to prevent salt water from moving upstream and affecting irrigation of agricultural lands (C.A.P.E. 2010a). These have, however, subsequently been removed.

In the 1950s a 20 m wide concrete channel was built along the banks of the Estuary mouth, followed by an artificial rubble weir to control the flow of water into the Bay (C.A.P.E. 2010a). This prevents water levels in the Estuary from dropping below a certain optimum level. These modifications, together with the intense urbanisation on the banks of Zandvlei, had serious consequences on the tidal flushing of the Estuary.

Before the development of the mouth, water levels in the Estuary would often reach up to 2.5-3.0 m above sea level before the sand bar was broken (Brown & Magoba 2009). This resulted in the flooding of areas surrounding Zandvlei and large amounts of sediment would be washed out to sea when the mouth breached. The mouth would be wide and up to 4 m deep, allowing strong tidal flushing and therefore increasing salinity in the Estuary. Nowadays, artificial breaching of the sand bar is required when water levels are only 1.1-1.4 m above sea level. This is due to the low-lying residential areas on the banks of the Zandvlei. However, in these events, breaching does not occur for a prolonged period of time as the water level is not high enough. As a result, tidal flushing is weak and there is little influx of sea water to the system. The situation is intensified by the presence of the rubble weir, which prevents water levels from dropping below a certain point. Sedimentation within the Estuary is therefore high and the true estuarine functioning of the system is compromised. In an effort to return the system to an estuarine state and restore the salinity gradient, the sandbar is bulldozed at high spring tides to allow water to flow into the Estuary from the sea.

In addition to these modifications to the mouth of the Estuary, a large proportion of the banks of the Estuary were cemented in the early 1960s (Morant & Grindley 1982). This was to stabilise the steep banks created through the dredging of the Estuary and also to increase the ease of entry and exit to the water for recreational users. This had great impacts on the ecology of the system and will be discussed in Chapter 2.

Plans to develop the eastern shores of Zandvlei were in existence for many years before the present Marina was actually established (Walker 2009). In 1902, a 500 acre piece of land adjoining the Muizenberg foreshore was rented out by the Foreshore Estate Syndicate. The plan was to develop this land into a township with roads, tramways and a pier onto the Zandvlei. However, the scheme was halted by an economic slump that lasted until 1907, following the Anglo-Boer War.

In 1939 plans were proposed to dredge the Estuary and stabilise water levels; however these were put on hold by World War II (Morant & Grindley 1982). Dredging commenced in 1946 and by 1961 parts of the existing Estuary were deepened and adjoining land was reclaimed. This created open water for yachting and the Imperial Yacht Club was reopened in 1962. The reclaimed land was also used for sports fields and recreational activities.

The plans for the Marina da Gama on the eastern side of the Estuary were put forward in 1969 (Walker 2009). These plans, proposed by the Anglo American Corporation, included the development of an inland marina on the eastern banks of the Zandvlei, with waterside housing, a golf course, parks and a yacht harbour connected to False Bay (Morant & Grindley 1982). It was thus to include nearly the entire Estuary. The eastern component was to be developed first and excavation of a canal system, which was later connected to the Estuary, was started in 1970. However, the economic recession of 1973 put a stop to all further developments and the ocean harbour, golf course and Westlake developments were never completed (Morant & Grindley 1982). The remaining undeveloped land was later sold by the Anglo American Corporation to local builders.

1.2.3 Biota

The following account deals only with the invertebrate component of the biota in Zandvlei. Other aspects of the flora and fauna are not of concern in this study and are therefore not addressed. The most comprehensive account of the flora and fauna in Zandvlei

Estuary is provided by Morant & Grindley (1982). However, there have been several physical changes in the system since this time and the biota has in turn responded to this (C.A.P.E. 2010a). The following description is based on a more recent account from C.A.P.E. (2010a), which details Morant & Grindley's (1982) report in conjunction with these biological responses.

The following groups of zooplankton are listed in Zandvlei: Protozoa, Turbellaria, Tardigrada, Gastrotricha, Rotifera, Nematoda, Ostracoda, Amphipoda, Copepoda, Cladocera and Decapoda, as well as aquatic invertebrates from the Bryozoa, Oligochaeta, Polychaeta, Isopoda, Mysidacea, and Mollusca. The most common species found on hard substrates within the Estuary is the introduced reef-building polychaete *Ficopomatus enigmaticus* (C.A.P.E. 2010a). This polychaete can have positive effects on water quality through its filter-feeding behaviour, but has also become a nuisance in areas where recreational use of the Estuary is high (C.A.P.E. 2010a). *Callianassa kraussi* is common in sandy substrates and the polychaete *Capitella capitata* is found in muddy anoxic areas. The crown crab *Hymenosoma orbiculare* and shrimp *Palaemon pacificus* are also common.

There are approximately 20 aquatic insect species present in Zandvlei and these include species from the orders Collembola, Ephemeroptera, Odonata, Hemiptera, Coleoptera and Diptera. Many of these are abundant as larvae (Morant & Grindley 1982).

1.2.4 Management and conservation

Zandvlei holds regional importance as an area for recreational activity (C.A.P.E. 2010b). Opportunities include various boating activities, picnicking, bird watching, hiking and some fishing, although fishing regulations for the Estuary are strict. It also hosts various competitions, including an international kite-flying competition, provincial canoe championships and yachting events (C.A.P.E. 2010b).

The development of the railway line and increased use of Muizenberg as a holiday destination led to the formation of a village management board in 1981 (C.A.P.E. 2010a) and municipality in 1987 (Walker 2009). With this came the development of laws regarding the control and development of fishing and fishing industries (Act No. 26 of 1897) (Walker 2009). The Zandvlei is accessible to the public for the most parts, with only sections of the Marina da Gama reserved for private use.

Over the years there has been increased awareness of the need to promote a safe and healthy estuarine system in order to maximise the recreational and conservational benefits of Zandvlei (C.A.P.E. 2010b). The first real recognition of this was the formation of the Zandvlei Nature Reserve in 1977 by the Cape Town City Council (C.A.P.E. 2010a). The borders of the nature reserve were expanded in 2000 to include the entire main Estuary, the Westlake Wetlands and the Sand River mouth. This then became the Greater Zandvlei Estuary Nature Reserve in 2006 (C.A.P.E. 2010a). In 1988 the Zandvlei Trust was formed in order to protect the indigenous fauna and flora of the Estuary.

Various projects have been put in place to facilitate on-going restoration, monitoring and educational programmes focussed on the Zandvlei (Brown & Magoba 2009). These are all aimed at the conservation and improvement of Zandvlei and involve various local government and community partnerships (Brown & Magoba 2009). An environmental education programme has been set up by the Greater Zandvlei Estuary Nature Reserve. This involves local schools and environmental clubs, who interact to identify problems and produce potential solutions (C.A.P.E. 2010b). These solutions are then brought to life through active campaigns, such as litter clean-up days, removal of alien vegetation or recycling initiatives (C.A.P.E. 2010b). Many local residents are also actively involved in the management of the area (C.A.P.E. 2010b).

Some of the projects include the rehabilitation of Park Island and the Westlake Wetlands, the Zandvlei Inventory and Monitoring Project, a community salinity monitoring programme and the Zandvlei Environmental Education Programme. Parties involved include the Marina da Gama Residents Association and Friends of Park Island, the Zandvlei Trust, City of Cape Town, the Cape Bird Club, the University of Cape Town, local residents of Muizenberg and Lakeside and users of the Estuary. In addition, there are organisations and projects focussed on management of the inflowing rivers, such as the Sand River Catchment Forum and the Keyzers River Restoration Project.

An Estuary Management Plan was recently published as part of the Cape Action for People and Environment Estuaries Programme (C.A.P.E. 2010b). This outlines the biophysical status of the Estuary, its socio-economic importance and regulatory framework and proposes improvements for the management of the Estuary in order to reach a situation where the conservation and functioning of the system is balanced with the needs of its users.

1.2.5 Current ecological issues

The biodiversity of an estuary is based mainly on its physical and chemical characteristics (C.A.P.E. 2010a). All of the transformations to Zandvlei have played a role in greatly changing the ecology of the system so that the environmental conditions are now extremely unnatural (Day 1981b). This has been associated with many ecological issues and hence changes in the biodiversity of the system (C.A.P.E. 2010a).

Both indigenous and alien invasive species have been found in the Zandvlei system for many years. These include terrestrial and aquatic species, plants and animals, vertebrates and invertebrates (C.A.P.E. 2010b). Some of the species have been introduced intentionally, while others have arrived unintentionally (C.A.P.E. 2010b). One of the biggest threats to the endangered Western Leopard Toad, for example, is the introduced guttural toad

Amietophrynus gutturalis, which has recently been heard in the Zeekoevlei and Zandvlei areas (C.A.P.E. 2010a).

Weed infestation has been an on-going problem in Zandvlei, dating back to the early 1900's, when the Imperial Yacht Club was forced to disband (Brown & Magoba 2009). The cosmopolitan pondweed *Potamogeton pectinatus* grows in extremely dense clumps during the summer months and is concentrated in the upper sections of the Estuary (Day 1981b). *Ruppia maritima*, another aquatic weed, grows closer to the lower reaches of the system (Day 1981b). These weeds can be an extreme nuisance, obstructing water flow and affecting recreational users of the Estuary by restricting boat movement (C.A.P.E. 2010a). In some years these weeds have been mowed in order to open space for boat activity and clear the system (Day 1981b). In addition, they have been associated with blooms of toxic algae, such as *Cladophora* and *Enteromorpha*, which have led to major fish mortalities (Morant & Grindley 1982). They may also alter the benthic habitat and produce toxic gases and are therefore controlled using mechanical methods.

Another highly invasive and problematic species in Zandvlei is the non-indigenous reef-building polychaete, *Ficopomatus enigmaticus*. A number of faults in the design of the Marina have led to ideal conditions for explosive growth of this species (Davies et al. 1989). Firstly, there are only two narrow openings connecting the canals of the Marina to the main Estuary and most of the canals are blind-ending. The canals were dredged to a mean depth of 2 m, which is deeper than the main Estuary, and as a result there is oxygen and salinity stratification, anoxic bottom water formation and hydrogen sulphide production. Finally, the design of the Marina is such that the canals are sheltered from wind action, greatly decreasing mixing of the water column. All of these features, together with the stabilisation of water levels and construction of cement canal walls, have created favourable conditions for the growth of *F. enigmaticus* in Zandvlei (Davies et al. 1989).

The construction of a weir near the mouth for stabilisation of water levels also played a role in decreasing the numbers of juvenile fish recruiting into the Estuary (Day 1981b). As a result, recruitment success decreased greatly. Day (1981b) recorded only eight fish species in the Zandvlei and attributed this to the closure of the mouth and presence of the weir, which prevented post-larval fish from entering the Estuary. Linefish populations also decreased, with the exceptions of Leervis (*Lichia amia*) and flathead mullet (*Mugil cephalus*), as did the populations of bottom-dwelling species, such as Gobiidae and Blackhand Sole (*Solea bleekeri*) (C.A.P.E. 2010a). This is a result of toxic benthic layers brought about by low water quality. However, the recent artificial mouth opening events have helped restore some of the estuarine functioning of the Zandvlei and juvenile fish are once more able to recruit into the system. In addition, the weir was lowered in 2001 (C.A.P.E. 2010a). Populations of Pipefish (*Syngnathus temminckii*), Blackhand Sole and Barehead Goby (*Caffrogobius nudiceps*) have begun to appear in the system again, indicating that there has been some successful recovery of fish populations in the Zandvlei. Juvenile White Steenbras have been recorded for the first time in 11 years and the sand prawn *Callinassa kraussi* has also moved further upstream, so that more food and benthic habitat is now available for fish (C.A.P.E. 2010a).

Finally, the construction of the railway line had major implications for the flora of the Westlake wetlands. The wetlands are now linked to the main Estuary by only a narrow causeway and as a result conditions in the wetlands resemble those of a freshwater environment. Consequently, the flora in this area is mainly freshwater species (C.A.P.E. 2010a).

CHAPTER 2.

Long-term change in the invertebrates of Zandvlei Estuary, with focus on the invasive reef worm *Ficopomatus enigmaticus*

2.1 Introduction

2.1.1 Biological invasions

Most aquatic environments have exotic species associated with them (Schwindt et al. 2001). These may be introduced in many different ways, including natural expansion of an organism's distribution range, or human activities, such as shipping and aquaculture (Eno et al. 1997; Schwindt et al. 2004b; McQuaid & Arenas 2009). Some introduced species have little to no impact on the native environment, while others have major impacts on native communities and ecosystem functions (Eno et al. 1997; Schwindt et al. 2001; McQuaid & Arenas 2009). The latter are known as invasive species and may represent one of the greatest threats to global biodiversity (Bax et al. 2003).

Invasive species can change the structure of a community by displacing or outcompeting native species, or by altering processes at the ecosystem level, such as sedimentation rates, productivity, nutrient cycling and disturbance rates (Schwindt et al. 2001; Obenat et al. 2006). In addition, invasive species can play a role in determining resource availability for other species, by changing the state of living and non-living material. Organisms that change the environment in this way are called ecosystem engineers (Schwindt et al. 2001). One excellent example of a group of ecosystem engineers are the reef-building worms. These can displace epifauna and change the abundance and diversity of infauna by creating a new environment for colonization (Schwindt et al. 2001). They may generate

spatial heterogeneity and therefore increase biodiversity by creating habitat for infaunal species (Schwindt et al. 2001).

Estuaries as sites of biological invasions

Estuaries are one of the most prominent environments affected by introduction of exotic species through human activities (Schwindt et al. 2004b; Glasby et al. 2007). The risk of estuaries to biological invasions has increased greatly over the years due to changes in donor and recipient habitats, as well as increased shipping activity (Glasby et al. 2007; Dafforn et al. 2009). The movement of ships between ports has created links between different biotic provinces, allowing organisms to travel between previously separated habitats (Glasby et al. 2007).

In addition, estuaries have become more developed and urbanised through anthropogenic activity, often leading to the formation of hard surfaces in areas which were previously soft sand or sediment (Bulleri & Airoidi 2005; Glasby et al. 2007; Dafforn et al. 2009). These artificial structures are then colonised, often by nonindigenous species (Bulleri & Airoidi 2005; Glasby et al. 2007). As space is a common factor limiting the success of biological invasions, these hard surfaces may play a role in providing new habitat for exotic species, increasing their recruitment success (Glasby et al. 2007; Dafforn et al. 2009). They may also create a habitat that is suitable to invasives, but not to native biota (Wasson et al. 2005), or act as corridors, providing habitat across areas of otherwise unsuitable substratum (Bulleri & Airoidi 2005).

The introduction of artificial habitats to estuaries may therefore increase the success of invasions by nonindigenous species and thus threaten the diversity of the native biota (Wasson et al. 2005; Glasby et al. 2007). One such invasive species that is dependent on hard substrata and therefore greatly influenced by the construction of artificial structures is the tube worm, *Ficopomatus enigmaticus*.

2.1.2 Biology of *Ficopomatus enigmaticus*

Ficopomatus enigmaticus (= *Mercierella enigmatica*) is a well-known reef-building polychaete belonging to the family Serpulidae (Mead et al. 2011). It is originally from Australia (Mead et al. 2011) but due to its fast growth rates, encrusting nature and high tolerance to stress it has spread around the world by fouling ship hulls and is now distributed in brackish waters in many tropical and subtropical areas (Ten Hove & Weerdenburg 1978; Day 1981a; Fornós et al. 1997; Bianchi & Morri 2001; Mead et al. 2011). Many studies have been done on this polychaete in the Mar Chiquita coastal lagoon, an estuarine environment in Argentina (Obenat & Pezzani 1994; Schwindt & Iribarne 2000; Schwindt et al. 2001; Schwindt et al. 2004a; Schwindt et al. 2004b).

F. enigmaticus is a suspension feeder, consuming suspended detritus, as well as phytoplankton (Obenat & Pezzani 1994). It prefers high nutrient waters, can survive in a large range of temperatures and salinities and is extremely tolerant to stress, surviving low pH and pollution (Fornós et al. 1997; Bianchi & Morri 2001). *F. enigmaticus* has been recorded in salinities ranging from 1.5-50‰ and temperatures of 12-28°C (Day 1981a). At most of these salinities it acts as an osmoconformer, regulating only when in fresh or nearly fresh water conditions (Hill 1981). *F. enigmaticus* has also been recorded at depths from low water at neap tides to 32 m (Day 1981a).

F. enigmaticus makes large reefs, consisting of a dense network of calcareous tubes (Mead et al. 2011). These reefs originate when the planktonic larvae settle on hard substrata, such as rocks, reeds or hard objects on soft bottom sediments, like shells (Obenat & Pezzani 1994; Fornós et al. 1997; Bianchi & Morri 2001; Mead et al. 2011). This is the dispersal phase of the life cycle (Obenat & Pezzani 1994). *F. enigmaticus* reaches maturity after only six weeks (Day 1981a) and the adults then build tubes by secreting calcareous material from their collar glands (Schwindt & Iribarne 2000). Each polychaete builds a tube in which it

lives and these structures display distinct growth rings. It is important to note that *F. enigmaticus* is not an obligate reef constructor, and can therefore also build tubes singly (Ten Hove & Weerdenberg 1978; Bianchi & Morri 2001).

Larval recruitment and growth rates in *F. enigmaticus* are high and individual worms may live up to several years (Bianchi & Morri 2001). In the Mar Chiquita coastal lagoon, *F. enigmaticus* reefs were shown to grow at an average rate of 1.6 cm per month (Schwindt et al. 2004a), while single polychaetes have been shown to grow at a rate of approximately 2 cm. month⁻¹ (Bianchi & Morri 2001). The size of adult worms varies from 20-25 mm, with some exceptional cases of 40 mm long worms together with 100 mm long tubes recorded (Bianchi & Morri 2001). The reefs grow upwards and outwards, towards suitable suspension-feeding sites, and a reef of living tube worms is formed (Obenat & Pezzani 1994). Neighbouring clumps of reefs of similar size may join together to form larger platforms of several metres in diameter (Obenat & Pezzani 1994; Bianchi & Morri 2001; Schwindt et al. 2004a). Reefs can reach up to 7 m in diameter and 0.5 m in height or 3 m thick (Fornós et al. 1997; Schwindt et al. 2004a; Mead et al. 2011).

Schwindt et al. (2004a) showed that the growth of *F. enigmaticus* reefs is affected by many different environmental factors, including salinity, nutrient availability, current speed and depth. As the reef continues to grow, the centre part becomes dead, due to death of older worms and silt accumulation (Obenat & Pezzani 1994). The living parts of the aggregate are therefore around the edges and larval settlement continues to occur on these outer parts of the reef (Obenat & Pezzani 1994; Schwindt & Iribarne 2000). Reef parts that are exposed above the water quickly die, and as a result fluctuations in water level can affect reef structure (Fornós et al. 1997). However, recolonisation occurs rapidly when water levels rise again (Fornós et al. 1997). In areas of high salinity *F. enigmaticus* is found in lower biomass than in areas with brackish waters (Schwindt et al. 2004a). The abundance of *F. enigmaticus* is

therefore expected to be lower near the mouth of a lagoon or estuary and greater further upstream, where the water becomes brackish (Schwindt et al. 2004a). Reefs also have greater growth rates in summer, when the water is warmer (Schwindt et al. 2004a).

F. enigmaticus tubes collapse reasonably easily under weight and as a result, they are not highly resistant to wave action (Bianchi & Morri 2001). Bioerosion, through fish predation for example, can also be a major cause of reef degradation, as seen by Fornós et al. (1997) in the Albufera of Menorca. However, physical and human damage to the reef creates new areas for larval recruitment (Obenat & Pezzani 1994) and new tubes continue to be built around the old, collapsed tubes (Bianchi & Morri 2001).

2.1.3 Ecosystem impacts of *Ficopomatus enigmaticus*

F. enigmaticus can have major impacts on the systems it invades and is therefore considered an exotic and ecosystem engineer (Schwindt et al. 2001; Schwindt et al. 2004b). In the Mar Chiquita coastal lagoon it has one of the strongest ecological effects of all species introduced to the area (Schwindt et al. 2004a).

F. enigmaticus changes the physical environment by creating a network of tubes. This creates habitat complexity, which plays a major role in determining the abundance, diversity and distribution of associated organisms and alters the physical characteristics of the system (Coull & Wells 1983; Schwindt et al. 2001). In addition, *F. enigmaticus* has high growth rates, allowing for rapid expansion and further increasing its impact on the ecological dynamics of the invaded environment (Fornós et al. 1997).

F. enigmaticus can alter both biotic and abiotic aspects of a system. For example, in the coastal lagoon at Mar Chiquita, *F. enigmaticus* increases the abundance of a number of benthic species, and alters the hydrodynamics and sediment dynamics of the system (Schwindt et al. 2004a).

Impacts on biotic aspects of invaded system

In terms of the biotic aspects of a system, *F. enigmaticus* reefs are extremely important providers of shelter, food and substratum for many different infaunal species and the density and structure of infaunal communities may therefore be altered by their presence (Obenat & Pezzani 1994). Interactions between native species, such as competition, predation and parasitism, may also be affected by the presence of *F. enigmaticus*, as discussed below (Schwindt et al. 2001; Schwindt et al. 2004b).

F. enigmaticus reefs create refuge for organisms in the form of spaces between the tubes and associated organisms include polychaetes, amphipods, juvenile crabs and gastropods (Schwindt & Iribarne 2000; Schwindt et al. 2004b). In the Mar Chiquita lagoon large populations of the amphipod *Melita palmata* and the gastropod *Littoridina parchappi* were associated with the reefs (Schwindt & Iribarne 2000). The increased habitat complexity can lead to changes in predation rates, as a result of refuge availability, increased refuge from disturbance and increased attachment sites for associated fauna's food (Coull & Wells 1983). For example, the availability of refuge increases the survival of new settlers on *F. enigmaticus* reefs, particularly where predation pressure is strong (Schwindt & Iribarne 2000).

Schwindt et al. (2001) showed that in the Mar Chiquita lagoon the abundance of crabs changed in the presence of *F. enigmaticus*. *Cyrtograpsus angulatus*, a native southwestern Atlantic crab species, uses *F. enigmaticus* reefs as refuge and increased greatly in abundance when *F. enigmaticus* was introduced. This increase in crab abundance led to a decrease in the abundance of a native free-living soft-bottom polychaete. The introduction of *F. enigmaticus* therefore resulted in cascading effects on the native community, changing the community structure and interactions.

As well as forming large reefs, *F. enigmaticus* can be an important filter feeder, often competing with other native filter feeders (Mead et al. 2011). These changes in community assemblage associated with *F. enigmaticus* can alter the interactions of species within native communities and determine the distribution and density of infaunal species (Schwindt et al. 2004b).

Impacts on abiotic aspects of invaded system

In terms of the abiotic aspects of a system, the reefs created by *F. enigmaticus* introduce topographic heterogeneity and therefore increase habitat complexity (Schwindt et al. 2004b). This can play a role in modulating the availability of resources to the native community and altering sediment transport, relative water flow and therefore sediment deposition (Schwindt et al. 2004b).

F. enigmaticus reefs trap sediment from the water column, which results in the accumulation of silt in the reef system and death of affected worms (Schwindt et al. 2004b). The intensity and duration of these hydrodynamic effects differs according to distance and orientation from the reef (Schwindt et al. 2004b). Schwindt et al. (2004b) found that *F. enigmaticus* reefs greatly affected the hydrodynamics of the Mar Chiquita coastal lagoon by impacting bedload transport and sediment deposition. These changes in hydrodynamic processes can then affect recruitment success and larval survival (Schwindt & Iribarne 2000).

In addition, the benthic habitat can be greatly impacted by the build-up of skeletal debris of dead reefs and pseudofaeces produced through filter feeding (Fornós et al. 1997; Mead et al. 2011). This can increase the concentration of pesticides, heavy metals and other pollutants in the benthos that were absorbed by the worm (Mead et al. 2011).

2.1.4. *Ficopomatus enigmaticus* in South Africa

The distribution of *F. enigmaticus* along the coast of southern Africa is patchy. It was introduced into South Africa by ship fouling and was first recorded by Day (1961) in 1955. In

South Africa it ranges from Milnerton Lagoon, on the west coast, to Kosi Bay, on the east coast, but is only found at isolated sites along this range (Day 1981a).

***Ficopomatus enigmaticus* in Zandvlei**

F. enigmaticus was first recorded in the Zandvlei Estuary, 20 km south of Cape Town, South Africa, by Muir (1974) and is thought to have been introduced to the Estuary as a result of fouled boats moving between Zandvlei and other estuaries (Charles Griffiths, pers. comm.). An artificial cement wall was built around the edges of the Estuary in order to ease entry to the water by recreational users of the Estuary. This, together with several aspects of the Marina da Gama design, facilitated the expansion of *F. enigmaticus* (Davies et al. 1989).

The exotic polychaete was initially unable to invade successfully, as there was little to no hard substratum available for the larvae to attach to. With the development of cement walls along the banks of Zandvlei in the early 1960s and canals of the Marina da Gama in the 1970s, large areas of suitable substratum were created. This allowed larvae that entered the system to attach to a hard surface and grow, provided the physico-chemical conditions were favourable. In areas of high recreational activity, litter such as bottles and cans that are disposed of into the water may also be used by larvae as settlement sites and can therefore increase the density of *F. enigmaticus* within the system (Schwindt et al. 2004b).

Due to the rapid growth and physical tolerance of *F. enigmaticus*, the cement walls, boats and jetties in the Zandvlei have become covered in reef. Over the years there have been complaints from local canoeists and recreational users of the Estuary that the number of reefs has greatly increased, to a point where boat movement within the Estuary is now restricted (C.A.P.E. 2010a). Physical contact with the reef when stood on, or brushed against, can lead to minor cuts and bruises. Despite these complaints, little work has been done on *F. enigmaticus* within the Zandvlei Estuary. In a recent site assessment of Zandvlei by the Cape

Action for People and the Environment Estuaries Programme *F. enigmaticus* was mentioned as an invasive species, but no further information was provided.

2.1.5 Aims

The primary aim of this study is to shed light on long term change in *F. enigmaticus* biomass within the Zandvlei Estuary. This will be done by quantifying the biomass of *F. enigmaticus* in the Estuary and comparing total standing stock to a study carried out by Davis et al. (1989), in order to determine whether it has increased or decreased since that time. An additional aim is to identify the infauna associated with *F. enigmaticus* and estimate their abundance in the system.

2.2 Methods and Materials

2.2.1 Study site

The study was carried out at the Zandvlei Estuary, 20 km south of Cape Town, South Africa. This is a temporarily open/closed system and covers approximately 60 ha, opening into False Bay (Davies et al. 1989). For more information on the physical characteristics and ecology of the Zandvlei Estuary refer to Chapter 1.

2.2.2 Sampling

Estimating total standing stock

The sampling methods follow, but differ slightly from, those carried out by Davies et al. (1989). The perimeter of the Estuary was divided into 200 m sections, including the Marina da Gama canals and all of the islands. One random sample of reef, approximately 0.0044 m², was collected in each section, resulting in a total of 65 samples. Sections of reef were removed using a metal corer that was pushed into the reef and pulled out to extract a core sample. For each 200 m section an estimate of the percentage cover (m²) of the wall by

the reef was made by eye and the vertical height of the reef was recorded using a metal ruler. Samples were taken back to the laboratory where they were frozen in water until processing.

The weight of the reef infauna was assumed to be negligible and these were therefore not removed before weighing the reef mass. The wet weight of the worm tubes was obtained and converted to dry mass using a conversion ratio determined by oven-drying five samples for 24 hours at 70°C and calculating the mean ratio of wet weight to dry weight. Dry mass represented 46.15% (± 2.70 , S.D.) of total wet weight. The dry mass was then converted to dry mass of worm (excluding tube) using the conversion ratio calculated by Davis et al. (1989). Dry mass of worm, excluding tube, formed 3.2% of total dry mass. The biomass of each sample was then divided by 0.0044 to obtain estimates of biomass per m² of *F. enigmaticus*.

The biomass of *F. enigmaticus* in each 200 m section was calculated by multiplying the percentage cover of the section by the vertical height of the reef recorded in that section and the dry mass per m² of the respective sample. The estimates of each section were then added up to get estimates of total standing stock for the Marina da Gama, as well as the Estuary as a whole. Student's t-tests were used to test for significance differences in the dry reef mass and dry mass of worm recorded in the Marina and the main Estuary body in 2012. The mean total standing stock of *F. enigmaticus* in the Marina da Gama was also compared with the mean obtained for the same area by Davies et al. in 1989. Due to limitations in the historical data set no statistical analyses were possible for this comparison.

The sites sampled in the Marina da Gama did not correspond exactly to those sampled by Davis et al. (1989) because we chose to sample once in every 200 m section, while Davis et al. (1989) had several sites that were extremely close together. While *F. enigmaticus* does occasionally also attach to the submerged aquatic plant *Potamogeton pectinatus* and hard substrata on the bottom of the Estuary, such as rocks or bottles and cans, these contributions

to the total biomass are difficult to sample and were considered negligible in relation to the large area of reef on the cement walls.

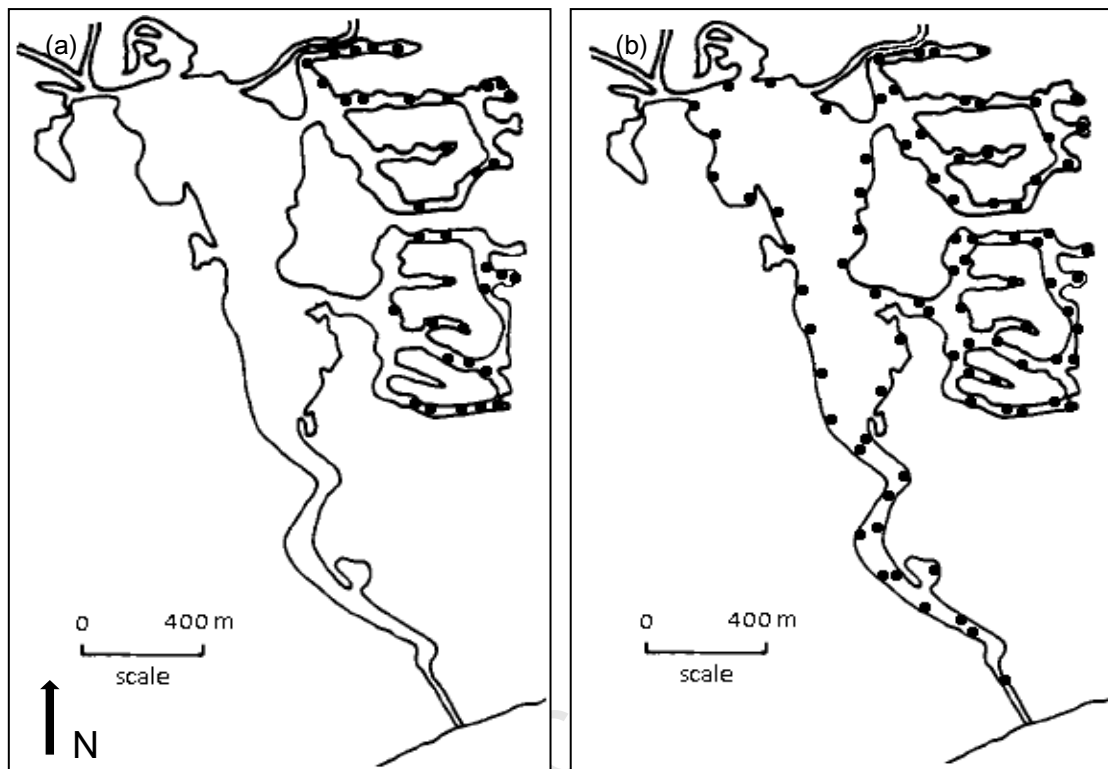


Figure 3. Zandvlei Estuary with sampling sites from (a) Davies et al. (1989) and (b) this study (2012). Maps adapted from Davies & Stewart (1984).

Identifying infauna

The 65 samples collected to determine total standing stock were also used to identify reef infauna. After being defrosted each reef sample was broken up into smaller pieces to release the infauna trapped between the tubes. The fauna were then counted and identified under a dissecting microscope where necessary, and a species list was created. Historical records of the invertebrates present in Zandvlei were also collated and presented in a table showing the species, reference and whether it was present or absent.

Salinity patterns

Historic salinity data were obtained from the Department of Scientific Services of the Cape Town City Council and the on-going Community Monitoring Programme for the period

1985-2011. These were used to determine general trends in salinity in Zandvlei from 1988-2012. In order to account for seasonal and spatial variation in salinity, readings from the same station and the same month were compared among years. The Imperial Yacht Club (Figure 1) was chosen as the station as it is in the centre of the main Estuary and the month of March was chosen randomly. Salinity readings in March were averaged and the average salinities compared among years. The number of readings taken in March varied between 2 and 6 among years and in 1996, 1999 and 2008 readings from April were used as no data from March was available. A linear regression was performed in Microsoft Excel 2010 in order to determine whether there was a significant trend.

The salinities from the mouth to the head of the Estuary were also compared for the month of March in 1989 and 2011, as the data set for 2012 was incomplete. A Student's t-test was used to test for a significant difference in the salinity recorded in the system at five stations in 1989 and 2012.

2.3 Results

2.3.1 Total standing stock

Patterns found in 2012

Table 1 shows the average, minimum, maximum and total dry mass and dry mass of worm recorded in the main Estuary and Marina da Gama in 2012. The average dry mass of *F. enigmaticus* in the main Estuary body was $6.66 \text{ kg m}^{-2} \pm 5.67 \text{ SD}$, the minimum 0.05 kg m^{-2} and the maximum 17.66 kg m^{-2} . In the Marina da Gama, these values were slightly higher, with an average dry mass of $8.05 \text{ kg m}^{-2} \pm 6.55 \text{ SD}$, a minimum of 0.25 kg m^{-2} and a maximum of 24.79 kg m^{-2} . However, no significant difference in the dry mass recorded in the Marina and the main Estuary body was found ($p > 0.05$). The total number of metres colonised by *F. enigmaticus* in the main Estuary was 843.4 m^2 , compared to 6138 m^2 in the Marina.

The complex canal system of the Marina has a much larger surface area for colonisation than the Estuary and had an approximate percentage cover of 98%, compared to only 30 % of the bank in the main Estuary. The total dry mass of *F. enigmaticus* estimated in the Estuary was 6.58 tonnes and 50.03 tonnes in the Marina.

In terms of dry mass of worm, excluding tube, the main Estuary again had lower recordings than the Marina da Gama. The average dry mass of worm in the Estuary was $213.25 \text{ gm}^{-2} \pm 181.49 \text{ SD}$, with a minimum of 1.61 gm^{-2} and a maximum of 565.01 gm^{-2} . The total dry mass of worm excluding tube was 0.21 tonnes. In the Marina, the average dry mass of worm was $257.59 \text{ gm}^{-2} \pm 209.65 \text{ SD}$, the minimum 7.92 gm^{-2} and the maximum 793.38 gm^{-2} . The total dry mass of worm excluding tube was 1.60 tonnes. However, Student's t-tests showed that there was no significant difference in the dry mass of worm recorded in the Marina and the main Estuary body ($p > 0.05$).

Table 1. Average, minimum, maximum and total dry mass and dry mass of worm excluding tube of *Ficopomatus enigmaticus* in the main Estuary and Marina da Gama in 2012.

	Main Estuary Body	Marina da Gama
Dry mass (kg)		
Average per $\text{m}^2 \pm \text{SD}$	6.66 ± 5.67	8.05 ± 6.55
Min per m^2	0.05	0.25
Max per m^2	17.66	24.79
No. m^2 of <i>F. enigmaticus</i>	843.4	6138
Total dry mass (tonnes)	6.58	50.03
Dry mass of worm excluding tube (g)		
Average per $\text{m}^2 \pm \text{SD}$	213.25 ± 181.49	257.59 ± 209.65
Min per m^2	1.61	7.92
Max per m^2	565.01	793.38
No. m^2 of <i>F. enigmaticus</i>	843.4	6138
Total dry mass of worm (tonnes)	0.21	1.60

The distribution of *F. enigmaticus* in the Zandvlei is shown in Figure 4. Near the mouth and head of the Estuary no *F. enigmaticus* was found. This is a result of either unsuitable physical conditions or lack of suitable substratum for attachment. The highest

biomasses of *F. enigmaticus* are concentrated in the Marina, where no null samples were collected. The average biomass of *F. enigmaticus* in the Marina is also greater than the average recorded in the main Estuary.

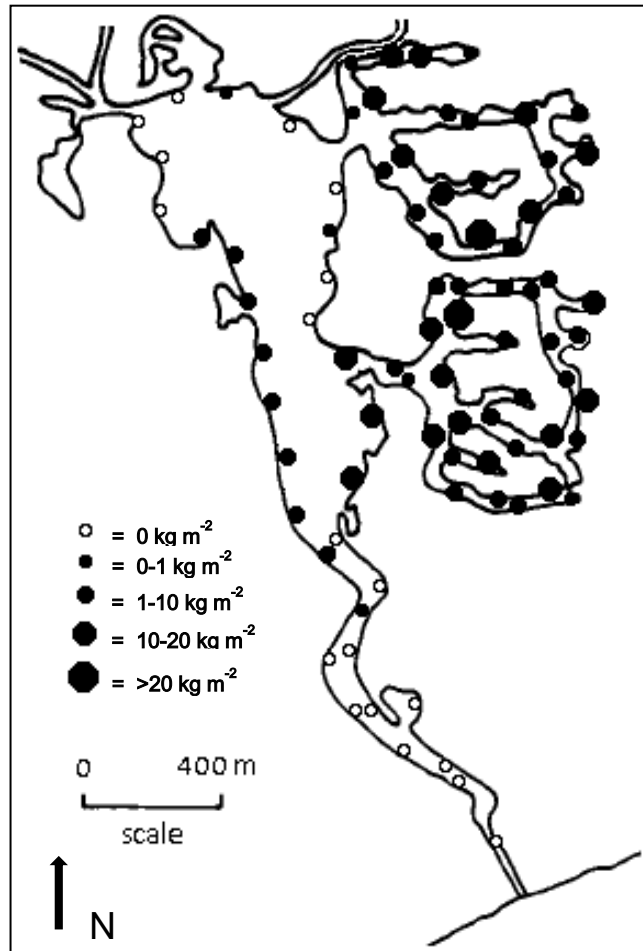


Figure 4. Distribution of *F. enigmaticus* biomass in Zandvlei Estuary in 2012. Circles represent samples taken, and the values given are dry mass. Map adapted from Davies & Stewart (1984).

Comparison with Davies et al. (1989)

Davies et al. (1989) used slightly different methods to calculate total standing stock. When estimating the surface area of the canal walls covered by *F. enigmaticus*, Davies et al. (1989) simply used a mean depth of 2 m, based on Morant & Grindley's (1982) description of the depth of the canals, and did not measure actual heights of the canal walls. In this study,

however, vertical height of the reef was recorded at each sampling site. The mean vertical height of reef in the canals was 0.6 m (± 0.25 m, S.D.) and the maximum reef height recorded was only 1.1 m. Davies et al. (1989) estimate of surface area covered by *F. enigmaticus* was therefore too high and was adjusted using the actual mean vertical reef height, as recorded in this study. This gave a more accurate representation of standing stock in the Marina in 1989 and allowed for comparison between the two studies.

A useful comparison can, however, be made between the estimates of percentage cover provided in each study. Davies et al. (1989) estimated a mean percentage cover of 73% of the walls by *F. enigmaticus*. In this study, *F. enigmaticus* was found to cover nearly the entire canal system, resulting in a mean percentage cover of 98%. A further difference in the methods of these studies was the use of average dry mass of reef per m² by Davies et al. (1989) to determine total standing stock. In my study the biomass of each sample was used along with its corresponding vertical reef height and percentage cover. Davies et al. (1989) multiplied the average dry mass by the total number of metres to give total standing stock.

The total standing stock in the Marina da Gama in 2012 was greater than that recorded by Davies et al. in 1989 (Table 2). This is the result of both an increased surface area covered by *F. enigmaticus* and an increase in average biomass per m². In 1989 the average dry mass of *F. enigmaticus* was 2.695 kg m⁻² \pm 2.1 SD, only a third of the average dry mass recorded in 2012, which was 8.050 kg m⁻² \pm 6.55 SD. The total area colonised by *F. enigmaticus* had also greatly increased, from 4 380 m² in 1989 to 6 138 m² in 2012. The total standing stock in the Marina da Gama in 1989, re-calculated using the adjusted wall area, was 11.80 t. This is lower than that recorded in 2012, which was 50.03 t.

The same patterns were seen for dry mass of worm excluding tube. In 1989, the average dry mass of worm excluding tube was 84.90 g m⁻² \pm 64.78 SD, compared to 257.59 g

$\text{m}^{-2} \pm 209.65$ SD in 2012. The total dry mass of worm estimated in 2012 was 1.60 t, while in 1989 only 0.37 t was recorded.

Unfortunately, limitations in the historical data set did not allow for statistical analyses of these results. In Davies et al. (1989) study only the final total standing stock value was recorded and I was unable to obtain any of the raw data for this paper. As a result statistical testing was not possible.

Table 2. Comparison of the average dry mass of *Ficopomatus enigmaticus*, average dry mass of worm excluding tube, total number of m^2 colonised and total standing stock in 1989 and 2012.

	Davies et al. (1989)	This study (2012)
Dry mass		
Average (kg m^{-2}) \pm SD	2.695 \pm 2.1	8.050 \pm 6.55
Area of <i>F. enigmaticus</i> (m^2)	4 380	6 138
Total dry mass (t)	11.80	50.03
Dry mass of worm excluding tube		
Average (g m^{-2}) \pm SD	84.90 \pm 64.78	257.59 \pm 209.65
Area of <i>F. enigmaticus</i> (m^2)	4 380	6 138
Total dry mass of worm (t)	0.37	1.60

2.3.2 Invertebrate community

Historical survey

Table 3 below shows historic and current data collected for the zooplankton, aquatic invertebrates and insects recorded in Zandvlei Estuary. The reference and year of identification is included. Bourgeois (1948) provided the earliest records of invertebrate species in the system. However, the most comprehensive list of invertebrates is provided by Morant & Grindley (1982) in their synopsis of available information on the Zandvlei Estuary. The table also shows the species recorded from *F. enigmaticus* reef in 2012.

Some species recorded by Bourgeois (1948) were not found by later authors, while others that were not recorded by her have been identified in later years. It is important to note

that the different sampling techniques and aims of each study will have resulted in much of the variation found. However, an interesting finding was the high diversity of cladocerans and low diversity of copepods recorded in 1948 and the low diversity of cladocerans and high diversity of copepods in 1982. These studies were carried out using similar sampling techniques and the results therefore point to a major change in the zooplankton community structure during those 30 years.

Table 3. Zooplankton, aquatic invertebrates and insects recorded in the Zandvlei Estuary (√ = present).

	Bourgeois 1948	Muir 1974	Shelton 1975	Morant & Grindley 1982	This study 2012
ZOOPLANKTON + AQUATIC INVERTEBRATES					
Amphipoda					
<i>Afrochiltonia capensis</i>	√	√	√	√	√
<i>Hyperia galba</i>	√				
<i>Melita zeylanica</i>		√	√	√	√
<i>Talorchestia ancheidos</i>	√			√	
<i>Talorchestia capensis</i>		√		√	
Bryozoa					
Bryozoa sp.		√		√	√
<i>Conopeum seurati</i>					√
Cladocera					
<i>Ceriodaphnia dubia</i>	√				
<i>Ceriodaphnia quadrangula</i>				√	
<i>Ceriodaphnia reticulata var. minor</i>	√				
Cladoceran sp.	√			√	√
<i>Daphnia propinqua</i>	√				
<i>Daphnia</i> sp.	√			√	
<i>Echinisca capensis</i>	√			√	
<i>Moina brachiata</i>	√				
<i>Moina dubia</i>	√			√	
<i>Simosa australiensis</i>	√				
<i>Simosa vetuloides</i>	√				
Copepoda					
<i>Centropages brachiatus</i>					√
Cyclopoid sp.	√			√	
<i>Elaphoidella bidens subtropica</i>				√	
Harpacticoid sp.				√	√

	Nauplii				√	
	<i>Paradiaptomus capensis</i>				√	
	<i>Paradiaptomus</i> sp.				√	
	<i>Pseudodiaptomus hessei</i>		√		√	
Decapoda						
	<i>Callinassa kraussi</i>	√		√	√	
	<i>Cyclograpsus punctatus</i>					√
	<i>Hymenosoma orbiculare</i>	√	√	√	√	√
	<i>Ovalipes punctatus</i>				√	
	<i>Palaemon pacificus</i>	√			√	
	<i>Potamonautes perlatus</i>	√	√		√	
	<i>Varuna litteratus</i>				√	
	Zoea larvae		√		√	
Isopoda						
	<i>Cinusa tetrodontis</i>	√				
	<i>Eurydice longicornis</i>	√				
	<i>Exosphaeroma</i> juv.	√				
	<i>Munna</i> sp.			√	√	
	<i>Pontogeloides latipes</i>	√				
Mollusca						
	<i>Assimineia</i>		√		√	
	<i>Hydrobia</i> sp.	√				
	<i>Physa (acuta)</i>				√	
	<i>Tomichia ventricosa</i>		√	√	√	√
	<i>Tomichia</i> sp.		√	√	√	
Mysida						
	<i>Gastrosaccus</i> sp.		√		√	
	<i>Mysida</i> sp.	√				
Nematoda						
	<i>Nematoda</i> sp.				√	√
Ostracoda						
	<i>Ostracod</i> sp.	√	√		√	
	<i>Cypris</i> sp.		√			
	<i>Paracypridinae</i> sp.					√
	<i>Sarscypridopsis</i> sp.					√
Polychaeta						
	<i>Aelosoma</i>				√	
	<i>Capitella capitata</i>		√	√	√	
	<i>Ceratonereis hircinicola</i>	√	√	√	√	
	<i>Ficopomatus enigmaticus</i>		√		√	√

AQUATIC INSECTS

Coleoptera

<i>Dyticus</i>	√
Gyrinidae	√

	Hydrophyllid larvae			√	√	
	<i>Hydroporus</i>				√	
Collembola						
	<i>Collembola</i>				√	
Diptera						
	<i>Chironomus</i> sp.	√			√	√
	<i>Culicine</i> sp.	√	√		√	
	<i>Ephydra</i> sp.		√		√	
	<i>Eristalis</i>				√	
	<i>Nemotelus</i> sp.		√		√	
	<i>Pentaneura</i> larvae sp.		√	√	√	
	<i>Tendipes chironimus</i>		√	√	√	
	<i>Tubifera</i>				√	
Ephemeroptera						
	<i>Cloen lacunosums</i>	√	√	√	√	
Odonata						
	<i>Crocothemis erythraea</i>		√		√	
	<i>Ischnura senegalensis</i>	√	√	√	√	√
	<i>Isotomus</i>		√		√	
Hemiptera						
	<i>Anisops aglaea</i>	√	√		√	
	<i>Plea pallula</i>	√	√		√	
	<i>Plea piccanina</i>	√				
	<i>Plea</i> sp.			√		
	<i>Sigara meridionalis</i>	√	√	√	√	
TOTAL NUMBER OF SPECIES		34	29	16	56	16

Infauna associated with *F. enigmaticus*

The following infaunal species were found associated with *F. enigmaticus* in this study: two species of amphipod, *Afrochiltonia capensis* and *Melita zeylanica*; a Cladoceran species; two species of copepod, *Centropages brachiatus* and a Harpacticoid species; two species of crab, *Hymenosoma orbiculare* and *Cyclograpsus punctatus*; the estuarine snail *Tomichia ventricosa*; a nematode species; two species of ostracod, a *Sarscypridopsis* species and a Paracypridinae species; the nymphs of the damselfly *Ischnura senegalensis* and the larvae and pupae of a *Chironomus* species. There were also many empty shells of the marine snail *Turritella sanguinea* recorded in the Marina da Gama samples. Notably, two species of bryozoan were identified in this study: the alien species *Conopeum seurati* (ex Europe),

identified by Wayne Florence (Iziko South African Museum), and an unidentified species. In previous years there has been only one unidentified bryozoan recorded in the system. The only other alien species found associated with *F. enigmaticus* was the wide-spread brackish amphipod *Melita zeylanica*. The infaunal species found are shown in Figure 5.

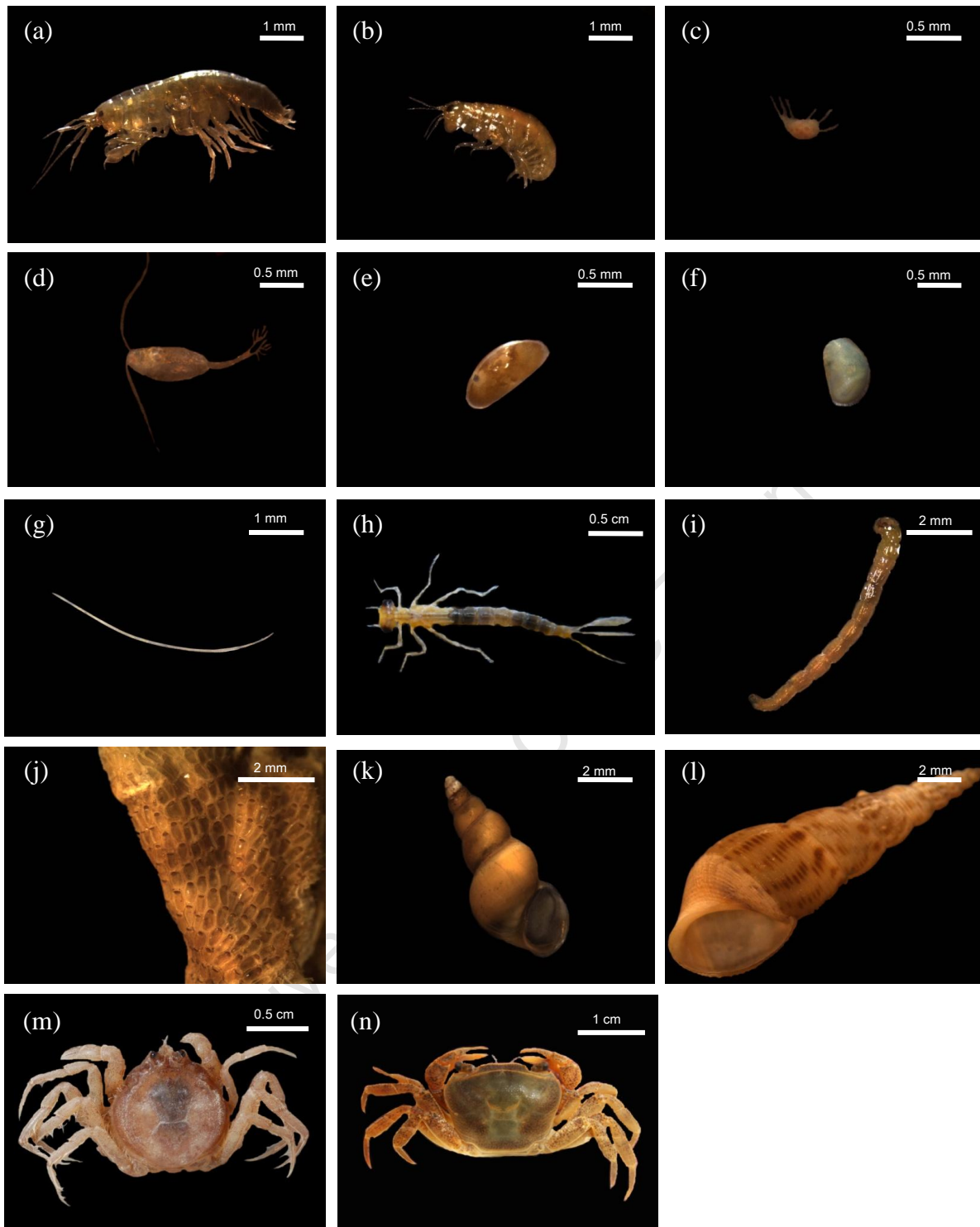


Figure 5. Infauna associated with *Ficopomatus enigmaticus*: (a) *Melita zeylanica* (b) *Afrochiltonia capensis* (c) Cladoceran sp. (d) *Centropages brachiatus* (e) Paracypridinae sp. (f) *Sarscypridopsis* sp. (g) Nematode sp. (h) *Ischnura senegalensis* (i) *Chironomus* sp. (j) Bryozoan sp. (k) *Tomichia ventricosa* (l) *Turritella sanguinea* (m) *Hymenosoma orbiculare* and (n) *Cyclograpsus punctatus*.

The minimum, maximum and average number of individuals of each species was calculated per m² of *F. enigmaticus* reef. In addition, the total number of individuals of each species in Zandvlei was estimated using the percentage cover of *F. enigmaticus* in the system (Table 4). No differentiation was made between the two species of bryozoan when they were counted, due to the difficulty in distinguishing between the two. Similarly, the two species of copepod recorded were counted together.

Table 4. Minimum, maximum and average number of infauna per m² of *Ficopomatus enigmaticus* with estimated total density in Zandvlei Estuary. * Bryozoan expressed as percent (%) cover of *F. enigmaticus* (can exceed 100% due to the highly complex, folded surface of the reef).

	Min	Max	Average ± SD	Total
<i>Sarscypridopsis</i> sp.	0	295 454	50 765 ± 238	34.20 x 10 ⁷
<i>Afrochiltonia capensis</i>	0	341 818	48 325 ± 249	33.80 x 10 ⁷
<i>Chironomus</i> larvae	455	177 727	40 951 ± 139	29.87 x 10 ⁷
<i>Tomichia ventricosa</i>	0	273 863	32 007 ± 207	23.50 x 10 ⁷
Paracypridinae sp.	0	1 255 681	31 265 ± 681	21.66 x 10 ⁷
Nematode	0	295 454	23 752 ± 181	17.32 x 10 ⁷
<i>Melita zeylanica</i>	0	227 272	20 328 ± 186	11.12 x 10 ⁷
Copepods	0	113 636	10 010 ± 78	7.09 x 10 ⁷
Cladoceran sp.	0	54 545	5 920 ± 43	3.96 x 10 ⁷
<i>Chironomus</i> pupae	0	2 727	406 ± 3	0.31 x 10 ⁷
<i>Ischnura senegalensis</i>	0	4 545	427 ± 3	0.29 x 10 ⁷
<i>Hymenosoma orbiculare</i>	0	1 136	66 ± 1	0.03 x 10 ⁷
<i>Cyclograpsus punctatus</i>	0	227	7 ± 0.2	0.006 x 10 ⁷
Bryozoans	0	300	28 ± 53.67	33.29

The most abundant infaunal species was the ostracod *Sarscypridopsis*, which was found in every sample, except for one taken at the south of the main Estuary, and averaged 50 765 individuals ± 238 SD per m² of *F. enigmaticus*. The next most abundant infaunal species was *Afrochiltonia capensis*, which was also found in every sample except one (in the canal before it widens into the main Estuary). *A. capensis* reached an average density of 48 325 individuals ± 249 SD per m² and was more abundant than the second, but much

larger, amphipod species, *Melita zeylanica*. *M. zeylanica* was found at an average of only 20 328 individuals \pm 186 SD per m² reef. The most abundant aquatic insect was the larvae of a *Chironomus* species. These were found in every sample, with a minimum of 455 individuals per m² reef. The average number of larvae per m² was 40 951 \pm 139 SD. Following this in descending order of abundance in terms of total density in Zandvlei were: *Tomichia ventricosa*, the Paracypridinae ostracod, the nematode species, *Melita zeylanica*, the copepods, the cladoceran species, *Chironomus* pupae, *Ischnura senegalensis* nymphs, *Hymenosoma orbiculare* and *Cyclograpsus punctatus*. The bryozoan species were found to cover an average of 28% \pm 53.67 SD of each m² of *F. enigmaticus* and a total of 33.29% of the reef in the whole system. The maximum percentage cover was over 100%. This is because the reef creates a highly complex surface which, if flattened, would cover more than 1 m².

2.3.3 Salinity patterns

The mean salinity of the top water in the Zandvlei Estuary in March was compared from 1989-2012. The estimates of mean salinity calculated in this study are extremely coarse and a linear regression shows there is no significant trend in salinity from 1989-2012, $R^2 = 0.1332$ (Figure 6). The maximum mean salinity over the observed period of time was 20‰ \pm 0.82 SD in 2004. The next highest mean salinity was recorded in 2005 at 15.4‰ \pm 1.36 SD. This was followed closely by 2011, at 14.8‰ \pm 1.34 SD, and then 2003, 2007 and 2008, all of which had an average of 14.5‰, \pm 0.5, 1.12 and 0 SD respectively.

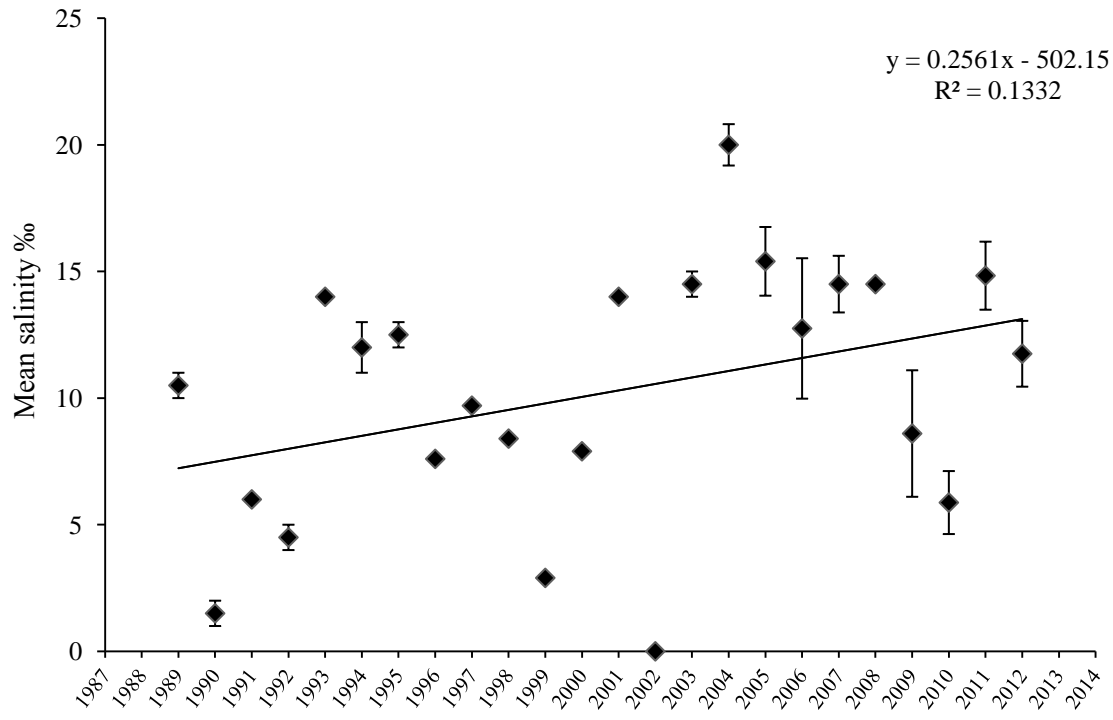


Figure 6. Mean salinity of surface water in the centre of Zandvlei, opposite the Imperial Yacht Club, in March 1988-2012.

The salinity gradient from the mouth to the head of Zandvlei was compared between 1989 and 2011 (Figure 7). The mean salinity in March was calculated for five stations within the Estuary. Data from 2011 were used as the data set for 2012 was incomplete for some of the stations. There is a significant trend of increased salinity throughout the Estuary from 1989 to 2011, ($p < 0.05$). The highest salinity recorded in 1989 was 15‰, near the mouth of the Estuary. In 2011, the equivalent salinity was recorded in the south of the main Estuary, before it narrows into the channel leading to the mouth. The salinity recorded in the centre of the Estuary in 2011 was nearly 5‰ higher than that recorded in 1989 and the salinity recorded at the mouth is approximately 7‰ higher. Not only is the salinity greater in 2011, but the salinity gradient is steeper. The difference between the salinity at the mouth and the head of the Estuary is greater in 2011 than in 1989. There was therefore a greater range of salinities experienced in Zandvlei in 2011 than in 1989. The maximum salinity at which *F.*

enigmaticus was recorded in March 2012 was approximately 18‰ in the south of the main Estuary, based on the salinity in 2011. The minimum salinity was less than 14‰, at the head.

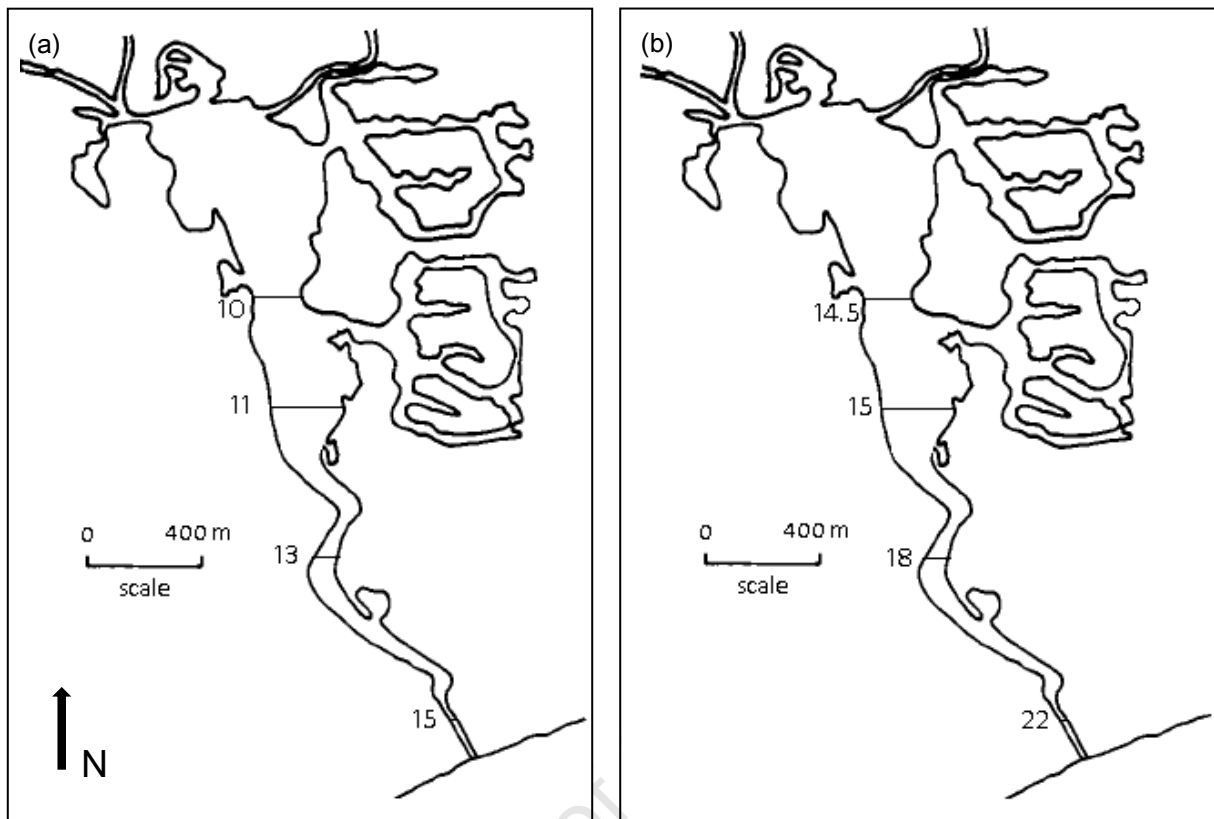


Figure 7. Salinity gradient in Zandvlei Estuary in (a) March 1989 and (b) March 2011. Maps adapted from Davies & Stewart (1984).

2.4 Discussion

2.4.1 Total standing stock

There has been a great change in total standing stock of *F. enigmaticus* in the Zandvlei Estuary over time. This was noted by local residents (C.A.P.E. 2010a) and some action was taken to remove *F. enigmaticus* reef from bridges in the Marina da Gama (Joshua Gericke, pers. comm.). This study, however, provides the first quantitative evidence that large increases in abundance have occurred and sheds light onto these changes. In addition, the

distribution of *F. enigmaticus* biomass in the Estuary was explored so that comparisons between the Marina da Gama and the main Estuary body can be made.

There has been a clear increase in *F. enigmaticus* in Zandvlei from 1989 to 2012. The total standing stock of *F. enigmaticus*, dry mass per m² and dry mass of worm recorded in 2012 are all higher than those observed in 1989. In addition, the total area covered by *F. enigmaticus* and the percentage cover of canal walls have both increased. When Davies' study was carried out in 1989, the banks of the Estuary had been cemented for approximately ten years. During this time the population of *F. enigmaticus* established within Zandvlei, and now, nearly 25 years later, there has been much more time for it to expand and consolidate. Changes in the physical conditions of the Estuary could also have played a role in the expansion of the population and will be discussed later.

Davies et al. (1989) used slightly different methods in their calculation of total standing stock and this was therefore adjusted to allow for comparison with this study. Using the corrected value, the total standing stock in 1989 was approximately 25% of that recorded in 2012. This great increase in biomass is the result of a great increase in the mass of *F. enigmaticus* per unit area, as well as an increase in the total area covered by reef.

The Marina da Gama had a much higher biomass of *F. enigmaticus* than the main Estuary. This could be attributed to several factors. The surface area of the Marina canals is greater than that of the banks of the main Estuary. The canals create a folded, complex matrix and are much deeper than in the Estuary. This greatly increases the area that could potentially be colonised by *F. enigmaticus*. Also, all of the walls in the Marina are cemented, creating a hard surface for *F. enigmaticus* to attach to. In the main Estuary, only sections of the bank are cemented, limiting hard substrate for larval attachment.

In addition, conditions in the canals are relatively stable when compared to the main Estuary. The salinity gradient from the mouth to the head of the Estuary is not found in the

Marina and the canals are sheltered from wind action, limiting vertical mixing of the water column. The stabilisation of water levels through the construction of the weir, the reduction in turbulence and the stabilisation of the canal walls with cement have all contributed to creating suitable conditions for high growth of *F. enigmaticus* (Davies et al. 1989). In the main Estuary, however, there is a different situation. At the mouth of the Estuary the banks are cemented, creating suitable habitat for *F. enigmaticus*. However, no reef is found in this region. This is likely because the salinity at the mouth of the Estuary is too high for it to survive. At the head of the Estuary, on the other hand, there is no suitable substratum for attachment. The banks are sandy, with some reeds and aquatic plants. No *F. enigmaticus* was found on the submerged stems of the reeds, even where conditions were favourable for growth. This is in contrast to the Mhlanga Estuary, where *F. enigmaticus* was found colonising the common reed, *Phragmites*. It would be interesting to investigate the reasons for this. One sample of *F. enigmaticus* was collected at the head of the Estuary where a jetty had been built. The biomass of *F. enigmaticus* at this site was low, but suggested that it could survive close to the head if suitable substratum were present. The Marina therefore provides more suitable substratum and environmental conditions for growth of *F. enigmaticus* than in the main Estuary. These patterns in the distribution of biomass can be seen in Figure 4.

Further research is required to understand the potential ecological response to removal of *F. enigmaticus* from the Zandvlei. Local residents and users of the Estuary are keen to remove some of the biomass in order to ease boat movement in the Estuary. However, the impact that this would have on water quality and the infaunal community are unknown (Davies et al. 1989). Furthermore, it would be interesting to investigate whether there is a maximum total standing stock that the system can support after which the population would stabilise. This would aid in management decisions regarding the control of *F. enigmaticus* in Zandvlei.

2.4.2 Invertebrate community

Historical survey

The comparison of historical and recent invertebrate data in the Zandvlei suggests some changes in the invertebrate community have occurred since 1948. Some invertebrates, such as the estuarine crab *Hymenosoma orbiculare* and the damselfly *Ischnura senegalensis*, were recorded in all five of the studies examined. Others, like three of the isopod species, were recorded only by Bourgeois (1948) and have not been recorded since. However, these trends are most likely due to the different sampling methods used in each study and the thoroughness with which it was carried out. For example, Bourgeois (1948) and Morant & Grindley (1982) recorded many cladoceran and copepod species, suggesting that they could have used much smaller mesh sizes when collecting samples.

Bourgeois (1948) sampled the planktonic and non-planktonic invertebrates in the system. There is no description of the methods used but this suggests a thorough study of the invertebrate community. She recorded a total of 34 zooplankton, aquatic invertebrates and aquatic insects. Muir (1974) sampled the benthic fauna, plankton and weed epifauna. This also indicates a comprehensive over-view and 29 species were recorded. However, a 1 mm mesh was used to sieve the samples, which could explain the absence of many of the smaller species, such as Cladocerans and Copepods, recorded by Bourgeois (1948) and Morant & Grindley (1982). Shelton (1975) then examined the benthic infauna and epifauna using core sampling and sieving. He also took samples of the weed epifauna. Only 16 species were recorded and most of those missing were planktonic species, which he did not sample. In addition, he used a mesh size of 1 mm², which would have limited the fauna he collected. Morant & Grindley (1982) collated all of the available data from the time into a summary of the invertebrate community in Zandvlei. Their study therefore included zooplankton, benthic fauna and weed epifauna. They recorded a total of 56 species in the system. This is the most

comprehensive listing of the invertebrate community available. My study looked only at the infauna associated with *F. enigmaticus* reef. This is the first study of this nature in Zandvlei. 16 species were recorded, only one of which had not been found previously in the system. The new bryozoan species has, however, most likely been recorded in the system before but grouped together with the other bryozoan species, due to the difficulty in distinguishing between the two. I used a mesh size of 125 µm when sieving my samples and therefore did collect some of the smaller species.

In addition, there are discrepancies in the taxonomic resolution of identifications among studies. There may therefore be duplication of species in the list, where an unidentified species in one study is identified in another. For example, the second bryozoan in Zandvlei was unidentified until this study. However, it is possible that both species have been present in the system for some time, but remained unrecorded due to the difficulty in distinguishing between the two. Similarly, the ostracod species have been unidentified until this study and as a result there are four species recorded on the list, two unidentified and two identified, while there are most likely only two species in the system.

The most important, and relevant, difference in the invertebrates recorded in Zandvlei is the presence of *F. enigmaticus*. There was no *F. enigmaticus* recorded in the system by Bourgeois (1948). This survey was carried out before the banks were stabilised with cement and clearly indicates that *F. enigmaticus* was not able to establish in the system before this time. Muir (1974) then recorded *F. enigmaticus* but Shelton (1975) did not. This could be because *F. enigmaticus* was present in the Estuary but only in extremely low biomass. Certainly it could not have been missed by Shelton (1975) if densities were anything approaching those found now. The concrete banks were constructed in the early 1960s and the population of *F. enigmaticus* was therefore probably still in the process of establishing within the Estuary. Morant & Grindley (1982) then recorded that *F. enigmaticus* was

common on the hard substrate of the banks and was found in large masses. Finally, *F. enigmaticus* was recorded in high abundance in this study. This pattern provides a timeline for the invasion of *F. enigmaticus* in the Estuary that corresponds with the construction of cement banks and canal walls.

Infauna associated with *Ficopomatus enigmaticus*

The invertebrates associated with *F. enigmaticus* in Zandvlei are similar to those found in Mar Chiquita. Schwindt & Iribarne (2000) recorded amphipods, ostracods, copepods, nematodes, juvenile crabs and gastropods. In the Mar Chiquita coastal lagoon *F. enigmaticus* had major impacts on the abundance of many benthic species (Schwindt et al. 2004a). It provided habitat between the tubes for large populations of amphipods and gastropods and provided shelter for the crab species *Cyrtograpsus angulatus* (Schwindt & Iribarne 2000). *F. enigmaticus* in Zandvlei is proposed to have had similar significant impacts on the structure of the benthic invertebrate community. The abundance and structure of the benthic community will have changed dramatically from when there were only sandy sediments, to the initial invasion by *F. enigmaticus* as a result of the formation of the cement walls, to the current situation. It clearly supports a high density and biomass of invertebrates and must therefore play an important role as an ecosystem engineer. The great increase in *F. enigmaticus* observed in Zandvlei will have increased food, habitat and substratum availability, thereby increasing the density of infauna in the system.

There are many factors which affect the distribution of marine organisms. These include temperature and salinity (Epelbaum et al. 2009). In Zandvlei, the highest mean number of species and individuals was found in the centre of the main Estuary. After this the next highest was in the Marina da Gama, followed by the south part of the Estuary and finally the lowest number of species and individuals was recorded at the head of the Estuary. The centre of the Estuary will have a mix of species that are tolerant to both fresh and saline

water, whereas those found at the mouth and head of the Estuary will be adapted to more extreme conditions. Day (1981a) recorded the highest number of benthic macrofauna species in the middle of four estuaries in southern Africa. It is interesting to note that the highest mean number of species and individuals was not found where the highest biomass of *F. enigmaticus* was located. Conditions in the main Estuary body are clearly more favourable for reef infauna than conditions in the Marina da Gama. This could be linked to the shallower water, greater turbulence or absence of anoxic bottom waters and toxic gases.

Future research should continue to explore the role of *F. enigmaticus* as an ecosystem engineer and its importance as a provider of habitat, food and substratum.

2.4.3 Salinity patterns

The growth of *F. enigmaticus* is affected by many different environmental factors. These include water depth, temperature, salinity, direction of water flow and nutrient availability (Schwindt et al. 2004a). Environmental conditions may, in fact, be the most important factors determining the growth and expansion of *F. enigmaticus* (Schwindt et al. 2004a). It is therefore interesting, and useful, to link growth patterns of *F. enigmaticus* to environmental conditions.

This can, however, be difficult in highly variable environments where conditions change constantly and rapidly. One of the characteristic features of estuaries is that they are extremely variable with respect to salinity. Salinity within an estuary will change depending on whether readings are taken from top or bottom water, at high or low tide, in summer or winter and at the head or mouth of the system (Allanson & Baird 1999). Using time averages or instantaneous snap-shots as representative of an estuary can therefore be extremely misleading (Allanson & Baird 1999).

The estimates of mean salinity calculated in this study are coarse and serve only to identify general trends. In some years there was only one data point available and 2002 had

no readings of salinity taken in March. Similarly, the averages obtained to show the salinity gradient from the mouth to the head of Zandvlei in 1989 and 2011 provide only an extremely rough picture of the conditions at these times.

There was no significant trend in salinity recorded in Zandvlei from 1989 to 2012. The salinity in the Estuary since 2000 has generally been higher than beforehand; however this pattern is not significant. Statistical analysis shows a significant increase in salinity throughout the Estuary when comparing data for 1989 and 2011 alone. The maximum salinity recorded in 1989, at the mouth of the Estuary, was found at the centre of the Estuary in 2011. This increase in salinity could have allowed *F. enigmaticus* to expand further towards the head of the Estuary, if it had been limited by low salinity in this area beforehand. However, it is important to remember that the data used to obtain these values provides only a snapshot in time and that estuaries are extremely variable environments.

The habitats invaded by *F. enigmaticus* worldwide have similar physical characteristics and it is therefore possible to compare invaded environments (Schwindt et al. 2004a). In the Mar Chiquita coastal lagoon *F. enigmaticus* was shown to have lower growth rates in areas of high salinity than in brackish waters (Schwindt et al. 2004a). *F. enigmaticus* near the mouth of the lagoon grew slower than polychaetes in the centre, where the water was brackish. This same pattern was seen in Zandvlei, where the highest biomasses of *F. enigmaticus* in the main Estuary were recorded in the centre. Future studies could investigate the effects of long-term salinity changes on the growth rate of *F. enigmaticus*. Changes in salinity could also have an effect on the reef infaunal by affecting community structure and population densities.

CHAPTER 3.

Conclusions on the impact of *Ficopomatus enigmaticus* invasion

There have been many physical modifications to the Zandvlei Estuary over the years and these changes have affected the flora and fauna of the area. The construction of concrete banks and canal walls facilitated the expansion of *F. enigmaticus* in the Zandvlei by providing a hard substratum on which larvae could settle and grow. Physical conditions in the centre of the main Estuary and Marina da Gama are favourable for rapid growth of the polychaete and as a result the biomass of *F. enigmaticus* in Zandvlei increased rapidly over time. When compared to the standing stock recorded in the system 25 years ago, the population of *F. enigmaticus* has increased greatly. *F. enigmaticus* now covers more surface area of the Marina canal walls and is found in greater mass per m². It is important to note that the establishment and consequent success of *F. enigmaticus* in the Zandvlei was initially driven by the construction of concrete banks and canal walls.

The increase in *F. enigmaticus* observed has had negative impacts on recreational users of the Estuary, restricting boat movement and causing discomfort when touched. There has been some attempt to remove sections of reef where it forms large platforms, and this activity has mainly been focussed on bridges in the Marina da Gama area (Joshua Gericke, pers. comm.). There are concerns, however, about the effect that this will have on the water quality in the system. *F. enigmaticus* has been recognised as an important filter-feeder and its removal may therefore impact water quality (Davies et al. 1989; Eno et al. 1997; Mead et al. 2011).

The increase in reef biomass has likely had positive impacts on reef infauna. With the increase in abundance of *F. enigmaticus*, there has been an increase in the availability of shelter and substratum for infaunal species. The density of infauna within the system is therefore suggested to have increased greatly with the increase in reef. In addition, the population growth has increased *F. enigmaticus* as a food source for some fish species, such as White Steenbras (Day 1981a). However, it is important to note that *F. enigmaticus* can also decrease food availability for other native filter feeders by reducing phytoplanktonic material and suspended organic matter (Eno et al. 1997; Bruschetti et al. 2008). *F. enigmaticus* is likely to have had a great impact on the functioning of the zooplankton food web through its filter-feeding activity. It is also likely to have affected sedimentation rates, through the accumulation of sediments in the reef, nutrient cycling even the productivity of the system.

CHAPTER 4.

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