

Intertidal salt-marsh foraminifera as sea-level indicators: Lessons from the South African coastline

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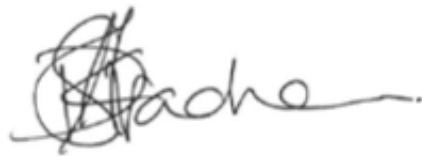
Submitted in fulfilment of the academic requirements for the degree of Doctor
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Preface

The experimental work described in this dissertation was carried out in the School of Agriculture, Earth and Environmental Science, University of KwaZulu-Natal, Pietermaritzburg, from January 2013 to January 2016, under the supervision of Prof T.R Hill and Dr J.M. Finch.

The Studies represent the original work of the author and have not otherwise been submitted in any form of degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.



K.L. Strachan (candidate)



Prof T.R. Hill



Dr J.M. Finch



Salt-marsh vegetation from Knysna Estuary

Abstract

Microfossils of the group foraminifera are widely used as robust, high-precision sea-level proxy indicators associated with salt marshes. These microfossils exhibit vertical zones related to elevation across the intertidal zone, and are well preserved within salt marsh sediments, leaving a permanent record of sea-level change. This research explores the application of intertidal salt-marsh foraminifera as sea-level indicators along the southern African coastline. It further describes the development of a regional transfer function and assesses its performance in reconstructing sea-level change. Three permanently open estuarine environments were selected for this study, Kariega and Keiskamma along the eastern coastline, and Knysna along the southern coastline.

Foraminiferal sea-level records depend on the accurate characterisation of modern foraminifera-environment relationships and salt-marsh zonation representative of a study site. Contemporary foraminiferal assemblages were surveyed across the intertidal zone, and corresponding vegetation and environmental data (pH, salinity, soil properties and elevation) were collected. Multivariate ordination was used to examine the correlation between living foraminiferal assemblages and environmental parameters. It was established that elevation was the key environmental variable governing the distribution of salt-marsh foraminifera at the Keiskamma and Knysna estuaries. Salinity had a significant but opposite influence to elevation at the Keiskamma Estuary. At Knysna Estuary, pH was the secondary driver of foraminiferal composition.

The contemporary intertidal environments at Keiskamma and Knysna estuaries were described in relation to the zonation of foraminifera across each salt marsh. Cluster analysis was performed to separate foraminifera into salt-marsh zones. Whilst the composition and vertical ranges of assemblage zones vary between sites, we suggest that South African salt marshes can be classified according to four broad subdivisions. The mudflats have the most diverse assemblages, consisting predominately of calcareous species. *Ammonia* spp., dominates the lower marsh zone followed by *Miliammina fusca*, which dominates the middle- to lower marsh vegetated zone. The high marsh zone is characterized by the high abundance of *Trochammina inflata*.

Modern training datasets from the selected study sites were used to investigate the suitability of local versus regional datasets for reconstructing recent sea-level trends. The results suggest that a regional transfer function using weighted averaging models is suitable for the analysis of fossil material, producing sea-level reconstructions with an error of ± 0.22 m. As a validation exercise the regional transfer function was applied to a sediment core from Kariega, and compare with tidal gauge data. Sea-level records from far field sites offer important constraints on the timing and amplitude of global sea-level changes and improve our understanding of the driving mechanisms behind the late Holocene sea-level change. The regional transfer function has the potential to link short-term instrumental records with longer-term relative sea-level reconstructions, advancing research into past sea-level fluctuations along the South African coastline, and provide a baseline understanding of the nature and causes of sea-level variation. Intertidal salt-marsh foraminifera provide South African sea-level studies with an indicator that is reliable and can be used at multiple sites, allowing for comparisons between studies.

Intertidal salt-marsh foraminifera as sea-level indicators: Lessons from the South African coastline

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Thesis contents

This doctoral thesis consists of an introduction, three appended papers and a synthesis.

List of papers

The papers appended are:

- I. Strachan, K.L., Finch, J.M., Hill, T.R., Barnett, R.L., Morris, C.D. and Frenzel, P., (2016): Environmental controls on the distribution of salt-marsh foraminifera from the southern coastline of South Africa. *Journal of Biogeography*, DOI: 10.1111/jbi.12698.
- II. Strachan, K.L., Hill, T.R., Finch, J.M., Barnett, R.L. and Frenzel, P. Distribution of salt-marsh foraminifera in two South African estuaries, and application as sea-level indicators. Submitted to *Journal of Coastal Research*.
- III. Strachan, K.L., Barnett, R.L., Finch, J.M. and Hill, T.R. A regional-based transfer function from South African marshes: Implications for sea-level studies along the South African coast. Target Journal: *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Co-authorship

KLS led the writing of all three papers and performed all analysis. CDM assisted the statistical analysis for paper I. PF assisted with the SEM images for Paper II. RLB assisted with the transfer function and diagrams for paper III. The co-authors contributed with improvements of the text, data interpretation and scientific discussions in all three papers.

Introduction

INTRODUCTION

The fundamental characteristic of the earth is one of constant change, varying in size and magnitude, through time (Hidore, 1996; Oldfield, 2005). The earth has been warmer and cooler, wetter and drier, whilst species (communities and populations) have disappeared and evolved (Oldfield, 2005), and sea levels have fluctuated, inundating and draining coastal environments (Lambeck *et al.*, 2004). Over the last decade there has been a growing concern with regards to the consequences of climate change; with a realization that either the climate may cool and give rise to another ice age or warm as a result of greenhouse gases (Brulle *et al.*, 2012). The Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5) provides a consensus view on future climate change along with a summary regarding the effects of increased levels of CO₂ on recent and future climate change together with consequences of expected sea-level rise. AR5 identifies sectors in which our ability to predict future scenarios is less certain, including change in ice-sheets and sea level, and future precipitation patterns. Unfortunately, such uncertainties limit the ability of governments and organisations to plan adaption and mitigation strategies (Bindoff *et al.*, 2007; Solomon, 2007). Reducing uncertainty concerning future climate change is therefore a high research priority.

Variability within the environment takes place at different timescales; it can be diurnal, semidiurnal; seasonal and in the form of cycles over years, decades or centuries. Therefore, there can be short-term variability and long-term change, however there is still a fine line between variability and change (Murray, 1991; Church *et al.*, 2006). Unfortunately, many instrumental records cover a limited period of time and are often missing data; this limits our ability to fully understand spatial and temporal patterns associated with natural climate variability (Church *et al.*, 2006; Henderson *et al.*, 2009).

Palaeoclimate research provides a variety of tools, which can reduce uncertainty around future predictions. As a consequence,

palaeoecological records both terrestrial (e.g. Pollen, plant biomarkers and tree-rings) and aquatic (e.g. ostracods, diatoms, chironomids, testate amoebae and foraminifera) can be used to measure and evaluate past climatic changes and overcome the confines of instrumental climatic records (Bigler *et al.*, 2002; Henderson *et al.*, 2009). Therefore palaeontology offers a tool, which can assist in understanding the resilience of ecosystems to past disturbances (Culver, 1987; Henderson *et al.*, 2009; Seddon *et al.*, 2014).

Studies, which incorporate the use of microfossils to understand late Holocene environmental change, can provide useful information that should be incorporated into conservation planning and policy-making (Seddon *et al.*, 2014). With increased awareness of anthropogenic impacts on the natural environment, micropalaeontologists are using the past as a key to the future (Willis *et al.*, 2010; Seddon *et al.*, 2014). In other words, by understanding how organisms responded to past environmental changes, we are able to use that information to predict how future change (natural or anthropogenic) might impact the earth (Froyd and Willis, 2008). Palaeoecological research using a variety of proxies and tools can analysis environmental change at different spatial and temporal scales, from which concerns regarding future environmental changes, including sea-level rise can be addressed (Willis and Birks, 2006; Froyd and Willis, 2008).

The Quaternary period was characterized by fluctuations in sea level; during cold glacial periods the sea level was significantly lower and somewhat higher during interglacial periods. Preserved within our coastal environments are a wide variety of sea-indicators representing past coastal environments. Coastal evolution is cumulative, and therefore the present coastal landscape is the result of past coastal processes and landforms (Masselink and Gehrels, 2014). Coastal landforms and sediment sequences potentially exist beyond the present day coastal zone (Davidson-Arnott, 2010; Masselink and Gehrels, 2014). Constraining past sea-level change is therefore an essential

component to understanding the evolution of the coastal zone and predicting the impacts of future sea-level change (Compton, 2006).

During the Holocene, sea-levels fluctuated as a result of changes in the gravity field linked with the exchange between land ice and the ocean (Masselink and Gehrels, 2014), as well as meteorological and oceanographic factors (Pugh and Woodworth, 2014). A growing body of literature suggests that the recent warming trend is likely to last for some time and as a result sea levels will continue to change in the future at an increasing rate. Therefore, sea-level rise from melting polar ice sheets and meteorological effects are some of the greatest threats of future climate change (Nicholls and Cazenave, 2010). Some of the world's largest populations and cities are concentrated in low-lying coastal areas and thus vulnerable to sea-level rise (Overpeck *et al.*, 2006; Nicholls and Cazenave, 2010; Masselink and Gehrels, 2014; Pugh and Woodworth, 2014).

The drivers of relative sea-level change include tectonic (uplift and subsidence), eustatic (fluctuations in global ice volume or ocean basin volume), and hydro-isostatic processes, as well as fluctuations in sediment supply (Carr and Botha, 2012), meteorological dynamics, and seawater densities as a result in varying salinities and ocean temperatures (Pugh and Woodworth, 2014). Eustatic sea-level change is one of the most important drivers due to changes in ocean volume (Gornitz *et al.*, 1982; Pugh and Woodworth, 2014). This is the result of growing and melting ice sheets, along with isostatic adjustment of the earth's crust caused by the decline and growth of ice sheets, and the associated change in ocean volume (Gornitz *et al.*, 1982). Thermal expansion of ocean water is likely to be the dominant driver of sea-level change having a greater contribution than the melting of glaciers and ice caps. As the ocean warms as a result of the increasing greenhouse gases, so the ocean's mass increases (Lombard *et al.*, 2005; Nicholls and Cazenave, 2010). Ocean temperature data collected over a period of 10 years indicated that thermal expansion has contributed to sea-level rise by 0.5 ± 0.05 mm/year prior to 2005 (Lombard *et al.*, 2005). At a local scale, tectonic movement and

sedimentation can generate sea level adjustments, which are comparable to eustatic or isostatic changes (Gornitz *et al.*, 1982; Pugh and Woodworth, 2014). Sea levels can also be influenced by local and regional meteorological effects, which include storm surges, the El Niño-Southern Oscillation, as well as sea surface and land movement long-term trends (Church and White, 2011). Reliable estimations are scarce, however anthropogenic changes in terrestrial water storage through unsustainable ground water use, reservoir operations and irrigation are likely to also have an impact on sea level rise (Pokhrel *et al.*, 2012).

The southern African south and east coastlines have been tectonically stable throughout the late Quaternary (Carr *et al.*, 2010), which means that sea levels would have been marginally influenced by postglacial eustatic rise during this period (Miller *et al.*, 1995). Southern African sites are classified as 'far field sites', situated away from the large ice sheets in the northern hemisphere, and offer important constraints on the timing and amplitude of global sea-level changes (Carr *et al.*, 2010). 'Far field' locations were not directly glaciated during the Quaternary period and therefore may have experienced local neotectonic effects or hydro-isostasy, compared to locations situated in higher latitudes which would have experienced glacio-isostasy (Murray-Wallace and Woodroffe, 2014). Such sites can provide important insights regarding the driving mechanisms responsible for Holocene sea-level change (Flemming *et al.*, 1998; Milne and Mitrovica, 2008; Woodroffe *et al.*, 2005). The southern cape coastline in South Africa is an example of a passive margin located in the far field of past ice-sheets, its coastal successions during the last interglacial age may be related to hydro-isostatic processes rather the tectonic uplift (Murray-Wallace and Woodroffe, 2014). In the southern African context, information related to past environmental changes has been limited due to the lack of researchers, funding, tidal gauge data (Woodworth and Player, 2003) and environmental limitations regarding the recovery of palaeoenvironmental data (Chase and Meadows, 2007). Instrumental evidence of recent sea-level change was confined to tide gauge data prior to 1993, when satellite

altimetry was introduced (Mather *et al.*, 2009). In many ways, satellites have increased the number sea-level records available; however, there is still a need for accurate long-term tidal gauge data to calibrate and correct the satellite altimeter results (Mitchum, 1998; Mather *et al.*, 2009). Unfortunately, not many of the tide gauge records for the southern hemisphere and especially South Africa extend beyond 50 years (Woodworth and Player, 2003; Mather, 2007). The South African tide gauge network consists of 10 stations with the oldest one going back as far as 1926, though with large periods of missing data. The majority of the other stations only started recording around the 1970's (PSMSL, 2015). Brundrit (1984) focused on sea-level changes using tidal gauge information along the west coast of South Africa, and since then very little research has been conducted (Mather *et al.*, 2009).

During the Holocene, both large and small sea-level fluctuations had enormous impacts on the coastal environment (Compton and Franceschini, 2005; Compton, 2006; Franceschini and Compton, 2006). It is therefore vital to understand how the South African coastline responds to changes in relative sea level, so that future changes can be predicted (Compton, 2006). To quantify

Holocene sea-level variations it is important to find site-specific sea-level indicators (Miller *et al.*, 1995). A number of potential sea-level indicators have been applied to the South African coast, including dating of beachrock (Ramsay and Cooper, 2002; Kelly *et al.*, 2014; Mauz *et al.*, 2015), pollen (Carr *et al.*, 2015), salt marsh deposits (Baxter and Meadows, 1999), tree stumps (Marker, 1997), intertidal erosional features (Green and Uken, 2005), plant biomarkers (Carr *et al.*, 2015), oyster-rich bioclastic gravel (Compton, 2001), luminescence dating of eolianite (Carr *et al.*, 2010), mollusc assemblages (Compton, 2006), and estuarine shells (Marker and Miller, 1993 and 1995)(Table 1). South African researchers tend to have relied on 'global records' as a comparison for dating shorelines, which are compared with particular elevations (Ramsay and Cooper, 2002). As a result, chronological control for most sea-level studies, whether it is depositional or erosional in nature, is weak (Carr *et al.*, 2010). The Holocene sea-level records for the eastern and western coastlines show partial but not a complete overlap at the current resolution (Miller *et al.*, 1995). For this reason there is a need for higher resolution studies, which may reveal a clearer picture of coastal sea level changes through time.

Table 1: Summary of South African late-Holocene sea-level indicators.

Lab code	¹⁴ C yr BP	cal yr BP (2 std dev)	Mean sea level relative to present (m)	Material	Locality	Reference
TOP83	450 ± 70	319 - 537 (95)	-0.4	bulk organic matter	Langebaan (South Africa)	Compton, 2001
SP2-48	560 ± 45	497 - 563 (86)	-0.2	bulk organic matter	Langebaan (South Africa)	Compton, 2001
SP2-82	840 ± 45	664 - 774 (93)	-0.5	bulk organic matter	Langebaan (South Africa)	Compton, 2001
TOP159	1390 ± 50	1171 - 1345 (94)	+0 to -0.7	bulk organic matter	Langebaan (South Africa)	Compton, 2001
SP1-87	4260± 80	4529-4879	0 to -0.7	bulk organic matter	Langebaan (South Africa)	Compton, 2001
SP3-99	4850± 70	4800-5084	0 to +1	<i>P. capensis</i>	Langebaan (South Africa)	Compton, 2001
SL2-105	3470± 60	2973-3321	-0.5 to 1.0	Shell, mixed	Langebaan (South Africa)	Compton, 2001
SL3-48	2920± 50	2333-2684	-0.5 to 1.0	Shell, mixed	Langebaan (South Africa)	Compton, 2001
BOT126	4510± 50	4370-4606	-1 to 1	Shell, mixed	Langebaan (South Africa)	Compton, 2001
BOT176	6460± 70	6617-6900	0 to +3	<i>O. atherstonei</i>	Langebaan (South Africa)	Compton, 2001
Y-467	1905± 60	1624-1919	-1 to 0	Organic mud	Groenvlei	Deevey <i>et al.</i> , 1959
Y-466	6870± 160	7386-7928	-4 to -3	Organic mud	Groenvlei	Deevey <i>et al.</i> , 1959
5860	5910± 30	6296-6385	2.8 to 3.8	Estuarine mudbank	Knysna	Marker and Miller, 1993
4462	4280± 60	4222-4523	0.2 to 1.2	Estuarine channel	Keubooms	Reddering, 1988
4317	5580± 70	5840±6154	1.7 to 2.7	Estuarine terrace	Keubooms	Reddering, 1988
Pta-7201	770 ± 50	628 - 736 (78)	-2 to -0.7	tree stump	Knysna (South Africa)	Marker, 1997
interpolated range		0 - 790	-0,2 to 0	bulk organic matter	Macassa Bay (Mozambique)	Norstrom <i>et al.</i> , 2012
interpolated range		4700 - 790	-1,1 to -0,2	bulk organic matter	Macassa Bay (Mozambique)	Norstrom <i>et al.</i> , 2013
Pta-4311	1450 ± 50	1242 - 1394 (92)	1.6	shell	Verlorenvlei (South Africa)	Miller <i>et al.</i> , 1993
unknown	910 ± 120	631 - 980 (92)	0	beach rock cement	Vilanculos (Mozambique)	Siesser, 1974
unknown	920 ± 140	627 - 1057 (92)	0	beach rock cement	Vilanculos (Mozambique)	Siesser, 1974
Pta-4972	1610 ± 70	1307 - 1569 (94)	1.5	coral in beach	Kosi Bay (South Africa)	Cooper, unpub (in Ramsay, 1995)

Salt-marsh environments

Coastal wetlands of the world such as salt marshes and mangrove stands provide key ecological services. They are indicators of both modern day anthropogenic impacts on climate and the natural environment, and are natural archives of palaeoecological changes throughout the earth's history (Scott *et al.*, 2014). Estuaries, coastal lagoons and salt marshes are some of the most biologically productive, but also severely altered ecosystems globally (Van Dyke and Wasson, 2005). Coastal wetlands are areas of high primary and secondary productivity, whereby soils and sediments are successfully able to sequester carbon (Beck *et al.*, 2001; Kathilankal *et al.*, 2008). Salt marshes are globally valued, due to their halophytic vegetation being confined to these environments (Adam, 1990). Such environments are said to have maintained equilibrium, naturally adjusting to the migration of the sea along the coastline, thereby providing a natural protective barrier from coastal hazards such as flooding (Constanza *et al.*, 2008). The elevation of the salt marsh relative to the local mean sea level will determine, the daily inundation frequency, duration, and the productivity of the marsh.

Coastal wetlands provide a wealth of information regarding Holocene sea-level change. Emery and Garrison (1967) conducted one of the first studies using salt marsh peat as a sea-level indicator. The sediment sequence can provide a record of coastal history; that has the potential to reveal past estuary, lagoonal or delta floors and ancient marsh deposits. The recognition of ancient depositional environments is important, but, salt-marsh peat can also provide essential information regarding key phases in marine transgression and regression (Frey and Basan, 1978; Scott *et al.*, 2014). Salt marshes are indicators of sea-level change due to their intimate relationship with the tidal frame, together with the distinct vertical zonation of flora and fauna (Horton and Edwards, 2006). Different plants form distinct vegetation zonation associated with tidal inundation and inter-specific competition. The relationship between elevation and salt-marsh vegetation has allowed researchers to date plant

fragments that are embedded in salt-marsh sediments, providing them with accurate ages of sea-level markers (Gehrels, 1994). The limitation of this method is the large and changeable vertical distribution of plants; however, plant fragments have the advantage of being visible to the naked eye (Gehrels, 1994).

Intertidal salt-marsh foraminifera

Foraminifera are single celled eukaryote organisms possessing a test, which remains fossilized in the sediment after death. They are abundant in both modern and ancient marine sediments (Murray, 1991) and their fossils are durable and easily collected and separated from the sediment, making them excellent tools for reconstructing historical environmental change (Scott and Leckie, 1990; Gehrels, 1994; Jennings and Nelson, 1992; Scott *et al.*, 2001). Intertidal foraminifera can be controlled by tidal elevation and by mean salinity of the surrounding water (Leorri *et al.*, 2010). Salt-marsh foraminifera occurring in temperate environments are all distributed according to the vertical zonation concept, and thereby considered to be accurate proxies for reconstructing the characteristics and timing of past sea levels (Scott and Medioli, 1978). Accurate sea-level information can be obtained as a result of the vertically zoned nature of salt-marsh foraminifera, related to tidal levels and altitude (vertical zonation concept; Scott and Medioli, 1978). Using salt-marsh foraminiferal assemblage zones, sea levels can be defined to within ± 0.05 m (Leorri *et al.*, 2010), as a result of the relationship between different foraminiferal taxa and elevation above mean sea level (Scott and Medioli, 1978).

Foraminifera have not only been used as accurate and precise tools for reconstructing sea-level changes during the Holocene (Scott and Medioli, 1978; 1980; Gehrels, 1994; Woodroffe *et al.*, 2005) but have also been applied to monitor pollution (Sen Gupta, 1999; Lee and Hallock, 2000; Martin, 2000). However, in South Africa few studies have utilized foraminifera (Albani, 1965; Moura, 1965; Martin, 1981; McMillan, 1986; 1990; 1993; Cooper and McMillan, 1987; Wright *et*

al., 1990; Rocha, 1995; Lindsay *et al.*, 1996; Franceschini *et al.*, 2005; Strachan *et al.*, 2014; Strachan *et al.*, 2015), relatively little has been published regarding their modern distribution, and their relationship with tidal levels remains inadequately quantified (Franceschini *et al.*, 2005; Strachan *et al.*, 2015).

AIM

The aim of this research is to explore the application of intertidal salt-marsh foraminifera as sea-level indicators along the southeast South African coastline, develop a regional transfer function, and assess its performance in reconstructing sea-level change. The objectives of this study are to: (i) establish a contemporary dataset of salt-marsh foraminifera, by confirming elevation (height above land levelling datum; LLD) as a statistically significant control on distribution; (ii) examine the extent to which salt-marsh foraminifera exhibit evidence of vertical zonation and (iii) develop a regional foraminifera based transfer function to calibrate fossil samples and produce a record of relative sea-level change for the past ± 300 years as a validation exercise. For the purpose of this research the aim is to extract an 'elevational signal' to explain species distribution patterns with regards to their relationship with environmental variables and therefore elevation is being used as a surrogate variable for the frequency of tidal inundation.

The South African coastal environment

South Africa is well situated in the southern hemisphere for studying large-scale environmental change during glacial and interglacial periods. Southern Africa is influenced by a number of atmospheric and oceanic circulation systems as it is positioned where the tropical, subtropical and temperate climate systems meet, along with the Indian, Atlantic and Southern oceans (Chase and Meadows, 2007). The South African climate is directly and indirectly influenced by four large scale processes, *viz.*, the seasonal movements of the Inter Tropical Convergence Zone (ITCZ), sea surface temperatures, the easterly trade winds and finally the expansion

and contraction of the circumpolar westerlies (Tyson and Preston-Whyte, 2000).

The most important large-scale oceanographic feature along the southeast coast of South Africa is the Agulhas current (Ramsay, 1995; Lubke and de Moor, 1998). As a consequence of the narrow shelf along the east coast, the Agulhas current flows relatively close inshore and can attain velocities of 1.5 m s^{-1} (Ramsay, 1995). This particular coastline is dominated by strong currents and consistently high wave energy with the tidal range in the area averaging ~ 2 m (Ramsay, 1995; Cooper, 2001; Hutchings *et al.*, 2002). The mixing of tropical warm waters and cold Antarctic waters along the coast, coupled with climatic changes moving north along the coast, makes for an extremely diverse coastal environment (Lubke and de Moor, 1998).

The north and eastern parts of the country fall within the summer rainfall zone (SRZ; Figure 1), in which the climate is influenced by the seasonal interactions between the subtropical high pressure cells and the movement of the easterly wind flows which are linked with the Intertropical Convergence Zone (ITCZ) (Chase and Meadows, 2007). The southern and western coastline experiences winter rainfall (winter rainfall zone; WRZ), resulting from temperate frontal systems attached to westerlies (Tyson and Preston-Whyte, 2000; Chase and Meadows, 2007). Between the SRZ and the WRZ is a narrow zone, which experiences both summer and winter rainfall (Cooper, 2001; Chase and Meadows, 2007). The South African coastline is approximately 3000 km in length, stretching from Namibia in the west to Mozambique in the east. The coastline is both climatologically and geomorphologically highly variable (Lubke and De Moor, 1998; Cooper, 2001). The southeast coast is characterized by linear, clastic sandy shorelines and bays sculptured by the waves. The beaches are protected by vegetated Pleistocene and Holocene sand dunes, with swamps, lagoons and old dunes (Ramsay, 1995). There are estuaries situated all the way along the South African coastline, which is a dominant component of the coastal geomorphology (Cooper, 2001). The majority of the estuaries originate in incised bedrock valleys, which were cut during the Pliocene

and Pleistocene epochs during low sea-level periods (Cooper *et al.*, 1999).

However, during the Holocene as sea levels rose, so the lower reaches of rivers were modified as a result of the landward retreat of the shoreline (Porat and Botha, 2008). On the most part, estuary channels engulfed the entire bedrock valley, though some have extensive floodplains, though still restricted to the bedrock valley (Cooper, 2001). South African estuaries are classified differently from one another due to contributing factors, *viz.*, size of the catchment and gradient; sediment supply from both upriver and the ocean, local climate and fluvial discharge (Cooper, 2001). The gradient of the coastline is variable due to mountains intersecting it; the west is gentler sloping and the east much steeper (Bird, 2011).

Whitfield and Kok (1992) suggest that there are five types of estuarine systems (estuarine bay, permanently open, river mouth, estuarine lake and temporarily closed) found along the southern and eastern coastline of South Africa, the two most prominent being permanently open or temporarily closed (Bornman and Adams, 2008). The state of the mouth is determined by large sand bars, which in return are controlled by the flow of the river (Bornman and Adams, 2008). According to Reddering and Rust (1990) there are only 37 true estuarine systems found in South Africa that continue to have a permanently open inlet to the ocean out of the 289 river mouths. Stratigraphical evidence suggests that many of these systems have been in a permanently open state throughout the Holocene period (Cooper, 1993), making them ideal locations for foraminifera-based sea-level studies.

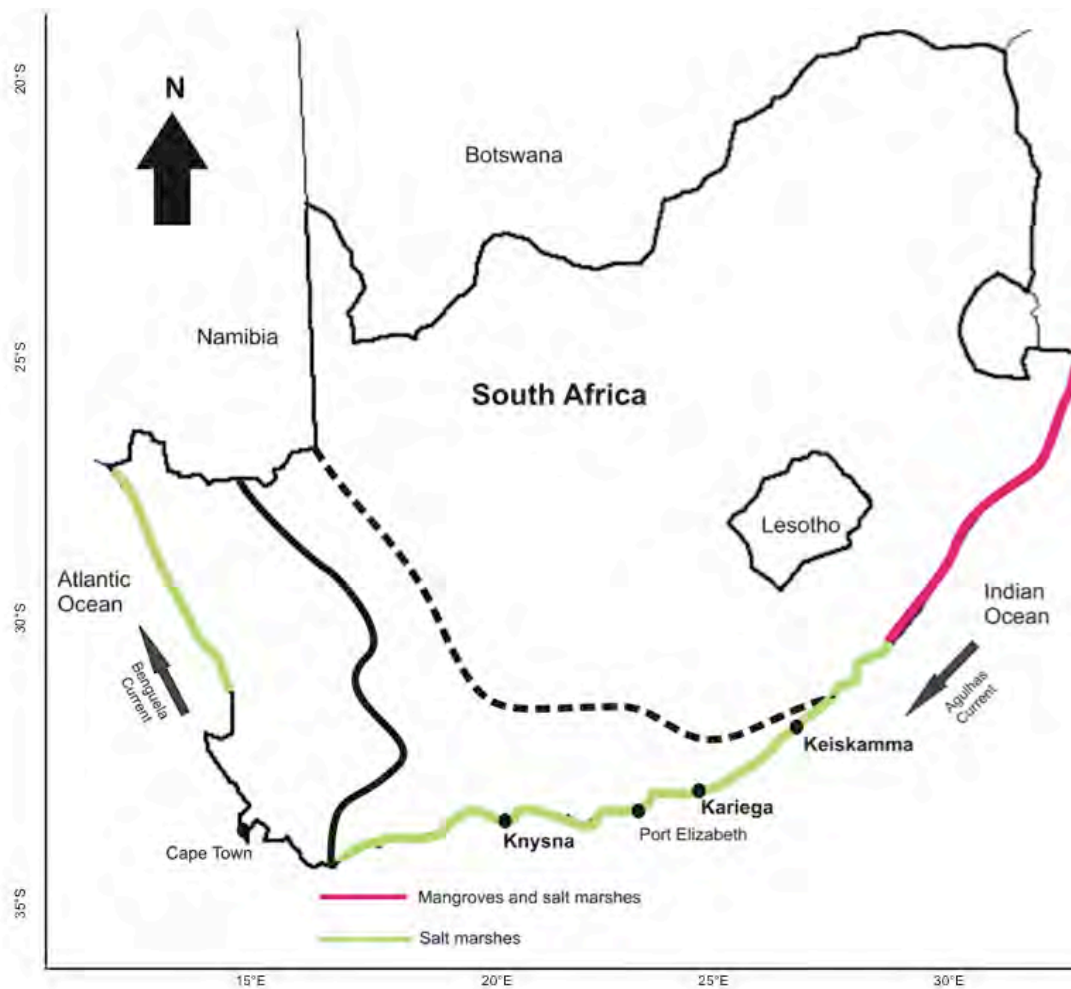


Figure 1: Map indicating the WRZ (solid line) and SRZ (dashed line) boundaries (Adapted from Chase and Meadows, 2007), salt marsh and mangrove distributions, along with major currents along the South African coastline (Adapted from Macnae, 1963).

Research structure

This research explores the application of intertidal salt-marsh foraminifera as sea-level indicators along the South African coastline. Three estuarine environments (Figure 1) were selected for this study based on their permanently open status and the size of their salt-marsh complex. Kariega and Keiskamma are situated along the eastern coastline and Knysna along the southern coastline. As sea-level reconstruction using foraminifera rely on accurately determining modern foraminifera-environment relationships, Paper I uses multivariate ordination analysis to examine the relationship between living foraminiferal assemblages and environmental variables *viz.* pH, salinity, sediment properties and elevation from Keiskamma and Knysna estuaries. Paper II, focussed on the same sites, describes the distribution, abundance and vertical zonation of dead and living foraminiferal assemblages, with which fossil foraminifera can be compared and constrained for sea-level reconstructions. In Paper III, modern training datasets from the three estuaries are used to investigate the suitability of local versus regional datasets for reconstructing recent sea-level trends. A regional foraminiferal transfer function is then applied to a sediment core from Kariega as a validation exercise. The sea-level reconstruction is compared against local tide gauge data to qualitatively validate the accuracy of the reconstruction and the use of a regional dataset. The research ultimately seeks to, explore the application of intertidal salt-marsh foraminifera as sea-level indicators along the southeast South African coastline, develop a regional transfer function, and assess its performance in reconstructing sea-level change.

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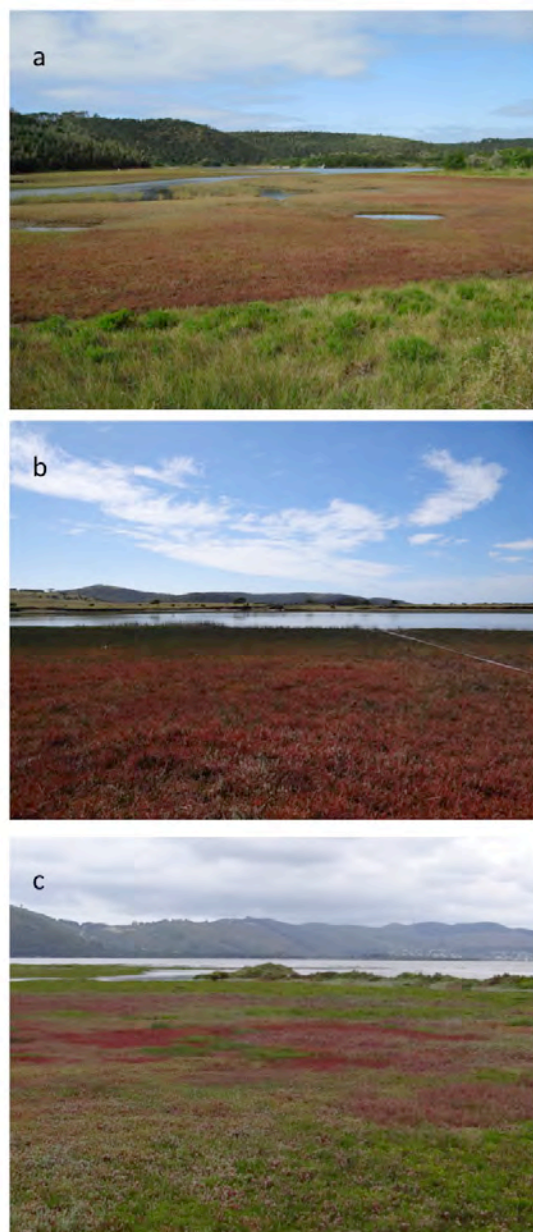


Plate 1: Study sites along the southeast coast of South Africa (a) Kariega Estuary, (b) Keiskamma Estuary and (c) Knysna Estuary.

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Paper I

Environmental controls on the distribution of salt-marsh foraminifera from the southern coastline of South Africa

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ABSTRACT

Aim Salt-marsh foraminifera are widely used as robust sea-level indicators. High-resolution Holocene sea-level reconstructions depend on the accurate characterisation of modern foraminifera-environment relationships representative of a study site. We investigate the relationship between modern foraminiferal assemblage distribution and key environmental variables, *viz.* elevation above mean sea level (MSL), sediment grain size, organic content, water pH and salinity. We hypothesize that the distribution of modern salt-marsh foraminifera is primarily controlled by elevation above MSL.

Location Knysna and Keiskamma estuaries along the southern coastline of South Africa.

Methods Salt-marsh surface sediment samples ($n = 97$) were collected along eight intertidal transects with corresponding environmental data (pH, salinity, organic content, sand, silt, clay and elevation). Multivariate ordination analysis (partial redundancy analysis; pRDA) was used to investigate the relationship between living foraminiferal assemblages and environmental controls, after accounting for spatial variability in community composition.

Results The pRDA suggests that species composition varied spatially within estuaries, but was strongly influenced by elevation at Keiskamma ($r = 0.63$) and Knysna ($r = -0.75$). At Keiskamma, the main gradient in composition was also influenced by salinity ($r = -0.63$), in an equal and opposite manner to elevation. Composition at Keiskamma was influenced to a much lesser extent by sediment organic content ($r = 0.20$) and the clay fraction ($r = -0.13$). At Knysna, pH ($r = 0.455$) was a secondary determinant of composition, and sediment characteristics covaried with elevation.

Main conclusion Elevation was found to be a key environmental variable controlling the distribution of salt-marsh foraminifera at both estuaries, thereby validating the use of foraminifera as sea-level indicators. Certain species were particularly sensitive to elevation changes and could thus serve as

useful indicators of past sea-level change. This is an important first step towards the development of high-resolution sea-level reconstructions for the South African coastline.

Keywords: elevation, environmental controls, foraminifera, grain size, organic content, pH, salinity, salt-marsh, sea level

INTRODUCTION

Our understanding of future sea-level rise is dependent on identifying, explaining and constraining past sea-level fluctuations. Trends obtained from instrumental data can be extended back in time using geological and micropalaeontological evidence (e.g. diatoms, testate amoebae, foraminifera and ostracods; Donnelly *et al.*, 2004; Mills *et al.*, 2013). Foraminiferal assemblages have been extensively employed as indicators to address key environmental concerns (Jennings & Weiner, 1996; Scott *et al.*, 2001). In salt-marsh environments, foraminifera have been used to reconstruct late Holocene relative sea-level changes (e.g. Gehrels, 1994; de Rijk & Troelstra, 1997; Horton, 1999; Scott *et al.*, 2001; Gehrels & Newman, 2004; Horton and Edwards, 2006; Strachan *et al.*, 2014) to high precision (cf. Gehrels & Woodworth, 2013). The successful use of salt-marsh foraminifera as a proxy for sea-level reconstructions requires a detailed and accurate knowledge of their contemporary distributions and their relationship to environmental drivers (Scott & Medioli, 1980; Gehrels, 1994, 2002; Hayward *et al.*, 1999). Salt-marsh sediments are responsive to relative sea-level changes, and distinct foraminiferal assemblages can be applied to track these changes (Murray, 2006), due to their strong and quantifiable relationship with elevation (Hayward *et al.*, 2010; Rossi *et al.*, 2011; Kemp *et al.*, 2011). The primary controls on salt-marsh foraminifera include duration of subaerial exposure linked to elevation, vegetation cover, effects of drying, salinity, and pore water pH (Murray, 2006). Quantification of environmental controls on foraminiferal distribution is thus a prerequisite to employing foraminifera as robust sea-level indicators.

Foraminiferal assemblages form discrete vertical zones across a salt marsh, where the relative abundance of species correlates with tidal levels (Scott, 1976; Scott & Medioli, 1980; Scott *et al.*, 2001; Gehrels & Newman,

2004). This ‘vertical zonation concept’ (de Rijk & Troelstra, 1997) reflects responses to changing environmental variables such as tidal submergence. Salt-marsh surface elevation can be used as an approximation of tidal inundation, and thus represents a key variable for sea-level studies (Scott & Medioli, 1980; Wright *et al.*, 2011). Change in elevation is regularly cited as the dominant variable influencing foraminiferal distributions of both agglutinated and calcareous taxa (Horton, 1999; Horton & Murray, 2007). Studies from the Americas (Jennings & Nelson, 1992; Gehrels, 1994; Williams, 1994; Guilbault *et al.*, 1995; Jennings *et al.*, 1995; Jennings & Weiner, 1996; Goldstein & Watkins, 1998), New Zealand (Hayward *et al.*, 1999), Australia (Horton *et al.*, 2003) and Great Britain (Horton, 1999; Edwards and Horton, 2000) support this notion. Even though elevation is the basis for investigating changes in sea level, it must be acknowledged that elevation is not a true environmental variable (Kemp & Telford, 2015). Elevation itself is not able to exert a controlling influence on modern foraminiferal distributions. The correlation between species distribution and elevation is explained as a consequence of co-variation with other environmental variables (Edwards & Wright, 2015). Elevation serves as a useful substitute, or surrogate variable, for frequency of tidal inundation. Where ecologists aim to identify and understand the relative importance of controlling variables, palaeoecologists simplify this approach to explain patterns in terms of their relationship with target variables (Edwards and Wright, 2015), in this case extracting an ‘elevational signal’ from the data. Thus, in developing a transfer function to reconstruct sea-level change, elevation is accepted as a surrogate variable for true controlling variables (Kemp & Telford, 2015).

Nonetheless, some studies have indicated that alternative environmental drivers may supersede elevation as the dominant variable.

Evidence from sea-level studies conducted by de Rijk and Troelstra (1997), Jonasson and Patterson (1992), and Hayward *et al.* (2004), found that high marsh foraminiferal distributions correlated more strongly with salinity than elevation. Further to this, sediment grain size (Matera & Lee, 1972; de Rijk & Troelstra, 1997) and pH (Horton, 1999; Woodroffe *et al.*, 2005) have been reported to influence foraminiferal distributions.

Since the 1970s, estuarine benthic foraminiferal assemblages have been used as proxies for salinity gradients (Nichols, 1974), with de Rijk (1995) the main advocate of salinity as a controlling environmental variable. Research conducted in the Great Marshes of Massachusetts, USA, recorded positive correlations between abundance and salinity for *Jadammina macrescens* and *Tiphotrecha comprimata*, however, this could have been related to the variable topography of the marsh (de Rijk & Troelstra, 1997). Horton & Murray's (2007) work at Cowpen Marsh, UK, found that species dominant in the lower reaches of the marsh and the tidal mudflats demonstrated a clear relationship with salinity. Under natural environmental conditions, foraminiferal distributions tend to reflect the relative inflow of salt versus fresh water, which ultimately influences salinity. Interpreting the spatial distribution of foraminifera with respect to salinity is complex (de Rijk, 1995), a number of factors influence the salinity of a salt marsh at any point in time e.g. flooding characteristics, groundwater flow and surface seepage (Kemp *et al.*, 2009). According to Kemp *et al.* (2009: 232), the "flooding of salt marsh surfaces is the primary control of salinity and is described by the frequency and duration of inundation as well as the salinity of the water itself".

Sea-level reconstructions depend on marsh assemblages being strongly correlative to elevation (Berkeley *et al.*, 2007), bearing in mind that controls will vary in both time and space. Elevation and salinity may be important in different zones of a marsh, and each species will have an individual response to any changes that may occur (Horton & Murray, 2007). A distinction should be made between

factors affecting major distributional patterns and those which affect abundance (Horton & Murray, 2007). For example, *J. macrescens* and *Trochammina inflata* are rarely found in unvegetated tidal mudflats. Plants provide shelter, detrital food and contribute to the low pH of pore water which encourages the existence of these species at higher elevations where there are significant periods of subaerial exposure (Gehrels, 2002; Murray, 2006). In shallow water environments, temperature and salinity are primary controls on foraminiferal distributions. Oxygen availability is significant when values drop to very low levels (Murray, 2006; Horton & Murray, 2007).

The range of environmental variables associated with foraminifera, and the fact that surface populations are not uniformly distributed between marshes (Murray, 2006), means that local studies to determine the relative influence of environmental drivers are imperative prior to attempting sea-level reconstructions. However, in South Africa, there is limited baseline research into environmental controls on contemporary salt-marsh foraminifera (e.g. Franceschini *et al.*, 2005; Strachan *et al.*, 2015). Without such understanding, studies attempting to develop pre-industrial sea-level data, while useful for investigating regional patterns of sea-level rise, will forcibly result in low confidence interpretation.

The aim of this paper is to identify dominant environmental variables controlling foraminiferal distribution along the southern coastline of South Africa, and thereby test the hypothesis that the distribution of modern salt-marsh foraminifera is primarily controlled by elevation. Two estuarine salt marshes were selected with minimal potential influence from development and agriculture. The objectives were to: (1) quantitatively describe the influence of seven environmental variables (*viz.* elevation, water pH and salinity, and sediment organic matter, sand, silt and clay content) on living assemblage composition, and (2) identify and describe the distribution of indicator species responsiveness to environmental controls.

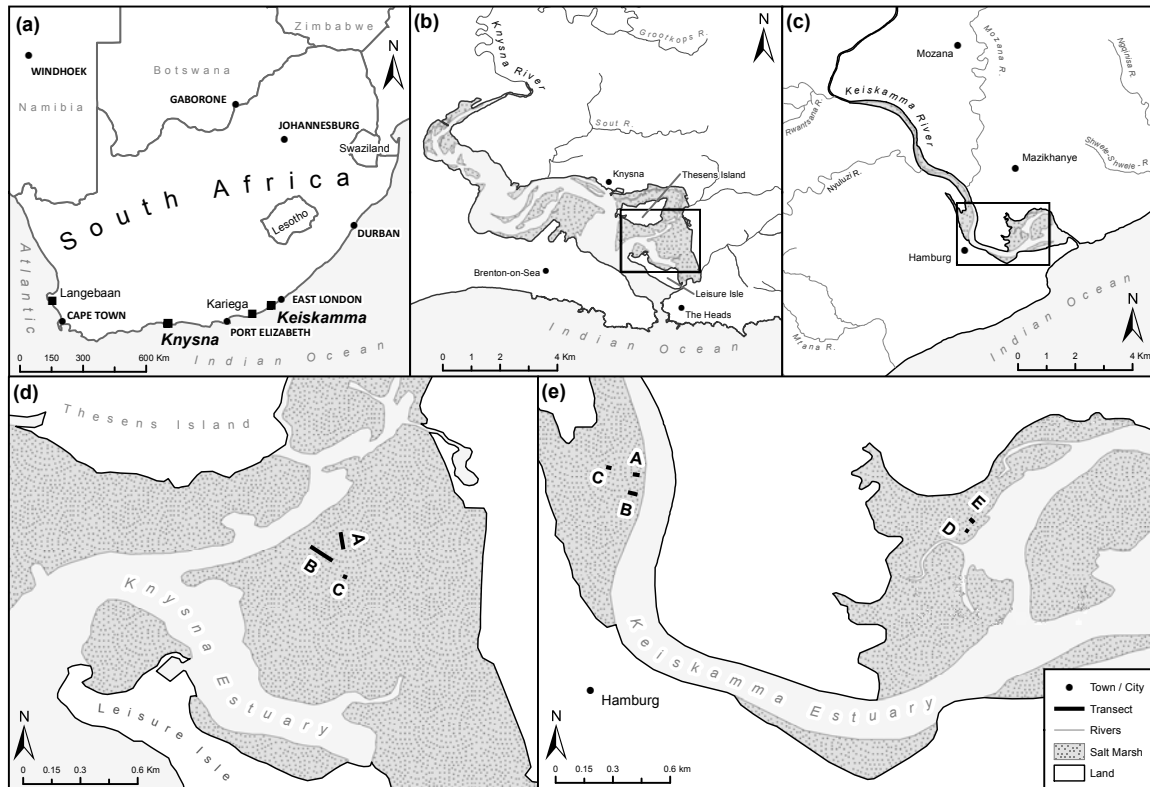


Figure 1: Map of (a) South Africa and locations of the (b) Knysna and (c) Keiskamma estuaries along the southern coastline. Position of transects surveyed in the (d) Knysna and (e) Keiskamma estuaries.

ENVIRONMENTAL SETTING

Keiskamma Estuary

The Keiskamma Estuary is situated alongside Hamburg, 80 km from East London (Fig. 1a; 33°16'45" S and 27°29'50" E). Mean annual precipitation varies from 600 mm along the coast to 1200 mm in the upper catchment, and predominantly falls in the summer months (mid-October to mid-February), with an average temperature of 23°C. The Keiskamma River has a catchment area of 2745 km² (Allanson & Baird, 2008).

The estuary extends ~12 km upriver and the coastal embayment near the mouth (0.5 to 2 m deep) is permanently open to the ocean. Salinity in the channel ranges seasonally from 0 to 35 ‰ (Allanson & Baird, 2008), decreasing with distance up the estuary. The spring tidal range is between 1.8 and 2.0 m, and neap tides are typically between 0.6 and 0.8 m (Cooper, 2001). Sediment samples from the channel consist predominately of silt,

whereas samples from the mouth consist of fine-grained sands. The estuary hosts intertidal salt marshes, reeds, sedges and submerged macrophytes, along with extensive intertidal sand and mudflats. Salt marsh vegetation (344 ha) is characterised by *Triglochin striata* Ruiz and Pav., *Sarcocornia perennis* (Miller), *Sarcocornia pillansii* (Moss), *Sarcocornia natalensis* (Bunge ex Ung.-Sternb.), *Chenolea diffusa* Thunb., *Cotula filifolia* Thunb. and *Limonium scabrum* Thunb. (Allanson & Baird, 2008).

Knysna Estuary

The estuarine bay at Knysna (Fig. 1b; 34°1' S and 23°0' E) is situated 260 km west of Port Elizabeth. The Knysna River is approximately 60 km in length and arises in the Outeniqua Mountains. The estuary is permanently open and marine dominated. Knysna experiences a semi-diurnal M2 tide with a microtidal range, between 0.4 and 2.0 m (Largier *et al.*, 2010).

A salinity gradient exists with the lowest salinity values near the river source (0 ‰), increasing toward the mouth (35.2 ‰) (Maree, 2000). Rainfall occurs throughout the year and is heaviest from September to February. The average temperature in the summer is 25°C and 18°C in winter.

The total area of Knysna Estuary is 1827 ha, of which 1000 ha consists of intertidal salt marshes (Maree, 2000). Dominant upper marsh species include *Sarcocornia perennis* (Miller), *Sarcocornia pillansii* (Moss), *Sarcocornia natalensis* (Bunge ex Ung.-Sternb.), *Limonium scabrum* Thunb., *Chenolea diffusa* Thunb. and *Triglochin striata* Ruiz and Pav., and *Plantago crassifolia* Forssk (Maree, 2000). *Spartina maritima* (Curtis) is common in the middle marsh (Morant & Grindley, 1982; Maree, 2000), whereas the sedge *Juncus kraussii* Hochst. var. *australiensis* occurs predominantly along the spring high tide mark and covers the mudflats in the upper reaches of the estuary (Maree, 2000). Mudflats are colonised by the marine grass *Zostera capensis* Setch. in the lower reaches (Morant & Grindley, 1982).

METHODS

Field sampling

Surface sediment samples were collected from transects that ran along gradients of elevation, following Scott & Medioli (1980) and Gehrels (2002). Transects were positioned according to the vertical zonation of salt-marsh vegetation,

with the aim of incorporating all the distinct salt marsh zones, along with the tidal mudflats (Table 1). Here, elevation refers to elevation above mean sea level (MSL). Transect surface profiles were surveyed using a theodolite, back-sighting to a benchmark of known elevation (estimated survey error: ± 0.03 m), precisely located using a Trimble ProXRT relative to the TrigNet reference stations at Bisho (for Keiskamma) (error: ± 0.10 cm) and Beaufort West (for Knysna) (error: ± 0.22 cm). Five transects were sampled at Keiskamma in September 2013 (1 – 42 m, 2 – 42 m, 3 – 20 m, 4 – 13 m, 5 – 26 m) and three at Knysna in October 2013 (1 – 91 m, 2 – 132 m, 3 – 20 m) (Fig. 1). Surface sediment samples (10 cm diameter by 3 cm deep) were collected using a Pitman corer along the transects at regular changes in elevation (vertical increments of <0.05 m) and stored in airtight containers for subsampling later that day. Corresponding pH and salinity at each sample site were recorded by measuring a sediment-distilled water solution (ratio 1:2) from the sample locations using a HANNA pH and temperature meter and WTW conductivity meter. Two 5 cm³ subsamples were extracted from the upper 1 cm of each sediment sample on the evening of collection and transferred to a buffered Rose Bengal-ethanol solution, which was stored at 4°C for two weeks prior to laboratory processing and analysis (Gehrels, 2002). Rose Bengal stains protoplasm of live foraminifera, allowing for the separation of living and dead tests (Walton, 1952). Sediment samples were transported to the University of KwaZulu-Natal for sedimentological analysis.

Table 1: Number of samples used from each transect containing living foraminiferal assemblages and elevational range covered.

Site	Transect	Number of samples	Elevational range (m above LLD)	Vegetational zones			
				Mudflats	Low marsh	Middle marsh	High marsh
Keiskamma	1	20	0.286 to 1.116	x	x	x	
	2	20	-0.025 to 1.054	x	x	x	
	3	1	1.477				x
	4	13	0.439 to 1.059		x	x	x
	5	11	0.166 to 0.951		x	x	x
Knysna	1	16	0.293 to 0.923		x	x	x
	2	11	0.399 to 1.075	x	x	x	x
	3	5	1.402 to 1.627			x	x

Laboratory analysis

For each sample location, a 5 cm³ subsample was washed through nested 500 and 63 µm mesh sieves. The 63 to 500 µm fraction was retained, suspended in 1.5 litres of distilled water, and volumetrically sub-divided into eight aliquots using a wet splitter (Gehrels, 2002). Aliquots were counted (Appendix C and D) wet using a Leica M205C stereomicroscope at 40x to 100x magnification, with both living and dead foraminifera recorded. Dead assemblages represent an accumulation of tests over time, with taphonomic factors needing to be taken into consideration (Sarita *et al.*, 2015), whereas the living fauna mirrors the foraminiferal response to the present environmental conditions (Sarita *et al.*, 2015). However, it should be noted that some authors advocate the use of living foraminiferal assemblages to be used if observed over a considerable period of time and believe dead assemblages accurately represent the fossil assemblages, which are the focus of palaeoenvironmental reconstructions (Buzas, 1968; Horton *et al.*, 2005; Horton and Murray, 2006). Furthermore, dead assemblages are considered to show less spatial and temporal fluctuations in comparison to living assemblages (Horton *et al.*, 2005).

For all samples, a total of ~150 to ~250 foraminiferal tests were counted (Gehrels, 2002). Both living and dead specimens were counted, though only living foraminiferal assemblages were assessed to 'interpret the ecological meaning of the assemblages', thereby determining the association between species and their dependence and response to present environmental variables (Sarita *et al.*, 2015; 4). Dead assemblage count data will be utilized in future studies for reconstructing past sea-level changes. Counts of 100 ensure a 99% probability of recording all the important species ($\geq 5\%$) (Fatela & Taborda, 2000), this is reduced to approximately 92% when a count of 48 is used (Sarita *et al.*, 2015). To avoid loss of data, a minimum count of 50 living tests was established, leaving 65 samples at Keiskamma and 32 at Knysna (see Appendix H - S1). Of these, 52 of 97 samples contained >100 living tests (54%). Foraminiferal

abundance is expressed as the number of individuals per 5 cm³.

Taxonomy follows Murray (1979), Horton and Edwards (2006) and Debenay (2012). Species identifications were confirmed by comparison with type and figure material at the Smithsonian Institution, Washington, D.C.

Sediment grain size and organic matter content were analysed using remaining sediment corresponding to each foraminiferal sample. Organic content was calculated using the loss on ignition (LOI) at 550 °C for 16 hours (Ball, 1964). Grain size of the inorganic fraction was analysed using a Malvern Mastersizer 2000, to establish the percentage clay (0-2 µm), silt (2-20 µm) and sand (20-2000 µm) (Atterberg, 1905).

Data analysis

Multivariate ordination methods were used to describe assemblage variations relative to environmental variables (Jongman *et al.*, 1995). Ordination was undertaken using CANOCO 5 (ter Braak & Šmilauer, 2012) to examine spatial and environmental determinants of foraminiferal populations at each estuary. Species counts were $\ln(x+1)$ transformed to reduce the influence of dominant species, allowing patterns in subordinate species to emerge.

On inspection of foraminiferal composition, it was evident that allochthonous calcareous foraminifera were present in both datasets. *Cibicides lobatulus* is characterised as a marine open water species (Murray, 2006) and therefore, it is anomalous that a marine species would show a preference for the higher elevations of a salt marsh. Exotic species may be transported in from storm events resulting in the reworking of sediments from deeper water (Mills *et al.*, 2013). Therefore, exotic species (*C. lobatulus*), and species with a single occurrence (singletons) in each estuary, were screened from the data set as they were considered to contribute to noise not pattern (Gauch, 1982; Tables 2 and 5). Species classified as exotic either originated or were characteristic of marine open water environments.

Initial detrended correspondence analyses (DCA) was used to indicate species turnover along the gradient of elevation, to determine an appropriate form of ordination. The Keiskamma and Knysna datasets demonstrated turnover responses of 2.4 and 3.5 standard deviation (SD) units respectively, implying that ordination methods based on linear or unimodal (non-linear) responses were appropriate (Smilauer & Leps, 2014). Community compositional variation was examined using redundancy analysis (RDA; Mills *et al.*, 2013), the canonical form of principal component analysis (PCA), that employs multiple regression to constrain extracted gradient to be a function of the fitted environmental variables (Birks, 2012). Spatial variability in composition between transect locations in each estuary was extracted and tested by using dummy variables for transect ($n = 5$ for Keiskamma; $n = 3$ for Knysna) in an RDA (Leps & Smilauer, 2000; Yang *et al.*, 2009; Mills *et al.*, 2013). Thereafter, a partial RDA (pRDA) was used to partial out spatial variability across the estuary (by specifying transect as a covariable) and then fit measured environmental variables to describe community composition along elevation, and sediment gradients within transects (Leps & Smilauer, 2000; Smilauer & Leps, 2014). By accounting for spatial differences in composition (using transect as a covariable) and then fitting and testing the effects of (or reduced subset) environmental variables to the remaining variability, the analysis will then be free of spatial differences attributed to transect location in the estuary.

To address the problem of potential multicollinearity among environmental variables that are closely correlated and do not have an independent influence on composition, variance inflation factors (VIF) were calculated to identify problematic collinear variables (ter Braak & Smilauer, 2012; Birks, 2012). After fitting all environmental variables together, a series of RDAs were run, identifying and then dropping the variable with the highest VIF each time until all VIFs were acceptably low (Zuur *et al.*, 2009), close to, or below a value of five. The final pRDA for each estuary thus included only variables that had a unique contribution to controlling foraminiferal community composition. Monte-Carlo permutation tests (n

= 9999) were used to test the significance of canonical (constrained) axes in RDA and pRDA for spatial and environmental influences, respectively with permutations for pRDAs constrained within the covariable (transect). Indicator species were identified as those with the highest proportion of their variance accounted for by the most important environmental axes in pRDA.

RESULTS

Keiskamma Estuary

Eighteen foraminiferal species were recorded at Keiskamma, with a total of four species removed on account of low numbers (*Brizalina variabilis*, *Cibicides lobatulus*, *Glabratella milletti* and 'Unknown species 1'; Table 1). Tests were well preserved and showed little sign of corrosion. The most frequently encountered agglutinated species were *Miliammina fusca* and *T. inflata*. The most frequently encountered calcareous species were *Ammonia tepida*, and *Quinqueloculina seminula* (Table 2). Species composition varied significantly across transect locations in the estuary (RDA: pseudo-F for all axes = 3.7, $p = 0.0001$). Transect 2 (-0.02 m to 1.05 m above MSL), was characterised by an absence of *Spirillina vivipara*, and a greater abundance (relative to the other transects) of *J. macrescens*, *Balticammina pseudomacrescens*, *Spiroloculina laevigata* and *Brizalina pseudopunctata*. Transects 4 and 5 were the only other two transects to have a presence of *Balticammina pseudomacrescens*. Transect 2 had a similar species composition to that of Transect 1, however abundance was significantly lower. Only four species were present along Transect 3 viz., *Ammonia tepida*, *Miliammina fusca*, *J. macrescens* and *T. inflata* (Appendix F).

The pRDA including all variables accounted for a significant portion of the non-spatial variability in composition at Keiskamma (pseudo-F for all axes = 2.5, $p = 0.0001$), but many of the fitted environmental variables were collinear (see Appendix H - S2). Variance inflation factors (VIF) for all sediment components, except organic matter content, were particularly large because of the

high correlation ($r = 0.82 - 0.99$) between sand, silt and clay (data not shown). Sandy sediments were low in clay and silt, and were distributed across the elevation gradient ($r = -0.24$). In the full pRDA, environmental variables and species were closely ($r = 0.80$) and moderately ($r = 0.56$) associated with variation in composition along the first and second axes, respectively (see Appendix H - S2).

The final pRDA that included elevation, salinity and sediment organic and clay contents, and excluded the collinear variables, sand, pH and silt, explained significant non-spatial variability in composition at Keiskamma (pseudo-F for all axes = 3.1, $p = 0.0001$) (Table 3). All environmental variables appeared to have a relatively independent influence on foraminifera as VIFs were all low (<2.4 ; Table 3). The main gradient in composition (axis 1), which represented more than 75% of the environmental effect, primarily defined the marked elevation and

salinity gradient ($r = 0.80$); both elevation (0.63) and salinity (-0.63) have important, but opposite, influences on composition (Figure 2). The second pRDA axis, representing a further 16% of the environmental effect, was most closely correlated with organic content ($r = 0.45$; Fig. 2 and Table 3). The third and fourth canonical axes were small and did not describe any important environmental effects (Table 3).

Trochammina inflata was the species most sensitive to changes in elevation and salinity within transects from Keiskamma (Table 4). This species was most abundant at higher elevations (>0.4 m), where salinity was low. *Balticammina pseudomacrescens* also decreased towards the deeper, more saline waters, where *Lagena* spp. and *S. vivipara* were prevalent (Fig. 2, Table 4). There were no other species with notable fits along the first or second environmental axis (Table 4).

Table 2: Full list of species (and codes) found at Keiskamma Estuary and the number (frequency) of occurrences in samples ($n = 65$). Species removed from the analysis are shown in bold.

Species name	Code	Frequency	Test
<i>Ammonia tepida</i> Cushman, 1928	AMSP	54	Calcareous
<i>Balticammina pseudomacrescens</i> Brönnimann, Lutze & Whittaker, 1989	BAPS	15	Agglutinated
<i>Brizalina pseudopunctata</i> (Höglund, 1947)	BIPS	11	Calcareous
<i>Brizalina variabilis</i> (Williamson, 1858)	BRVA	*	Calcareous
<i>Cibicides lobatulus</i> (Walker & Jacob, 1798)	CRLO	*	Calcareous
<i>Elphidium</i> spp.	ELSP	4	Calcareous
<i>Glabratella milletti</i> (Wright, 1911)	GLMI	*	Calcareous
<i>Jadammina macrescens</i> (Brady, 1870)	JAMA	36	Agglutinated
<i>Lagena</i> spp.	LASP	11	Calcareous
<i>Miliammina fusca</i> (Brady, 1870)	MIFU	56	Agglutinated
<i>Quinqueloculina seminula</i> (Linnaeus, 1758)	QUSE	46	Calcareous
<i>Quinqueloculina</i> spp.	QUSP	3	Calcareous
<i>Scherochorella moniliformis</i> (Siddall, 1886)	REMO	4	Agglutinated
<i>Spirillina vivipara</i> Ehrenberg, 1843	SPVI	11	Calcareous
<i>Spiroloculina laevigata</i> Cushman & Todd, 1944	SPLA	8	Calcareous
<i>Triloculina</i> sp.	TRSP	7	Calcareous
<i>Trochammina inflata</i> (Montagu, 1808)	TRIN	40	Agglutinated
Unknown 1	UK01	*	Calcareous

Table 3: Partial redundancy analysis (pRDA) fitting spatial location (transect) as a covariable and only significant (VIF <5) explanatory environmental variables (MSL, salinity, organic content and clay) to variation in foraminiferal species composition in the Keiskamma Estuary.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.1127	0.0237	0.0079	0.0026
Explained variation (cumulative %)	14.08	17.05	18.03	18.36
Pseudo-canonical correlation (r)	0.7982	0.4518	0.2936	0.215
Explained fitted variation (cumulative %)	76.69	92.85	98.21	100
<u>Environmental variable</u>	<u>Correlations (r)</u>			
Elevation	0.6327	0.2592		
Salinity	-0.6327	0.2467		
Organic content	0.2032	0.272		
Clay	-0.1323	0.1819		
Permutation test of all canonical axes:	pseudo-F = 3.1; p = 0.0001			

Knysna Estuary

Fifteen foraminiferal species were recorded at Knysna, of which ten were used in the final analysis (Table 5). Five species were removed on account of low numbers (*Brizalina pseudopunctata*, *Brizalina variabilis*, *Cibicides lobatulus*, *Lagena* species and *Spirillina vivipara*; Table 6). The majority of the tests were well preserved and identifiable. *Miliammina fusca*, *T. inflata*, *A. tepida*, *Quinqueloculina* spp., and *J. macrescens* (Table 5) were dominant, while *Helena anderseni* and *Scherchorella moniliformis* were relatively rare and found in fewer than 10% of the samples. The RDA of transect differences revealed significant spatial variation in community composition across the estuary (pseudo-F for all axes = 4.5, p = 0.0003). The composition of transect C differed from transects 1 and 2 due to higher counts of *J. macrescens* and *T. inflata*, and lower counts of *M. fusca*.

A pRDA using all environmental variables extracted significant variability in composition (pseudo-F for all axes = 2.9, p = 0.0001) in the Knysna Estuary. Environment and species were closely (r = 0.88) and moderately (r = 0.67) associated along axis one and two, respectively. However, similar to Keiskamma, sand, silt and clay, as well as organic content, in the Knysna sediments varied closely

together (r = 0.89 – 0.99) and had high VIFs in the ordination (see Appendix H - S3). Sediments were low in sand, silt and organic content (data not shown). Unlike Keiskamma, however, the sand-to-clay/silt sediment gradient was strongly correlated with elevation (r = -0.97), with sands being most prevalent in deeper waters. Sequentially eliminating the explanatory variables with the highest VIFs resulted in the exclusion of all the sediment variables that were collinear with elevation (Table 6).

Table 4: The percentage variance of each species accounted for by the first two axes of a partial redundancy analysis (pRDA) of the foraminiferal composition in the Keiskamma Estuary.

Species name	Percentage variance	
	Axis 1	Axis 2
<i>Ammonia tepida</i>	0.06	6.91
<i>Balticammina pseudomacrescens</i>	24.68	0.13
<i>Brizalina pseudopunctata</i>	2.31	0.32
<i>Elphidium</i> spp.	3.74	0.04
<i>Jadammina macrescens</i>	0.10	3.02
<i>Lagena</i> spp.	8.78	0.81
<i>Miliammina fusca</i>	4.50	4.61
<i>Quinqueloculina seminula</i>	1.09	0.53
<i>Quinqueloculina</i> spp.	4.50	4.61
<i>Scherchorella moniliformis</i>	2.23	0.07
<i>Spirillina vivipara</i>	5.93	0.00
<i>Spiroloculina laevigata</i>	0.54	2.84
<i>Triloculina</i> sp.	3.40	2.37
<i>Trochammina inflata</i>	53.94	0.54

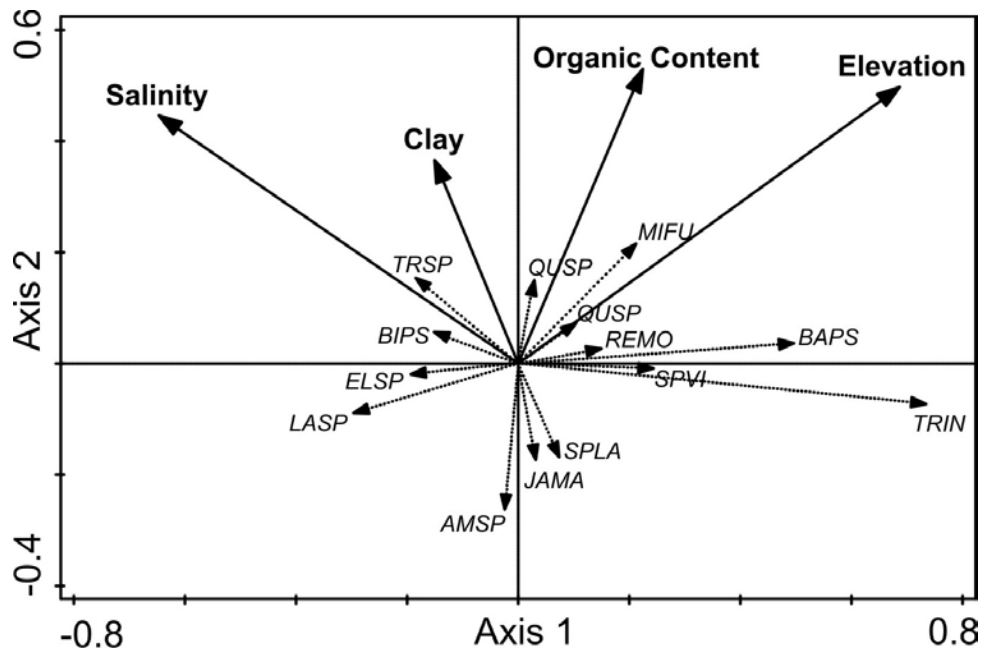


Figure 2: Partial redundancy analysis (pRDA) plot of species (dotted arrows) and environmental variables (solid arrows) that had a significant influence ($p = 0.0001$) on the species composition of salt-marsh foraminiferal assemblages in the Keiskamma Estuary. Full species names provided in Table 1.

Table 5: Full list of species (and codes) found at Knysna Estuary and the number (frequency) of occurrences in samples ($n = 32$). Species removed from the analysis are shown in bold.

Species name	Code	Frequency	Test
<i>Ammonia tepida</i> Cushman, 1928	AMSP	21	Calcareous
<i>Balticamina pseudomacrescens</i> Brönnimann, Lutze & Whittaker, 1989	BAPS	3	Agglutinated
<i>Brizalina pseudopunctata</i> (Höglund, 1947)	BIPS	*	Calcareous
<i>Brizalina variabilis</i> (Williamson, 1858)	BRVA	*	Calcareous
<i>Cibicides lobatulus</i> (Walker & Jacob, 1798)	CRLO	*	Calcareous
<i>Elphidium</i> spp.	ELSP	6	Calcareous
<i>Helenina anderseni</i> (Warren, 1957)	HIAN	1	Calcareous
<i>Jadammina macrescens</i> (Brady, 1870)	JAMA	8	Agglutinated
<i>Miliammina fusca</i> (Brady, 1870)	MIFU	23	Agglutinated
<i>Lagena</i> spp.	LASP	*	Calcareous
<i>Quinqueloculina</i> spp.	QUSP	16	Calcareous
<i>Scherochorella moniliformis</i> (Siddall, 1886)	REMO	2	Agglutinated
<i>Spirillina vivipara</i> Ehrenberg, 1843	SPVI	*	Calcareous
<i>Triloculina</i> sp.	TRSP	5	Calcareous
<i>Trochammina inflata</i> (Montagu, 1808)	TRIN	26	Agglutinated

Table 6: Partial redundancy analysis (pRDA) fitting spatial location (transect) as a covariable and only significant (VIF <5) explanatory environmental variables (MSL, salinity and pH) to variation in foraminiferal species composition in the Knysna Estuary.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.1788	0.0551	0.0214	0.1512
Explained variation (cumulative %)	23.45	30.68	33.48	53.31
Pseudo-canonical correlation (r)	0.8236	0.5954	0.4279	0
Explained fitted variation (cumulative %)	70.04	91.63	100	
<u>Environmental variable</u>	<u>Correlations (r)</u>			
Elevation	-0.7504	0.0809		
pH	0.4488	0.4975		
Salinity	0.0327	-0.774		
Permutation test of all canonical axes:	pseudo-F = 4.4; p = 0.0001			

The final pRDA that included only elevation, pH and salinity explained significant non-spatial variability in composition (pseudo-F for all axes = 4.4, p = 0.0001; Table 6). The first axis in the final pRDA primarily described the influence of elevation (r = -0.75; Fig. 3), and represented most (70%) of the influence of environment on the foraminiferal community composition. The second, much smaller axis, was associated with pH (r = 0.50; Fig. 3), and, together with pRDA axis 1, explained over 90% of the environmental effect. (Table 6; Fig. 3). Salinity, which partially controlled composition at Keiskamma, did not appear to have a significant influence on community composition at Knysna (Table 6 and Fig. 3).

The species with the largest proportion of its variance accounted for by elevation in the pRDA was *T. inflata* (Table 7), which was dominant in the upper reaches of the salt marsh. Also sensitive to elevation (Table 7) were *A. tepida* and *Elphidium* spp., both of which were most prevalent in the lower reaches of the salt marsh (Fig. 3). *Quinqueloculina* spp. showed a notable negative response to increasing pH (Table 7 and Fig. 3).

Table 7: The percentage variance of each species accounted for by the first two axes of a partial redundancy analysis (pRDA) of the foraminiferal composition in the Knysna Estuary.

Species name	Percentage variance	
	Axis 1	Axis 2
<i>Ammonia tepida</i>	23.39	1.50
<i>Balticammina pseudomacrescens</i>	16.11	4.05
<i>Elphidium</i> spp.	28.14	1.28
<i>Helenina anderseni</i>	0.36	0.00
<i>Jadammina macrescens</i>	16.64	6.39
<i>Miliammina fusca</i>	0.04	1.83
<i>Quinqueloculina</i> spp.	5.69	20.07
<i>Scherochorella moniliformis</i>	5.22	0.47
<i>Triloculina</i> sp.	19.70	0.82
<i>Trochammina inflata</i>	45.09	2.58

DISCUSSION

In South Africa, two previous studies have documented the modern distribution of salt-marsh foraminiferal assemblages (Franceschini *et al.*, 2005; Strachan *et al.*, 2015). Research at Langebaan Lagoon assessed the relationship between marine benthic foraminiferal assemblages (living plus dead) and the environment, and determined that assemblages showed a vertical zonation related primarily to elevation and secondarily to type and abundance of vegetation (Franceschini *et al.*, 2005). A study at Kariega Estuary investigated the relationship between salt-marsh foraminifera (living vs. dead) and vegetation zonation, but did not consider

additional environmental variables beyond elevation (Strachan *et al.*, 2015).

The current study assesses the influence of a range of environmental controls on salt-marsh foraminiferal distribution. Results indicate that foraminiferal species compositions at both estuaries were spatially heterogeneous, but local environmental conditions also significantly influence community composition. Elevation emerged as a key

determinant of composition in both estuaries. However, it is also apparent that elevation (surrogate for flooding frequency) is not the only ‘environmental variable’ controlling foraminiferal distribution. At Keiskamma, species composition changed most along the elevation-salinity gradient, whereas at Knysna, elevation had the largest influence on composition but covaried closely with sediment substrate.

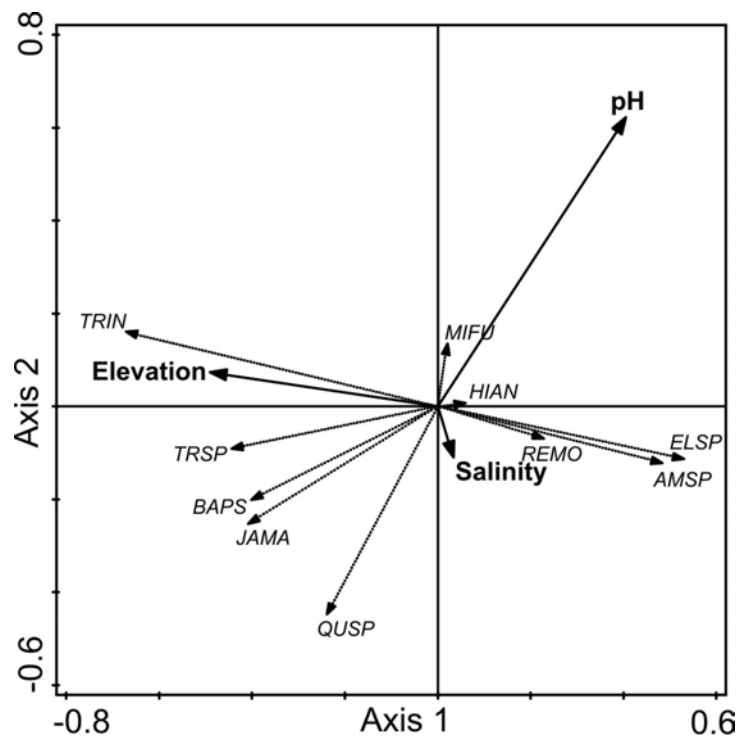


Figure 3: Partial redundancy analysis (pRDA) plot of species (dotted arrows) and environmental variables (solid arrows) that had a significant influence ($p = 0.0001$) on the species composition of salt-marsh foraminiferal assemblages in the Knysna Estuary. Full species names provided in Table 5.

At Keiskamma, species dominating the middle elevations were influenced by both elevation and salinity, most notably *M. fusca*. This corroborates the findings of Jonasson and Patterson (1992) at the Fraser River delta (British Columbia, Canada) and de Rijk (1995) from the Great Marshes (Massachusetts, USA). At Knysna, species predominantly controlled by elevation include *T. inflata* and *B. pseudomacrescens* from the higher elevations, and *A. tepida* and *Elphidium* spp. from the lower elevations.

At Knysna, the agglutinated species *T. inflata* and *B. pseudomacrescens*, and calcareous

species *A. tepida* and *Elphidium* spp., were primarily constrained by elevation, although grain size and organic content exhibited a considerable degree of covariance with elevation (Appendix G). Similarly, Horton (1999) found surface abundances of agglutinated species (*J. macrescens*, *T. inflata* and *M. fusca*) to be strongly controlled by tidal elevation at Cowpen Marsh (UK). At this site, grain size, pH, organic matter content and vegetation cover covaried with tidal elevation (Horton, 1999).

In contrast, a study conducted along the shoreline of the Great Barrier Reef in Australia

(Woodroffe *et al.*, 2005) suggests that a low pH creates a stressful environment for calcareous foraminifera by causing dissolution, thereby limiting their distribution (Woodroffe *et al.*, 2005). At Knysna, pH was identified as a secondary controlling environmental variable, which could explain the decline in overall abundance of calcareous species in the upper reaches of the marsh coinciding with low pH.

The species most responsive to elevation at both Keiskamma and Knysna were *T. inflata* and *B. pseudomacrescens*, both of which are agglutinated and appear to prefer higher elevations (Figs. 2 and 3). *Ammonia tepida* and *Elphidium* spp. were the most responsive species characteristic of lower elevations at Knysna. Particularly at Keiskamma Estuary this could be as a result of the low energy environment as both living and dead assemblages of *T. inflata* and *B. pseudomacrescens* display similar patterns in distribution along each of the transects (Appendix F). Therefore, there is little reworking or transportation of tests specially in the upper reaches of the marsh. At Knysna *T. inflata*, *B. pseudomacrescens*, *Ammonia tepida* and *Elphidium* spp. along Transect 1 (Appendix G; Figure G1) both living and dead assemblages display similar distributional patterns. However, along transects 2 and 3 (Figures G4 and G7) only living and dead assemblages of *Ammonia tepida* indicate similar distribution patterns. Living and dead assemblages of *T. inflata* and *B. pseudomacrescens* almost display opposite patterns, indicating that dead assemblages may not have the same response as living assemblages.

Jadammina macrescens was also responsive to elevation at Knysna, but only accounted for <18 % of the species abundance in the middle marsh, and <10% in the high marsh. Keiskamma exhibited similar abundances of living *J. macrescens*, with <30% of species abundance in the middle marsh, and <8% in the higher elevations. A scattered presence of *J. macrescens* has been observed in other studies along the South African coastline (Franceschini *et al.*, 2005; Strachan *et al.*, 2015). At Langebaan, *J. macrescens* (total assemblages) ranged between 1 and 2% in the

high marsh, and between 19% and 24% in the middle marsh (Franceschini *et al.*, 2005), and at Kariega (living *J. macrescens*) it accounted for <38% of abundance in the middle marsh and <40% in the high marsh (Strachan *et al.*, 2015). The low abundance of living *J. macrescens* at Keiskamma and Knysna could be explained by the prevalence of sandy and silty sediments. Agglutinated assemblages use clay particles for building their tests; thus, a low proportion of clay may limit the occurrence of agglutinants (de Rijk & Troelstra, 1997). The grain size distribution along transects 4 and 5 at Keiskamma (Appendix F; Figures F10 and F13) and transects 1 and 2 at Knysna (Appendix G; Figures G2 and G5) show a general coarsening sequence from the upper elevations to the lower elevations.

The study of living foraminiferal assemblages and corresponding environmental variables provides knowledge regarding the ecological trends and distribution patterns, which is useful for the interpretation of fossil foraminifera assemblages. This baseline knowledge is essential to understanding and identifying post-mortem changes that could effect the preservation of calcareous tests and the disintegration of agglutinated tests, along with the transportation of exotic species (Horton & Murray, 2007). However, living assemblages only represent a short period in time and highlight the behaviour of foraminiferal assemblages to present environmental conditions and therefore do not integrate seasonal changes as that of fossil foraminifera, to which they will be applied (Duchemin *et al.*, 2005). A study conducted over a three year period in Delaware, USA, however found that dead assemblages in the upper 10 cm showed a strong correlation with living assemblages and their patterns mirrored that of the living, suggesting that contemporary dead assemblages reflect the most recent input (Leorri & Martin, 2009).

The results from this study indicate that the high marsh species *T. inflata* and *B. pseudomacrescens* are potentially reliable indicators for reconstructing past sea-levels for the southern coast of South Africa. This is noteworthy as agglutinated assemblages experience limited post-mortem taphonomic

alteration compared with post-mortem loss of calcareous taxa from intertidal mudflats. Calcareous tests are more likely to be lost due to post-mortem dissolution (Culver & Horton, 2005) in cold climate regions. Along the Indian Ocean coastline of South Africa there are several localised outcroppings of calcareous sandstone. Many of these outcrops were lost during wetter climatic periods of the Quaternary, whereby the calcium carbonate cement was dissolved and washed out of the system (Bateman *et al.*, 2004; Norman & Whitfield, 2006). With the presence of beachrock, aeolianites and calcareous sandstones, the preservation of calcareous tests in South African salt marshes is better than those preserved in marshes from colder climates. Therefore, even though *A. tepida* is a calcareous species, it is responsive to elevation, and may be a reliable indicator along the South African coastline.

Foraminiferal assemblage composition across both the Keiskamma and Knysna estuaries were significantly influenced by elevation. This supports the hypothesis that foraminiferal assemblages from the southern coast of South Africa are strongly controlled by elevation.

Spatial heterogeneity between sites complicates the use of a single indicator species for sea-level studies, resulting in low and variable precision reconstructions. Whatever explanations might account for spatial variability, we concur with the recommendations of Scott & Medioli (1980) that the elevational relationship of salt-marsh foraminifera should be determined for each estuary prior to attempting to reconstruct regional sea-level curves using modern foraminifera as an analogue. However, in the case of a no-modern-analogue scenario, training datasets may benefit from inclusion of extra local data (e.g., Barnett *et al.*, unpubl. data). Studies seeking to produce high resolution reconstructions will need to use quantitative methods capable of combining information from multiple sites to develop foraminifera-environment relationships which capture spatial variability (Edwards *et al.*, 2004).

SUMMARY AND CONCLUSION

Vertical zonation underpins the sea-level proxy value of fossilised foraminiferal assemblages in salt-marsh sediment cores. Elevation as the primary distributional control on living salt-marsh foraminifera is an important first step towards high-resolution regional sea-level reconstructions. Grounded in the assumption that the environmental association of a species is unchanged through time, the modern observation of an assemblage therefore constitutes a suitable analogue for interpreting fossilized assemblages in the sedimentary record.

This study applied multivariate ordination analyses to determine the dominant environmental variables controlling living foraminiferal distributions along the southern coastline of South Africa. Results indicate significant intra- and inter-site variability for the occurrence and distribution of foraminifera, and we caution against the use of single indicator species for sea-level reconstructions.

The results support the hypothesis that living salt-marsh foraminiferal assemblages are predominantly controlled by elevation at both study sites. Salinity was found to have an important but opposing influence to elevation on species composition at Keiskamma. pH was found to be a secondary driver of foraminiferal distribution at Knysna. At both estuaries the species most strongly associated with changes in the elevation gradient were *T. inflata* and *B. pseudomacrescens*, followed by *A. tepida*. Therefore, these species could prove reliable indicators for sea-level reconstructions in this region.

The modern distribution of salt-marsh foraminifera from this study indicate strong potential for reconstructing past sea levels in South Africa, when well preserved foraminiferal assemblages from salt-marsh sedimentary sequences can be found with elevation as the primary controlling environmental variable.

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BIOSKETCH

Kate L Strachan is a PhD student with an interest in understanding sea-level change through the use of foraminifera, particularly along the South African coast. This paper contributes to her PhD thesis. All authors have a common interest in environmental and climatic change.

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contributed to research design and commented on the manuscript.

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Paper II

Distribution of salt-marsh foraminifera in two South African estuaries, and application as sea-level indicators

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Short running heading: Foraminiferal distribution in South African salt marshes

ABSTRACT

Global sea levels are rising as a result of climate change, and could affect millions of people. It is therefore important to understand and quantify past sea-level changes in order to predict future changes. Salt-marsh foraminifera have become a favourable indicator for reconstructing Holocene sea-level changes. In this study we describe the distribution of living and dead surface foraminifera from two study sites along the southeast South African coastline. In South Africa little is known about the distribution of salt-marsh foraminifera, thereby limiting their application in sea-level research. A hundred and thirty-nine surface samples were collected, identified and the modern distribution recorded. Cluster analysis defined four salt-marsh foraminiferal zones, namely high, middle, and low and mudflats. In the higher marsh areas, where environmental conditions reach the survival threshold, there is a greater abundance of agglutinated foraminiferal species. In the lower intertidal marsh zone, where sub-aerial exposure is restricted and environmental conditions are usually stable, there is a greater diversity of assemblages comprising predominantly of calcareous species. The highest salt-marsh zone, alongside the terrestrial edge, is characterised by *Trochammina inflata*, while the middle marsh zone is dominated by *Miliammina fusca* and an increase of calcareous species. The third zone is characterised by *Miliammina fusca*, and a greater abundance of *Ammonia* spp. and *Quinqueloculina* spp. The tidal mudflats have the highest diversity of calcareous assemblages with some agglutinated taxa present. The two study sites displayed similar living population distributions to those of dead, particularly in the lower reaches. However, in the upper reaches of both sites the living to dead ratio and distributions were different, which could be as a result of different influences of environmental variables along with seasonal variations. This study provides new insights into foraminiferal distributions along southeast South African coast, which can be further used in interpreting Holocene sea-level change.

Keywords: Salt-marsh, Foraminifera, Distribution, Vertical zonation

INTRODUCTION

Tidal salt marshes grow horizontally and vertically with sediment accretion, resulting in tidal flats gaining elevation relative to mean sea level (MSL) (Scott *et al.*, 2014). Tides govern the vertical range of salt marshes, which define different zones within which salt marsh fauna and flora occur (Davy, 2000; Rogers and Woodroffe, 2014), reflecting the different tolerances to strong environmental gradients (Scott and Medioli, 1980; Debenay, 1990; Jennings and Nelson, 1992; Debenay and Guillo, 2002). Salt marshes are widely used as geological archives and have the potential to reveal past estuary, lagoon or delta floors and ancient marsh deposits as well as information regarding key phases of marine transgression and regression (Scott *et al.*, 2014). Microfossils such as diatoms, foraminifera, pollen and testate amoebae are preserved in the marsh sediment sequence and underlying mudflat sediment and can provide a wealth of information regarding late Holocene relative sea level (RSL) and past climates (Gehrels, 1994; Zong and Horton, 1999; Edwards, 2001; Gehrels *et al.*, 2001, Gehrels *et al.*, 2005; Horton and Edwards, 2006; Woodroffe and Long, 2009; Charman *et al.*, 2010; Barnett *et al.*, 2013).

Since the pioneering work of Scott and Medioli (1978; 1980), the use of salt-marsh foraminifera as indicators of RSL change has attracted the attention of scientists worldwide (Edwards *et al.*, 2004). Modern salt-marsh foraminifera were first studied at Barnstable Harbour, Massachusetts by Phleger and Walton (1950). Phleger (1965) suggested that salt-marsh foraminifera were vertically zoned in a similar way to that of salt-marsh flora relative to tidal inundation, but more tightly constrained, and this was subsequently documented by Scott (1976), and Scott and Medioli (1978) in southern California. Much of their early work was based on visual assessment, with vertical assemblage zones described based on the dominant taxa present (Edwards and Wright, 2015). Later, marsh studies in Greece, Italy and Canada provided detailed descriptions of the vertical zonation of foraminiferal assemblages (Scott and Medioli, 1980; Petrucci *et al.*, 1983). Subsequent studies provided additional

knowledge and detailed descriptions regarding the vertical distribution of foraminifera, particularly along the Atlantic Ocean (Gehrels, 1994; Edwards and Horton, 2000; Scott *et al.*, 2001; Gehrels and Newman, 2004; Patterson *et al.*, 2004) and the eastern Pacific coast (Patterson *et al.*, 1999; Williams, 1989). Studies conducted in Australia (Haslett, 2001; Horton and Edwards, 2003), New Zealand (Southall *et al.*, 2006) and South Africa (Franceschini *et al.*, 2005; Strachan *et al.*, 2015) illustrate that salt-marsh foraminiferal zones in the southern hemisphere mirror those of the northern hemisphere (Scott and Leckie, 1990).

There is a need for higher resolution Holocene sea-level reconstructions along the South African coastline. Salt-marsh foraminifera can be used as Holocene sea-level indicators, though their distribution first needs to be determined. Foraminiferal transfer function based sea-level reconstructions rely on the relationship between foraminiferal zones and elevation relative to the tidal frame. The aim of this study is to examine the distribution, abundance and vertical zonation of dead and living foraminiferal assemblages from two South African salt marshes. A comparison of foraminiferal zonations from the two study sites, as well as from two previous studies on salt marsh foraminifera is executed to evaluate the applicability of regional training sets in analysing sediment cores from South African salt marshes.

STUDY AREA

Two permanently open estuaries were selected for this study (Figure 1); Keiskamma Estuary (33°16'45" S and 27°29'50" E) on the east coast and Knysna Estuary (34°1' S and 23°0' E) on the south coast of South Africa. Climatologically, the South African coastline can be divided into three rainfall zones (Chase and Meadows, 2007). The north-eastern and east coast experience summer rainfall and the west coast, winter rainfall. Between these two zones, is a narrow zone, which experiences both summer and winter rainfall (Cooper, 2001; Chase and Meadows, 2007), in which both study sites are situated.

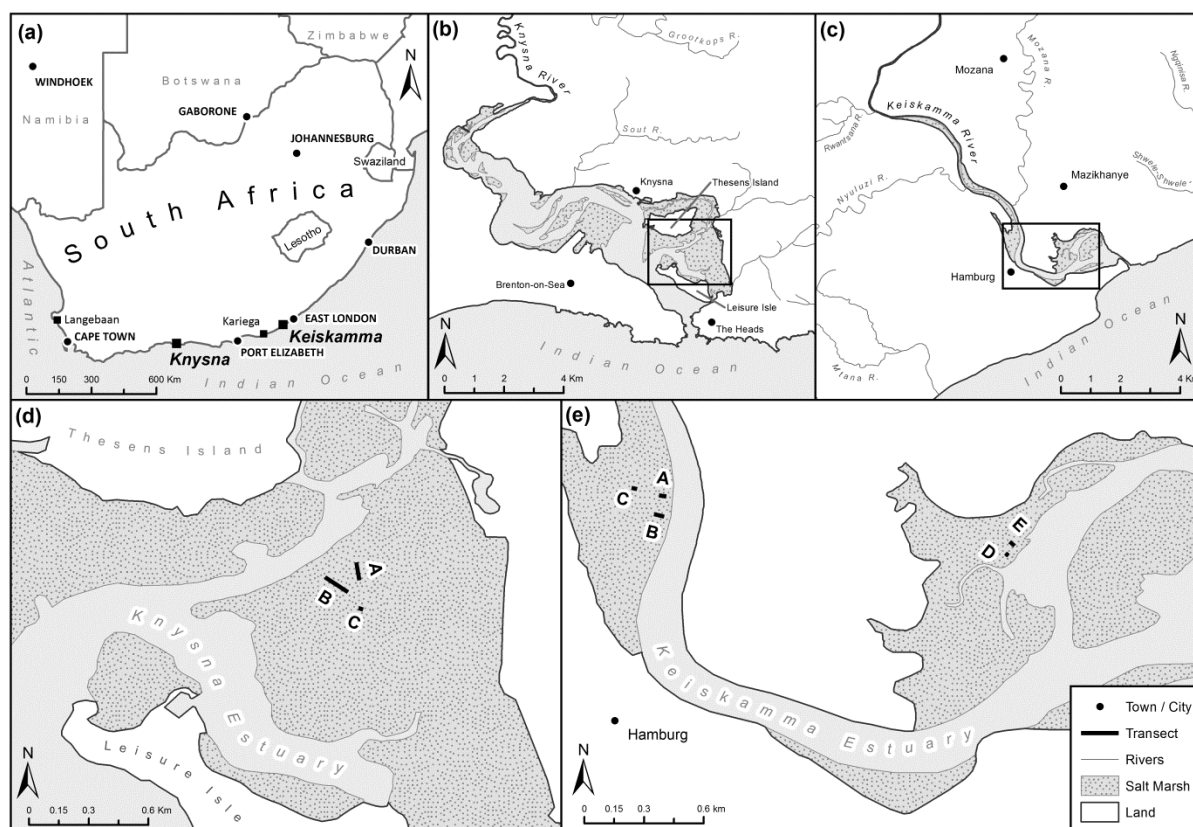


Figure 1: Map of (a) South Africa and locations of the (b) Knysna Estuary on the south coast and (c) Keiskamma Estuary along the eastern coastline. Position of transects surveyed in the (d) Knysna and (e) Keiskamma estuaries.

Keiskamma Estuary, adjacent to the village of Hamburg in the Eastern Cape, is host to extensive intertidal salt marshes and mudflats, though large areas of salt marsh in the upper reaches of the estuary have been converted to croplands. Covering an area of approximately 344 ha, the salt marshes are characterised by the following flora species, *Triglochin striata* Ruiz and Pav, *Sarcocornia perennis* (Miller), *Sarcocornia pillansii* (Moss), *Sarcocornia natalensis* (Bunge ex Ung.-Sternb.), *Chenolea diffusa* Thunb., *Cotula filifolia* Thunb. and *Limonium scabrum* Thunb (Allanson and Baird, 2008).

Knysna Estuary is located on the northern shore of the town Knysna in the Western Cape, South Africa. The intertidal salt marshes cover an area of approximately 1000 hectares (Maree, 2000). A total of 54 salt-marsh plant species and 27 local endemics have been identified at Knysna Estuary (Day, 1981; Grindley, 1985; Maree, 2000). The upper marsh zone is dominated by

Sarcocornia perennis, *Sarcocornia pillansii*, *Sarcocornia natalensis*, *Limonium scabrum*, *Chenolea diffusa*, *Triglochin striata* and *Plantago linnaeus*, while *Spartina maritima* (Curtis) is more abundant in the middle marsh (Morant and Grindley, 1982; Maree, 2000). Occurring predominately along the spring high tide mark and covering the upper reaches of the estuary is the sedge *Juncus kraussii* Hochst. var., *australiensis* (Maree, 2000). In the lower reaches of the estuary the mudflats are dominated by the marine grass *Zostera capensis* Setch. (Morant and Grindley, 1982).

MATERIALS AND METHOD

Field sampling

For each site, transects were established across the elevational range between the tidal mud flats and terrestrial edge according to the vertical zonation of the salt-marsh vegetation present. The aim was to ensure that all salt marsh zones

were incorporated by using the zonation of the vegetation as a guide. At Keiskamma Estuary five transects were sampled; two on the northern bank (13 m, 26 m) and three on the southern bank (42 m, 42 m, 20 m) covering an elevational range of 1.94 m. Three transects (91 m, 132 m, 20 m) were sampled on the eastern side of the Knysna Estuary, with an elevational range of 1.8 m. The sampling stations were positioned at marked changes in elevation (~5 cm) and vegetation along each transect. A total of 86 samples were collected at Keiskamma and 53 at Knysna Estuary. Transects were surveyed using a theodolite and back-sighted to a benchmark of known elevation (estimated survey error: ± 0.03 m) which was precisely located using a Trimble ProXRT relative to the TrigNet reference stations at Bisho (for Keiskamma) (error: ± 0.10 m) and Beaufort West (for Knysna) (error: ± 0.22 m). Sample elevations were recorded as height above land levelling datum (LLD), referred to as elevation. At each sample station a standardised surface sediment sample (10 cm diameter by 3 cm deep) was collected using a Pitman hand corer. Each sample was stored in a labelled airtight container for subsampling later that day. Floral assemblages were described using the Braun Blanquet scale (Poore, 1955; Adam, 1981). The relative abundance for each plant species and total cover (%) were estimated for each 1 m² quadrant.

Laboratory analysis

On the evening of collection, two 5 cm³ subsamples were extracted from the upper 1 cm of each surface sediment sample and placed in a buffered Rose Bengal-ethanol solution, which was stored at 4°C prior to analysis. Rose Bengal is used to differentiate living from dead foraminifera (Scott and Medioli, 1980; Murray 1991). Species living at the time of collection will have brightly stained pink protoplasm; it is assumed tests with the protoplasm stained in the last few chambers were living at the time of collection (Murray and Alve, 2000).

The foraminiferal samples were prepared following Gehrels (2002). For each sample station a 5 cm³ subsample was wet-sieved through 500 and 63 µm mesh sieves, the material in the 63 µm sieve was retained and volumetrically sub-divided into eight aliquots using a wet splitter (Gehrels, 2002). Aliquots

were counted wet using a Leica M205C stereomicroscope with an attached camera at 40 x to 100 x magnification. Whenever possible, a total (dead and living) of between ~150 and 250 specimens were counted from each sample, starting with a single aliquot, adding additional aliquots where necessary to achieve minimum count size, whilst always analysing individual aliquots to completion. In some instances a count of 250 was not possible, and a lower count was considered sufficient given the low species diversity (Patterson and Fishbein, 1989; Southall, *et al.*, 2006). The foraminiferal taxonomy follows Murray (1979), Horton and Edwards (2006) and Debenay (2012). Species identifications were confirmed by comparison with type and figure material at the Smithsonian Institution, Washington, D.C. For the purpose of this study all *Quinqueloculina* species were grouped except for *Quinqueloculina seminula*. Scanning electron microscope (SEM) imaging of foraminiferal test was conducted at Friedrich-Schiller-Universität Jena.

Data analysis

Relative abundances of modern surface foraminiferal assemblages (living and dead) were plotted as frequencies against elevation using Psimpoll version 4.263 (Bennett, 2005). Foraminiferal abundance is expressed as the number of individuals per 5 cm³. For each site all transects were combined to create a synthetic profile of each of the marshes. The vertical zones were determined using constrained incremental sum of squares (CONISS) cluster analysis (Grimm, 1987) on total assemblages from each site as changes within a site can be identified and then compared with other sites (Massey *et al.*, 2006; Lloyd *et al.*, 2007). CONISS in comparison to an unconstrained cluster analysis is good for local data and identifies parts along the gradient where significant changes take place (Massey *et al.*, 2006). Four zones were identified for both Keiskamma (H-1, H-2, H-3 and H-4) and Knysna (F-1, F-2, F-3 and F-4) estuaries. Salt-marsh plant distributions were plotted as kite diagrams using Microsoft Excel.

To assess the relationship between modern surface foraminiferal assemblages and elevation, and between sites, the programme C² (Juggins, 2003) was used, using Weighted Averaging

(WA) regression. The WA analysis of the height-normalized data set yields the tolerance ranges for each species. In order to compare our two study sites with previous studies along the South African coastline total (living plus dead) foraminiferal assemblage counts were used. To compare sites, height above LLD was converted to height above local mean sea level (MWL) using vertical offsets provided by the Hydrographic Office, South Africa, and available from the Permanent Service for Mean Sea Level (www.psmsl.org).

RESULTS

The most frequently encountered species at Keiskamma were *Miliammina fusca* and *Ammonia tepida*, while *Quinqueloculina seminula*, *Trochammina inflata* and *Jadammina macrescens* were the next most prevalent (Table 1; Plate 1; Appendix H). Calcareous species, in comparison to agglutinated forms, were highly diverse yet found in lower abundance. Assemblages from Knysna were typically dominated by agglutinated foraminifera (e.g. *Miliammina fusca*, *Trochammina inflata* and *Jadammina macrescens*) and contained lower counts of certain calcareous species such as *Ammonia tepida* and *Quinqueloculina* spp. (Table 1; Plate 1; Appendix J). *Helenina anderseni*, *Cibicides lobatulus* and *Scherochorella moniliformis* were relatively rare at Knysna.

Inter-site spatial variability at Keiskamma Estuary

Transect 1 (Appendix F; Figure F1) has the greatest diversity of foraminiferal assemblages. The upper reaches of the transect is dominated by agglutinated assemblages viz., *T. inflata* and *M. fusca*. *A. tepida* is also abundant in the upper reaches especially between 1.2 and 0.8 m above LLD, but declines thereafter and increases again in the lower reaches of the transect at 0.5 m above LLD. Living *Quinqueloculina seminula* fluctuates along the entire reach of the transect, but percentage abundance increases significantly at 0.2 m above LLD. The lower reaches of the transect is dominated by a diversity of calcareous species and highlights the transition from the middle marsh to the lower marsh and mudflats. The fluctuations and presence of living assemblages of *A. tepida* and *Q. seminula*

correspond relatively well with the spikes in salinity along Transect 1 (Figure F2). The highest presence of *M. fusca* is between 19 and 29 m along the transect (± 0.8 m above LLD) and corresponds with the presence of *Sarcocornia perennis* a middle marsh flora species.

Transect 2 (Figure F4) also has a diverse foraminiferal assemblage and shows similar trends to Transect 1 with an increase in the diversity of calcareous species in the lower reaches. The percentage of agglutinated species (except for *J. macrescens*) rapidly decreases at the transition between low marsh and tidal mudflats to be replaced by more diverse calcareous assemblages. Living foraminiferal assemblages are far more abundant than dead assemblages. The presence of both *J. macrescens* and *T. inflata* in the lowest reach of this transect and few living calcareous assemblages may be as a result of the sudden decrease in salinity (Figure F5). This is further supported by the presence of living calcareous foraminifera where there is a peak in salinity and pH along the transect around 0.3 m above LLD. Transect 3 (Figure F7) was situated in the upper most reaches of the marsh at Keiskamma and was dominated by both living agglutinated and calcareous assemblages. The distribution patterns of *A. tepida* and *Q. seminula* correspond with the spikes in pH, however both species do not show the same trend.

Transects 4 (Figure F9) and 5 (Figure F12) cover the entire intertidal range (high, middle and low) of the marsh. The most prominent difference between the two transects is the dominance of living *M. fusca* in the upper reaches of Transect 4 to that of dead along Transect 5. Aside from *M. fusca*, dead assemblages display similar trends to that of their living equivalent along Transect 4. The sudden increase of *A. tepida* and *Q. seminula* in the lower reaches of Transect 4 corresponds with the increase in pH and salinity and decrease of organic content (Figure F10), and the present of mud and *Spartina maritime* (Figure F11).

Inter-site spatial variability at Knysna Estuary

Transect 1 (Appendix G; Figure G1) has a greater abundance of agglutinated assemblages to that of calcareous. Dead assemblages are also

more prevalent than living, especially with regards to agglutinated species. Agglutinated species viz., *J. macrescens*, *Balticammia* decrease in abundance corresponding with the general coarsening sequence of grain size (Figure G2). The lack of calcareous species may be as a result of the relatively constant salinity and pH gradient along the transect.

Living and dead *J. macrescens* assemblages are only found in the upper reaches of Transect 2 (Figure G4). As the abundance of *J. macrescens* decreases so it is replaced by the presence of living *Elphidium* spp., *Quinqueloculina* spp., *Triloculina* sp. and *A. tepida*. This change is also parallel with the sudden decrease in organic content and steady increase in pH and salinity

pseudomacrescens and *T. inflata* are the most abundant in the upper most reaches, with the

(Figure G5). The abundance of assemblages both living and dead along Transect 3 (Figure G7) was far less abundant than that of transects 1 and 2, with dead assemblages dominating. In the upper reaches only dead assemblages of *J. macrescens*, *T. inflata* and *A. tepida*, with few living *T. inflata* assemblages were present. At the end of the transect majority of species peak and then drop off to '0' with the exception of dead *T. inflata*. The salinity gradient (Figure G8) in the upper reaches remains around '0', corresponding with the absence of living assemblages with the exception of *T. inflata*.

Table 1: List of species found at Keiskamma and Knysna estuaries and number of occurrences (total, dead and living).

Species name	Keiskamma (N)				Knysna (N)				Test
	Total	Dead	Aliquotes	Living	Total	Dead	Living	Aliquotes	
<i>Balticammia pseudomacrescens</i> Brönnimann, Lutze & Whittaker, 1989	18	3	52	15	6	3	3	5	Agglutinated
<i>Jadammina macrescens</i> (Brady, 1870)	39	3	318	36	24	16	8	54	Agglutinated
<i>Miliammia fusca</i> (Brady, 1870)	69	13	511	56	39	16	23	169	Agglutinated
<i>Scherochorella moniliformis</i> (Siddall, 1886)	4	0	20	4	4	2	2	9	Agglutinated
<i>Trochammia inflata</i> (Montagu, 1808)	43	3	317	40	42	16	26	150	Agglutinated
<i>Ammonia tepida</i> Cushman, 1928	62	8	450	54	31	10	21	166	Calcareous
<i>Brizalina pseudopunctata</i> (Höglund, 1947)	12	1	110	11	3	3	0	1	Calcareous
<i>Brizalina variabilis</i> (Williamson, 1858)	4	4	24	0	1	1	0	4	Calcareous
<i>Cibicides lobatulus</i> (Walker & Jacob, 1798)	12	12	91	0	2	2	0	3	Calcareous
<i>Elphidium</i> spp.	10	6	74	4	9	3	6	57	Calcareous
<i>Glabratella milletti</i> (Wright, 1911)	3	3	8	0	0	0	0	0	Calcareous
<i>Helenina anderseni</i> (Warren, 1957)	0	0	0	0	2	1	1	1	Calcareous
<i>Lagena</i> spp.	12	1	218	11	1	1	0	2	Calcareous
<i>Quinqueloculina seminula</i> (Linnaeus, 1758)	56	10	233	46	0	0	0	0	Calcareous
<i>Quinqueloculina</i> spp.	6	3	8	3	27	11	16	108	Calcareous
<i>Spirillina vivipara</i> Ehrenberg, 1843	13	2	84	11	1	1	0	8	Calcareous
<i>Spiroloculina laevigata</i> Cushman & Todd, 1944	11	3	101	8	0	0	0	0	Calcareous
<i>Triloculina</i> sp.	9	2	66	7	9	4	5	32	Calcareous
Unknown 1	2	2	24	0	0	0	0	0	Calcareous

Species zonation and abundance for Keiskamma Estuary

Cluster analysis on the total assemblages distinguishes four distinct biozones at Keiskamma Estuary (Figure 2). Zone H-1 is dominated by living and dead calcareous species, most notably *Ammonia tepida*, and to a lesser extent *Elphidium* spp., *Jadammina macrescens* and *Triloculina* sp. and living *Lagena* sp. Living specimens are more abundant.

Zone H-1 extends from -0.2 to 0.5 m with several estuarine species having the upper limit of their distribution in H-1 to H-2. *Trochammia inflata* and *Miliammia fusca* dominate zone H-

2, which ranges from 0.5 to 1.2 m. The abundance of both living and dead *Trochammia inflata* and *Miliammia fusca* substantially increases in this zone, with relatively high frequencies of living *Ammonia tepida* and *Quinqueloculina* spp. Living and dead *Balticammia pseudomacrescens*, a minor agglutinated species, only occurs in this zone (H-2). The upper reaches of zone H-2 contain the highest abundance of both living and dead specimens of *Trochammia inflata*, which abruptly disappear higher up the marsh, though appearing in lower abundances in the lower reaches of the marsh. Zone H-3 is dominated by living *Quinqueloculina seminula* and is sparsely populated by live specimens of *Ammonia tepida* and *Miliammia fusca*. CONISS bounded the

highest zone H-4 between 1.69 to 1.75 m, which is inhabited by living specimens of *Ammonia tepida* and *Miliammina fusca* and a lower number of dead *Miliammina fusca* tests. This zone contains few foraminiferal taxa, which

could be related to the upper reaches of this particular salt marsh receiving limited daily tidal inundation. The relative abundance of agglutinated living species increases with increasing elevation.



Plate 1: 1 = *Ammonia tepida*, spiral; 2 = *Ammonia tepida*, umbilical; 3 = *Quinqueloculina* sp., lateral; 4 = *Miliammina fusca*, lateral; 5 = *Miliammina fusca* lateral; 6 = *Spiroloculina laevigata*, lateral; 7 = *Quinqueloculina triangularis*, lateral; 8 = *Triloculina* sp., lateral; 9 = *Jadammina macrescens*, umbilical; 10 = *Trochammina inflata*, apertural; 11 = *Trochammina inflata*, spiral; 12 = *Trochammina inflata*, umbilical. Scale bar = 60 μ m

Species zonation and abundance for Knysna Estuary

The salt marsh at Knysna had a slightly greater elevational limit (1.79 m above LLD; Figure 3) relative to Keiskamma (1.74 m). The greater elevational limit sampled at Knysna reveals a succession of common foraminiferal species. Four marsh zones were likewise identified using CONISS. Zone F-1 extends from 0 to 0.6 m and is characterized by a high abundance of both living and dead *Ammonia tepida* and *Elphidium* spp., and live specimens of *Ammonia tepida* are particularly abundant (Figure 3b). F-2 is a narrow zone; and, together with F-3, represent transitional zones between agglutinated dominated assemblages to dominated assemblages. *Ammonia tepida* and *Miliammina fusca* dominate F-2, though there is also a high presence of dead *Trochammina inflata*. Zone F-3 is also narrow with a limited diversity and presence of foraminiferal associations. Dead assemblages of *Miliammina fusca* and living *Quinqueloculina* and *Ammonia tepida* specimens are the most prevalent but in low numbers. The upper reach of the marsh is represented by zone (F-4), and is dominated by *Trochammina inflata* (particularly dead specimens) with living and dead *Miliammina fusca* though the abundance of the latter decreases as elevation increases. The upper limit of the zone is situated above the highest astronomical tide (HAT) level. *Trochammina inflata* is present in both zones F-2 and F-4 though the presence of *Trochammina inflata* almost completely disappears in zone F-3. Dead *Trochammina inflata* are far more abundant than living forms. Once again, there is a significant increase in the relative abundance of agglutinated foraminifera as elevation increases. Calcareous species appear to be present predominately in zones F-1, F-2 and F-3 up to 1.0 m.

Foraminiferal tolerance ranges

Keiskamma Estuary exhibits high and low marsh zonations based on species tolerance ranges (Figure 4) as determined by WA analysis and the CONISS defined zones. Approximately 60 % of the transect can be described as low marsh, according to assemblages present. Tolerance ranges for individual species demonstrates that *Elphidium* spp., *Jadammina*

macrescens, *Ammonia tepida*, *Miliammina fusca* and *Trochammina inflata* occupy the low to upper middle-high marsh at Keiskamma from 0.0 and 1.1 m. Compared to other species at Keiskamma, *Jadammina macrescens* and *Ammonia tepida* display wide tolerance ranges. Based on species tolerance ranges as determined by WA analysis and the CONISS defined zones at Knysna Estuary, there is evidence of broad high and low marsh zones, and a very narrow middle marsh zone. The middle marsh zone between 0.9 and 1.1 m is based on the overlap and presence of *Balticammina pseudomacrescens*, *Jadammina macrescens*, *Miliammina fusca* and *Trochammina inflata*. The tolerance range for *Trochammina inflata* extends throughout the high marsh, whereas the range for *Jadammina macrescens* extends from the high marsh down into the low marsh. Tolerance ranges for *Balticammina pseudomacrescens* and *Ammonia tepida* also occupy the low marsh.

Keiskamma Estuary Salt-marsh plant zonations

The salt marsh at Keiskamma Estuary exhibits predominately an upper and lower marsh zonation based on flora distribution across the marsh (Figure 5). The lower 0.38 m was contined *Triglochin striata*, which was dominant throughout most of the lower marsh zone. Between 0.75 and 0.83 a thin band of *Sporobolus virginicus* was present along with *Sarcocornia perennis*, which gradually increased in abundance as elevation, increased. *Sarcocornia perennis* has the highest percentage cover between 0.91 and 1.40 m, and *Chenolea diffusa* sparsley distributed in the upper reaches of the marsh. *Carpobrotus edulis* and *Pennisetum cladestinum* were restricted to elevated areas towards the terrestrial edge. *Juncus kraussii* was limited to a thin band at the edge of the tidal mudflats.

Knysna Estuary Salt-marsh plant zonations

Knysna Estuary had a similar floral species composition and cover to Keiskamma Estuary, possibly due to similar elevation profiles. The salt marsh at Knysna Estuary shows distinct salt-marsh flora zones (Figure 6). The lower elevations were dominated by *Spartina maritima* with *Zostera capensis* between 0.3 and 0.4 m.

Triglochin striata was relatively abundant and present throughout the salt marsh. *Limonium scabrum* co-dominated with *Triglochin striata* towards the higher elevations of the marsh. *Sarcocornia perennis* was present in a thin band between 0.5 and 0.7 m. The highest reaches of

the intertidal zone, closest to the terrestrial edge, were occupied by *Chenolea diffusa* and *Carpobrotus edulis*. *Juncus kraussii* and *Sarcocornia pillansii* were only present along the terrestrial edge of the marsh.

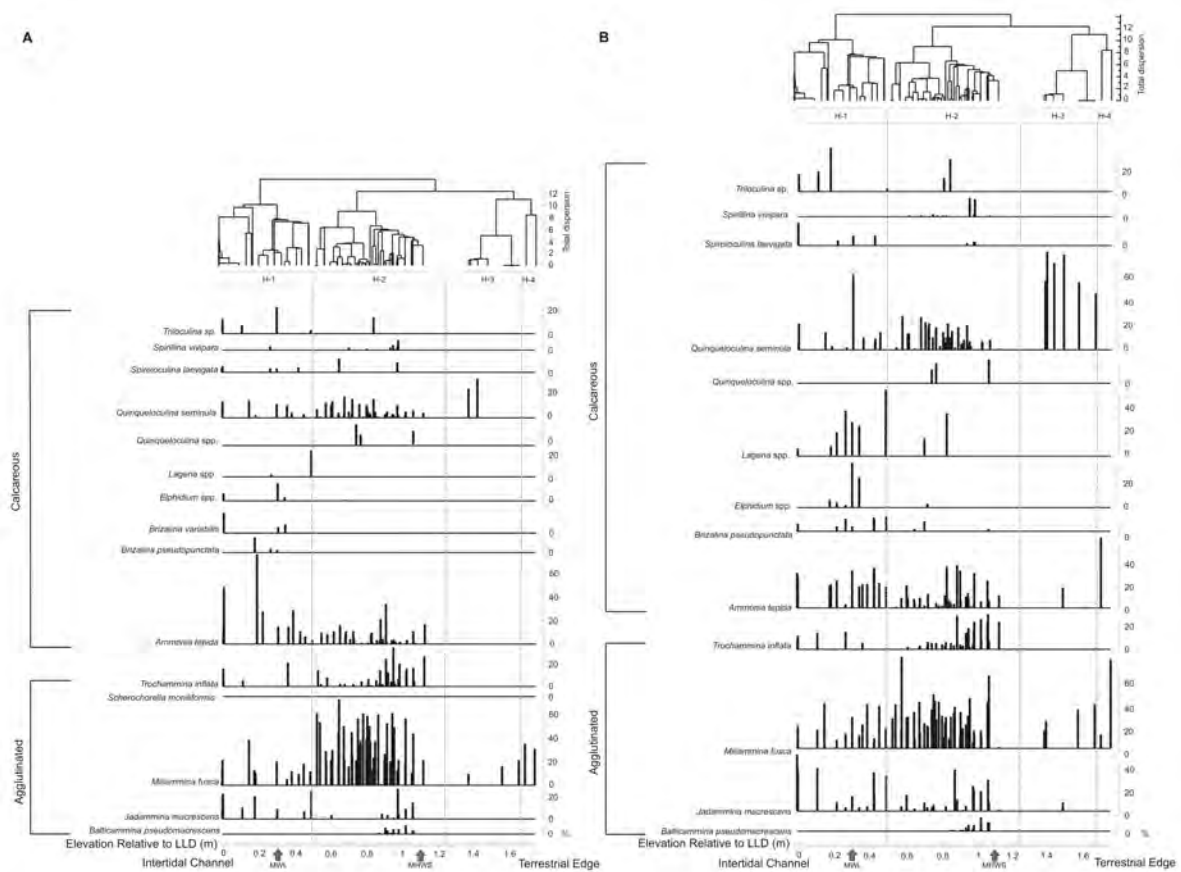


Figure 2: Distribution of surface (A) dead and (B) living foraminiferal assemblages at Keiskamma Estuary. Zonations are based on CONISS.

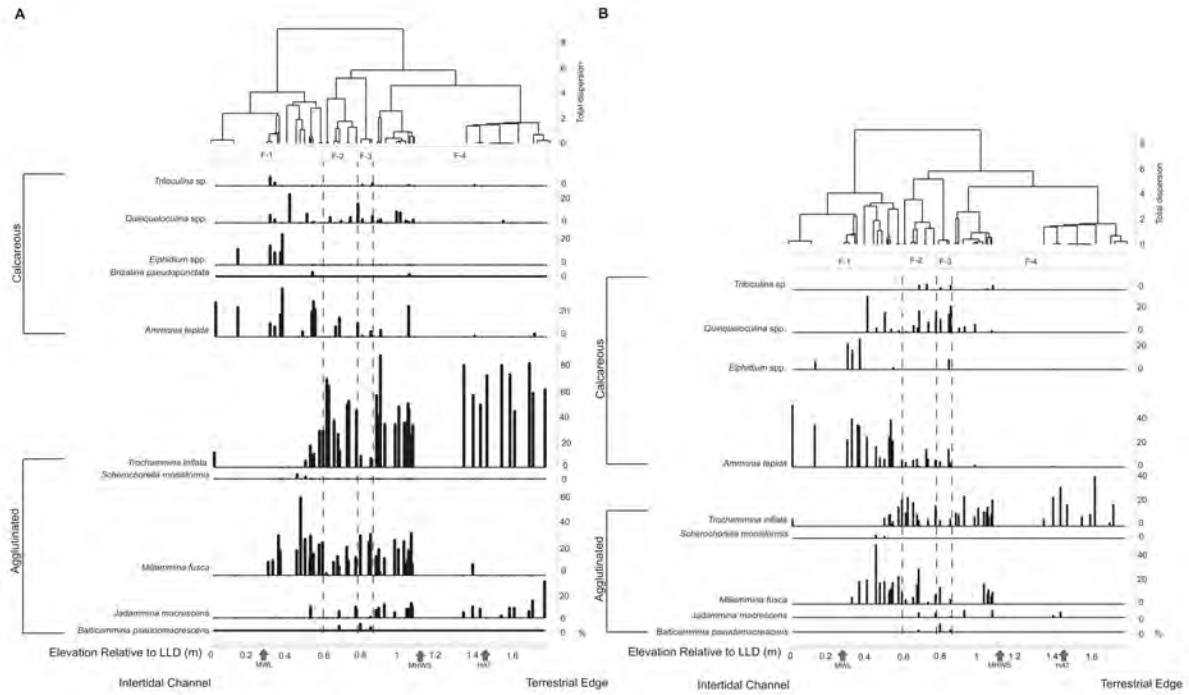


Figure 3: Distribution of surface (A) dead and (B) living foraminiferal assemblages at Knysna Estuary. Zonations are based on CONISS.

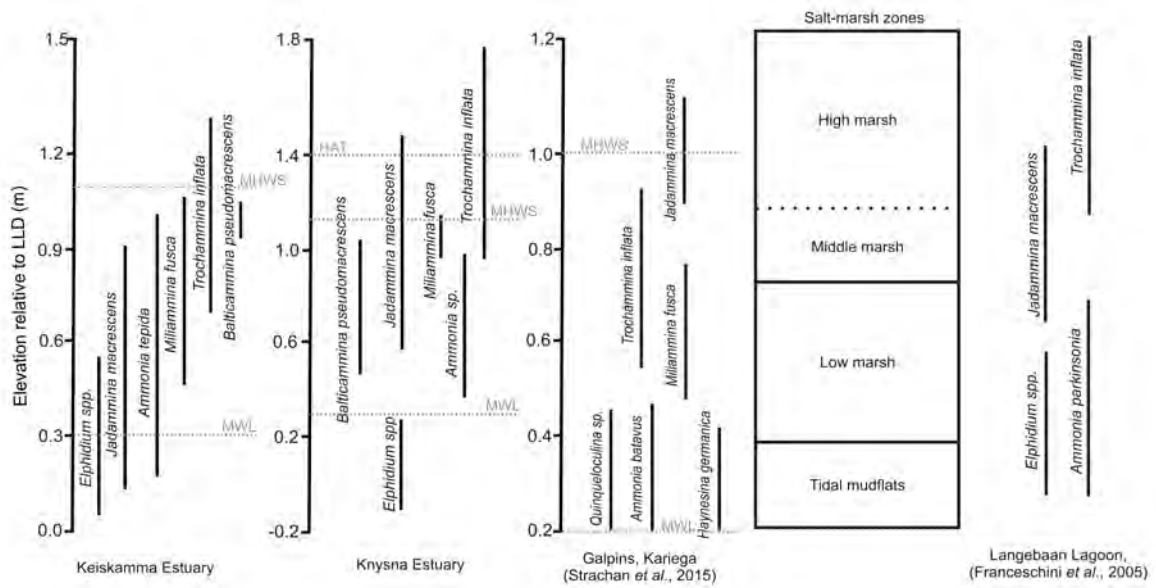


Figure 4: Foraminiferal tolerance ranges from Keiskamma and Knysna estuaries, determined by WA analysis and the CONISS defined zones. For illustrative purposes, a comparison is given with Kariega Estuary (Strachan *et al.*, 2015). Height above LLD from Keiskamma, Knysna and Kariega estuaries were converted to height above local mean sea level (MWL) using vertical offsets provided by the Hydrographic Office, South Africa. Foraminiferal zones provided by Franceschini *et al.* (2005) for Langebaan Lagoon are also illustrated.

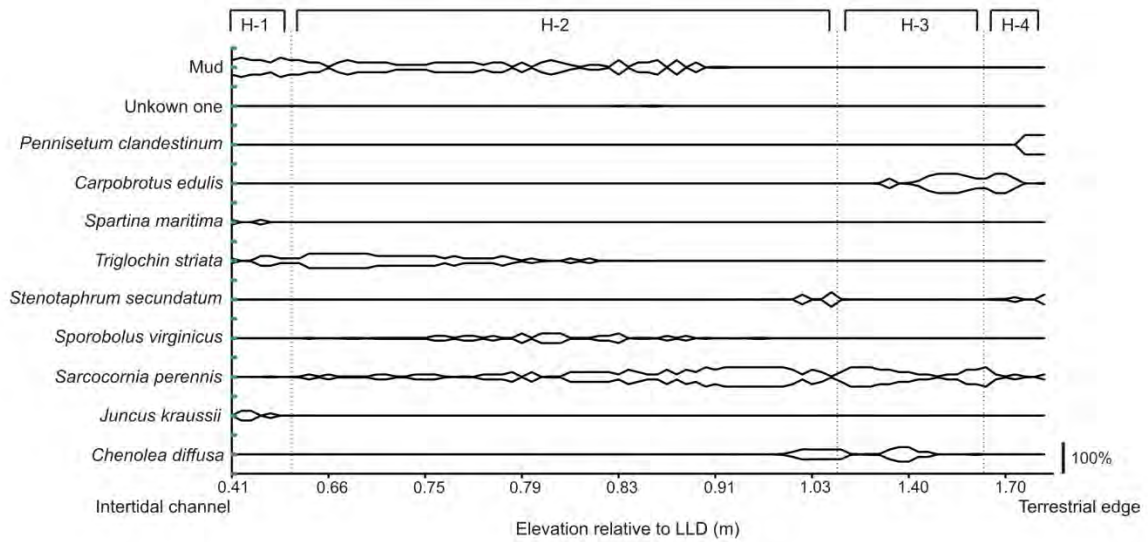


Figure 5: Kite diagram showing changes in flora distribution across Keiskamma Estuary salt marsh. Foraminiferal zonation based on CONISS indicated above (H-1 to H-4).

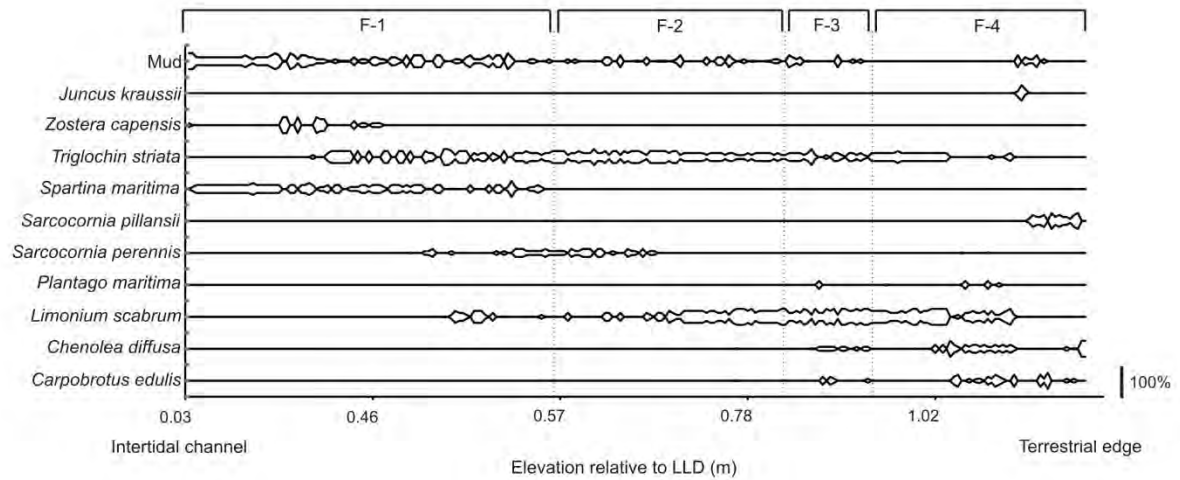


Figure 6: Kite diagram showing changes in flora distribution across Knysna Estuary salt marsh. Foraminiferal zonation based on CONISS indicated above (F-1 to F-2).

DISCUSSION

The greatest diversity of foraminifera was found in the lower elevations where assemblages were predominantly composed of calcareous tests. Transitions between low elevation assemblages composed of calcareous tests into higher elevation assemblages containing mainly agglutinated species correspond to foraminiferal

zonations seen at other South African sites at Galpins salt marsh (Kariega), and Langebaan Lagoon (Figure 4). Similar studies from Europe and North America also identify high foraminiferal diversity throughout intertidal mudflats (Patterson, 1990; Horton, 1999). Several estuarine species from this study have

the upper limit of their distribution in the mudflats and low marsh zones including *Elphidium* spp. (Keiskamma and Knysna), *Cibicides lobatulus* and *Glabratella milletti* (Keiskamma). Calcareous species are rare and tend to be restricted to marsh surfaces near tidal channels (Scott and Leckie, 1990). Changes in species diversity and dominance along the marshes elevational gradient can be an indication of stressful conditions, as environmental conditions become more stressful so diversity decreases and dominance increases (Murray, 2003). However, it should be noted that spatial variability could be substantial even at a local scale (Horton *et al.*, 2005). Studies such as this one demonstrate that when multiple transects are obtained from a single site the precise composition and elevation of specific foraminiferal species depends entirely on where transects are located (Strachan *et al.*, *ud*).

The results from this study suggest that foraminiferal assemblages exhibit evidence of vertical zonation. Comparisons could only be made with the two existing South African studies (Franceschini *et al.*, 2005; Strachan *et al.*, 2015) and other temperate salt marshes. Species tolerance ranges revealed broadly similar foraminiferal zonation between the Keiskamma and Knysna datasets. The highest faunal zone consists of predominantly *Trochammina inflata* with a presence of *Jadammina macrescens*. Common agglutinated species such as *Trochammina inflata* and *Jadammina macrescens* are typically found in abundance and dominate the highest elevations of the salt marsh above the mean high water spring tide (MHWST) (Horton *et al.*, 1999; de Rijk and Troelstra, 1997; Horton and Edwards, 2006). Investigations of foraminiferal distributions at Langebaan (Franceschini *et al.*, 2005), the Fraser River delta in British Columbia (Patterson, 1990) and Nova Scotia, New Zealand (Southall *et al.*, 2006) also observed the high abundance of agglutinated taxa in the upper reaches and particularly the dominance of *Trochammina inflata*. In our study, a second faunal zone was observed around and above MHWS in which *Trochammina inflata* and *Jadammina macrescens* are present but it is characterised by the presence of *Balticamina pseudomacrescens* and a high abundance of *Miliammina fusca*. *Miliammina fusca* is often restricted to the middle marsh between mean

tidal level (MTL) and MHWST (de Rijk and Troelstra, 1997). Even though the highest abundance *Jadammina macrescens* corresponds with the most elevated zones at both marshes it is also found else where along the elevational gradient, however always correspondence with the presence of vegetation (Appendix F and G) and therefore is sheltered. The third zone is a mixed assemblage zone at both study sites situated above the mean water level (MWL), where calcareous taxa were substantially more abundant. Whilst *Miliammina fusca* is still prevalent in this zone, the abundance of *Ammonia* spp. and *Quinqueloculina* spp. is considerably greater. This last assemblage zone is altitudinally constrained below MWL and has the highest abundance of calcareous foraminiferal assemblages, particularly *Elphidium* spp. Typically, agglutinated forms are abundant in the vegetated upper reaches of the salt marsh, and calcareous forms in the lower elevations and the unvegetated mudflats (Debenay and Guillou, 2002; Berkeley *et al.*, 2007). The lower elevations and mudflats are associated with calcareous foraminifera such as *Elphidium* spp., *Ammonia* spp. and *Quinqueloculina* spp. (de Rijk and Troelstra, 1997; Woodroffe *et al.*, 2005). However, at Keiskamma Estuary calcareous species were found throughout the entire sampled range. There can be a number of environmental variables responsible for the distribution of foraminifera (Murray, 2006), and it is evident at Keiskamma that the environmental conditions are favourable for calcareous assemblages to survive throughout the marsh. Only agglutinated are usually able to survive the extreme and variable conditions of the upper marsh, however at Keiskamma the pH values along each of the transects (Transects 1-4; Appendix F; Figures F2, F5, F7 and F10) in the upper reaches were relatively high and constant and thus more favourable for calcareous assemblages. This is further validated by the fact that along Transect 5 there were no calcareous assemblages in the upper reaches and the pH was significantly lower. It may also be as a result of the presence of localized outcroppings of calcareous sandstone along the South African coastline, many of which were lost during the Quaternary (Bateman *et al.*, 2004; Norman and Whitfield, 2006). This may have resulted in a high presence of calcium carbonate in the Keiskamma salt-marsh environment and possibly at Kariega and Knysna, as there is

evidence of calcareous assemblages at higher elevations.

The studies of salt-marsh environments at Keiskamma and Knysna displayed similar living foraminiferal population distributions to those of dead, particularly in the lower reaches. However, in the upper reaches the living to dead ratios and distributional patterns were different. At Keiskamma Estuary the abundance of living foraminifera, including for example *Miliammina fusca*, *Ammonia* spp. and *Quinqueloculina* spp. was greater. Living *Quinqueloculina* spp. were far more abundant in comparison to other species. Studies conducted at Cowpen Marsh, UK (Horton and Murray, 2007) and a southern England marsh (Swallow, 2000), found *Quinqueloculina* spp. to be most abundant and present in the middle and upper reaches of the salt marsh generally. Surprisingly, only dead *Miliammina fusca* tests were present in the upper reaches alongside the living assemblages present (Horton and Murray, 2007). At Knysna Estuary many of the upper reach surface samples were void of living foraminifera with the exception of *Trochammina inflata*. In both the upper and lower reaches there was almost double the number of dead specimens present in comparison to living. This stark contrast between concentrations of living and dead foraminiferal assemblages, especially in the higher elevations, is a common feature characterising low sedimentation environments (Murray, 1979). This is further evidence of inter-site spatial variability and the fact that not all living forms are retained within the dead assemblages, and certain dead assemblages are never found among the living population (Appendix F and G). Controversially, dead *Trochammina inflata* and *Miliammina fusca* and living *Trochammina inflata* were present above the highest astronomical tide (HAT) at 1.13 m above MWL. Lake Onoke, New Zealand is one of the few other places in the world to have also recorded living salt-marsh foraminifera well above the astronomical tide level (Hayward *et al.*, 2011).

The differences in foraminiferal distributions between study sites could be as a result of different influences of environmental variables. Even though elevation was found to be the primary control of living salt-marsh foraminifera at both study sites, secondary drivers at each of

the sites differed (Strachan *et al.*, *ud*). At Keiskamma Estuary, salinity was identified as having an important but opposing influence on distribution to that of elevation. Sediment organic content and the clay fraction also had an influence but to a much lesser extent. At Knysna Estuary pH was found to be a secondary controlling variable along with sediment grain size (sand, silt and clay), which covaried with elevation (Strachan *et al.*, *ud*). Seasonal variations may have a significant effect on the differences in distribution patterns between sites. A study conducted at Cowpen Marsh, UK found relative abundances of agglutinated and calcareous tests to differ during the summer and winter months. Agglutinated species were more abundant during the winter months, while calcareous species reached their peak abundances during summer (Horton and Edwards, 2003). Seasonal variations in salt-marsh foraminiferal composition have also been documented by Scott and Medioli (1980), Alve and Murray (2001), Murray (2003) and Horton *et al.*, (2005). Differences observed in species distribution between the two study sites and Kariega and Langebaan (Figure 4) may be related to seasonal variations, time of sampling along with different influences of environmental and climatic factors. Sampling at Keiskamma took place in September and higher densities and diversities are reported in samples from the upper most reaches of a salt marsh during the winter months (Sarita *et al.*, 2015). Debenay *et al.*, (1998) and Horton and Murray (2007) found a notable number of *Quinqueloculina* species in samples with high marsh assemblages also during the winter months.

Salt marsh flora zones described at Keiskamma and Knysna estuaries exhibit similar patterns to those described by Day (1981), O'Callaghan (1994) and Adams *et al.*, (1992). Salt-marsh plant zonations at each of the sites are to a certain extent similar to the surface foraminiferal transitional zones indicated by CONISS. Vegetation zones are based on the relative abundance of dominant plants present. However, at Keiskamma flora species *viz.*, *Sporobolus virginicus* and *Juncus kraussii* in the low marsh zone are usually associated with the terrestrial edge experiencing limited tidal inundation. Salt-marsh flora and foraminiferal zones corresponded well to a certain extent at Langebaan (Franceschini *et al.*, 2005) and

Kariega (Strachan *et al.*, 2015), though there is no definite overlap.

Salt-marsh foraminiferal zones, determined by species tolerance ranges, are important tools for reconstructing relative sea level using salt-marsh sediment cores (Scott and Medioli, 1980; Scott and Leckie, 1990; Jennings and Nelson, 1992). Sea level is able to be interpreted based on changes in fossil foraminifera assemblages, which become indicative of different modern environments (Jennings and Nelson, 1992). The precision of reconstructing relative sea-level change is governed by the ability to develop training sets of contemporary modern analogues (Jorissen and Wittling, 1999) to interpret fossil assemblages.

A training set of only living assemblages will include foraminifera which are only suited to the conditions at the time of sampling and does not take into consideration seasonal change (Murray, 1991). The use of total (living plus dead) assemblages, however, would not take into consideration post-mortem changes. Evidently, the distributional patterns exhibited here suggest that post-mortem transportation may occur. Therefore, the use of exclusively dead foraminiferal assemblages is recommended as they are not susceptible to seasonal changes and are more likely to accurately reflect subsurface (buried) assemblages. The distributional patterns and the vertical zonation of foraminiferal assemblages from Keiskamma and Knysna provide the foundation for documenting late Holocene sea-level fluctuations in this region.

CONCLUSION

The contemporary salt-marsh foraminiferal distributions indicated that agglutinated and calcareous foraminiferal assemblages were found throughout the entire sampled range. Foraminiferal species diversity and abundance fluctuated in accordance with environmental tolerance ranges and possibly the timing of sampling. Cluster analysis was used to determine foraminiferal assemblage zones, which were broadly similar between sites. The highest zone (F-4 and H-4) was characterised by high numbers of *Trochammina inflata* and the presence of other agglutinated species with few calcareous species present. The second zone (F-

3 and H-3) was dominated by *Miliammina fusca* with an increase of calcareous species. The mixed assemblage third zone was characterised by the presence of *Miliammina fusca*, however the abundance of *Ammonia* spp. and *Quinqueloculina* spp. increased. The tidal mudflats had the highest diversity of calcareous foraminifera though agglutinated taxa were present. Well-defined contemporary foraminiferal zones, increases the accuracy of fossil foraminifera deposits down salt-marsh cores, as indicators of Holocene sea-level change. By having well defined local assemblage zones, the precision of the estimated changes in past sea levels is greater than if modern assemblage zones were only broadly defined. Furthermore, the selection of the most appropriate foraminiferal assemblages is important for transfer function performance and where living populations are spatially variable; including them into a total assemblage dataset will impact the reliability of the dead assemblages for interpreting past sea-level trends. The data analysed in this study provides new insights into foraminiferal distributions and will aid in interpreting sea-level change along the southeast South African coast.

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Paper III

A regional foraminifera-based transfer function from South African marshes: Implications for sea-level studies along the South African coast

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ABSTRACT

Holocene sea-level reconstructions exist for various coastal sites in the northern hemisphere, however few exist along the South African coastline. Modern training datasets from three South African estuaries were used to investigate the suitability of local versus regional datasets for reconstructing recent sea-level trends. The results suggest that a regional transfer function using weighted averaging with inverse deshrinking and tolerance downweighting regression model is most suitable for the analysis of fossil material, producing sea-level reconstructions. As a form of validation the regional transfer function was applied to a sediment core from Kariega Estuary, to produce a record of recent sea-level change over the last ± 250 years, and compared with local tide gauge data. Sea-level records from far field sites offer important constraints on the timing and amplitude of global sea-level change, and advance our understanding of the driving mechanisms behind the late Holocene sea-level changes. The regional transfer function has the ability to link short-term instrumental records with longer-term relative sea-level reconstructions, advancing research into understanding sea-level fluctuations. Intertidal salt-marsh foraminifera have the potential to produce high-precision sea-level curves from the South African coastline, to provide a baseline understanding of the nature and causes of sea-level variation and coastal evolution.

Keywords: salt-marsh foraminifera; sea-level reconstruction

INTRODUCTION

Sea-level reconstructions extending back over the past ~2000 years provide us with insight into the nature and causes of contemporary sea-level trends (Kemp *et al.*, 2011). Recently, sea level has been monitored using satellite altimetry (Cabanes *et al.*, 2001), and tide gauges (Douglas, 1991; 2001). Proxy measurements are routinely used to reconstruct precise sea-level

histories to extend knowledge beyond relatively short length instrumental data. A variety of salt-marsh proxies, including plant macrofossils (Donnelly and Bertness, 2001; Reed, 2002), foraminifera (Horton and Edwards, 2006; Kemp *et al.*, 2013; Scott and Medioli, 1978), diatoms (Palmer and Abbott, 1986; Zong and Horton, 1999) and testate amoebae (Charman *et al.*, 1998; Gehrels *et al.*, 2001), can be used as sea-level indicators by establishing relationships

between the proxy and elevation (c.f., Barlow *et al.*, 2013). Typically, modern analogues of contemporary assemblages are developed into training sets and used to build transfer functions capable of predicting marsh-surface elevations based on fossil assemblages derived from sediment cores (e.g. Birks *et al.*, 2003; Horton *et al.*, 1999; Leorri *et al.*, 2008).

Mathematically, a transfer function would be expressed as a function of complex variables, whereby the input-output relation for a linear system is described. For example, a transfer function has the ability to quantify the relationship between a chosen environmental variable (e.g. elevation) and the environmental proxy, so that the variable can be expressed as a function of the proxy (Kemp and Telford, 2015). Developing modern training sets of assemblage data is a vital component in the transfer function development process. There is regular discussion on whether local (i.e. site specific) or regional (multi-site) datasets are most suitable for sea level reconstructions (Allen and Haslett, 2002; Gehrels, 1994; Horton *et al.*, 1999; Horton and Edwards, 2005; Kemp and Telford, 2015; Zong *et al.*, 2003). Local training sets, such as those developed from sampling transects taken from a single site (e.g., Allen and Haslett, 2002; Gehrels, 1994; Strachan *et al.*, 2014), have the benefit of producing sea-level reconstructions with smaller uncertainties, as the influence of environmental factors other than elevation is reduced (Allen and Haslett, 2002; Gehrels, 1994; Kemp and Telford, 2015). However, the predictive power of local training sets is often hindered due to 'no modern analogue' situations (Horton and Edwards, 2005). In contrast, regional training sets, such as those developed from samples deriving from multiple sites will incorporate a greater range and variety of modern analogues. This may be suitable for the development of a transfer function used for reconstructing relative sea level (RSL) at sites with no modern analogue. (e.g., Gehrels, 2000; Horton and Edwards, 2005; Leorri *et al.*, 2008; Massey *et al.*, 2006). Thus Horton and Edwards (2005) recommend that transfer functions established using a regional training set are better suited for developing reconstructions from fossil material.

Several studies have found that local influences are important controls on the distribution of salt-

marsh foraminifera (Edwards and Horton, 2000; Gehrels, 1994; Goldstein and Watkins, 1998; Guilbault *et al.*, 1995; Hayward *et al.*, 1999; Horton *et al.*, 2003; Jennings and Nelson, 1992; Jennings *et al.*, 1995; Jennings and Weiner, 1996; Williams, 1994). For example, the relationship between flooding duration and foraminiferal distributions is stronger for a local training set than for one using multiple sites (Gehrels *et al.*, 2001). Regional training sets, however, are able to cover a diversity of environments, and increase the likelihood that modern environmental data and foraminiferal distributions correctly reflect palaeoenvironmental conditions (Gehrels *et al.*, 2001).

Salt-marsh proxy based transfer functions have been concentrated in the northern hemisphere, and mostly along the North Atlantic seaboard (see references in Gehrels and Woodworth, 2013; Gehrels *et al.*, 2001; Nicholls *et al.*, 2011); to date, few transfer functions have been developed for the southern hemisphere. Recently, however, late Holocene RSL reconstructions derived from salt-marsh foraminifera transfer functions have been produced for New Zealand (Gehrels *et al.*, 2008), Tasmania (Callard *et al.*, 2011), and South Africa (Strachan *et al.*, 2014). In all of these studies, an acceleration in sea-level rise has been recorded during the early 20th century, warranting further research to provide comparisons between northern and southern hemisphere drivers of sea-level change. Furthermore, southern African coastal sites are located in the far field relative to polar ice masses, which can be useful for investigating sea-level mechanisms in the absence of vertical land motion or tectonic instability (Nicholls and Cazenave, 2010). Sea-level records from far field sites offer important constraints on the timing and amplitude of global sea-level change, and advance our understanding of the driving mechanisms behind late Holocene sea-level changes (Flemming *et al.*, 1998; Milne and Mitrovica, 2008; Woodroffe *et al.*, 2005). Therefore, studies conducted along the South African coastline could contribute towards resolving the timing and magnitude of the Mid-Holocene High Stand, as well as the nature of late Holocene sea fall for the southern hemisphere (Woodroffe and Horton, 2005). There is a need to understand how sea level has varied over different timescales; thus

quantifying changes in the rate of sea-level rise is critical to improving our understanding of 20th century sea-level rise and predicting future changes (Church and White, 2011).

Monitoring and management of recent sea-level change can inform remediation initiatives related to changing coastal land use (Poulter *et al.*, 2009; Scott *et al.*, 2001). Large-scale environmental and climatic changes are predicted for the future, and therefore insight into the effects of past climatic changes can contribute to a better understanding of future conditions (Anderson *et al.*, 2007). If we understand which processes have contributed to past sea-level changes, we can use that information to predict how future natural or anthropogenic changes might affect mean sea level (Pugh and Woodworth, 2014). The rise and fall of future sea levels is of significant interest, in particular due to the large portion of the population residing along the coast. There are predictions that sea levels in 2100 may be similar to those of the last interglacial, which were several meters higher than the present (Overpeck *et al.*, 2006).

Although salt-marsh foraminifera are considered to be an accurate and precise tool for reconstructing sea-level changes during the Holocene (Gehrels, 1994; Scott and Medioli, 1978; Woodroffe *et al.*, 2005), there has been limited application of this proxy in southern Africa with regards to sea-level change (Franceschini *et al.*, 2005; Strachan *et al.*, 2014; Strachan *et al.*, 2015). This study will develop

training sets of salt-marsh surface foraminifera from the southeast coastline of South Africa to investigate the suitability of local versus regional datasets for reconstructing recent sea-level trends. Using three study areas, our objectives are to: (1) present a transfer function for each of the study sites from the modern distributions of foraminifera recorded at each site; and (2) evaluate the applicability of using a regional (multi-site) training set for the development of a transfer function used to produce high-resolution sea-level reconstructions from salt-marsh foraminifera along the South African coastline.

REGIONAL SETTING

This study makes use of contemporary salt-marsh foraminiferal assemblages from three locations along South Africa’s coastline (Figure 1). The South African coastline is dominated by strong currents and consistently high wave energy, tides are regular, semi-diurnal and their range seldom exceeds 2.2 m (Cooper, 2001; Hutchings *et al.*, 2002; Ramsay, 1995; SA Navy, 2011; Table 1). The South African south coast experiences varying rainfall regimes with some areas experiencing higher rainfall during the summer and others the winter (Cooper, 2001; Heydorn and Tinley, 1980). South African estuaries vary considerably in discharge variation in rivers, sediment supply rate, fauna and flora due to both geomorphological and climatological factors (Cooper, 2001).

Table 1: Tidal characteristics above Chart Datum for tide gauges situated near study sites (SA Navy, 2011). Keiskamma and Kariega Estuaries are situated between Port Elizabeth and East London.

PLACE	LAT	MLWS	MLWN	ML	MHWN	MHWS	HAT
Knysna	0	0.22	0.82	1.06	1.32	1.91	2.21
Port Elizabeth	0	0.21	0.79	1.04	1.29	1.86	2.12
East London	0	0.23	0.78	1.02	1.25	1.82	2.08

Lowest Astronomical Tide (LAT); Mean Low Water Spring (MLWS); Mean Low Water Neap (MLWN); Mean Level (ML); Mean High Water Neap (MHWN); Mean High Water Spring (MHWS); Highest Astronomical Tide (HAT).

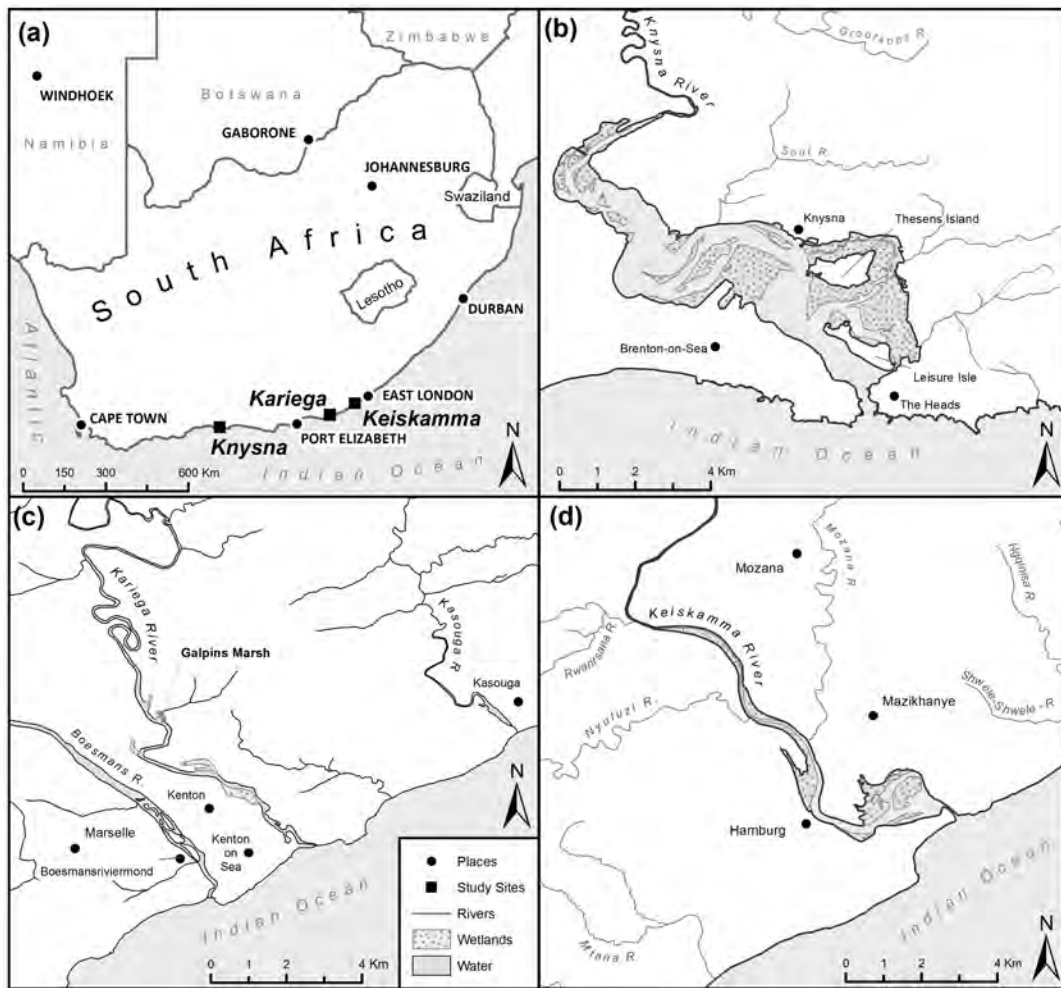


Figure 1: Map of (a) South Africa and locations of the (b) Knysna, (c) Kariega and (d) Keiskamma estuaries along the southern coastline.

The site at Knysna is an estuarine bay located on the south coast of South Africa ($34^{\circ}11''$ S, $23^{\circ}0''$ E) containing ~ 330 km² of salt-marsh environments (Maree, 2000; Whitefield and Kok, 1992). Knysna experiences a semi-diurnal M2 tide with a microtidal reach, between 0.2 and 2.0 m (Largier *et al.*, 2010; Table 1). Keiskamma Estuary ($33^{\circ}16''$ S, $27^{\circ}29''$ E) is located on the east coast, and extends 12 km inland (Allanson and Baird, 2008). Typically, Keiskamma Estuary experiences a spring tidal range between 1.8 and 2.5 m, and neap tides between 0.2 and 0.8 m (Cooper, 2001; SA Navy, 2011; Table 1). The third site is Galpins salt marsh on the Kariega Estuary ($33^{\circ}41'$ S, $27^{\circ}44'$ E), on the east coast of South Africa. The estuary stretches approximately 18 km inland

from the mouth. Salt marshes and mud flats are found on either side of the estuary, while further up it is bordered by steep vertical slopes (Grange *et al.*, 2000).

METHODS

Sample collection and preparation

Contemporary surface foraminiferal samples were extracted along cross-marsh transects at Keiskamma and Knysna, covering tidal flat to high marsh, as near to or above highest astronomical tidal levels. Sample stations were placed at ~ 5 cm vertical intervals and at marked changes in the flora. Foraminiferal sample preparation followed Gehrels (2002), and

taxonomy followed Debenay (2012), Horton and Edwards (2006) and Murray (1979). Dead tests were defined as those, which failed to retain Rose Bengal pigment, which is designed to stain protoplasm tissue pink (Walton, 1952). Previous modern samples from Kariega (Strachan *et al.*, 2015) following the same procedures will also be used in this study. Assemblages of salt-marsh foraminifera from Keiskamma, Knysna and Kariega (Strachan *et al.*, 2015) were screened to remove samples with low-test abundance. Samples compiled of fewer than 100 'dead' tests. Elevation was used as a surrogate variable for inundation frequency and duration (Telford and Kemp, 2015). Sample elevations were measured in the field using a Trimble ProXRT relative to the Land Levelling Datum of South Africa (LLD). Height above LLD was converted to height above local mean sea level (MWL) using vertical offsets provided by the Hydrographic Office, South Africa, and available from the Permanent Service for Mean Sea Level (www.psmsl.org).

Statistical analysis

Species response to changes in elevation was assessed using detrended correspondence analysis (DCA) in the software package Canoco 5 (ter Braak and Smilauer, 2002). A unimodal response suggests complete compositional turnover occurs and is represented by a DCA score of greater than 2 standard deviation (SD) units, whereas a linear response results in scores of less than 2 SD units (ter Braak and Prentice, 1988). This analysis was used to determine the suitability of using different available regression models in transfer function development (Birks, 1995). Surface datasets displaying unimodal response distributions (i.e., relatively larger DCA scores) are favoured in sea-level reconstructions (Gehrels, 2000). This is due to their ability to capture a greater expanse of ecological variety, resulting in reconstructions that more accurately reflect environmental changes through time (Birks *et al.*, 2010; ter Braak and Prentice, 1988).

Transfer function development

Transfer functions were built for each site using a suite of regression models in C2 (Juggins, 2003). Knysna and Keiskamma have DCA scores of 2.7 and 3.3 respectively. The training

were removed on account of low counts (Fatela and Taborda, 2002). This screening process resulted in local training set sizes of 42 samples for both Knysna and Keiskamma, and 34 samples for Kariega. Due to the presence of 'rare' taxa, i.e., those making up a small percentage of the populations (Patterson and Fishbein, 1989), taxa occurring in low numbers (less than 5 %) in a single sample were screened following Gauch (1982) as they were considered to contribute to noise rather than pattern.

set from Kariega returned a DCA score of 1.9, implying that regression models suitable for both linear and unimodal distributions were available (Birks, 1995; Juggins and Birks, 2012). Regression models suitable for unimodal distributions were used at Keiskamma and Knysna, whereas for Kariega unimodal and linear models were used. Model performance was compared using the root mean square errors (RMSEP) and correlation coefficients (r^2) of the internally cross-validated (using leave-one-out; Manly, 1997) model prediction values versus measured values and the systematic error terms, mean and maximum biases (ter Braak and Juggins, 1993). Leave-one-out, in turn excludes one sample and uses the remaining samples to predict the left out samples environmental value (Edwards and Wright, 2015). As a result of samples being situated along intertidal transects only a few meters apart as well as between sites, leave-one-out was chosen to take into consideration spatial autocorrelation (Payne *et al.*, 2012). Cross-validation methods such as 'bootstrapping' and 'leave-one-group-out' are better suited for training sets in which samples are greater distances apart (Telford and Birks, 2009).

The three datasets were combined into a single training set to investigate how a regional model compared against the performance of local transfer functions. The regional training set had a DCA score of 3.1, and the same suite of regression models were applied to the new regional dataset for comparison with the local transfer functions. Sample elevations required standardising as the three locations had varying tidal ranges (Table 1). A standardised water level index (SWLI) was developed for each site following Gehrels (1999) and Horton *et al.*, (1999). Local MWL and highest astronomical tide (HAT) were used as reference water levels, with a standardised vertical difference of 100

SWLI units (e.g., Wright *et al.*, 2011) so that 0 and 100 SWLI units equates to MWL and HAT, respectively.

As a validation exercise, the regional transfer function was used to reconstruct recent sea-level change at Kariega Estuary to demonstrate the use of the new model. Strachan *et al.*, (2014) used a local training set and a regression model designed for linearly responsive distributions to reconstruct sea-level changes at Kariega over the past ~1000 years. Here, we revisit the site and present new higher resolution counts of recent fossil foraminifera from archived sediment cores of Strachan *et al.*, (2014). The top 20 cm of the archived sediment core was sub-sampled at 1 cm contiguous resolution and counts of fossil foraminifera (averaging over 250 per sample) were performed based on taxonomies in Horton and Edwards (2006) and Murray (1979). The new regional transfer function, built using a regression model designed for unimodally responsive data, was applied to the fossil dataset to derive estimations of palaeo-marsh surface elevations (PMSEs). Model uncertainty values (RMSEP) and PMSEs were used to provide indicative ranges (c.f., Shennan, 2007), which were converted to estimations of former sea level following Gehrels (1999). Performance measures such as RMSEP provide information on the reliability of the transfer function and little information on how 'realistic' the estimated values of SWLI determined by the transfer function are (Horton and Edwards, 2006). In an ideal situation independent transfer functions using different environmental proxies could be run and compared thus determining which reconstruction provides an ecologically realistic picture (Manly, 1997). To provide validation, a minimum dissimilarity coefficient (minDC) was established using the modern analogue technique (MAT; Birks, 1995) to determine assemblage similarities between modern and fossil samples (Simpson, 2012; Barlow *et al.*, 2013; Edwards and Wright, 2015). Estimations of 'good', 'close' and 'poor' modern analogues were based on the 5th, 10th and 20th dissimilarity coefficient percentile threshold values following Watcham *et al.*, (2013). While "good modern analogues" are important for estimating "reliable" palaeomarsh-surface elevations, this does not necessarily mean they will be realistic (Edwards and Wright, 2015). High percentiles (10th and 20th) were particularly chosen as a result of the fairly

homogenous modern training sets, thus reducing the chance of fossil samples that have a similar biological composition to that of the modern training set and thus exceed the chosen threshold and are considered to have no modern analogue (Kemp and Telford, 2015). In addition, the revised sea-level reconstruction was compared against local tide gauge data from Port Elizabeth the closest station to qualitatively validate the accuracy of the regional model in reconstructing local trends (PSMSL, 2015).

RESULTS AND DISCUSSION

Surface foraminiferal distributions

The highest occurrence of foraminifera is encountered above the level of mean high water springs (MHWS) at Keiskamma and Kariega (Figure 2). This is consistent with other sea-level studies, which present distributions of salt-marsh foraminifera in the southern hemisphere (Callard *et al.*, 2011; Franceschini *et al.*, 2005; Hayward *et al.*, 1999). In contrast, foraminifera at Knysna are encountered above HAT (Figure 2), consisting of dead assemblages of *Trochammina inflata* and *Miliammina fusca* and living assemblages of *Trochammina inflata* (Strachan *et al.*, in review). This seems unusual as salt-marsh foraminifera are typically limited to the intertidal realm (Scott *et al.*, 2001). Though, a similar trend is demonstrated with living salt-marsh foraminifera at Lake Onoke, New Zealand also in the southern hemisphere (Hayward *et al.*, 2011). Dead tests with no living assemblage at this elevation may have transported during storm surge events or increase in wave height. As sea temperatures warm with climate change, wind speeds increase along with wave height and storm surge events. A 10% change in wind speed intensity along the South African coastline can result in a 26% increase in wave height (Riddin and Adams, 2010). The 'abnormal' counts are retained in the local and regional training sets as they represent natural ecological diversity, which should be included when attempting to capture full spatial variability in species distribution (Murray and Alve, 2000).

Agglutinated foraminifera dominate the surface datasets and demonstrate zonation relative to changes in elevation typical for salt-marsh environments (Franceschini *et al.*, 2005; Horton,

1999; Jennings and Nelson, 1992; Massey *et al.*, 2006; Scott *et al.*, 1979; Scott *et al.*, 1981; Scott and Leckie, 1990). *Trochammina inflata* and *Jadammina macrescens* characterise the highest reaches of the marshes, the abundance of *Miliammina fusca* increases with decreasing elevation, and calcareous taxa are most commonly encountered in the low marsh and near MWL (Figure 2; Appendix F and G). Preservation of calcareous tests in low pH salt-marsh environments along South Africa's coastline appear to be better in comparison to sites from other latitudes (Appendix F and G) (e.g., the Georgia coast (Goldstein and Watkins, 1999); Fraser River delta, British Columbia (Jonasson and Patterson, 1992); UK salt marshes (Edwards and Horton, 2000)). The preservation of calcareous tests in South African salt marshes may be better than those from colder climates, due to the presence of beachrock, aeolianites and calcareous sandstones along the South African coastline (Bateman *et al.*, 2004; Norman & Whitfield, 2006), increasing the amount of calcium present in salt-marsh environments. Therefore, fossil calcareous foraminiferal assemblages in South African core samples may be reliable indicators of previous low marsh environments in sea-level studies.

Local transfer function development

Transfer function performance criteria for the three local training sets are summarised in Table 2. Regression models based on the local training set from Knysna are capable of predicting marsh-surface elevations to within precisions of ± 0.27 m as demonstrated by the weighted averaging model using inverse deshinking. Comprehensive overviews of the models displayed in Table 2 are provided by Birks (1995) and Juggins and Birks (2012), whom we refer the reader to for details on the different model parameters available. For Knysna, five of the six available models have similar RMSEP values (± 0.27 to 0.29 m), which represent approximately 20 % of the total measured environmental gradient and *c.* 17 % of the spring tidal range at that location. In contrast, the training set from Keiskamma (Table 2) is capable of predicting marsh-surface elevations to higher precisions (five of the six models have RMSEP values of ± 0.19 to 0.22 m). These lower RMSEP values similarly represent *c.* 20 % of the measured environmental gradient. Combined

with the fact that the dataset from Keiskamma has a greater DCA score (3.3 SD units) in comparison to that from Knysna (2.7 SD units), it appears that a more complete turnover of species has been captured by the sampling which occurred over a shorter environmental gradient at Keiskamma, thus driving greater precision in the transfer function models. This results in improved RMSEP values at Keiskamma as a function of spring tidal ranges (12 to 15 %). Correlation coefficients between model predicted elevations and sample elevations (as measured in the field) are broadly similar for both Knysna and Keiskamma (r^2 values of 0.5 to 0.6 in five out of six cases). The effects of applying different deshinking methods (i.e., classical or inverse; c.f. Birks, 1995) to the training sets can be noticed in the maximum bias values. Inverse deshinking results in greater precision towards the centre of environmental gradients (ter Braak and Juggins, 1993) but generates greater maximum bias values compared to classical deshinking methods driven by greater imprecision in samples from the ends of the environmental gradients (Table 2). Regression models designed for unimodally responsive datasets (i.e., forms of weighted averaging and weighted averaging partial least squares) are less successful in comparison to models designed for linearly responsive species data, as shown by the results for the Kariega dataset. The best models for the training set from Kariega return precision capabilities of ± 0.16 to 0.18 m. This represents approximately 10 % of the spring tidal range, comparable to transfer functions from studies elsewhere in the world, which return similar high precisions as a function of tidal range size (Callard *et al.*, 2011; Gehrels, 2000; Horton *et al.*, 1999; Leorri *et al.*, 2008). However, despite having the best RMSEP precision and some of the highest correlation coefficients, the partial least squares models based on the Kariega dataset do not necessarily represent the most robust or honest transfer functions developed in this study, and a transfer function based on a unimodal species response may be more appropriate (Telford and Birks, 2005). Simply assessing the model performance based on the RMSEP and r^2 values is not recommended, and other statistical parameters should be considered before selecting the final component from which to base the reconstruction (Telford *et al.*, 2004). In most Holocene sea-level investigations, species distributions are unimodal. Thus,

unimodal response models are generally considered more robust and reliable reconstruction techniques (Birks, 1995; Telford *et al.*, 2004; Telford and Birks, 2005) compared

to linear models, and are widely applied to salt-marsh foraminifera based sea-level reconstructions (Woodroffe and Long, 2010; Leorri *et al.*, 2011; Barlow *et al.*, 2013).

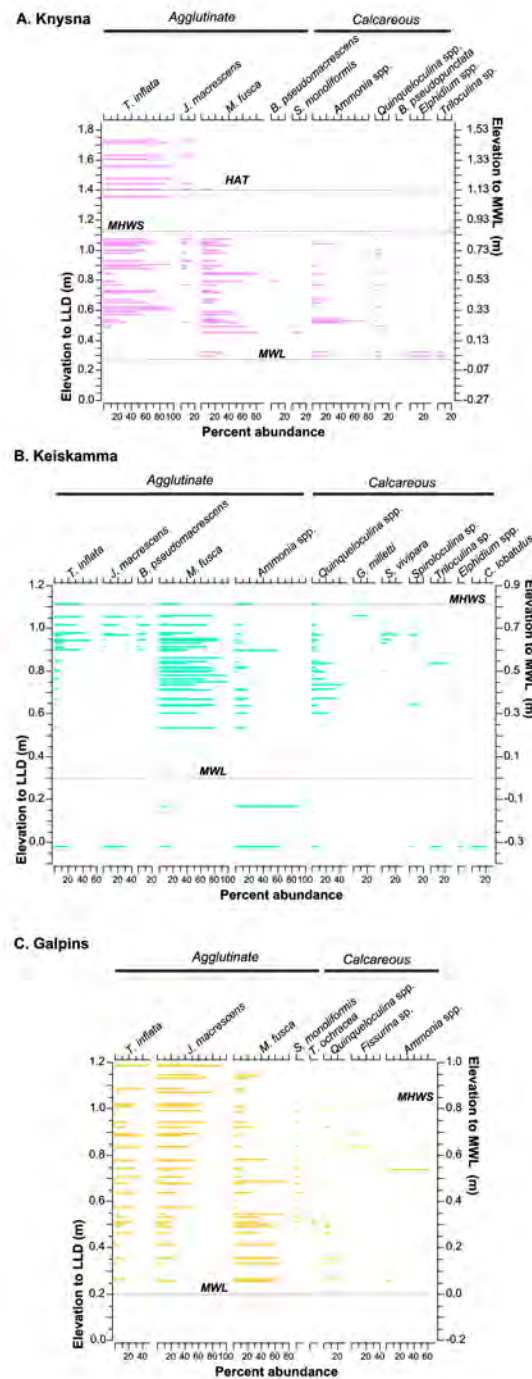


Figure 2: Training sets of surface foraminiferal data from (A) Knysna, (B) Keiskamma and (C) Kariega estuaries (independent scaling). HAT = Highest Astronomical Tide, MHWS = Mean High Water Springs, MWL = Mean Water Level.

Regional transfer function development

Sample elevations for the surface data from the three sites were standardised using a SWLI index, and the datasets were compiled into a single regional training set. The regional data has a DCA score of 3.1 SD units and captures greater compositional turnover in species data than the local training sets at Knysna and Kariega (Table 2). The performance criteria of the regression models based on the regional training set (Figure 3) are given in SWLI units. The highest precisions are demonstrated by weighted averaging models with inverse deshrinking, and the multi-component weighted averaging partial least squares models (RMSEP of ± 0.22 to 0.24 m). These SWLI RMSEP values correspond to marsh-surface elevation prediction precisions of *c.* ± 0.25 , ± 0.23 and ± 0.24 m at Knysna, Keiskamma and Kariega,

after correcting for tidal range size, which is broadly comparable to the best performing models using only local data. Whereas at Kariega, a regression model designed for species data demonstrating a linear response to change in elevation provides lower RMSEP values, the regional training set extends the sampled environmental range, encapsulates greater spatial variability in species occurrence, and is theoretically more robust at predicting surface elevations as it captures a broader range of ecological diversity. There is little loss in performance values in terms of RMSEP, r^2 and biases when using the regional training set (Figure 3) versus the local datasets. This implies that the regional transfer function is likely to be more robust and accurate when used to predict marsh-surface elevations along the South African coastline, and is preferred even at the cost of a small loss in model precision.

Table 2: Transfer function performance criteria for Knysna, Keiskamma and Kariega estuaries.

Training set	Model	RMSEP			r ²	Ave. Bias (m)	Max. Bias (m)
		(m)	(% gradient)	(% tidal)			
Knysna							
	WA_Inverse	0.29	20.1	17.2	0.55	0.00	0.44
	WA_Inverse+Tol	0.27	18.75	16.0	0.58	-0.02	0.27
	WA_Classical	0.37	25.7	21.9	0.55	0.00	0.37
	WA_Classical+Tol	0.28	19.4	16.6	0.58	-0.04	0.28
	WAPLS(2)	0.28	19.4	16.6	0.62	-0.01	0.36
	WAPLS(3)	0.28	19.4	16.6	0.69	0.00	0.3
Keiskamma							
	WA_Inverse	0.22	19.3	13.8	0.5	0.00	0.38
	WA_Inverse+Tol	0.19	16.7	11.9	0.64	-0.02	0.36
	WA_Classical	0.24	21.1	15.1	0.53	0.00	0.33
	WA_Classical+Tol	0.2	17.5	12.6	0.65	-0.02	0.25
	WAPLS(2)	0.22	19.3	13.8	0.53	0.00	0.39
	WAPLS(3)	0.21	18.4	13.2	0.55	0.00	0.31
Kariega							
	WA_Inverse	0.22	23.4	13.3	0.44	0.02	0.25
	WA_Inverse+Tol	0.26	27.7	15.8	0.34	0.04	0.27
	WA_Classical	0.28	29.8	17.0	0.46	0.03	0.25
	WA_Classical+Tol	0.33	35.1	20.0	0.37	0.05	0.37
	WAPLS(2)	0.33	35.1	20.0	0.26	0.06	0.43
	WAPLS(3)	0.53	56.4	32.1	0.12	0.09	0.77
	PLS(1)	0.17	18.1	10.3	0.61	0.00	0.23
	PLS(2)	0.16	17.0	9.7	0.64	0.00	0.16
	PLS(3)	0.18	19.1	10.9	0.60	0.01	0.18

Weighted Averaging (WA); Tolerance (Tol); Partial least squares (PLS): Root-mean-square error (RMSEP)

The regional transfer function was applied to fossil foraminifera from an archived sediment core taken from Kariega in 2011. The top ± 30 cm of the core (Figure 4) is characterised by decreasing grain size (increasing clay content) and becomes more organic rich. The top 20 cm of assemblages display a dominance of typical salt marsh agglutinated foraminifera such as

Jadammina macrescens, *Trochammina inflata* and *Miliammina fusca* (Figure 4). The weighted averaging with inverse deshrinking and tolerance downweighting regression model (Figure 3) was used to predict PMSEs based on the fossil assemblages (Figure 4). Assemblages containing a greater abundance of *M. fusca* tended to drive lower surface predictions in

comparison to assemblages with a relatively greater abundance of *T. inflata*. A minimum dissimilarity coefficient was used to analyse whether fossil assemblages had good or close modern analogues and were thus suitably driving transfer function results (Barlein and Whitlock, 1993; Birks, 1995; Barlow *et al.*, 2013). All 21 sampled fossil samples had good or close modern analogues within the regional training set, demonstrating the power of

including surface data from a wide geographical area (e.g., Barlow *et al.*, 2013; Watchman *et al.*, 2013). In the earlier study, fossil samples below 66 cm had a poor fit, representing foraminiferal assemblages, which had no close modern analogue (Strachan *et al.*, 2014). A regional transfer function may widen the geographical range of modern analogues, however in some instances it may give inaccurate reconstructions due to the spatial variability of species.

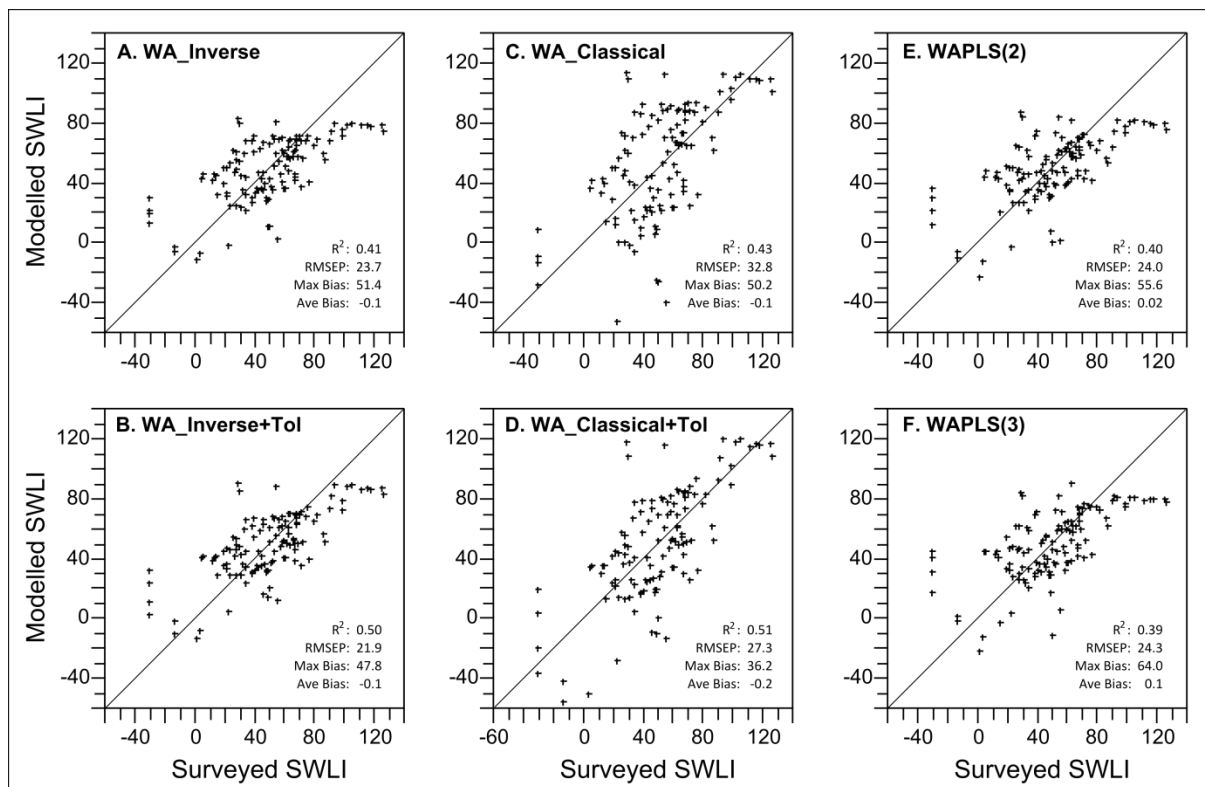


Figure 3: The six regression models used to predict marsh surface elevations based on the regional training set of surface assemblages. Weighted Averaging (WA); Tolerance (Tol); Partial least squares (PLS); Standardised water level index (SWLI).

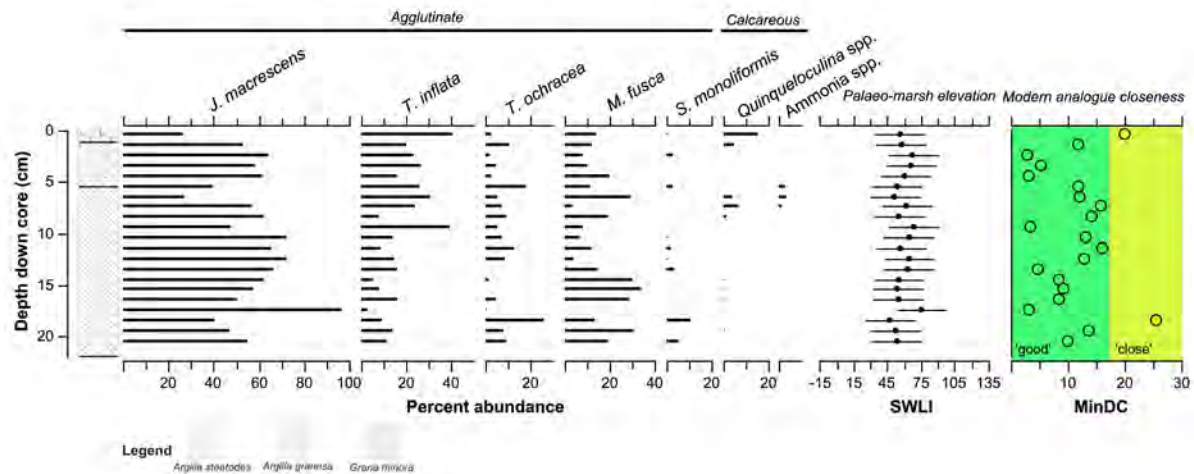


Figure 4: Foraminiferal concentrations encountered in the top 20 cm of an archived sediment core from Kariega. Indicative meaning and associated errors are quantified using the WA_Inverse+Tol regression model. Indicated in the figure is Troels-Smith stratigraphy. Standardised water level index (SWLI); Minimum dissimilarity coefficient (MinDC).

Transfer function validation

Surface prediction results (Figure 4) were used to derive estimations of former sea level by subtracting the indicative meaning (PMSE) from the height of the fossil sample relative to local MWL (c.f., Gehrels 1999). The model RMSEP value provided the indicative range of each estimation (vertical uncertainty) and both this and the PMSE estimation were corrected for the tidal range at Kariega. Strachan *et al.*, (2014) include an age-depth model (Appendix K) in their original reconstruction but for the purpose of this study data was plotted against the interpolated age ranges from the original age model (Figure 5). Recent tide gauge data from Port Elizabeth the closest station is included in Figure 5 to help validate the reconstruction. The commencement of tidal data (year AD) is plotted to coincide with the corresponding year from the original age-depth model in Strachan *et al.*, (2014). The time axis for the tide gauge data is then extrapolated linearly back (Figure 5). Figure 5 demonstrates the use of a regional transfer function in reconstructing sea-level changes on a local scale. One obvious benefit is the ability to extend sea-level records beyond the length of (sometimes very-) short tide gauge data. Figure 5 appears to show some overlap but not a direct correlation with the tidal gauge data from Port Elizabeth, which is situated 190 km away. It must be stressed that this analysis should be considered preliminary given the lack of chronological control. The reconstruction

implies a potential trend of decadal to centennial sea level oscillations. However, given the size of the error bars the possibility that oscillations especially with regards to the 0.8 m drop in sea level, did not occur cannot be entirely ruled out. Dramatic sea-level oscillations can be caused by interannual and decadal variations, such as water temperature, salinity and atmospheric pressure (van de Plassche *et al.*, 1998). Short-term fluctuations in sea level, however, are more likely to be related to climatic forcing (e.g., wind and atmospheric pressure) and variable sedimentation rates. At this location, on the southeast coast of South Africa, it is likely that short-term regional climatic effects such as monsoons (including storm surges), the southern oscillation/El Niño phenomenon (Church *et al.*, 2006), and sea surface temperatures will have a significant influence on decadal to centennial sea level trends, which have potential implications in a warming climate (Rasmusson and Wallace, 1983; Church and White, 2011). To date, salt marsh based sea-level reconstructions (as well as other proxy data) have been unable to explore sub-decadal scale trends. Bridging the gap between high resolution but short length tide gauge records with lower resolution but longer proxy records remains a significant challenge for the sea-level research community.

Uncertainty regarding historical sea-level rates is contributed to by the individual tide gauge records being short and missing data. High-resolution sea-level reconstructions from southern African locations will improve our understanding of how sea level has varied over longer time scales, which is useful for identifying pre- and post-industrial drivers of sea-level change. With a concentration of records in the northern hemisphere, additional data from e.g., South Africa will contribute significantly to the understanding of long-term trends (ocean surface and land movement), local

and regional meteorological influences, and modes of climate variability (El Niño-southern oscillation), which all affect mean sea level (Church and White, 2011; Tyson *et al.*, 2002). This is especially relevant along the southern Cape (Carr *et al.*, 2010; Goedhart, 2007) and the South African Indian Ocean (Woodroffe and Horton, 2005) coastlines, which have experienced limited tectonic activity during the Pleistocene and is useful in constraining the timing and amplitudes of past sea-level change (Carr *et al.*, 2010).

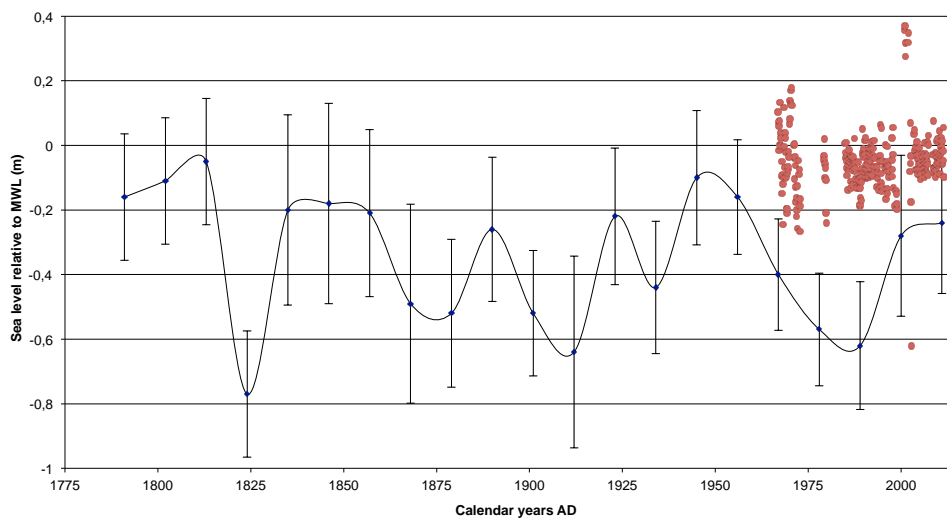


Figure 5: Estimation of former sea level (plotted against calendar years AD) at Kariega based on a reconstruction using the regional transfer function. Recent monthly tide gauge data from Port Elizabeth is shown in red with dates aligned with the original age-model presented by Strachan *et al.*, (2014).

CONCLUSION

Foraminiferal transfer functions are suitable for the reconstruction of high-resolution RSL changes. The reliability of this foraminiferal-based sea-level approach is reliant on the accurate and precise determination of relationships between contemporary foraminiferal assemblages and elevation relative to the tidal frame. Foraminiferal ecological studies were conducted to provide a modern training dataset from which core data can be compared with and interpreted. The results presented in this paper illustrate that a regional transfer function from the southeast South African coastline is suitable for the analysis of fossil foraminiferal material. While training sets

based on local data improved the model precision, their predictive power is restricted, as a regional training set incorporates a greater range and variety of modern analogues. Thus the use of a regional training set reduces the chance of a ‘no modern analogue’ scenario. A regional training set consisting of modern foraminiferal assemblages from three study sites shows through a validation exercise that past sea-level change can be predicted if applied to fossil foraminifera down a sediment core. The collection of additional sediment cores from salt-marshes along the South African coast, and the use of a regional foraminiferal-based transfer function has the potential to produce high-resolution sea-level records that can assist in

interpreting sea-level fluctuations and coastal evolution.

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Synthesis

Intertidal salt-marsh foraminifera as sea-level indicators: Lessons from the South African coastline

Synthesis

INTRODUCTION

Studies including the Intergovernmental Panel on Climate Change (IPCC) Fourth and Fifth Assessment Reports (AR4 and AR5) have shown that global sea level has increased significantly faster during the 20th century in comparison to the 19th century, and is expected to continue accelerating (Nicholls and Cazenave, 2010; Church *et al.*, 2013). Future rising sea levels are one of the most difficult consequences of climate change to adapt to (Nicholls and Cazenave, 2010) as many of the world's largest cities are situated along the coast, and survival is threatened by rising sea levels (Dasgupta *et al.*, 2009; Church *et al.*, 2013). The magnitude and rate of sea-level change is difficult to predict, partly because of the long timescales involved and the spatial variability (Church *et al.*, 2006). Therefore, in order to improve projections of future sea-level change, it is important to quantify changes in the rate of sea-level rise and understand the reasons for such changes (Church and White, 2011). The available meteorological data such as tide-gauges and satellite altimeter records have contributed to this understanding but are not long enough to provide valuable insight into how the climate system operates at a range of timescales (Gehrels *et al.*, 2012; Holgate *et al.*, 2013).

While interannual and decadal sea-level variations can be associated with climatic forcing (wind and atmospheric pressure) and steric variation (Tsimplis *et al.*, 2008), longer-term sea-level trends are related to glacial isostatic adjustment (GIA) and tectonic movements (e.g. Lambeck and Purcell, 2005; Furlani *et al.*, 2011). Geological evidence and proxy data are useful for inferring relative sea-level changes dating back to the last interglacial (Ferranti, 2008). During the past 30 years, proxy sea-level records have been derived from salt-marsh sediments providing data with which the timing of modern sea-level rise can be assessed

(Gehrels and Woodworth, 2013). A significant benefit of using such proxies is that their temporal range and resolution can provide information on sea-level variability beyond the short instrumental period (Leorri *et al.*, 2008; Kemp *et al.*, 2009).

Salt-marsh environments contribute towards understanding sea-level variability due to the quantifiable relationships between microfossils (e.g. intertidal foraminifera and diatoms) in the sediment and elevation (Scott and Medioli, 1980). From such understanding, transfer functions are used to apply this relationship to fossil assemblages in the sediment record and then combine with chronological data (radiocarbon dating) to produce past sea-level estimations (Gehrels *et al.*, 2005).

This synthesis will provide an overview of each of the papers presented and show how the controls and modern patterns of salt-marsh foraminifera, along with development and application of a regional transfer function, can contribute to understanding past sea-level changes. Furthermore, it will highlight the implications for future foraminiferal based sea-level studies in South Africa, along with the limitations of this approach and possible solutions to these issues.

DISCUSSION

This research has used contemporary foraminiferal distributions from three intertidal salt marshes to investigate the use of this proxy as a sea level indicator along the South African southeast coastline, and ultimately attempts to reconstruct past sea-level trends. Living and dead foraminiferal assemblages from Kariega, Keiskamma and Knysna estuaries provide baseline knowledge on ecological trends and

distribution patterns, which are essential for interpreting palaeo-assemblages. To accurately represent the fossil assemblages, seasonal contemporary samples should be collected; ensuring ecological variations are recorded under changing environmental conditions (Debenay *et al.*, 2006). However, this is rare for most ecological studies due to the time consuming task of counting and identifying foraminiferal assemblages and the fact that most studies are based on a single sampling period (Horton and Murray, 2007). For this reason, both live and dead assemblages were utilized for different components of this study. By assessing both live and dead assemblages, the most appropriate assemblage composition can be selected for the training set.

Controls on salt-marsh foraminiferal distribution

Salt-marsh foraminifera can be controlled by a number of environmental variables (e.g. salinity, pH, temperature etc., Murray, 1971; de Rijk, 1995; Patterson, 1990). Quantifying elevation (surrogate for flooding frequency), as an important controlling parameter of contemporary foraminiferal distribution is an essential prerequisite in transfer function based sea-level reconstructions (Kemp and Telford, 2015). To defend the reconstruction, it is important to demonstrate that elevation is statistically significant as the control of modern foraminiferal distributions. It is important with the transfer function technique that the environmental variable of interest, in this instance elevation, has remained the primary control over the entire depositional history of the sediment sequence (Birks, 1995; Kemp and Telford, 2015). Thus, to test this hypothesis other environmental data, such as sediment grain size and organic content, pH and salinity were collected along side foraminiferal assemblage data.

Initially, only living foraminiferal assemblages at Keiskamma and Knysna estuaries were used in determining which environmental parameters influence their distribution. Dead assemblages incorporate taphonomic factors and represent accumulation over time (Schönfeld *et al.*, 2012), whereas living assemblages mirror the present environmental conditions (Murray, 1971; Schönfeld *et al.*, 2012). A partial redundancy

analysis (pRDA) was used to correlate several environmental variables (elevation, sediment grain size, organic content, pH and salinity) and determine which are the most important variables controlling the distribution of living foraminifera at both sites.

At each of the estuaries, species composition varied spatially to some extent, however, the pRDA indicated that composition was strongly influenced by elevation at both Keiskamma ($r = 0.63$) and Knysna ($r = -0.75$). At Keiskamma even though the distributional composition of foraminiferal species was influenced by elevation it was also influenced by salinity, in an equal and opposite manner and to a much lesser extent the sediment organic content and clay fraction. At Knysna Estuary, pH was the secondary controlling variable, while sediment grain size covaried with elevation.

Elevation has been found to be statistically significant in explaining modern foraminiferal distribution variance (Horton *et al.*, 1999; Horton and Culver, 2008; Hawkes *et al.*, 2010). A study conducted by Horton and Edwards (2006) using data from sites around the UK and multiple environmental variables found that elevation explained 42 % of the explained variance. However, other studies have found alternative environmental parameters to exert greater control, for example in the Great Marshes in Massachusetts (de Rijk and Troelstra, 1997), it was demonstrated that salinity was more influential. Another study conducted in northwest England at the Mersey Estuary concluded that even though elevation was the primary variable, when the elevational range is low in comparison to the amplitude (<10 %), inter-correlation between variables becomes more significant (Mills *et al.*, 2013). The results obtained here indicate that elevational control on the distribution of salt-marsh foraminifera is apparent. Therefore, marsh foraminiferal species along the southeast South African coastline can be applied to reconstructing past sea-level changes.

Contemporary distributional patterns of salt-marsh foraminifera

To successfully apply salt-marsh foraminifera for reconstructing sea-level change it is important to have a well documented

relationship between modern distributions and controlling environmental variables (e.g., Scott and Medioli, 1978; 1980; Gehrels, 2002; Gehrels and Newman, 2004; Hayward *et al.*, 2004; Horton *et al.*, 2005). Based on the dominant species at each marsh, and their relation to elevation, it was possible from this research to define four main foraminiferal assemblage zones using constrained incremental sum of squares (CONISS) cluster analysis (Grimm, 1987).

At both Keiskamma and Knysna estuaries, dead and living foraminiferal populations displayed similar distributions and exhibited a vertical zonation comparable with those in other South African and temperate intertidal environments (Horton *et al.*, 1999; de Rijk and Troelstra, 1997; Franceschini *et al.*, 2005; Horton and Edwards, 2006; Strachan *et al.*, 2015). However, there are differences between sites in the zonation of species, and their vertical ranges. The highest salt-marsh zone at both Keiskamma and Knysna was characterised by *Trochammina inflata*, while the middle marsh zone was dominated by *Miliammina fusca* and an increased presence of calcareous species. It has been observed in other studies that the middle to lower marsh zone is characterised by *Miliammina fusca* with low frequencies of calcareous species (Scott and Medioli, 1978; 1980; Patterson, 1990; Scott *et al.*, 1990; Gehrels, 1994; Strachan *et al.*, 2015). The mixed assemblage low-marsh zone was also characterised by the presence of *Miliammina fusca*, and a greater abundance of *Ammonia* spp. and *Quinqueloculina* spp., while the tidal mudflats had the highest diversity of calcareous assemblages and few agglutinated taxa. At Kariega Estuary the lower marsh zone comprised of both living and dead species of *Trochammina inflata*, *Miliammina fusca*, and *Quinqueloculina* spp. (Strachan *et al.*, 2015). Franceschini *et al.*, (2005) encountered a similar species composition in the lower elevations to that of Kariega, however the diversity of calcareous species was greater. Similar studies from Europe found the tidal mudflats to be dominated by calcareous species (Phleger, 1970; Murray, 1991; Buzas *et al.*, 2002; Horton and Edwards, 2006). Calcareous foraminiferal assemblages zones are also common in tropical salt marshes; however, species composition may differ (Debenay *et al.*, 2000; Horton *et al.*, 2005; Woodroffe *et al.*, 2005). Typically, agglutinated

assemblages are abundant in the vegetated upper reaches of the salt marsh, and calcareous assemblages in the lower elevations and the unvegetated mudflats (Debenay and Guillo, 2002; Berkeley *et al.*, 2007), indicating environmental tolerances. Salt-marsh foraminiferal zones determined by their tolerance ranges are important tools for reconstructing relative sea level using salt-marsh sediment cores (Scott and Medioli, 1980; Scott and Leckie, 1990; Jennings and Nelson, 1992). The vertical zonation of each of the study areas further confirms that foraminiferal distributions are controlled by elevation (surrogate variable for flooding frequency) and the key controlling factors are duration and frequency of tidal exposure.

Contemporary living and dead foraminiferal assemblage distributional patterns were compared (Appendix F and G) to determine the extent to which assemblage distribution is affected after death and which assemblages (living, dead or total) are the most appropriate to form a training set that can be used to interpret fossil assemblages in sea-level studies. Keiskamma and Knysna displayed considerably similar living and dead population distributions particularly in the lower reaches. In the upper reaches of both sites the living to dead ratios and distributions were different. The abundance of living populations was far greater at Keiskamma whereas at Knysna the upper reaches were void of living assemblages with the exception of living and dead *Trochammina inflata* (Appendix F and G). Dead specimens in comparison to living were more abundant throughout the marshes. Both living and dead assemblage populations at Kariega displayed similar distributional patterns, while the abundance of dead tests was greater (Strachan *et al.*, 2015). Total (living plus dead) assemblages will therefore take into consideration seasonal and temporal changes (Jennings *et al.*, 1995), however, post-mortem changes that may affect living assemblages are disregarded. A training set comprising of exclusively dead foraminiferal assemblages is not susceptible to seasonal changes, will accurately reflect subsurface assemblages (Murray, 1979; Horton *et al.*, 2005) and takes into the consideration post-mortem transportation and dissolution. However, according to study conducted in Delaware, USA dead assemblages in the upper most 10 cm are susceptible to seasonal changes as they reflect

the latest reproductive input (Leorri and Martin, 2009). Therefore, for this reason determining the ecological trends and distribution of modern foraminiferal assemblages, using only living is acceptable. Living assemblages are also the only assemblages responding to the current environmental parameters. Evidence from Keiskamma Estuary indicates that dead assemblages have greater species diversity, probably as a result of accumulation over time (Murray, 2003). Therefore, unlike an ecological study, it is recommended that a training set comprise of solely dead assemblages, thus will reliably reflect past assemblage-environment relationships and best represent fossil species present down a salt-marsh sediment core.

Development and application of a regional transfer function

The underlying response of salt-marsh foraminiferal distributions to environmental gradients is the foundation on which transfer function models are based. The most appropriate statistical technique for the transfer function is selected based on the species' linear or unimodal distribution (Birks, 1995). Using elevation as the only constraining variable, detrended correspondence analysis (DCA) revealed gradient lengths that indicated linear species distributions at Knysna and Keiskamma have DCA scores of 2.7 and 3.3 respectively. The training set from Kariega returned a DCA score of 1.9 implying that regression models suitable for both linear and unimodal distributions were available. In combining modern training sets (Keiskamma, Knysna and Kariega) comprising of only dead assemblages, the gradient length was still strongly linear at 3.1 SD units. In merging local training sets to create a regional training set, the strength of the association between foraminiferal assemblages and elevation is reduced. Whilst it may seem counterintuitive to combine datasets, a regional training set may provide a better representation of modern environments from which fossil assemblages can be compared (Gehrels *et al.*, 2001) depending on the past environments encountered down the core. Linear regression models are fairly uncommon in quantitative sea-level reconstructions, often as a result of the unimodal distribution of species in response to elevation (Woodroffe and Long, 2010; Leorri *et al.*, 2011; Barlow *et al.*, 2013).

The regional transfer function was used to reconstruct recent sea-level changes at Galpins salt marsh in the Kariega Estuary to demonstrate the use of the new model. The new regional transfer function, built using a regression model designed for unimodally responsive data, was applied to the fossil dataset to derive estimations of palaeo-marsh surface elevations (PMSEs). The highest precisions are demonstrated by weighted averaging models with inverse deshrinking and the multi-component weighted averaging partial least squares models (RMSEP of ± 0.22 to 0.24 m). Standardised water level index (SWLI) root-mean-square error (RMSEP) values correspond to marsh-surface elevation prediction precisions of *c.* ± 0.25 at Knysna Estuary, ± 0.23 at Keiskamma Estuary and ± 0.24 m at Kariega Estuary, after correcting for tidal range size, which is broadly comparable to other models using local data only. The weighted averaging with inverse deshrinking and tolerance downweighting regression model was used to predict PMSEs based on the fossil assemblages. Surface prediction results were used to derive estimations of former sea level by subtracting the indicative meaning (PMSE) from the height of the fossil sample relative to local MWL (*c.f.*, Gehrels 1999). The model RMSEP value provided the indicative range for each estimation (vertical uncertainty) and both this and the PMSE estimation were corrected for the tidal range at Kariega. The results from the weighted averaging with inverse deshrinking and tolerance downweighting regression model were compared with the results from the other three WA models (Paper III) if there were applied to the same fossil assemblages (Figure 1) for further validation. All four approaches display similar results and respond in similar ways to the dataset. Models B and D (Figure 1) show a pattern which is more uniform and little variation in comparison to models A and C which show greater changes down the core.

At Kariega Estuary, two modern training sets (dead and total) were compared using a partial least squares (PLS) regression model (Strachan *et al.*, 2015). The two training sets performed equally well, being able to predict marsh elevation to precisions of ± 17 cm (RMSEP = 0.17). Even though the RMSEP precision is better, the transfer function is based on a linear species response and a unimodal response is more appropriate (Telford and Birks, 2005). Furthermore, model performance based on the

RMSEP and r^2 values is not recommended (Telford *et al.*, 2004). Larger proxies such as coral and beachrock which are commonly used as sea-level indicators have larger vertical errors in comparison to the precision of the microfossils (e.g. foraminifera, diatoms and mangrove pollen; Table 1) in predicting past sea levels. It is only recently that the quantified vertical error of sea-level indicators has been

utilized and this error applied to sea-level reconstructions (Horton *et al.*, 2007). A study conducted on UK saltmarshes found that by joining three groups of micro-organisms (foraminifera, testate amoebae and diatoms) together, the accuracy and precision of the reconstruction was far greater than if a single group was used (Gehrels *et al.*, 2001).

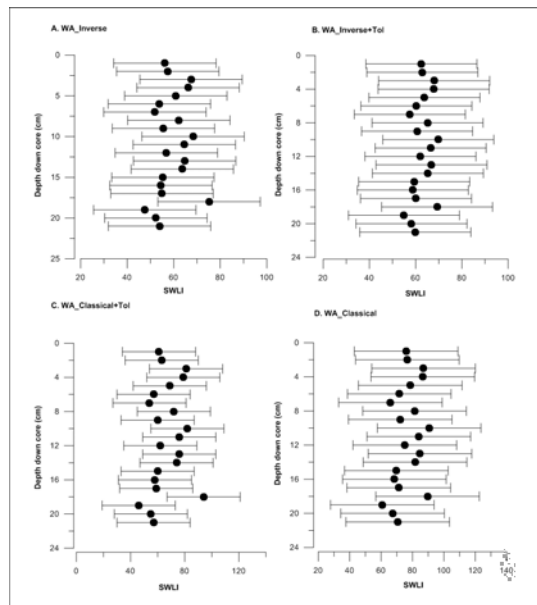


Figure 1: Comparison of three (A, C and D) of the regression models used to predict marsh surface elevations based on the regional training set of surface assemblages with the chosen WA_Inverse+Tot regression model (B). Weighted Averaging (WA); Tolerance (Tot); Partial least squares (PLS); Standardised water level index (SWLI).

To assess the validity of the reconstructed sea-level trend it was compared with an instrumental tide gauge record from Port Elizabeth. Unfortunately, not many of the tide gauge records for South Africa extend further back than 50 years and have missing data (Mather, 2007), especially if the vertical error is taken into consideration. Speculations made from this analysis however should be considered preliminary given the lack of chronological control (Appendix K). Nonetheless, the reconstruction shows some similarities with the tide gauge record. Both records indicate that sea level drops between 1960 and 1980, however there is no noticeable overlap. Most notably, both records similarly record an increase in mean sea level (MSL) to present and display resembling sea levels relative to MWL. The short-term fluctuations in sea-level rise indicated by the model are likely to be influenced by

regional or local-scale processes such as climatic forcing and variable sedimentation rates. Local-scale processes operating along the south east coast possibly influencing sea-level fluctuations include monsoons, the southern oscillation/El Niño phenomena and sea surface temperatures (Church *et al.*, 2006). Isla (1989) working on Holocene sea-level changes in the southern hemisphere concluded that the climate contributed significantly sea-level changes. Due to the low resolution of other South African archaeological and palaeoenvironmental based sea-level curves it is difficult to compare results. However, proxy evidence from the southwestern Cape (Miller *et al.*, 1995; Baxter and Meadows, 1999) and southern coastline (Ramsay, 1995) suggests that there were minor peaks in sea-level during the past 6000 years and a peak of ± 1.5 m between 1610 BP and 900 BP. Similarly, the earlier sea-level reconstruction at Kariega

Estuary (Strachan *et al.*, 2014), provides evidence that sea levels were lower than present around ± 300 cal years BP, followed by a steady rise to present levels. The high-resolution sea-level curve for Kariega presented in this study indicates minor sea-level fluctuations for past ± 300 years.

Table 1: Comparison of sea-level proxy precision (error)

Proxy	Error (m)	Reference
Veretid gastropods	± 0.10	Loborel, 1986
Diatoms	± 0.15	Horton <i>et al.</i> , 2007
Mangrove pollen	± 0.22	Engelhart <i>et al.</i> , 2007
Foraminifera	± 0.22	This study
	± 0.17	Strachan <i>et al.</i> , 2014
Coral	± 2.5	Bard <i>et al.</i> , 1990
Beachrock	± 1.4	de Oliveira Caldas <i>et al.</i> , 2006

Implications for future South African foraminifera based sea-level research

Approximately 40 years after salt-marsh foraminifera were first presented as sea-level indicators, they are still considered to be reliable high-resolution indicators of sea-level change (Horton and Edwards, 2006). Foraminifera continue to be used in research pursuing to improve our understanding of past sea-level change and how these fluctuations have influenced coastal evolution, as they are able to extend reconstructions further back than instrumental records (Bigler *et al.*, 2002). Such

This research illustrates that the foraminifera based transfer function approach to reconstructing sea-level change in South Africa remains a work in progress. There is scope to improve the reconstruction in terms of the reliability, accuracy and precision. This could be achieved by combining foraminiferal data with other quantitative proxies (e.g. diatoms, testate amoebae, ostracods). Although the aim of this project was to assess the utilization of salt-marsh foraminifera for reconstructing sea-level change, the use of additional proxies such as diatoms (e.g. Norström *et al.*, 2012), testate amoebae, biomarkers (e.g. Carr *et al.*, 2015) and pollen (e.g. Baxter and Meadows, 1999) would improve the reliability and precision of the sea-level reconstruction.

In terms of developing modern training sets, there are a number of questions that warrant further investigation. These questions include; is

valuable insights are further used to reduce the uncertainty around future predictions.

This research demonstrates that elevation controls the distribution of modern foraminifera, and these foraminifera do exhibit evidence of being vertically zoned, suggesting that intertidal salt-marsh foraminiferal assemblages can be utilized as sea-level indicators along the South African coastline. This foraminiferal ecological information provides an important baseline for the interpretation of past sea levels. Late Holocene sea-level change was reconstructed for Kariega Estuary using a regional training set, which suggested a similar trend to that observed in the tide-gauge data, implying that the foraminifera-based reconstruction is reflecting real changes in sea level over time. Therefore, intertidal salt-marsh foraminifera can be used as indicators of sea-level change, which can extrapolate changes beyond the limit of tide-gauge records. The combination of intertidal foraminiferal data and the regional transfer function approach to reconstructing past sea-level change offers a number of advantages to sea-level research in South Africa. Sea-level reconstructions will have quantified error terms; sea-level records can be reconstructed at the same resolution; the methodology is replicable and therefore records can be compared with one another along the South African coastline.

PROBLEMS AND PROSPECTS

there an ‘optimum’ sample size for a modern training set; is there an elevational threshold at which point the vertical relationship between salt-marsh foraminifera and the tidal frame no longer exists; and, lastly, what constitutes a ‘region’ in particular in terms of creating a regionally based foraminiferal transfer function? The fundamental assumption of this approach is that fossil and surface assemblages co-vary with ‘elevation’ in a consistent manner. However, in some cases this assumption may be incorrect due to various taphonomic processes altering fossil assemblage composition. Calcareous assemblages can be lost as a result of dissolution and agglutinated through bacterial degradation (Goldstein and Watkins, 1999). Even though there was no evidence of dissolution and foraminiferal tests were well preserved it would still be important to examine taphonomic processes in South African intertidal environments along with the transportation of

both exotic and common species, which could result in anomalies. For example at Knysna Estuary living salt-marsh foraminifera were recorded well above the astronomical tide level. A good understanding of both the ecology and taphonomy of intertidal foraminifera is key to transfer function development and application (Horton and Edwards, 2006).

The further development of foraminifera-based transfer functions along the South African coastline will need to be supported by advances in the dating of core material and thereby reduce chronological uncertainties. A significant component of a transfer function is the chronology as this is used to accurately depict changes in sedimentation that may reflect sea-level fluctuations (Marshall *et al.*, 2007). The chronology established for the core at Kariega Estuary was restricted due to dating limitations and the lack of macrofossils and organic material suitable for radiocarbon dating (Strachan *et al.*, 2014). The marine carbon reservoir correction or ΔR value is used to calibrate samples with a marine carbon component (Dewar *et al.*, 2012). This correction is necessary for comparing marine and terrestrial samples, however, as a result of ocean circulation complexities; each location will have its own correction. Due to the limited number of coastal studies in South Africa and the fact that many researchers have calibrated not taking into consideration the marine reservoir effect, there are few ΔR values along the South African coastline (Woodroffe *et al.*, 2005; Dewar *et al.*, 2012) and it is difficult to establish a marine carbon reservoir correction. It is therefore necessary for further research to be conducted on constraining the marine reservoir effect for South Africa.

An alternative approach to radiocarbon dating would be to introduce the use of lead isotopes (e.g. ^{210}Pb ; Kemp *et al.*, 2012). ^{210}Pb occurs naturally in marine environments and is part of the ^{238}U decay series, widely used to develop modern chronologies (Corbett and Walsh, 2015). ^{210}Pb and ^{137}Cs are radionuclides commonly used as chronological markers for the past 100 to 150 years. Pb isotopes assist in constraining observed inflexions in sea-level studies, which in many cases are not sea-level trends but rather dating limitations (Corbett and Walsh, 2015). In situations where organic

material for radiocarbon dating is lacking, luminescence dating could provide a useful alternative. However, one needs to take cognizance of the fact that in waterlogged coastal sedimentary environments, poorly bleached sediments can limit this approach (Edwards, 2004).

Pollen analysis is one of the longest established climate proxies and is used to investigate changes in vegetation cover over time. In addition to being a palaeoenvironmental proxy, pollen can be used to estimate the depositional age of sediment through chronostratigraphy. Using an established dated pollen record for an area, one can use this to identify unique events in the vegetation history of the area. Alternatively, pollen can document anthropogenic events, for example the introduction of a new species in agricultural practices (Marshall, 2015). Pollen records are therefore also useful for constraining chronological records as a result of indirect and unique event dating, although chronostratigraphic frameworks for pollen markers are poorly established in the southern African context (e.g. Thamm *et al.*, 1996; Turner and Plater, 2004). Mangrove pollen in tropical environments has also been indicated to be a suitable proxy for reconstructing sea-level change. A study conducted in Indonesia developed a mangrove pollen transfer function with a precision of ± 0.22 m (Engelhart *et al.*, 2007).

Few tide gauge records for the southern hemisphere extend further back than 50 years (Mather *et al.*, 2009), thus making it difficult to validate foraminifera-based sea-level reconstructions using instrumental data. Another major problem is that many of the countries tide gauges are not always functional and therefore are unable to provide complete records (Woodroffe *et al.*, 2005). There is a great need not only in South Africa but also in Africa to increase the accessibility and availability of sea-level measurements to support both sustainable development and sea-level research.

Another problematic area with measuring past sea levels, is that datums such as 'mean sea level' are commonly used as reference points when measuring elevation (Roberts *et al.*, 2012). However, sea level is continually changing both

spatially and temporally on local and global scales, and therefore such datums are ‘fixed’ (Roberts *et al.*, 2012). This is especially true in the South African context as it is known that mean sea level has fluctuated over time and is never consistent along the coastline, as a result of variation in barometric pressure (Chandler and Merry, 2011; Mather *et al.*, 2009; Roberts *et al.*, 2012). Therefore, in order to standardise sea-level studies in South Africa it may be advisable to express all elevational measurements relative to orthometric zero. In South Africa this can then be directly linked to international geodetic standards (e.g. WGS84). It is then possible to correct elevations using National Geo-spatial Information (NGI) benchmarks, which are referred to as ‘orthometric heights’ (precision of ± 5 mm) above or below Land Levelling Datum (LLD) zero. LLD zero was set in the 1900s based on mean sea-level measurements at that time (Roberts *et al.*, 2012).

In South Africa, estuaries are one of the most threatened habitats, making it difficult to acquire suitable study sites for this research. Over the last decade there has been an increase in coastal developments and growing human disturbances and exploitation. In many of the estuaries the freshwater inflow has been compromised affecting salinity profiles, nutrient supply, sediment scouring or an increase in pollution (Turpie *et al.*, 2002). As a consequence, many estuaries have become functionally degraded and species have been lost making it difficult to extract viable sediment cores and modern foraminiferal data for sea-level studies. We unfortunately have a very limited understanding of how intertidal foraminifera respond to pollution, especially with regards to abundance and diversity patterns, including taphonomic processes (Alve, 1995; Pati and Patra, 2012).

Estuaries are dynamic environments and therefore geomorphologically can change instantaneously (flood events) or over a long period of time. A number of factors along the South African coastline influence the geomorphology of estuaries, *viz.*, climate, variations in river discharge, gradients, rate of sediment supply from rivers, and sediment supply and type from the coastal zone (Harrison *et al.*, 2000). Extracting undisturbed sedimentary archives from South African estuaries can be difficult as some are periodically scoured from

flood events and accumulated sediment is removed, or sediment is transported through the system to the sea and does not accumulate (Harrison *et al.*, 2000). The chronology from the sediment core extracted from Kariega (Strachan *et al.*, 2014) demonstrated this in a hiatus in the upper 30 cm of the core.

Table 2: List of permanently open estuaries in South Africa (CERM, ud). Sites visited are indicated in bold text. *Sites investigated in this study.

Estuary Name	Type of estuary	Information available	Salt marsh status
Berg (Groot)	Permanently open	Good	
Bot/Kleinmond	Estuarine lake	Excellent	
Bre'	Permanently open	Moderate	
Buffalo	Permanently open	Poor	
Bushmans	Permanently open	Moderate	
Duiwenhoks	Permanently open	Moderate	
Durban Bay	Estuarine bay	Good	Absent
Gamtoos	Permanently open	Good	
Gourits	Permanently open	Moderate	Absent
Gqunube	Permanently open	Poor	
Great Fish	Permanently open	Good	Disturbed
Great Kei	Permanently open	Moderate	Disturbed
Heuningnes	Permanently open	Moderate	
Kaaimans	Permanently open	Poor	
Goukou	Permanently open	Moderate	
*Kariega	Permanently open	Good	Relatively undisturbed
*Keiskamma	Permanently open	Moderate	Relatively undisturbed
Keurboms	Permanently open	Good	
Klein	Estuarine lake	Good	
*Knysna	Estuarine bay	Excellent	Relatively undisturbed
Kobonqaba	Permanently open	Poor	
Kosi	Estuarine lake	Excellent	Relatively undisturbed
Kowie	Permanently open	Good	Absent
Kromme	Permanently open	Excellent	Relatively undisturbed
Kwelera	Permanently open	Poor	
Langebaan Lagoon	Permanently open	Excellent	
Matigulu/Nyoni	Permanently open	Poor	
Mbashe	Permanently open	Moderate	Disturbed
Mdumbi	Permanently open	Nil	
Mgobezeleni	Estuarine lake	Moderate	Absent
Mhlathuze	Estuarine bay	Moderate	
Mkomazi	Permanently open	Moderate	
Mlalazi	Permanently open	Moderate	
Mngazana	Permanently open	Good	
Mngazi	Permanently open	Poor	
Mintafufu	Permanently open	Moderate	
Msikaba	Permanently open	Moderate	
Mtakatye	Permanently open	Nil	
Mtata	Permanently open	Moderate	
Mtentu	Permanently open	Poor	
Mzamba	Permanently open	Moderate	
Mzimkulu	Permanently open	Moderate	
Mzintlava	Permanently open	Nil	
Nahoon	Permanently open	Moderate	
Ngqusi/Inxaxo	Permanently open	Poor	Absent
Nhlabane	Estuarine lake system	Poor	
Nqabara	Permanently open	Poor	
Olifants	Permanently open	Moderate	
Palmiet	Permanently open	Good	
Qolora	Temporarily open	Poor	Absent
Qora	Permanently open	Poor	Absent
Richards Bay	Estuarine bay	Good	Absent
Shixini	Permanently open	Poor	
Sout (Oos)	Permanently open	Moderate	
St Lucia	Estuarine lake system	Excellent	Absent
Steenbras	Permanently open	Moderate	
Sundays	Permanently open	Excellent	
Swartkops	Permanently open	Excellent	
Swartvlei	Estuarine lake system	Excellent	Disturbed
Uilkraals	Permanently open	Moderate	
Wilderness	Estuarine lake system	Excellent	Absent
Xora	Permanently open	Poor	

During this study numerous permanently open estuaries were visited to assess the state of the salt marshes and suitability for foraminifera-based sea-level studies (Table 2). The majority

of sites visited were found to be unsuitable for this research, for the following reasons: (i) absent or highly restricted salt marsh; (ii) no evidence of floral zonation; and/or (iii) highly disturbed salt marsh as a result of cattle grazing (e.g. Great Kei and Great Fish) or development. However, a number of potential sites remain unexplored, for example the Groot Brak Estuary that is temporarily open, but is host to an extensive salt marsh complex. It may be valuable to subsample this site for contemporary foraminiferal data if it was open for a considerably long period of time. Other sites have potential for further research, for example Langebaan Lagoon and Kariega Estuary could be resampled to improve modern data, or the Knysna Estuary, which has potential for obtaining a sediment core.

Future palaeoenvironmental studies focusing on past sea-level change in South Africa should focus on attaining at least two cores per region (east, south and west coasts) and sampling at a higher resolution to further our understanding of sea-level change based on the work conducted by Kemp *et al.*, (2011) along the east coast of the USA. Contemporary data may not be available from salt marshes with disturbed surfaces, however underlying sediment may not be disturbed and a sea-level reconstruction may be possible with the use of a regional transfer function. A regional transfer function incorporating multiple microorganism proxies may be worth further exploring, as it is likely that the precision of the reconstruction will increase but greater chance that modern training set information will better reflect palaeoenvironmental conditions as more contemporary environments are represented.

CONCLUSION

1. Elevation proved to be the most important parameter controlling the distribution of living salt-marsh foraminifera from both Keiskamma and Knysna estuaries.

2. Analysis of contemporary dead and living foraminiferal species distribution and abundances from Keiskamma and Knysna showed that salt-marsh foraminifera are vertically zoned confirming that foraminiferal distribution is a direct function of elevation.

3. Keiskamma and Knysna displayed similar living and dead foraminiferal distributions in the lower reaches, however in the upper reaches the distribution of dead foraminifera differed to that of living assemblages. Therefore, it was recommended that a training set comprise solely of dead assemblages, thus differing from an ecological study focusing on determining which environmental variables control the distribution of living assemblages. The environmental information from a modern training set comprised of only dead assemblages is likely to better reflect palaeoenvironmental conditions encountered down a sediment core.

4. The regional training set consisting of modern foraminiferal assemblages from Kariega, Keiskamma and Knysna, showed that past sea-level change can be predicted and if applied to fossil foraminifera from a sediment core can provide a valuable assessment of sea-level change.

From this study one can conclude that distinct foraminiferal assemblages inhabit different vertical intervals along the intertidal zone and distribution is controlled by elevation. Therefore, frequency and duration of tidal inundation is the primary controlling factor of intertidal salt-marsh foraminiferal distribution. By analysing modern foraminifera one is able to quantify the relationship between species and elevation. With this information one is then able to infer past marsh surface elevations from fossil assemblages down a sediment core and produce high-resolution relative sea level reconstructions. The high precision of this foraminiferal approach makes it a favourable tool for reconstructing sea-level change.

The findings of this study therefore indicate that South African intertidal salt-marsh foraminifera are reliable sea-level indicators and a regional transfer function can predict past sea-level change. The use of salt-marsh foraminifera and a regional transfer function along with other palaeoenvironmental data gives South African researchers unprecedented opportunities to advance sea-level research. As this technique becomes more widely used along the coastline, more data will become available, and not only will this provide new relative sea-level reconstructions for the coastline but will also provide insight into further advantages. Future

sea-level reconstructions will need to proceed in conjunction with the continued advancements in the understanding of the ecology intertidal foraminifera and the development and testing of the transfer function. Therefore, salt-marsh foraminifera are valuable sea-level indicators and can be used to construct high-resolution sea-level curves thus advancing sea-level research in South Africa.

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Appendices

Appendices

Appendix A: Keiskamma Estuary transect elevational data

Table A1: Elevational data for Keiskamma Estuary, Transects 1. Fusca. - 3

Transect 1				Transect 2				Transect 3			
Distance along transect (m)	Height of dumpy (m)	Surface sample	Elevation to LLD (m)	Distance along transect (m)	Height of dumpy (m)	Surface sample	Elevation to LLD (m)	Distance along transect (m)	Height of dumpy (m)	Surface sample	Elevation to LLD (m)
0	1,260	X	1,116	1	1,250		1,029	1	1,370	X	1,727
1	1,325	X	1,051	2	1,265	X	1,014	2	1,330	X	1,767
2	1,342		1,034	3	1,310	X	0,969	3	1,375	X	1,722
3	1,360	X	1,016	4	1,350	X	0,929	4	1,400	X	1,697
4	1,390		0,986	5	1,380		0,899	5	1,415	X	1,682
5	1,395		0,981	6	1,385		0,894	6	1,445		1,652
6	1,400	X	0,976	7	1,400	X	0,879	7	1,445	X	1,652
7	1,435	X	0,941	8	1,410		0,869	8	1,440		1,657
8	1,470		0,906	9	1,410		0,869	9	1,420		1,677
9	1,475		0,901	10	1,445	X	0,834	10	1,450		1,647
10	1,480	X	0,896	11	1,470		0,809	11	1,515	X	1,582
11	1,495		0,881	12	1,470		0,809	12	1,570	X	1,527
12	1,510	X	0,866	13	1,485		0,794	13	1,605	X	1,492
13	1,555	X	0,821	14	1,480	X	0,799	14	1,700	X	1,397
14	1,545		0,831	15	1,510		0,769	15	1,710		1,387
15	1,560		0,816	16	1,525		0,754	16	1,785	X	1,312
16	1,565		0,811	17	1,520		0,759	17	1,840	X	1,257
17	1,560	X	0,816	18	1,525	X	0,754	18	1,850		1,247
18	1,580		0,796	19	1,540		0,739	19	1,890	X	1,207
19	1,590		0,786	20	1,545		0,734	20	1,880	X	1,217
20	1,600	X	0,776	21	1,585	X	0,694	21	1,870		1,227
21	1,595		0,781	22	1,610		0,669	22	1,880		1,217
22	1,600		0,776	23	1,640	X	0,639	23	1,880		1,217
23	1,625		0,751	24	1,670		0,609	24	1,850		1,247
24	1,630	X	0,746	25	1,685		0,594	25	1,860		1,237
25	1,635		0,741	26	1,800	X	0,479	26	1,860		1,237
26	1,665	X	0,711	27	1,870	X	0,409	27	1,840		1,257
27	1,675		0,701	28	2,030	X	0,249	28	1,810		1,287
28	1,680		0,696	29	2,080	X	0,199	29	1,810		1,287
29	1,710	X	0,666	30	2,100		0,179	30	1,820		1,277
30	1,740	X	0,636	31	2,110		0,169				
31	1,730		0,646	32	2,120	X	0,159				
32	1,720		0,656	33	2,140		0,139				
33	1,810	X	0,566	34	2,150		0,129				
34	1,900	X	0,476	35	2,150	X	0,129				
35	1,965	X	0,411	36	2,190	X	0,089				
36	2,050	X	0,326	37	2,210		0,069				
37	2,090	X	0,286	38	2,210		0,069				
38	2,090	X	0,286	39	2,220		0,059				
39	2,090	X	0,286	40	2,225		0,054				
40	2,090	X	0,286	41	2,300	X	-0,021				
41	2,090	X	0,286								
42	2,090	X	0,286								

Table A2: Elevational data for Keiskamma Estuary, Transects 4 and 5

Transect 4				Transect 5			
Distance along transect (m)	Height of dumpy (m)	Surface sample	Elevation to LLD (m)	Distance along transect (m)	Height of dumpy (m)	Surface sample	Elevation to LLD (m)
0,5	1,205		1,059	1	1,230		0,921
1	1,195		1,069	2	1,220		0,931
1,5	1,200		1,064	3	1,220		0,931
2	1,185		1,079	4	1,225		0,926
2,5	1,210		1,054	5	1,225		0,926
3	1,195		1,069	6	1,240		0,911
3,5	1,205		1,059	7	1,210	X	0,941
4	1,205		1,059	8	1,210		0,941
4,5	1,205	X	1,059	9	1,210		0,941
5	1,215		1,049	10	1,210		0,941
5,5	1,230		1,034	11	1,220		0,931
6	1,235		1,029	12	1,230		0,921
6,5	1,250	X	1,014	13	1,240		0,911
7	1,290	X	0,974	14	1,200	X	0,951
7,5	1,320	X	0,944	15	1,290	X	0,861
8	1,335		0,929	16	1,330		0,821
8,5	1,365	X	0,899	17	1,340	X	0,811
9	1,420	X	0,844	18	1,360		0,791
9,5	1,470	X	0,794	19	1,390	X	0,761
10	1,550	X	0,714	20	1,415	X	0,736
10,5	1,595	X	0,669	21	1,450		0,701
11	1,670	X	0,594	22	1,550	X	0,601
11,5	1,700	X	0,564	23	1,620	X	0,531
12	1,750	X	0,514	24	1,780	X	0,371
12,5	1,825	X	0,439	25	1,985	X	0,166
13	1,920	X	0,344	26	2,020	X	0,131

Appendix B: Knysna Estuary transect elevational data

Table B1: Elevational data for Knysna Estuary, Transects 1 and 2

Transect 1				Transect 2							
Distance along transect (m)	Height of dump (m)	Surface sample	Elevation to LLD (m)	Distance along transect (m)	Height of dump (m)	Surface sample	Elevation to LLD (m)	Distance along transect (m)	Height of dump (m)	Surface sample	Elevation to LLD (m)
1	1,360		0,878	1	1,290		1,049	88	1,745		0,594
2	1,350		0,888	2	1,290		1,049	89	1,745		0,594
3	1,315	X	0,923	3	1,285	X	1,054	90	1,745		0,594
4	1,335		0,903	4	1,290		1,049	91	1,770	X	0,569
5	1,325		0,913	5	1,295		1,044	92	1,770		0,569
6	1,345	X	0,893	6	1,295		1,044	93	1,760		0,579
7	1,345		0,893	7	1,295		1,044	94	1,760		0,579
8	1,350		0,888	8	1,280		1,059	95	1,750		0,589
9	1,450		0,788	9	1,270	X	1,069	96	1,760		0,579
10	1,355		0,883	10	1,290		1,049	97	1,760		0,579
11	1,375		0,863	11	1,295	X	1,044	98	1,760		0,579
12	1,375		0,863	12	1,285		1,054	99	1,750		0,589
13	1,390	X	0,848	13	1,275		1,064	100	1,760		0,579
14	1,400		0,838	14	1,264	X	1,075	101	1,770		0,569
15	1,410		0,828	15	1,285		1,054	102	1,780		0,559
16	1,445	X	0,793	16	1,270		1,069	103	1,780		0,559
17	1,450		0,788	17	1,270		1,069	104	1,790		0,549
18	1,450		0,788	18	1,300		1,039	105	1,770		0,569
19	1,470	X	0,768	19	1,310	X	1,029	106	1,770		0,569
20	1,510	X	0,728	20	1,300		1,039	107	1,770		0,569
21	1,560	X	0,678	21	1,315		1,024	108	1,770		0,569
22	1,590	X	0,648	22	1,310		1,029	109	1,775		0,564
23	1,620	X	0,618	23	1,330		1,009	110	1,780		0,559
24	1,630	X	0,608	24	1,330		1,009	111	1,790		0,549
25	1,630		0,608	25	1,320		1,019	112	1,800		0,539
26	1,650	X	0,588	26	1,340	X	0,999	113	1,810		0,529
27	1,690		0,548	27	1,340		0,999	114	1,820	X	0,519
28	1,700	X	0,538	28	1,340		0,999	115	1,820		0,519
29	1,700		0,538	29	1,345		0,994	116	1,825		0,514
30	1,700		0,538	30	1,345		0,994	117	1,830		0,509
31	1,710		0,528	31	1,330		1,009	118	1,830		0,509
32	1,700		0,538	32	1,330		1,009	119	1,840		0,499
33	1,710		0,528	33	1,340		0,999	120	1,850		0,489
34	1,710	X	0,528	34	1,360	X	0,979	121	1,860		0,479
35	1,710		0,528	35	1,365		0,974	122	1,870	X	0,469
36	1,715		0,523	36	1,350		0,989	123	1,870		0,469
37	1,715	X	0,523	37	1,390		0,949	124	1,870		0,469
38	1,715		0,523	38	1,390		0,949	125	1,880		0,459
39	1,720		0,518	39	1,440	X	0,899	126	1,885		0,454
40	1,720		0,518	40	1,430		0,909	127	1,890		0,449
41	1,720		0,518	41	1,440		0,899	128	1,940	X	0,399
42	1,730		0,508	42	1,480		0,859	129	1,940		0,399
43	1,740		0,498	43	1,495		0,844	130	1,950		0,389
44	1,745	X	0,493	44	1,450	X	0,889	131	1,980	X	0,359
45	1,765		0,473	45	1,500	X	0,839	132	1,990	X	0,349
46	1,765		0,473	46	1,545		0,794	133	1,990		0,349
47	1,770		0,468	47	1,500		0,839	134	2,000		0,339
48	1,785		0,453	48	1,500		0,839	135	2,000		0,339
49	1,790	X	0,448	49	1,520		0,819	136	2,000		0,339
50	1,810		0,428	50	1,520		0,819	137	2,040	X	0,299
51	1,810		0,428	51	1,520	X	0,819	138	2,050		0,289
52	1,800		0,438	52	1,570	X	0,769	139	2,060		0,279
53	1,810		0,428	53	1,580		0,759	140	2,180		0,159
54	1,820		0,418	54	1,580		0,759	141	2,200	X	0,139
55	1,830	X	0,408	55	1,560		0,779	142	2,200		0,139
56	1,850		0,388	56	1,520		0,819	143	2,160	X	0,179
57	1,870		0,368	57	1,530		0,809	144	2,160		0,179
58	1,880	X	0,358	58	1,540		0,799	145	2,160		0,179
59	1,860		0,378	59	1,550		0,789	146	2,200		0,139
60	1,860		0,378	60	1,600		0,739	147	2,160	X	0,179
61	1,880		0,358	61	1,600		0,739				
62	1,920	X	0,318	62	1,620	X	0,719				
63	1,930		0,308	63	1,620		0,719				
64	1,930		0,308	64	1,630		0,709				
65	1,940		0,298	65	1,650		0,689				
66	1,940		0,298	66	1,650		0,689				
67	1,945	X	0,293	67	1,660		0,679				
68	1,940		0,298	68	1,670	X	0,669				
69	1,940		0,298	69	1,670		0,669				
70	1,940		0,298	70	1,680		0,659				
71	1,940		0,298	71	1,680		0,659				
72	1,940		0,298	72	1,670		0,669				
73	1,950		0,288	73	1,690		0,649				
74	1,950		0,288	74	1,690		0,649				
75	1,950		0,288	75	1,700		0,639				
76	1,950		0,288	76	1,680		0,659				
77	1,950		0,288	77	1,700		0,639				
78	1,960		0,278	78	1,700		0,639				
79	1,970		0,268	79	1,710		0,629				
80	1,985	X	0,253	80	1,710		0,629				
81	2,004		0,234	81	1,720	X	0,619				
82	2,110		0,128	82	1,730		0,609				
83	2,120	X	0,118	83	1,730		0,609				
84	2,150		0,088	84	1,740		0,599				
85	2,185		0,053	85	1,740		0,599				
86	2,200		0,038	86	1,740		0,599				
87	2,240	X	-0,002	87	1,750		0,589				

Table B2: Elevational data for Knysna Estuary, Transects 3

Transect 3			
Distance along transect (m)	Height of dumpy (m)	Surface sample	Elevation to LLD (m)
0,5	1,500		1,792
1	1,480		1,812
1,5	1,500		1,792
2	1,500		1,792
2,5	1,525		1,767
3	1,555	X	1,737
3,5	1,550		1,742
4	1,565		1,727
4,5	1,565	X	1,727
5	1,610	X	1,682
5,5	1,680	X	1,612
6	1,700	X	1,592
6,5	1,765	X	1,527
7	1,750		1,542
7,5	1,770		1,522
8	1,785	X	1,507
8,5	1,830	X	1,462
9	1,865	X	1,427
9,5	1,890	X	1,402
10	1,900		1,392
10,5	1,935	X	1,357
11	1,985		1,307
11,5	1,995		1,297
12	2,015	X	1,277
12,5	2,005		1,287
13	2,010		1,282
13,5	2,000		1,292
14	2,000		1,292
14,5	2,000		1,292
15	2,020		1,272
15,5	2,035		1,257
16	2,050	X	1,242
16,5	2,070		1,222
17	2,085		1,207
17,5	2,090	X	1,202
18	2,090		1,202
18,5	2,090	X	1,202
19	2,100		1,192
19,5	2,130		1,162
20	2,140	X	1,152

Appendix C: Foraminiferal assemblage count sheets Keiskamma Estuary

Table C1: Transect One at Keiskamma Estuary, South Africa

Species Name	Status	0	1	3	6	7	10	12	13	17	20	24	26	29	30	33	34	35	36	37	38	39	40	41	42	Total	
<i>Ammonia tepida</i>	Dead	42	16	8	0	0	64	3	0	10	0	0	16	12	13	0	0	9	0	12	0	0	4	4	8	221	
	Living	27	35	0	112	63	60	0	32	28	6	0	0	4	6	0	0	29	10	56	32	0	20	12	8	540	
<i>Jadammina macrescens</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	8	0	0	0	0	16	
	Living	3	0	0	0	0	0	5	0	14	0	8	4	0	0	0	0	12	2	9	17	4	0	0	0	78	
<i>Miliammina fusca</i>	Dead	54	16	121	78	131	40	0	12	133	186	84	66	83	37	12	2	8	0	0	28	0	4	8	0	1103	
	Living	3	60	20	42	54	20	5	0	94	122	68	28	64	26	44	3	7	6	8	36	25	8	25	0	768	
<i>Quinqueloculina seminula</i>	Dead	12	0	11	6	18	0	0	0	10	4	0	5	4	4	0	0	0	0	16	0	0	0	27	0	117	
	Living	3	0	14	0	20	8	0	20	39	9	0	29	0	1	0	0	8	0	8	24	10	8	152	0	353	
<i>Trochammina inflata</i>	Dead	66	0	32	72	162	0	2	0	4	0	0	0	4	0	4	0	0	0	0	0	0	0	0	0	346	
	Living	60	35	16	88	74	8	0	0	22	0	0	4	4	0	0	0	0	0	0	0	0	0	0	0	311	
<i>Elphidium</i> spp.	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	8	10	
	Living	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	14	0	0	0	0	0	20	39	
<i>Brizalina variabilis</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	5	0	0	0	9	
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	16	
<i>Brizalina pseudopunctata</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	6	0	7	
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	8	0	0	0	4	0	20	
Unknown 1	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	6	
<i>Lagena</i> spp.	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4	
	Living	0	0	0	0	0	0	33	0	0	0	0	0	0	0	0	10	0	14	20	0	28	36	0	0	141	
<i>Cibicides lobatulus</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	7	20	3	0	38	
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	16	0	0	40	12	0	70	
<i>Triloculina</i> sp.	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	12	
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Spiroloculina laevigata</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	4	
	Living	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	24	
Unknown	Dead	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	4	0	12	0	0	0	0	0	20	
	Living	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	4	0	16	0	0	0	0	0	24	
<i>Scherchorella moniliformis</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	Living	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	
Total number of dead		174	32	172	156	311	104	5	12	157	190	84	87	107	55	16	6	24	6	48	36	20	32	48	28	1910	
Total number of living		96	130	57	242	211	104	10	97	197	137	76	70	76	35	59	13	68	52	141	109	83	124	205	28	2420	
Total number of species		270	162	229	398	522	208	15	109	354	327	160	157	183	90	75	19	92	58	189	145	103	156	253	56	4330	
alliquotes		8	8	5	8	6	8	8	8	3	2	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	

Table C2: Transect two at Keiskamma Estuary, South Africa

Species Name	Status	0	2	3	4	7	10	14	18	21	23	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	Total
<i>Ammonia tepida</i>	Dead	0	8	0	10	4	0	0	0	6	0	4	4	0	14	0	0	0	0	6	44	4	49	24	19	16	15	7	234
	Living	0	16	0	30	30	9	0	0	4	8	20	42	4	12	6	0	0	0	2	10	16	12	20	10	36	25	44	356
<i>Jadammina macrescens</i>	Dead	36	35	92	0	4	0	0	0	0	0	25	0	0	0	6	0	10	3	0	20	12	16	19	0	28	24	9	339
	Living	72	70	78	12	8	0	0	0	12	4	32	44	4	4	0	0	38	8	12	30	16	14	46	0	56	39	70	669
<i>Miliammina fusca</i>	Dead	18	28	48	64	1	34	140	21	26	124	0	0	0	0	4	20	0	0	8	0	0	0	0	10	0	0	3	549
	Living	0	12	21	64	0	12	24	25	34	14	4	6	14	4	0	20	17	4	7	0	4	0	8	2	0	0	0	296
<i>Quinqueloculina seminula</i>	Dead	0	8	38	4		24	19	7	8	4	0	0	0	0	8	0	7	5	0	0	0	0	6	0	0	0	138	
	Living	0	24	0	68	16	16	26	12	37	0	0	8	2	0	0	8	0	11	0	0	0	0	4	2	8	0	0	242
<i>Spirillina vivipara</i>	Dead	0	0	12	8	0	0	0	0	4	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28
	Living	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
<i>Trochammina inflata</i>	Dead	42	53	24	14	2	0	15	0	0	4	0	0	0	0	0	6	0	0	4	0	4	0	12	0	0	0	180	
	Living	80	102	17	45	24	0	0	0	0	0	0	16	0	0	0	15	0	0	16	0	2	8	5	0	8	3	341	
<i>Balticammina pseudomacrescens</i>	Dead	8	32	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
	Living	21	46	8	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	84
<i>Elphidium spp.</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	4	0	0	11	
	Living	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	6
<i>Triloculina sp.</i>	Dead	0	0	0	0	0	21	0	0	0	4	0	0	0	0	0	8	6	0	0	0	0	10	0	0	0	0	49	
	Living	0	0	0	0	0	40	29	0	0	4	0	0	0	12	0	18	0	0	20	0	0	6	0	0	0	0	129	
<i>Brizalina variabilis</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	
<i>Brizalina pseudopunctata</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	4	0	4	0	0	0	0	0	0	0	0	0	0	0	0	8	
	Living	6	0	0	0	0	0	0	14	4	14	16	12	2	0	0	0	0	0	4	0	0	0	0	0	0	0	2	74
<i>Glabrattella milletti</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	4	
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cibicides lobatulus</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	13	
	Living	0	0	0	0	0	0	0	0	0	4	8	2	0	0	0	13	0	0	0	0	0	2	16	0	0	0	45	
<i>Spiroloculina laevigata</i>	Dead	0	0	30	0	0	0	0	0	20	0	6	4	0	0	0	0	0	0	6	0	0	6	0	0	0	0	5	71
	Living	0	0	13	8	0	0	0	0	0	0	12	0	2	0	0	0	0	0	0	0	0	0	0	0	24	12	71	
<i>Lagena spp.</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
	Living	0	0	0	0	0	0	24	0	0	0	0	42	10	0	0	0	0	0	4	0	0	0	0	0	0	0	80	
Unknown	Dead	0	0	0	0	0	0	0	0	0	8	0	0	2	0	0	0	0	0	0	0	6	0	0	0	0	0	16	
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Total number of dead		116	164	247	106	11	79	174	28	44	156	41	38	14	16	14	28	40	16	19	68	20	88	59	60	44	39	24	1753
Total number of living		221	270	153	240	78	77	79	37	125	30	74	132	104	38	20	28	115	36	21	76	44	28	92	23	116	96	131	2484
Total number of species		337	434	400	346	89	156	253	65	169	186	115	170	118	54	34	56	155	52	40	144	64	116	151	83	160	135	155	4237
alliquotes		6	3	5	8	8	8	2	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8

Table C3: Transect three at Keiskamma Estuary, South Africa

Species Name	Status	11	12	13	14	16	17	19	20	Total
<i>Ammonia tepida</i>	Dead	0	0	0	0	0	0	0	0	0
	Living	0	5	0	0	9	0	0	0	14
<i>Jadammina macrescens</i>	Dead	0	0	0	0	0	0	0	0	0
	Living	0	0	0	0	4	0	0	0	4
<i>Miliammina fusca</i>	Dead	2	3	4	4	0	0	2	0	15
	Living	5	1	7	8	0	0	3	4	28
<i>Trochammina inflata</i>	Dead	0	0	0	0	0	5	5	0	10
	Living	0	0	9	14	42	11	12	14	102
Unknown 1	Dead	0	0	5	0	0	0	0	0	5
	Living	0	0	3	0	0	0	0	0	3
Total number of dead		2	3	9	4	0	5	7	0	30
Total number of living		5	6	19	22	55	11	15	18	151
Total number of species		7	9	28	26	55	16	22	18	181
alliquotes		8	8	8	8	8	8	8	8	8

Table C4: Transect four at Keiskamma Estuary, South Africa

Species Name	Status	0	4,5	6,7	7	7,5	8,5	9	9,5	10	11	11	12	12	13	13	Total
<i>Ammonia tepida</i>	Dead	2	0	20	15	6	10	14	4	24	33	0	8	0	8	12	156
	Living	19	0	28	16	56	28	20	8	49	28	21	8	0	28	16	325
<i>Jadammina macrescens</i>	Dead	0	0	30	28	9	0	0	0	0	0	3	0	0	8	0	78
	Living	0	24	88	110	0	0	0	0	0	0	15	4	0	0	0	241
<i>Miliammina fusca</i>	Dead	330	131	110	20	88	120	158	134	102	68	24	28	26	24	4	1367
	Living	175	61	84	87	129	142	112	92	74	45	30	16	11	48	16	1122
<i>Quinqueloculina seminula</i>	Dead	17	0	0	0	27	15	24	36	68	60	12	12	3	4	8	286
	Living	23	0	40	0	57	25	66	52	92	90	15	28	0	20	8	516
<i>Spirillina vivipara</i>	Dead	0	0	0	48	35	0	0	4	0	0	0	0	0	0	0	87
	Living	4	3	0	88	120	0	0	4	0	4	0	0	0	0	0	223
<i>Trochammina inflata</i>	Dead	11	3	36	40	28	107	24	4	8	0	0	0	6	0	16	283
	Living	22	3	144	103	137	12	22	16	28	12	0	0	0	0	4	503
<i>Balticammina pseudomacrescens</i>	Dead	8	0	7	25	31	23	2	0	0	0	0	0	0	0	0	96
	Living	22	0	14	33	37	4	5	0	0	0	0	0	0	0	0	115
<i>Scherochorella moniliformis</i>	Dead	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2
	Living	0	0	0	0	24	0	0	4	0	0	0	0	0	0	0	28
<i>Elphidium</i> spp.	Dead	0	0	0	0	0	0	2	0	0	4	0	0	0	0	0	6
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Quinqueloculina</i> spp.	Dead	0	36	0	0	0	0	0	0	0	0	0	0	0	0	0	36
	Living	0	60	0	0	0	0	0	0	0	0	0	0	0	0	0	60
<i>Spiroloculina laevigata</i>	Dead	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	8
	Living	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	16
Total number of dead		368	170	203	184	224	275	224	184	202	165	39	48	35	44	40	2405
Total number of living		265	151	398	453	560	211	225	176	243	179	81	56	11	100	44	3153
Total number of species		633	321	601	637	784	486	449	360	445	344	120	104	46	144	84	5558
alliquotes		2	3	4	8	8	1	2	4	4	8	8	8	8	8	8	8

Table C5: Transect five at Keiskamma Estuary, South Africa

Species Name	Status	0	7	14	15	17	19	20	22	23	24	25	26	Total
<i>Ammonia tepida</i>	Dead	0	26	7	13	41	2		52	29	28	168	134	500
	Living	0	12	9	15	49	11	2	40	2	20	52	24	236
<i>Jadammina macrescens</i>	Dead	7	0	0	0	0	0	2	0	0	0	0	0	9
	Living	2	0	0	0	0	0	14	0	0	4	0	0	20
<i>Miliammina fusca</i>	Dead	128	373	165	260	227	102	80	143	164	12	28	8	1690
	Living	43	174	145	132	97	67	124	130	113	37	0	0	1062
<i>Quinqueloculina seminula</i>	Dead	13	0	6	5	17	0	0	68	3	4	0	4	120
	Living	22	6	11	10	30	0	40	67	8	0	8	4	206
<i>Spirillina vivipara</i>	Dead	0	0	3	0	0	1	0	0	0	0	0	0	4
	Living	0	0	0	0	5	4	7	3	0	0	0	0	19
<i>Trochammina inflata</i>	Dead	30	24	7	7	6	12	0	0	6	0	0	0	92
	Living	7	29	6	15	13	16	19	11	1	0	0	0	117
<i>Balticammina pseudomacrescens</i>	Dead	7	9	2	4	0	0	0	0	0	0	0	0	22
	Living	2	4	0	5	0	0	0	0	0	0	0	0	11
<i>Scherochorella moniliformis</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0
	Living	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Quinqueloculina</i> spp.	Dead	0	0	0	0	0	26	68	0	0	0	0	0	94
	Living	0	0	0	0	0	48	46	0	0	0	0	0	94
<i>Cibicides lobatulus</i>	Dead	0	0	0	0	0	3	0	0	0	0	0	0	3
	Living	0	0	0	0	0	2	0	0	0	0	0	0	2
<i>Lagena</i> spp.	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0
	Living	0	0	0	0	0	0	0	0	0	0	12	16	28
Total number of dead		185	432	190	289	291	146	150	263	202	44	196	146	2534
Total number of living		76	225	171	178	194	149	252	251	124	61	72	44	1797
Total number of species		261	657	361	467	485	295	402	514	326	105	268	190	4331
alliquotes		2	1	1	1	1	3	2	8	8	8	8	8	8

Appendix D: Foraminiferal assemblage count sheets Knysna Estuary

Table D1: Transect One at Knysna Estuary, South Africa

Species Name	Status	0	3	6	13	16	19	20	21	22	24	26	28	34	37	44	49	58	62	67	84	87	91	Total
<i>Ammonia tepida</i>	Dead	0	0	20	2	2	36	0	2	25	0	0	59	167	12	0	0	0	15	24	11	0	16	391
	Living	0	0	0	14	20	17	16	6	17	9	9	54	208	68	26	70	66	63	44	15	0	27	749
<i>Jadammina macrescens</i>	Dead	15	33	30	4	0	32	0	30	0	0	0	0	2	32	0	0	0	0	0	0	0	0	178
	Living	0	17	0	4	0	13	0	18	0	0	0	0	2	0	0	0	0	0	0	0	0	0	54
<i>Miliammina fusca</i>	Dead	36	42	79	134	132	50	28	38	32	4	42	48	50	116	114	90	42	20	24	0	0	0	1121
	Living	0	0	0	16	52	25	4	140	16	8	16	45	68	20	68	200	36	9	0	0	0	0	723
<i>Quinqueloculina</i> spp.	Dead	5	0	10	24	11	26	11	10	0	0	0	8	0	28	0	0	5	13	0	0	0	0	151
	Living	0	13	14	80	42	24	20	84	15	2	0	0	18	0	60	15	0	0	0	0	0	0	387
<i>Trochammina inflata</i>	Dead	134	108	152	28	38	68	124	70	112	158	46	30	0	36	20	0	0	0	0	0	0	7	1131
	Living	23	72	33	22	20	18	12	26	53	23	32	10	10	33	24	0	0	0	0	0	0	3	414
<i>Balticammina pseudomacrescens</i>	Dead	0	0	0	12	24	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54
	Living	0	0	0	8	26	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Elphidium</i> spp.	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	33	6	0	0	56
	Living	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	48	25	41	3	0	0	122
<i>Brizalina pseudopunctata</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	13
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	8
<i>Lagena</i> spp.	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Living	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Cibicides lobatulus</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Living	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
<i>Triloculina</i> sp.	Dead	0	0	0	6	4	0	0	0	0	0	0	0	0	0	0	0	0	5	16	0	0	0	31
	Living	0	0	0	13	8	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	39
<i>Brizalina variabilis</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
	Living	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Unknown	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	8
	Living	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
<i>Scherochorella moniliformis</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	7	16	0	0	0	0	0	0	0	23
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	8	11	0	0	0	0	0	0	0	19
Total number of dead		190	183	291	210	211	212	163	168	169	162	88	137	229	209	169	106	42	62	110	25	0	23	3159
Total number of living		23	102	47	161	170	97	52	311	101	42	57	114	306	121	186	304	150	97	85	18	0	30	2574
Total number of species		213	285	338	371	381	309	215	479	270	204	145	251	535	330	355	410	192	159	195	43	0	53	5733
alliquotes		1	2	1	2	1	2	4	2	8	4	8	1	2	8	4	5	8	8	8	8	8	8	8

Table D2: Transect two at Knysna Estuary, South Africa

Species Name	Status	0	3	9	11	14	19	26	34	39	45	52	57	62	68	81	91	114	122	128	132	Total	
<i>Ammonia tepida</i>	Dead	0	0	0	89	0	0	0	0	0	16	0	0	66	0	0	28	2	0	19	9	229	
	Living	0	0	0	0	0	0	0	4	0	48	0	26	27	0	0	32	3	40	3	16	199	
<i>Jadammina macrescens</i>	Dead	13	28	21	25	46	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	147
	Living	0	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27
<i>Miliammina fusca</i>	Dead	46	82	62	33	47	90	57	80	5	90	0	44	63	0	48	18	26	0	6	16	813	
	Living	32	43	12	0	45	51	0	0	0	0	0	0	60	0	4	14	7	32	0	0	0	337
<i>Quinqueloculina</i> spp.	Dead	0	0	5	4	0	6	21	26	0	0	8	0	0	8	0	0	0	40	0	0	0	118
	Living	0	0	3	0	0	0	0	17	0	48	8	0	15	0	4	0	0	48	0	0	0	143
<i>Spirillina vivipara</i>	Dead	0	0	0	0	0	0	0	0	0	88	0	0	0	0	0	0	0	0	0	0	0	88
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trochammina inflata</i>	Dead	188	187	48	134	165	118	131	98	143	0	24	96	110	120	56	25	0	0	0	0	1643	
	Living	53	28	16	41	101	36	36	21	0	0	8	0	37	40	28	12	0	0	0	0	0	457
<i>Elphidium</i> spp.	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	5	17	
	Living	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0	0	5	0	29
<i>Brizalina pseudopunctata</i>	Dead	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
	Living	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Triloculina</i> sp.	Dead	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
	Living	0	0	0	2	18	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	28
Total number of dead		253	297	136	289	258	214	209	218	148	194	32	140	239	128	104	71	28	40	37	30	3065	
Total number of living		85	71	31	43	191	87	36	42	0	120	16	34	139	40	73	58	10	120	8	16	1220	
Total number of species		338	368	167	332	449	301	245	260	148	314	48	174	378	168	177	129	38	160	45	46	4285	
alliquotes		1	1	1	1	1	3	3	2	8	8	8	8	3	8	8	8	8	8	8	8	8	8

Table D3: Transect three at Knysna Estuary, South Africa

Species Name	Status	6	6,5	8	9	9,5	11	12	16	18	19	20	Total
<i>Ammonia tepida</i>	Dead	0	6	0	0	0	0	0	0	0	2	0	8
	Living	0	0	0	0	0	0	0	0	0	3	0	3
<i>Jadammina macrescens</i>	Dead	11	34	11	23	18	4	0	24	31	16	9	181
	Living	0	0	0	0	0	0	0	14		5	0	19
<i>Miliammina fusca</i>	Dead	0	0	0	0	0	0	0	0	33	13	0	46
	Living	0	0	0	0	0	0	0	0	0	0	0	0
<i>Quinqueloculina</i> spp.	Dead	0	0	0	0	0	4	0	0	0	0	0	4
	Living	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trochammina inflata</i>	Dead	23	150	164	122	153	227	161	165	170	153	155	1643
	Living	0	42	5	102	19	21	36	96	77	48	11	457
<i>Elphidium</i> spp.	Dead	0	0	0	0	0	0	0	0	0	0	0	0
	Living	0	0	0	0	0	0	0	0	0	2	0	2
Unknown	Dead	0	0	0	0	0	0	0	0	0	0	0	0
	Living	0	0	0	0	0	0	0	0	2	0	0	2
<i>Cibicides lobatulus</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0
	Living	0	0	0	0	0	0	0	0	0	0	0	0
<i>Triloculina</i> sp.	Dead	0	0	0	0	0	0	0	0	3	0	0	3
	Living	0	0	0	0	0	0	0	0	0	0	0	0
<i>Helenina anderseni</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0
	Living	0	0	0	0	0	0	4	0	0	0	0	4
Total number of dead		34	190	175	145	171	235	161	189	237	184	164	1885
Total number of living		0	42	5	102	19	21	40	110	79	58	11	487
Total number of species		34	232	180	247	190	256	201	299	316	242	175	2372
alliquotes		8	3	4	6	1	1	1	1	1	1	1	

Appendix E: Environmental data for Keiskamma and Knysna estuaries

Table E1: Environmental variable data for Keiskamma and Knysna estuaries

Keiskamma Estuary								Knysna Estuary							
Transect	LLD (m)	pH	Salinity	LOI	Clay (%)	Silt (%)	Sand (%)	Transect	LLD (m)	pH	Salinity	LOI	Clay (%)	Silt (%)	Sand (%)
1	1,12	6,20	4,50	1,08	1,44	7,76	92,02	1	0,92	8,10	4,60	44,01	2,75	23,38	76,98
1	1,05	7,00	5,40	5,61	3,94	19,43	79,32	1	0,85	8,00	4,60	31,40	2,82	23,92	76,64
1	1,02	7,20	6,90	9,82	5,27	32,00	67,30	1	0,79	7,90	10,00	23,05	2,36	19,64	80,96
1	0,98	7,20	6,00	7,78	4,78	26,95	71,84	1	0,77	7,80	5,10	11,51	2,42	17,95	82,39
1	0,94	7,30	5,20	9,32	4,68	28,81	70,80	1	0,73	7,80	9,30	13,19	2,10	17,00	83,63
1	0,90	7,30	6,90	11,22	4,55	28,12	71,19	1	0,68	7,80	9,10	8,21	1,90	15,17	85,50
1	0,82	7,60	9,30	10,38	5,17	29,01	69,74	1	0,65	8,60	10,50	7,97	2,06	15,54	85,15
1	0,82	7,60	5,70	11,22	4,80	27,15	71,65	1	0,59	9,00	8,80	6,17	1,62	12,33	88,32
1	0,78	6,80	5,70	12,08	4,54	24,78	73,73	1	0,54	8,80	9,50	5,85	2,12	14,90	85,62
1	0,75	6,90	11,70	10,35	5,01	26,00	72,25	1	0,53	8,60	7,90	4,18	1,38	10,80	89,78
1	0,71	6,90	11,50	10,96	3,99	18,84	79,50	1	0,52	8,40	7,70	6,06	1,80	13,74	86,84
1	0,67	7,10	12,40	10,57	4,92	25,74	72,55	1	0,49	8,30	6,80	3,98	1,45	11,32	89,34
1	0,52	7,00	8,00	4,85	4,27	23,74	75,13	1	0,45	8,70	5,30	3,57	1,25	9,75	90,83
1	0,41	7,30	9,10	8,69	4,89	24,64	73,78	1	0,36	8,80	5,50	1,92	1,12	8,06	92,16
1	0,33	7,30	9,10	4,51	3,42	17,41	81,61	1	0,32	8,90	6,10	2,29	1,13	8,59	91,68
1	0,29	7,20	9,10	8,66	4,14	20,70	77,96	1	0,29	8,80	4,50	2,27	0,97	7,78	92,68
1	0,29	7,20	12,40	9,07	6,17	29,11	68,57	2	1,05	9,10	0,70	34,94	2,89	23,63	76,74
1	0,29	7,20	6,60	6,51	6,20	30,67	67,15	2	1,05	9,50	2,70	37,71	2,94	23,23	77,01
1	0,29	7,00	8,60	8,31	5,17	24,82	73,50	2	1,06	9,00	1,15	34,40	3,01	22,94	77,22
1	0,29	7,00	6,90	3,84	5,43	27,50	71,15	2	1,08	9,00	3,00	36,28	3,40	24,93	75,11
2	1,05	6,90	4,40	10,64	5,69	34,61	64,54	2	1,03	8,60	4,60	30,22	2,89	22,01	78,24
2	1,01	6,90	2,80	8,81	5,74	33,03	65,99	2	0,99	8,70	3,70	29,92	2,79	21,75	78,65
2	0,97	6,70	4,80	10,04	5,29	31,37	67,60	2	0,84	8,30	2,80	18,57	2,51	20,13	80,26
2	0,93	6,90	5,10	5,98	4,05	22,55	76,55	2	0,67	8,90	5,00	5,80	1,45	11,98	88,51
2	0,88	6,50	9,30	9,97	5,24	31,64	67,41	2	0,57	8,60	9,30	5,19	1,11	10,33	90,16
2	0,83	7,10	10,00	7,35	5,79	30,75	68,01	2	0,52	9,20	7,90	3,32	0,77	7,51	92,93
2	0,80	7,20	11,20	10,54	5,41	28,71	69,61	2	0,40	9,40	8,70	1,41	0,00	2,16	98,22
2	0,69	6,50	11,90	10,41	4,61	25,55	73,24	3	1,63	10,10	0,00	74,11	4,21	30,50	69,82
2	0,48	6,70	9,50	9,05	6,17	28,99	68,66	3	1,52	9,45	0,30	60,09	3,11	24,37	76,06
2	0,41	7,10	6,80	8,44	5,50	28,03	70,37	3	1,44	8,90	3,70	52,12	2,86	22,90	77,33
2	0,25	6,30	6,80	9,00	5,55	26,65	71,33	3	1,40	9,10	5,20	49,56	2,45	20,08	80,15
2	0,18	6,85	8,60	9,02	6,57	29,57	67,81	3	1,40	9,10	8,10	44,66	2,69	21,43	78,70
2	0,09	6,90	6,80	6,97	5,72	25,09	72,80								
2	-0,02	6,90	6,00	7,70	5,45	26,26	71,88								
2	-0,02	6,90	6,00	7,49	4,51	23,61	74,84								
2	-0,02	6,90	5,80	6,52	5,34	24,11	74,06								
2	-0,02	6,90	5,80	5,31	4,18	19,90	78,91								
2	-0,02	7,00	6,00	5,26	4,92	28,72	70,85								
2	-0,02	7,20	6,00	6,56	4,84	22,89	75,64								
2	-0,02	7,10	6,20	6,27	4,69	21,55	76,93								
3	1,48	5,90	2,60	9,14	5,81	35,18	64,23								
4	1,06	5,70	3,00	12,79	5,57	29,23	68,49								
4	1,06	5,30	3,50	12,21	5,71	27,64	69,81								
4	1,01	5,60	4,20	11,53	5,61	28,85	68,95								
4	0,97	6,20	3,20	10,57	5,80	30,47	67,26								
4	0,94	5,70	4,00	11,14	5,39	27,45	70,33								
4	0,90	5,20	4,50	10,57	5,53	28,70	69,02								
4	0,84	5,40	6,60	10,42	5,14	27,61	70,54								
4	0,79	5,20	3,90	10,68	6,35	28,47	68,47								
4	0,71	4,90	5,20	10,03	5,30	27,18	70,83								
4	0,67	5,40	6,60	10,79	4,67	26,35	72,19								
4	0,59	5,50	8,60	10,05	5,74	28,66	68,99								
4	0,56	6,20	8,30	9,75	6,55	30,41	66,65								
4	0,44	5,50	9,40	8,71	6,03	25,15	71,86								
5	0,91	5,20	3,40	13,22	5,11	29,78	68,34								
5	0,94	5,30	4,60	12,58	4,13	20,74	77,44								
5	0,95	5,10	2,40	11,97	5,92	29,15	68,12								
5	0,86	5,20	1,90	13,18	5,74	29,06	68,45								
5	0,81	5,30	4,40	8,47	4,51	29,37	70,55								
5	0,76	5,60	3,60	10,84	6,77	29,62	66,79								
5	0,74	5,50	3,20	11,58	6,18	28,82	68,21								
5	0,60	5,30	3,80	10,45	5,91	28,81	68,67								
5	0,53	5,20	5,60	5,72	2,89	15,12	83,95								
5	0,37	5,70	5,90	8,61	5,52	26,23	71,47								
5	0,17	5,60	5,50	7,58	4,12	20,56	78,04								

Appendix F: Dead and living species distribution and environmental data for each transect at Keiskamma Estuary

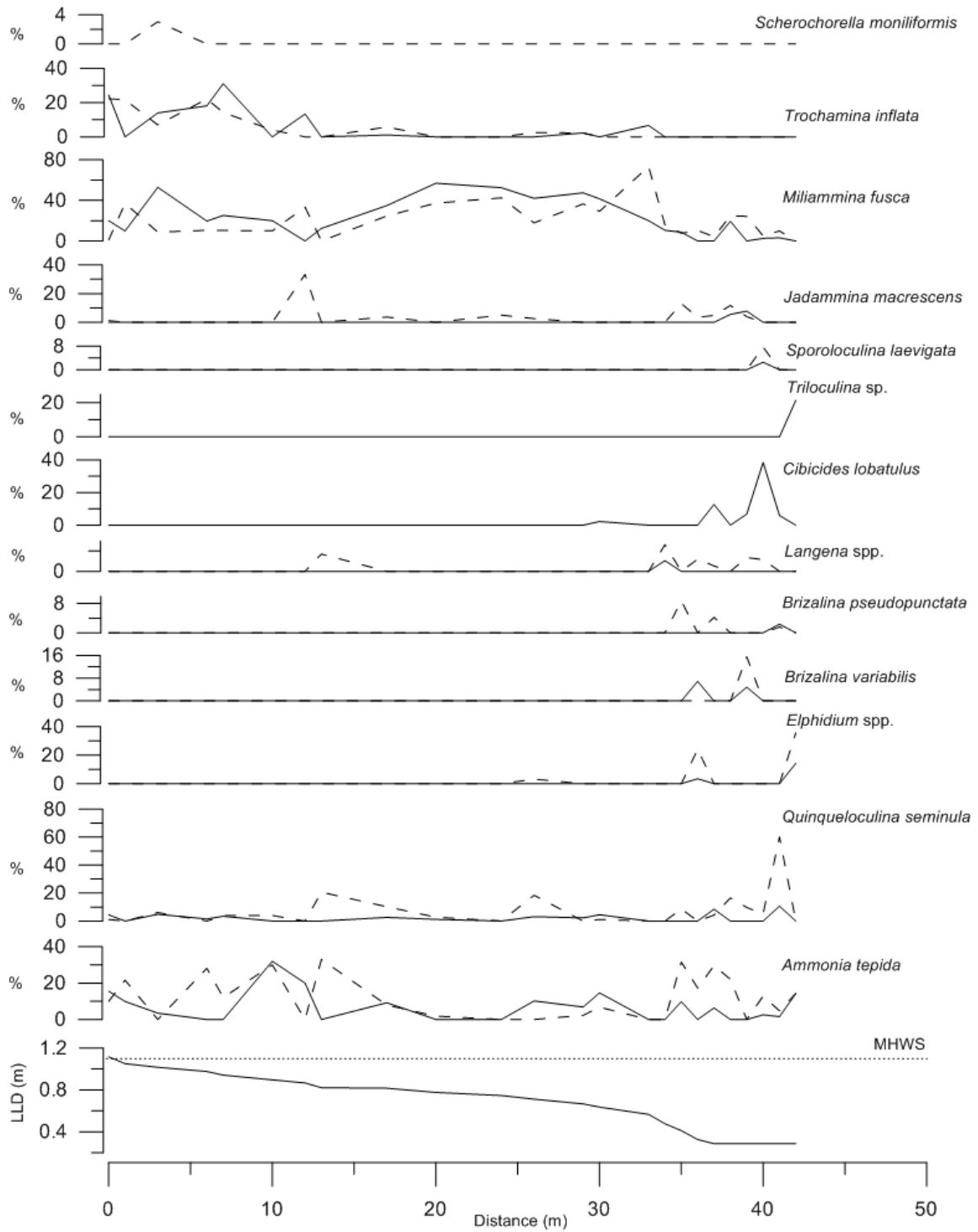


Figure F1: Species distribution along Transect 1 at Keiskamma Estuary. Solid line indicates dead assemblages and dashed line living assemblages.

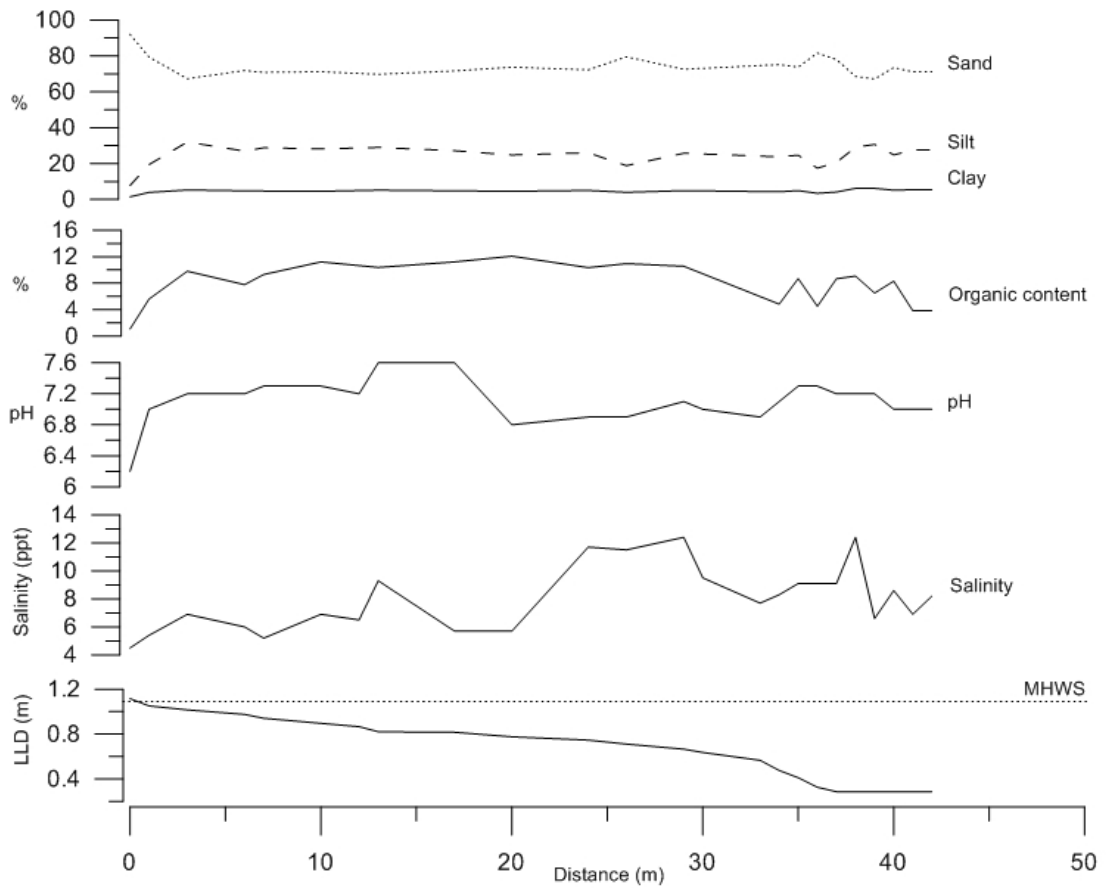


Figure F2: Salinity, pH, grain size and organic content variations along Transect 1 at Keiskamma Estuary.

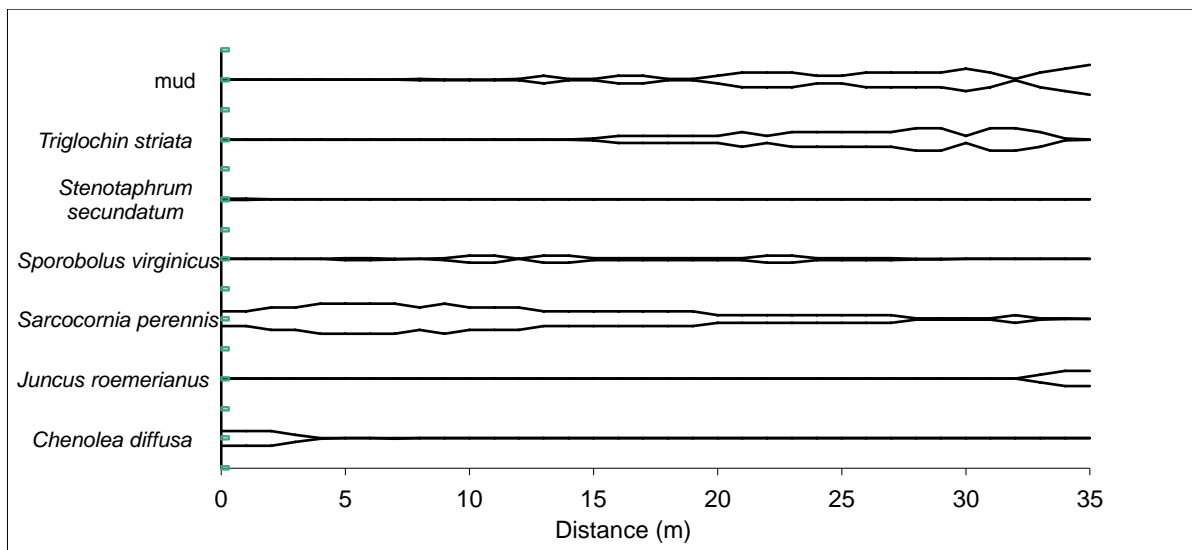


Figure F3: Vegetation distribution along Transect 1 at Keiskamma Estuary.

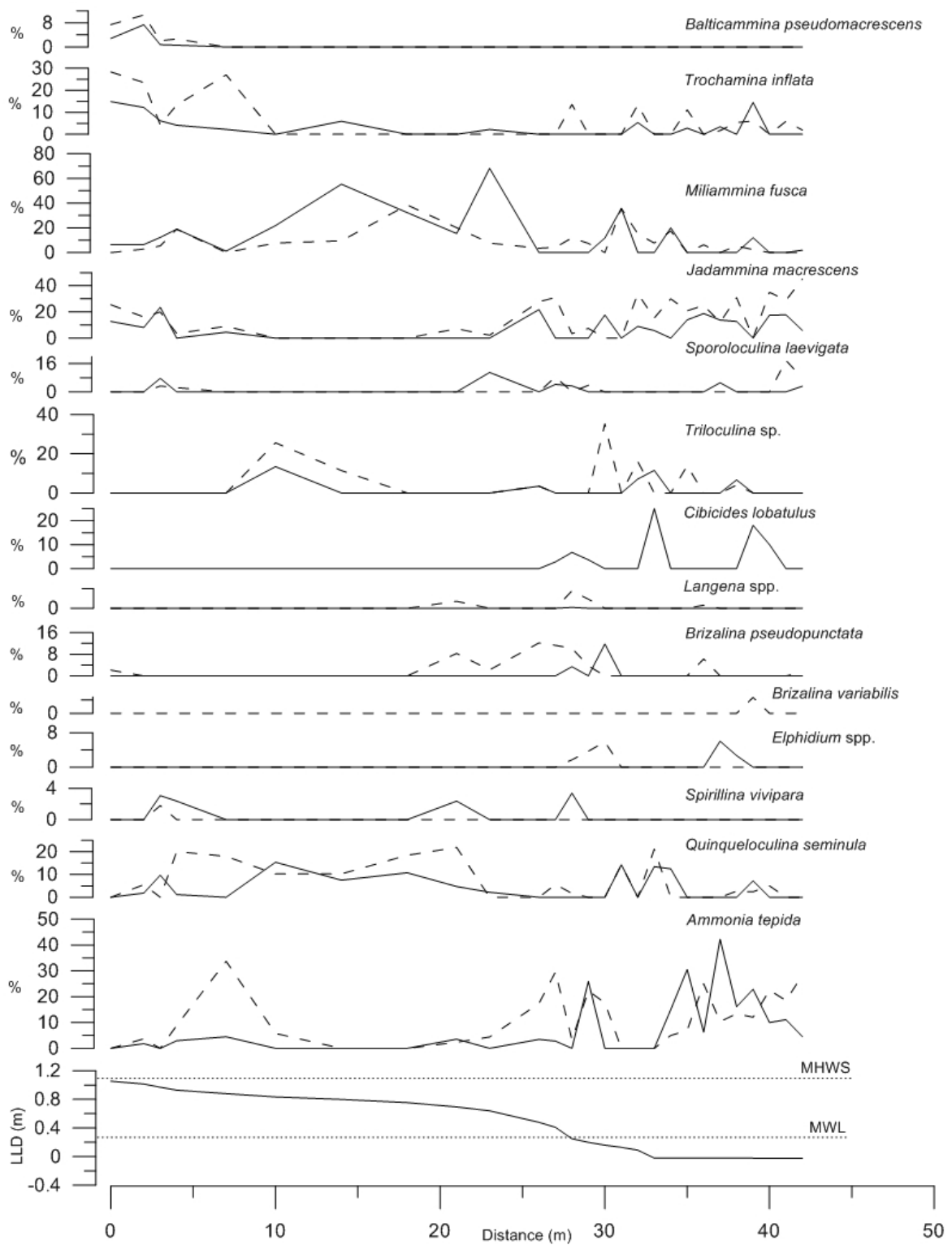


Figure F4: Species distribution along Transect 2 at Keiskamma Estuary. Solid line indicates dead assemblages and dashed line living assemblages.

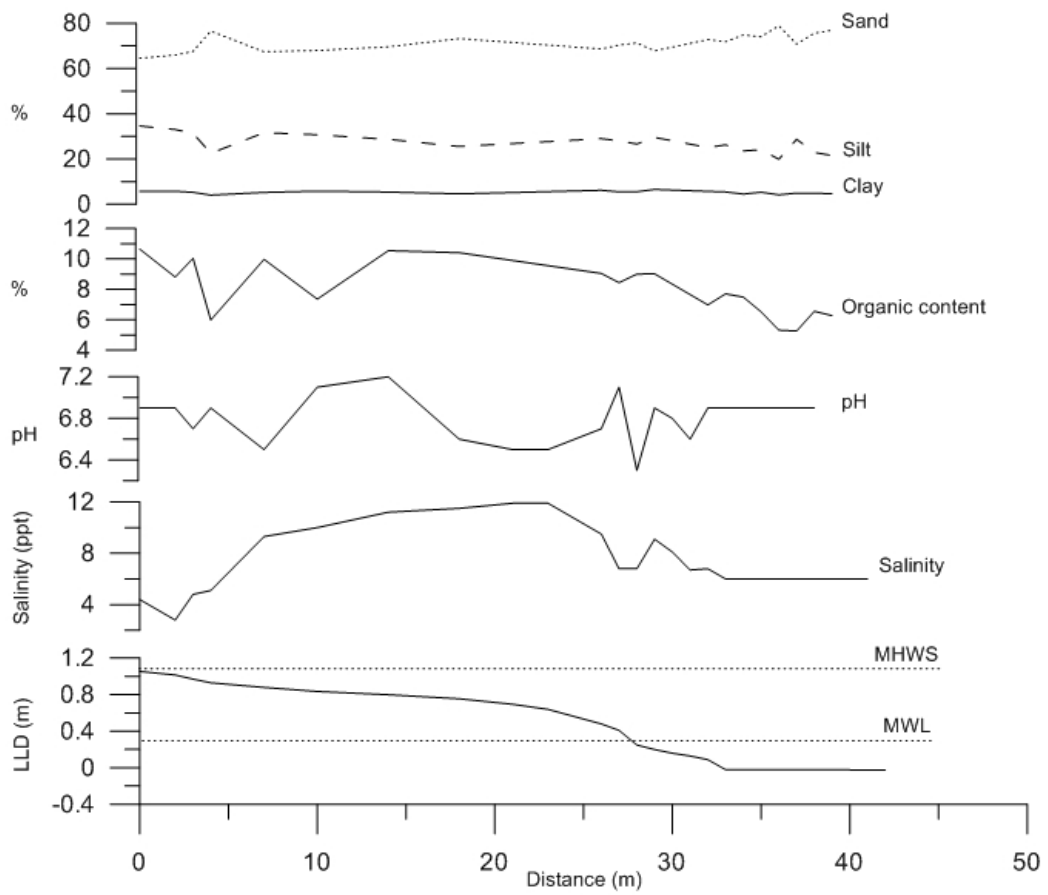


Figure F5: Salinity, pH, grain size and organic content variations along Transect 2 at Keiskamma Estuary.

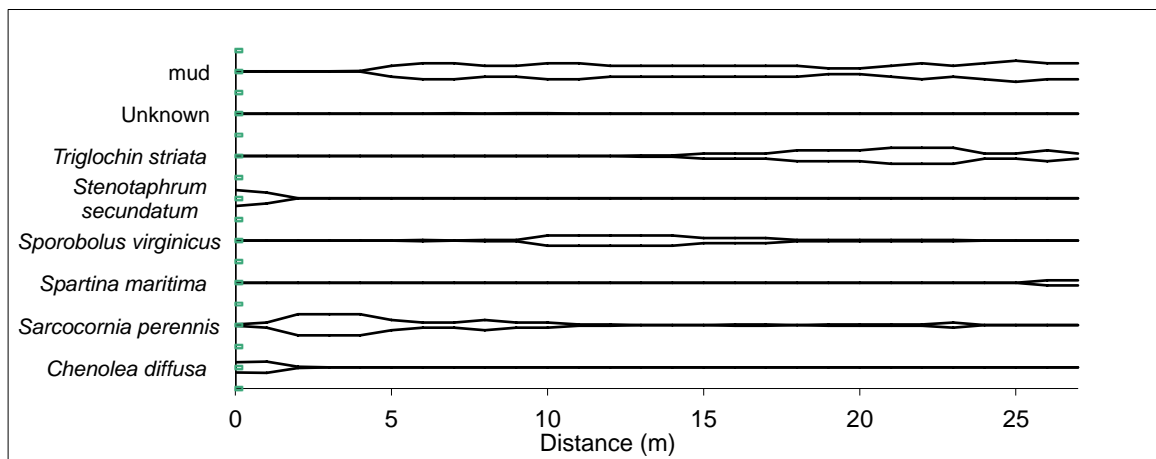


Figure F6: Vegetation distribution along Transect 2 at Keiskamma Estuary.

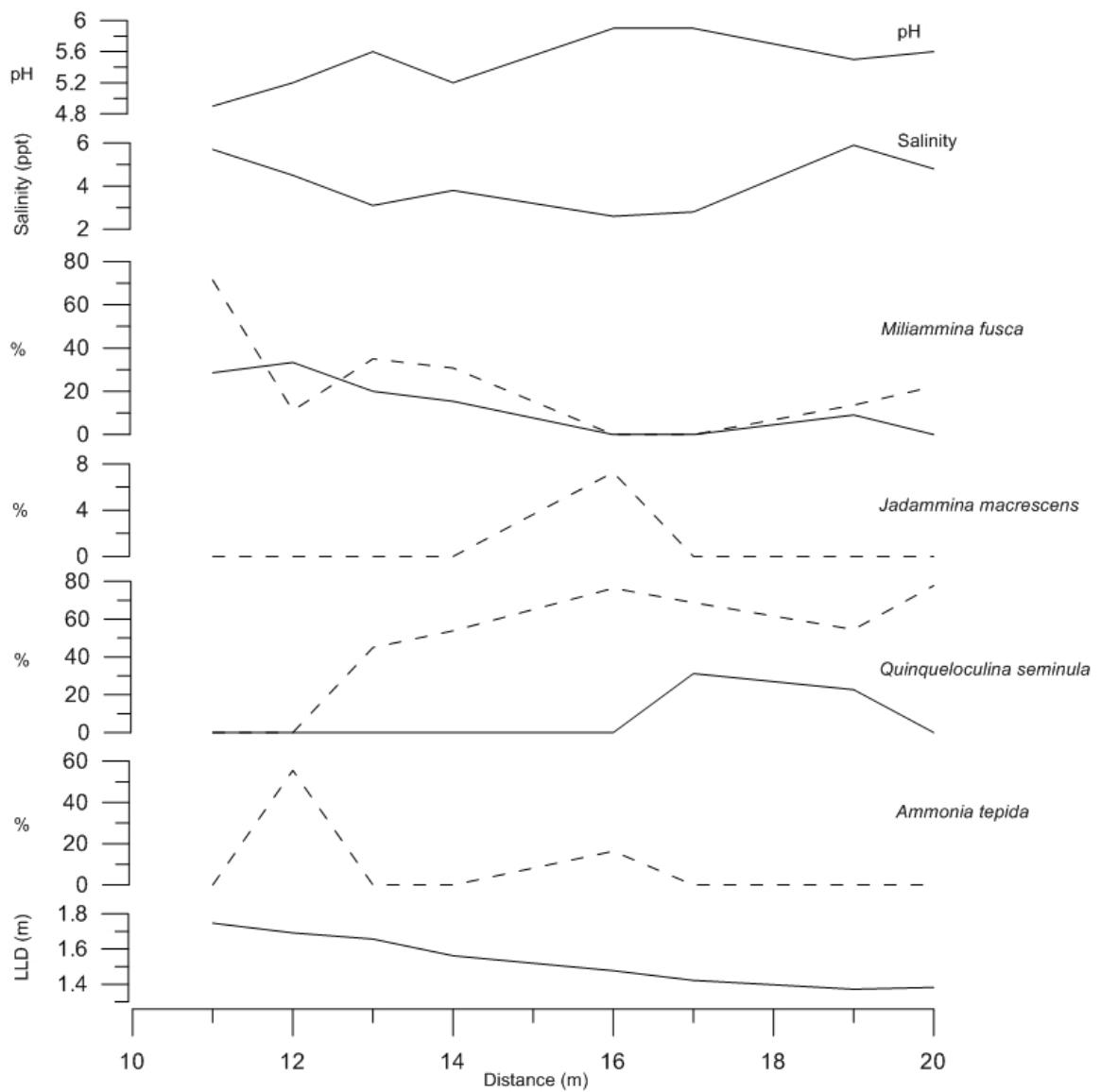


Figure F7: Species distribution, salinity and pH variations along Transect 3 at Keiskamma Estuary. Solid line indicates dead assemblages and dashed line living assemblages.

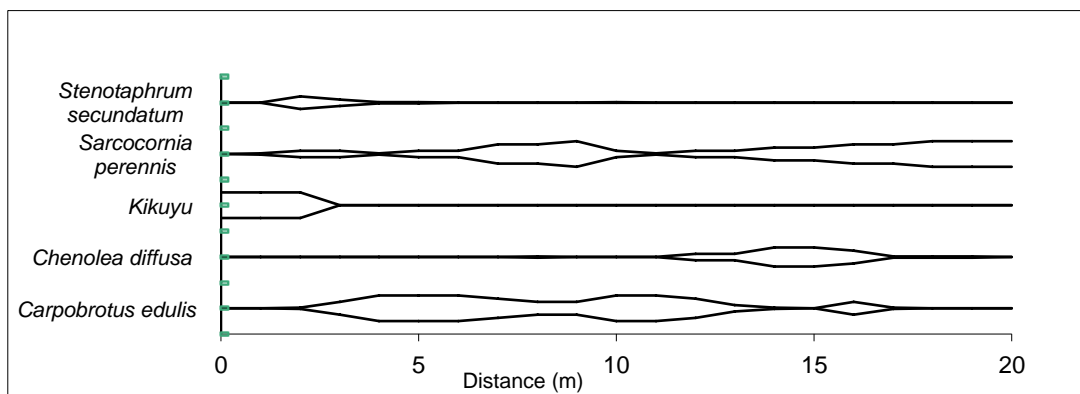


Figure F8: Vegetation distribution along Transect 3 at Keiskamma Estuary.

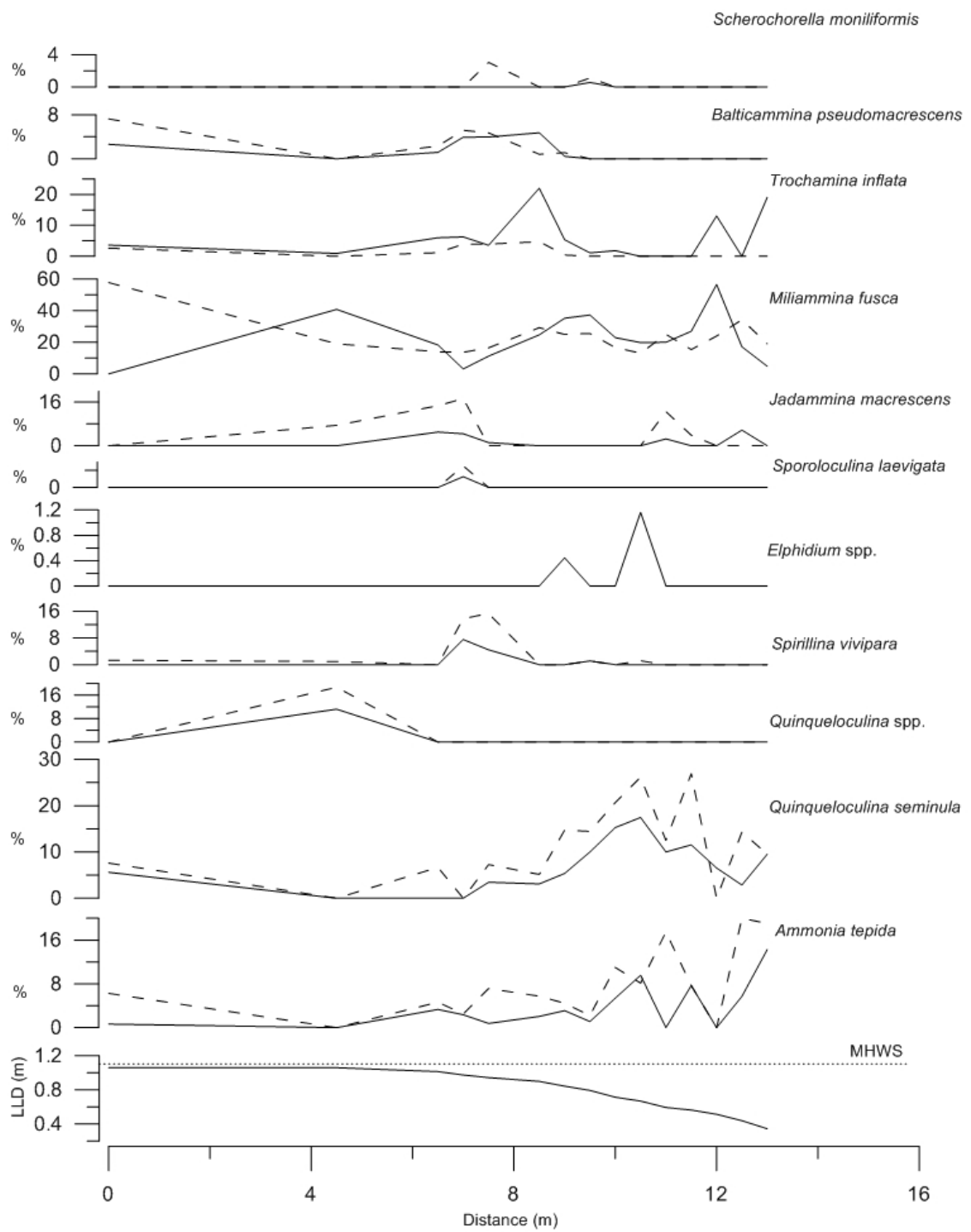


Figure F9: Species distribution along Transect 4 at Keiskamma Estuary. Solid line indicates dead assemblages and dashed line living assemblages.

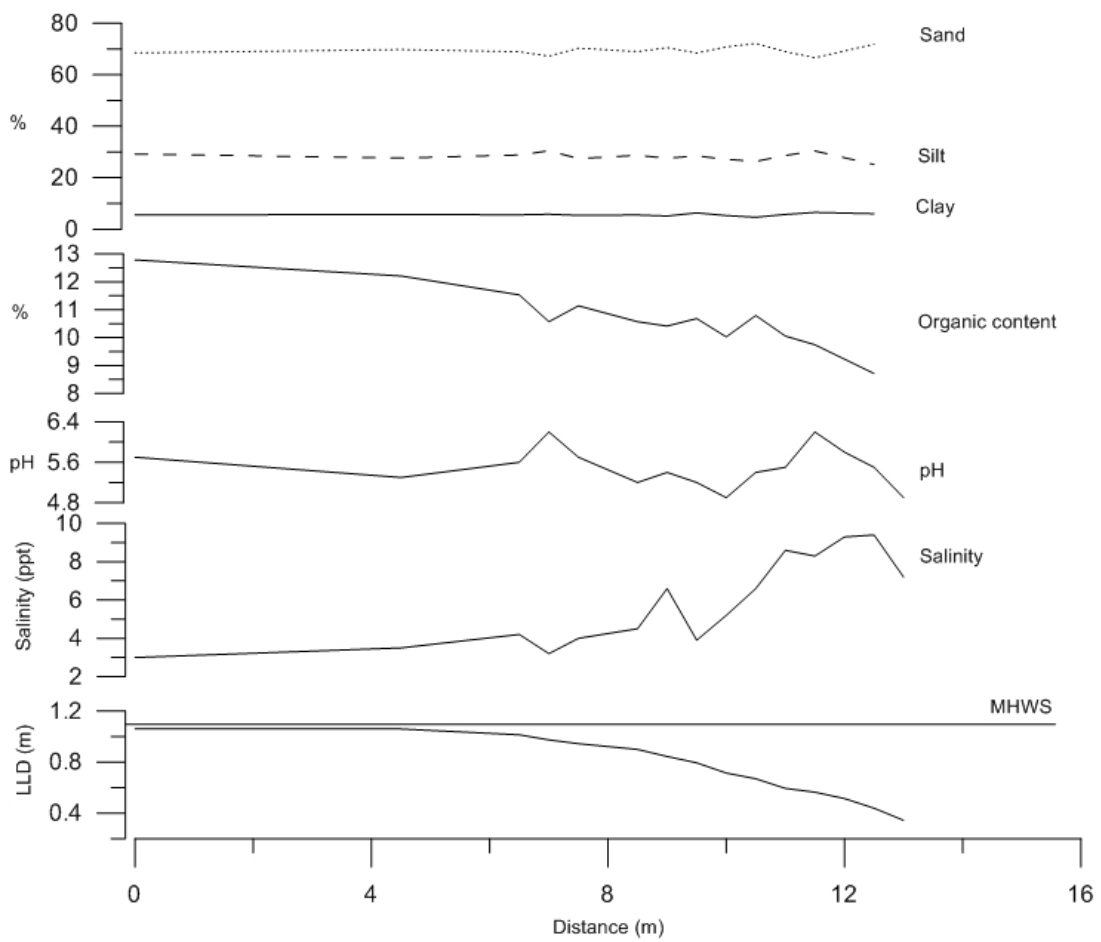


Figure F10: Salinity, pH, grain size and organic content variations along Transect 4 at Keiskamma Estuary.

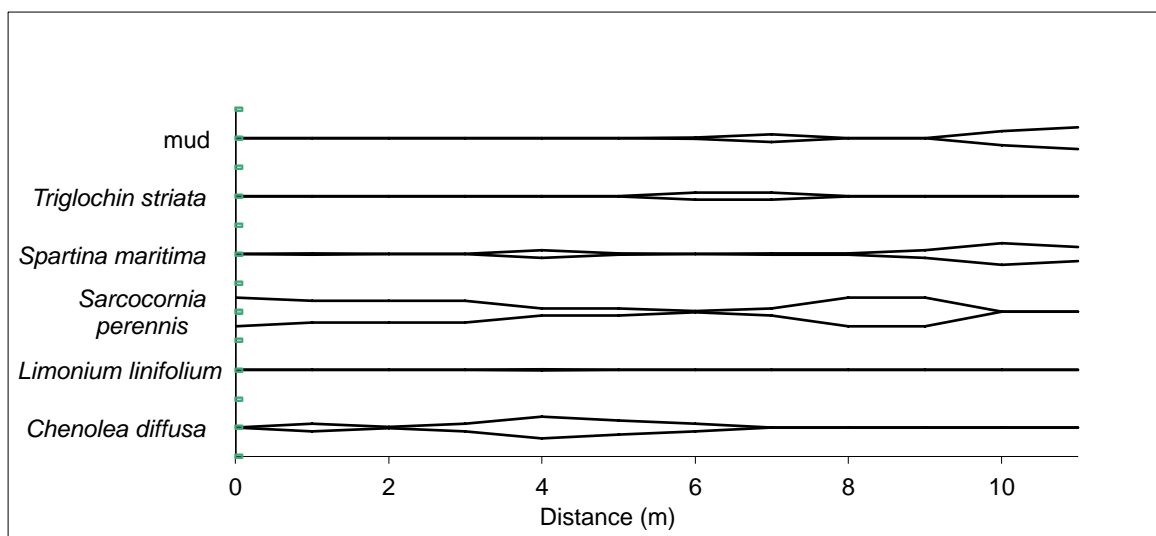


Figure F11: Vegetation distribution along Transect 4 at Keiskamma Estuary.

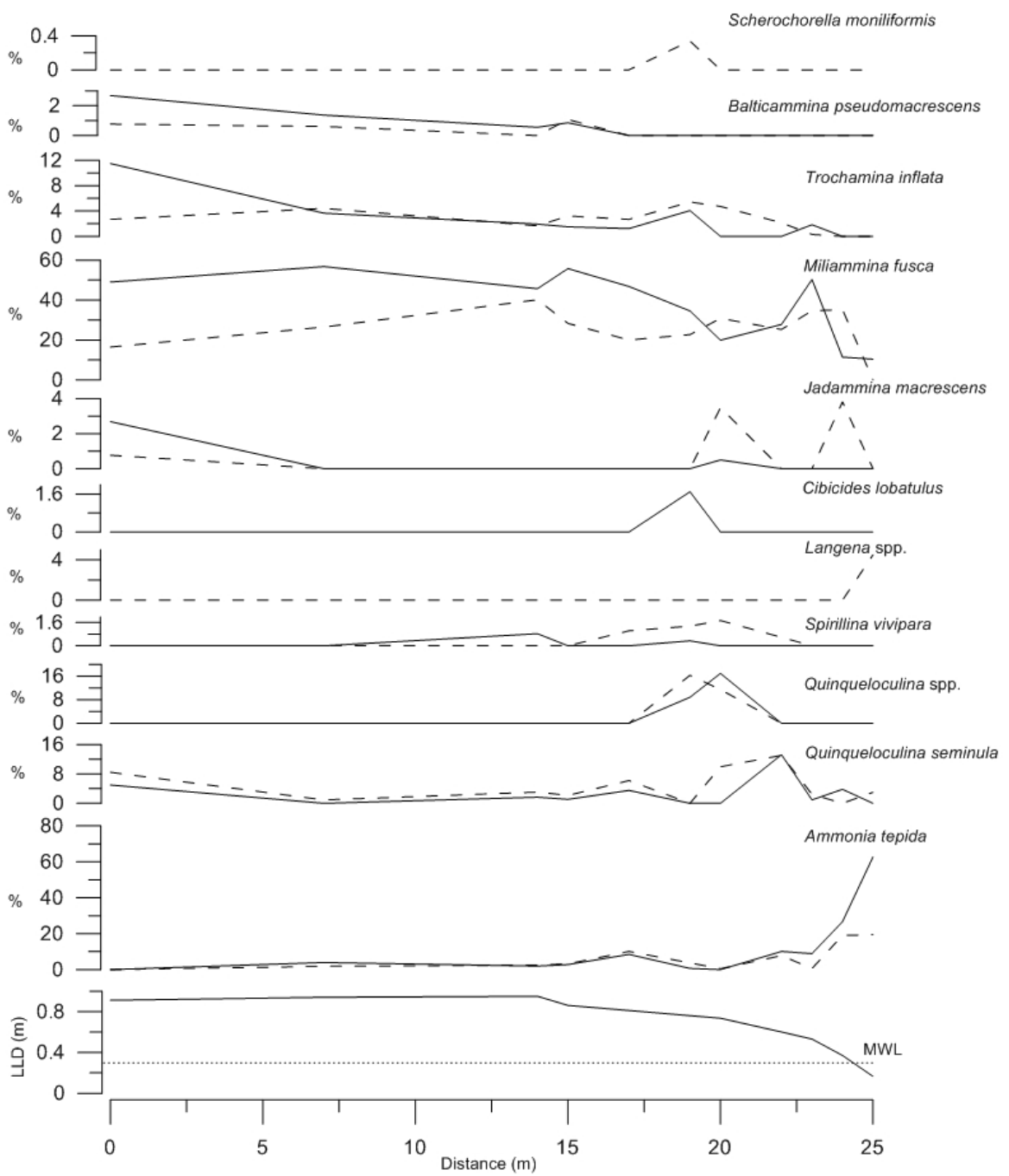


Figure F12: Species distribution along Transect 5 at Keiskamma Estuary. Solid line indicates dead assemblages and dashed line living assemblages.

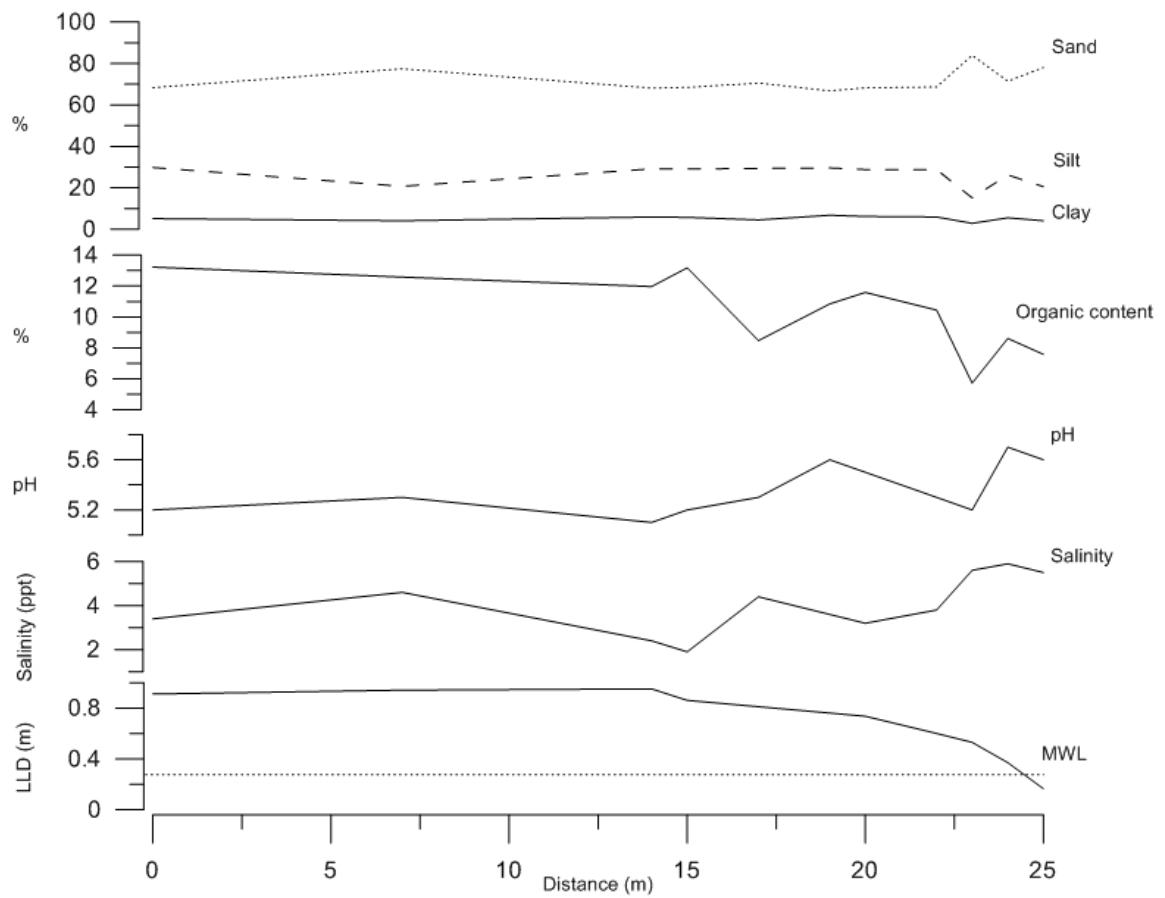


Figure F13: Salinity, pH, grain size and organic content variations along Transect 5 at Keiskamma Estuary.

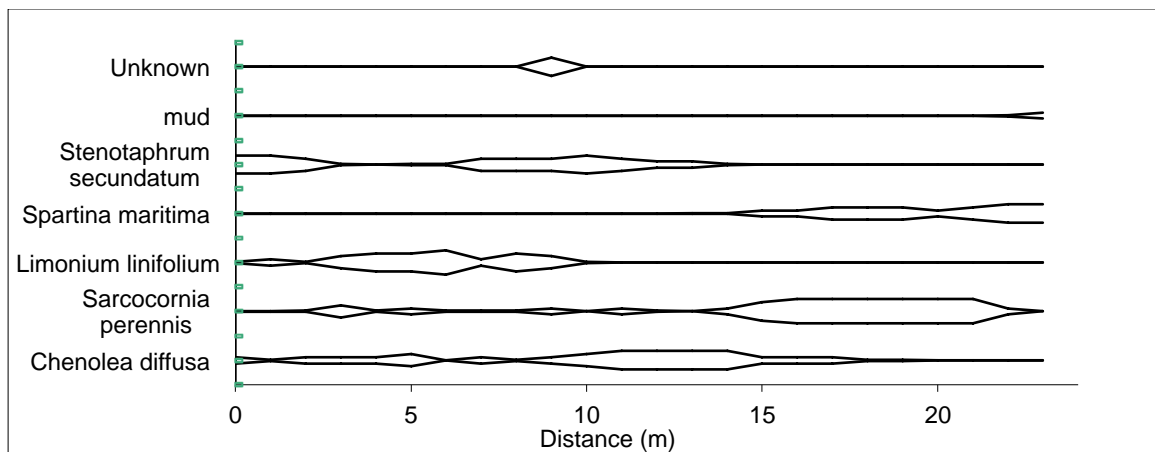


Figure F14: Vegetation distribution along Transect 5 at Keiskamma Estuary.

Appendix G: Dead and living species distribution and environmental data for each transect at Knysna Estuary

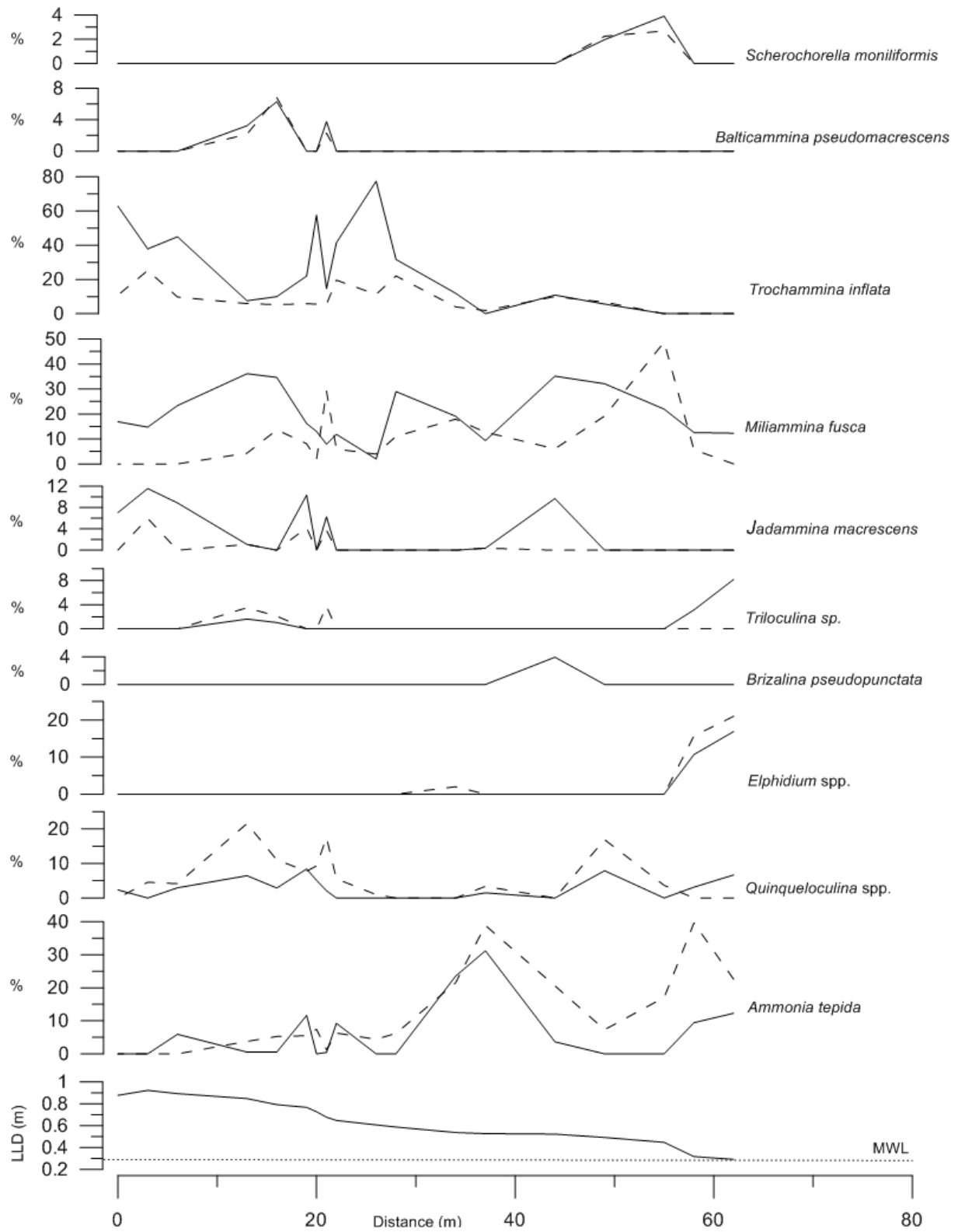


Figure G1: Species distribution along Transect 1 at Knysna Estuary. Solid line indicates dead assemblages and dashed line living assemblages.

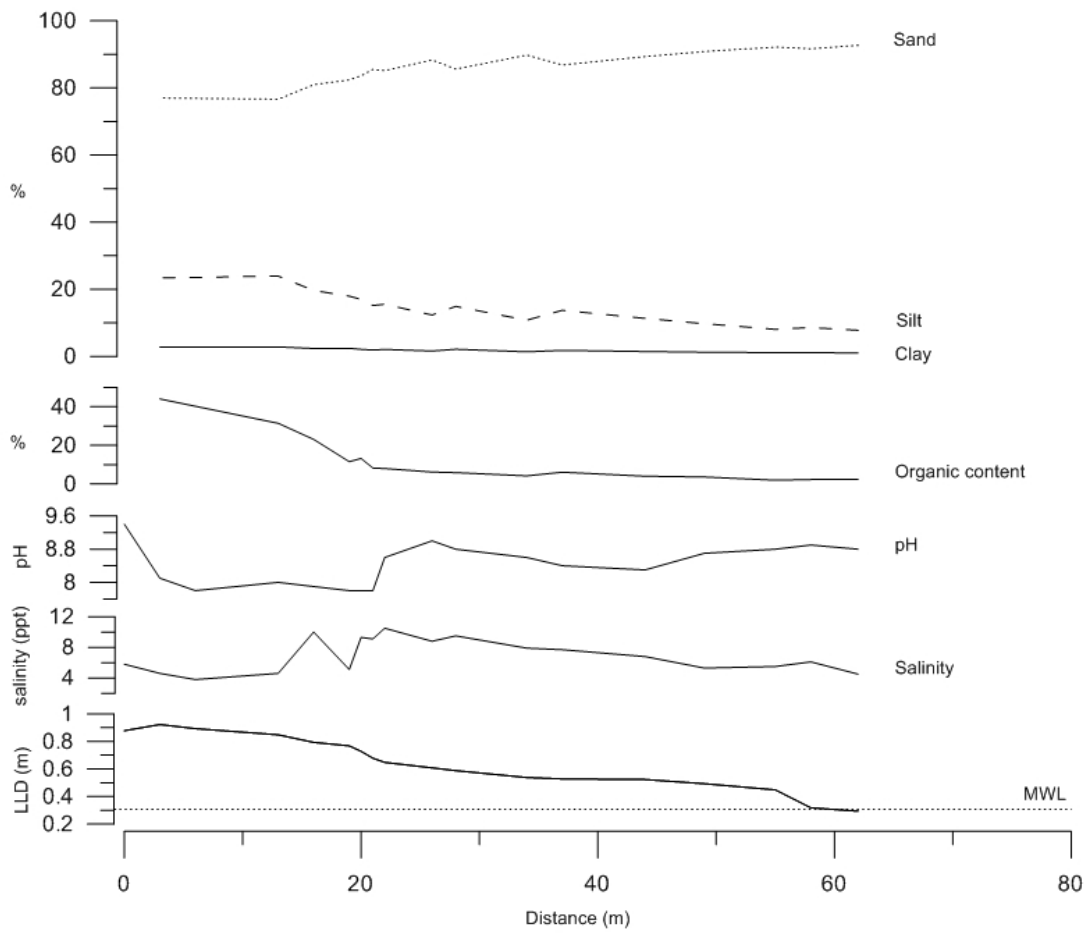


Figure G2: Salinity, pH, grain size and organic content variations along Transect 1 at Knysna Estuary.

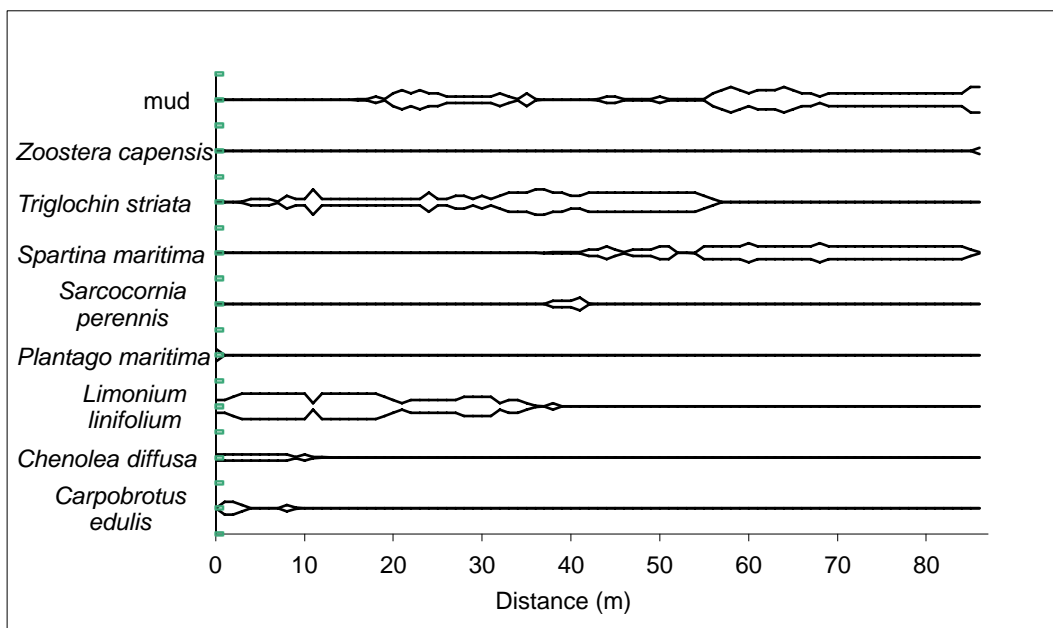


Figure G3: Vegetation distribution along Transect 1 at Knysna Estuary.

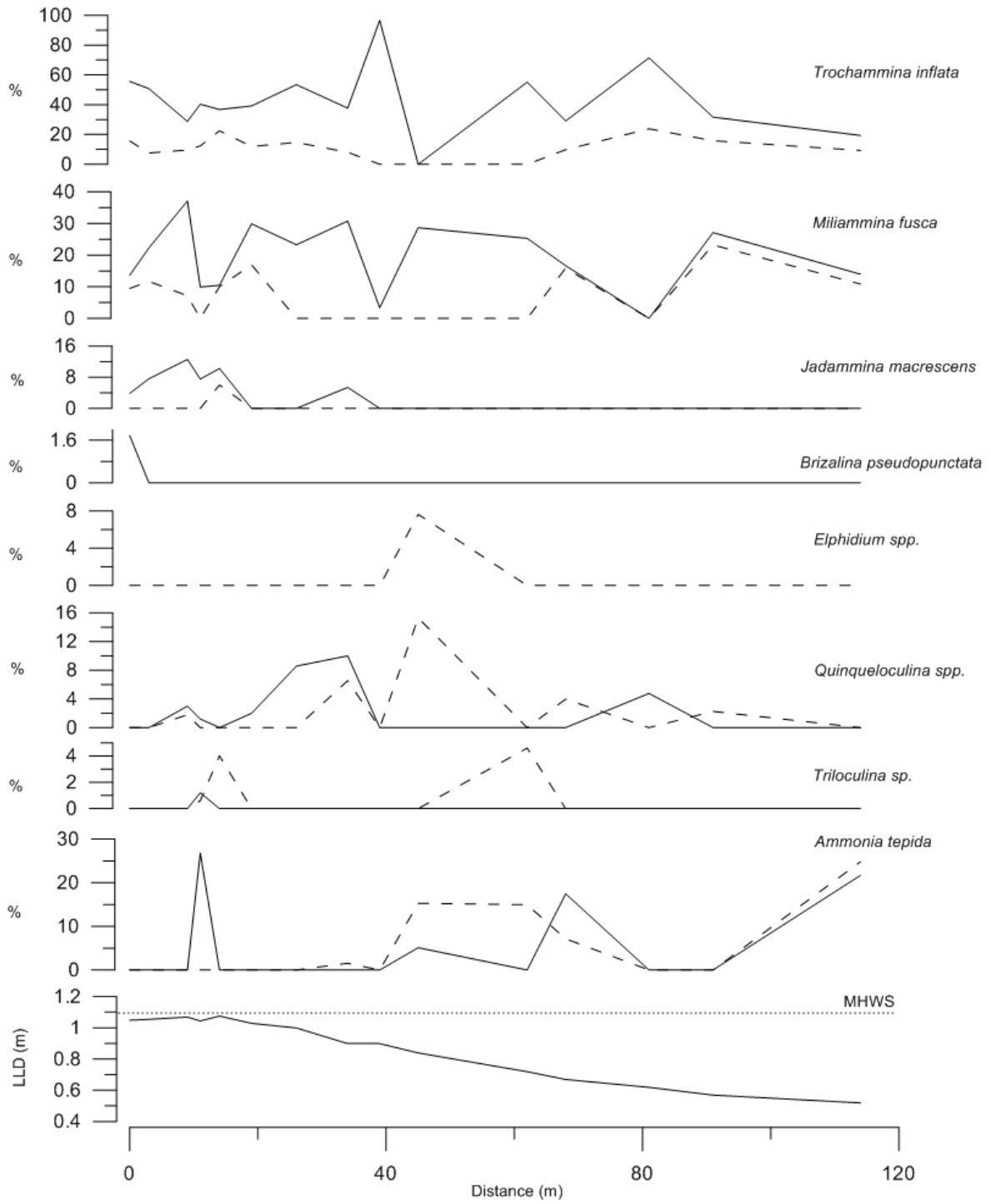


Figure G4: Species distribution along Transect 2 at Knysna Estuary. Solid line indicates dead assemblages and dashed line living assemblages.

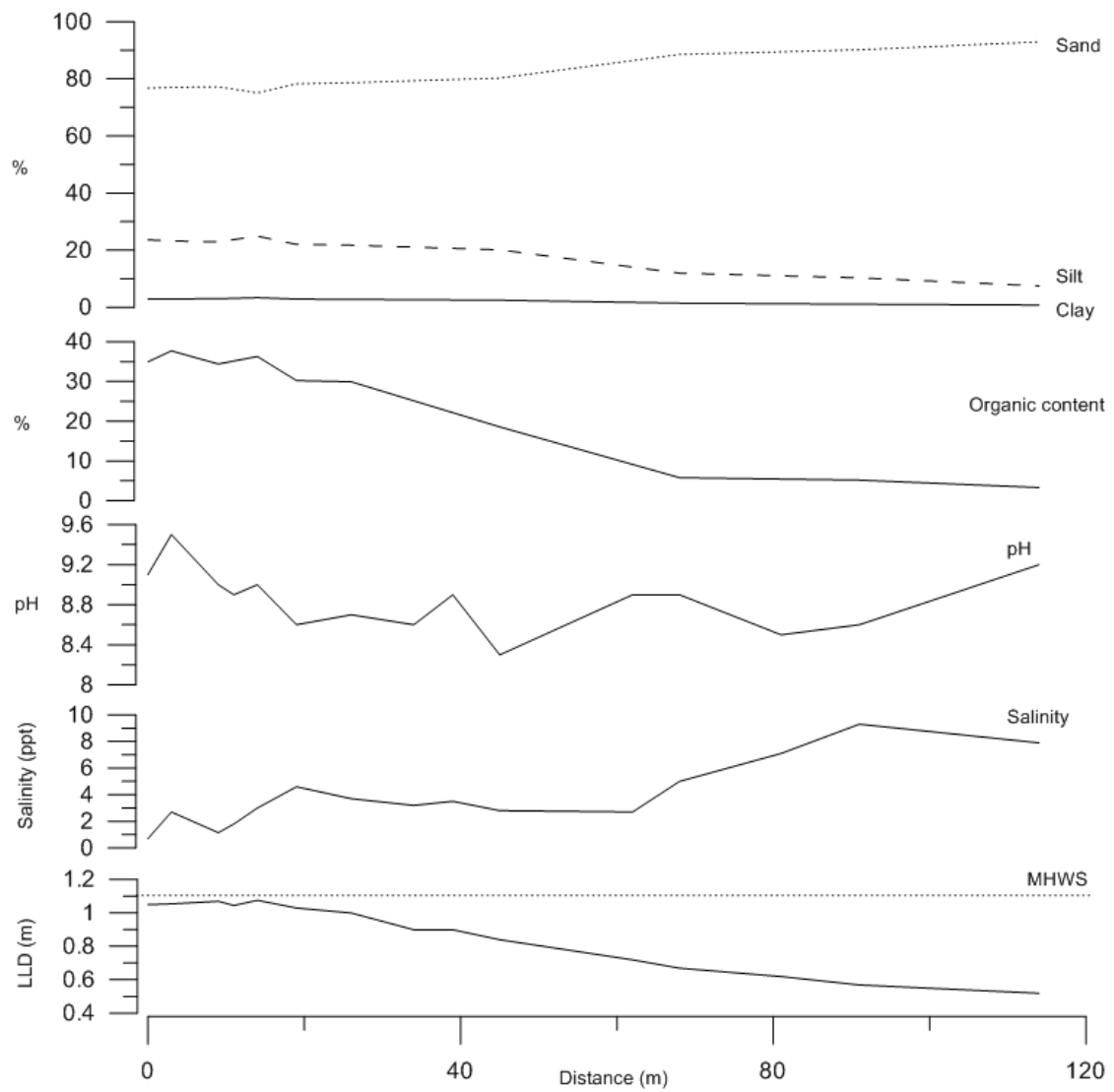


Figure G5: Salinity, pH, grain size and organic content variations along Transect 2 at Knysna Estuary.

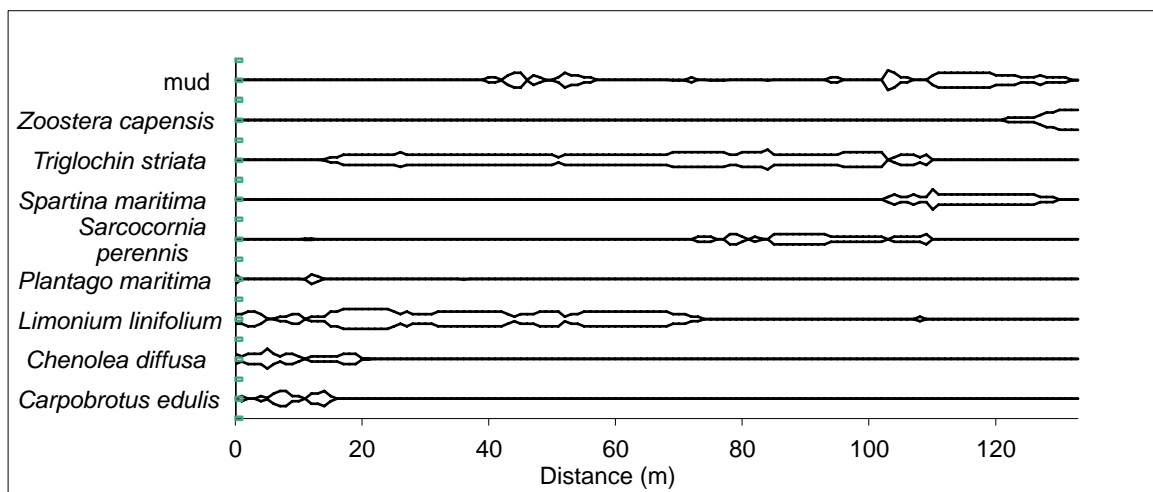


Figure G6: Vegetation distribution along Transect 2 at Knysna Estuary.

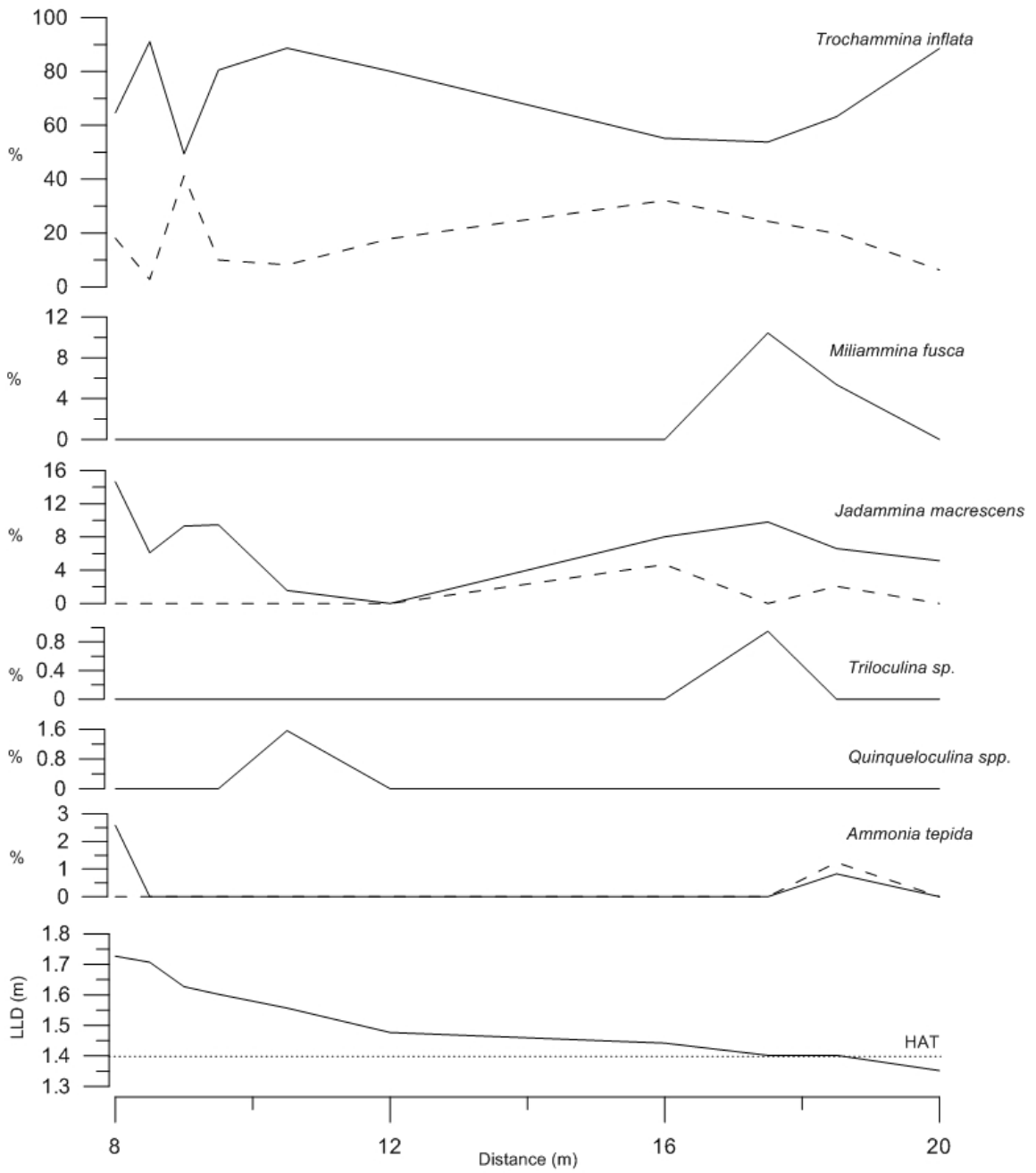


Figure G7: Species distribution along Transect 3 at Knysna Estuary. Solid line indicates dead assemblages and dashed line living assemblages.

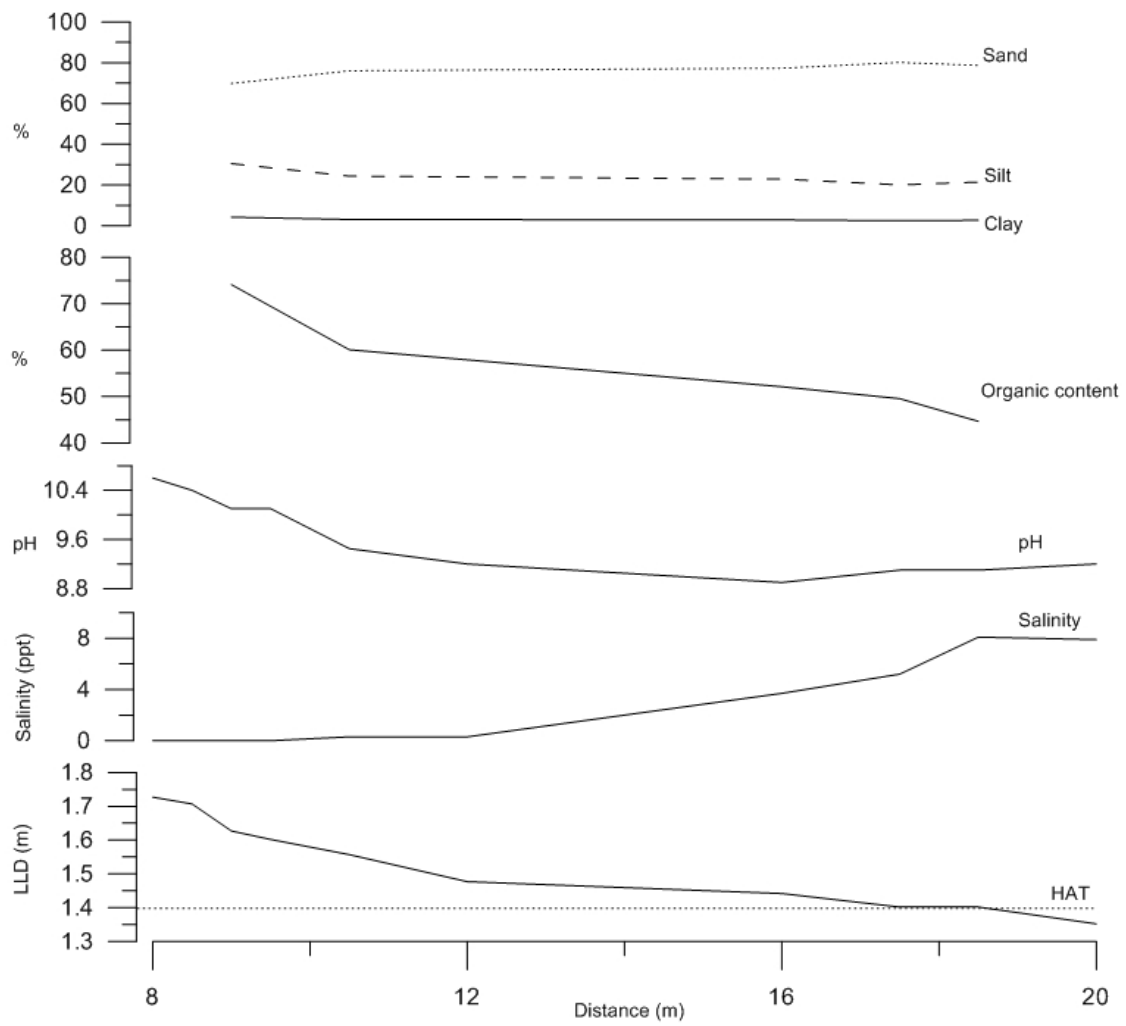


Figure G8: Salinity, pH, grain size and organic content variations along Transect 3 at Knysna Estuary.

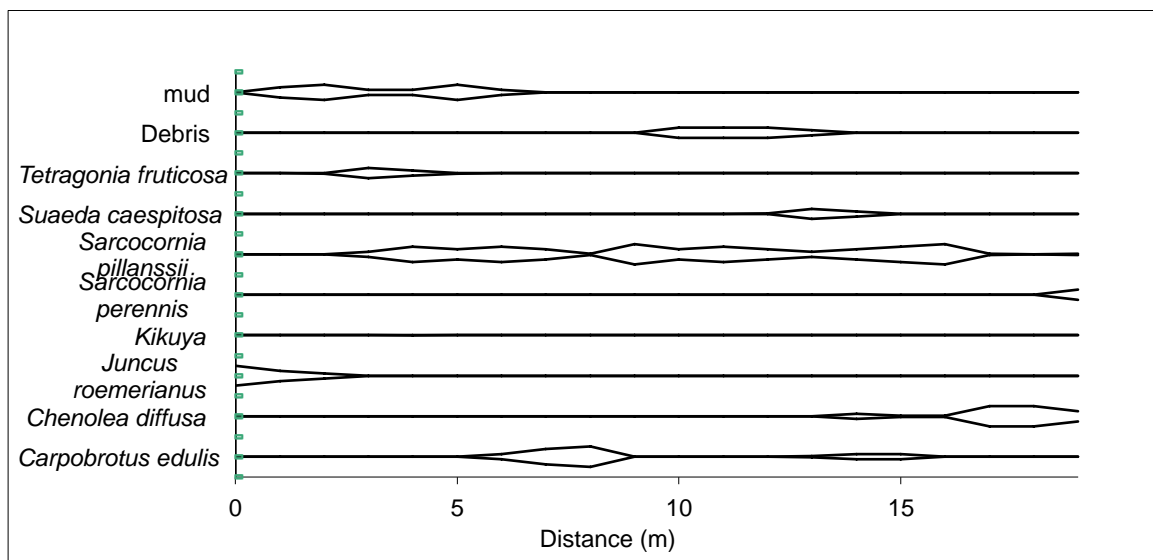


Figure G9: Vegetation distribution along Transect 3 at Knysna Estuary.

Appendix H: Supporting information for Paper I

Journal of Biogeography

SUPPORTING INFORMATION

Environmental controls on the distribution of salt-marsh foraminifera from the southern coastline of South Africa

Kate L. Strachan, Jemma M. Finch, Trevor R. Hill, Robert L. Barnett, Craig D. Morris & Peter Frenzel

Appendix S1 Foraminiferal census data for Keiskamma and Knysna estuaries

Site	Sample station	Total living	Total count	Living agglutinated (%)	Living calcareous (%)	Site	Sample station	Total living	Total count	Living agglutinated (%)	Living calcareous (%)
Keisk	A1	96	270	69	31	Keisk	D9	243	445	42	58
Keisk	A2	130	162	73	27	Keisk	D10	179	344	32	68
Keisk	A3	57	229	75	25	Keisk	D11	81	120	56	44
Keisk	A4	242	398	54	46	Keisk	D12	56	104	36	64
Keisk	A5	211	522	61	39	Keisk	D14	96	144	50	50
Keisk	A6	96	208	29	71	Keisk	E1	76	261	71	29
Keisk	A8	85	109	0	100	Keisk	E2	225	657	92	8
Keisk	A9	199	354	65	35	Keisk	E3	171	361	88	12
Keisk	A10	137	327	89	11	Keisk	E4	177	467	86	14
Keisk	A11	76	160	100	0	Keisk	E5	194	485	57	43
Keisk	A12	70	157	51	49	Keisk	E6	147	295	57	43
Keisk	A13	72	183	94	6	Keisk	E7	252	402	62	38
Keisk	A15.5	57	165	82	18	Keisk	E8	251	514	56	44
Keisk	A17	68	92	34	66	Keisk	E9	124	326	92	8
Keisk	A18	46	58	17	83	Keisk	E10	61	105	67	33
Keisk	A19	117	189	21	79	Keisk	E11	72	268	0	100
Keisk	A20	109	145	49	51	Kny	A2	102	285	87	13
Keisk	A21	67	103	43	57	Kny	A4	157	371	32	68
Keisk	A22	84	156	10	90	Kny	A5	168	381	58	42
Keisk	A23	193	253	13	87	Kny	A6	97	309	58	42
Keisk	B1	179	337	97	3	Kny	A7	52	215	31	69
Keisk	B2	270	434	85	15	Kny	A8	303	479	64	36
Keisk	B3	144	400	86	14	Kny	A9	101	270	68	32
Keisk	B4	236	346	55	45	Kny	A11	57	145	84	16
Keisk	B5	78	89	41	59	Kny	A12	114	251	48	52
Keisk	B6	77	156	16	84	Kny	A13	306	535	26	74
Keisk	B7	79	253	30	70	Kny	A14	121	330	44	56
Keisk	B9	125	169	37	63	Kny	A15	186	355	54	46
Keisk	B11	74	115	49	51	Kny	A16	296	410	71	29
Keisk	B12	128	170	39	61	Kny	A17	150	192	24	76
Keisk	B13	96	118	35	65	Kny	A18	97	159	9	91
Keisk	B14.5	56	88	14	86	Kny	A19	85	195	0	100
Keisk	B17	88	155	80	20	Kny	B1	85	338	100	0
Keisk	B18.5	54	92	70	30	Kny	B2	71	368	100	0
Keisk	B20	76	144	61	39	Kny	B3.5	74	499	93	7
Keisk	B21.5	72	180	50	50	Kny	B5	191	449	91	9
Keisk	B23	92	151	67	33	Kny	B6	87	301	100	0
Keisk	B25	100	160	56	44	Kny	B7.5	78	505	73	27
Keisk	B26	96	135	49	51	Kny	B10	120	314	0	100
Keisk	B27	131	155	56	44	Kny	B13	139	378	70	30
Keisk	C5	55	55	7	93	Kny	B15	73	177	95	5
Keisk	D1	265	633	83	17	Kny	B16	58	129	45	55
Keisk	D2	151	321	58	42	Kny	B18	120	160	27	73
Keisk	D3	398	601	83	17	Kny	C4	102	247	100	0
Keisk	D4	453	637	74	26	Kny	C6.5	61	446	93	7
Keisk	D5	560	784	58	42	Kny	C8	110	299	100	0
Keisk	D6	211	486	75	25	Kny	C9	77	316	100	0
Keisk	D7	225	449	62	38	Kny	C10	58	242	91	9
Keisk	D8	176	360	64	36						

SUPPORTING INFORMATION

Environmental controls on the distribution of salt-marsh foraminifera from the southern coastline of South Africa

Kate L. Strachan, Jemma M. Finch, Trevor R. Hill, Robert L. Barnett, Craig D. Morris & Peter Frenzel

Appendix S2 A partial redundancy analysis (pRDA) accounting for spatial variability among transect locations (fitted as a covariable) and the effects of all measured environmental variables on the composition of foraminiferal species in the Keiskamma Estuary.

		Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue		0.1142	0.036	0.0273	0.0082
Explained variation (cumulative %)		14.27	18.77	22.18	23.2
Pseudo-canonical correlation (r)		0.801	0.5601	0.4755	0.3819
Explained fitted variation (cumulative %)		57.85	76.08	89.89	94.02
Environmental variable	VIF*	Correlations (r)			
Elevation	2.80	0.62	0.29	0.03	-0.05
pH	10.43	-0.05	-0.35	-0.07	-0.21
Salinity	1.77	-0.64	0.20	0.00	-0.07
Organic content	3.80	0.19	0.26	-0.09	-0.21
Clay	63.87	-0.13	0.13	-0.19	-0.13
Silt	652.18	0.11	0.18	0.00	-0.24
Sand	1077.52	-0.07	-0.18	0.05	0.23
Permutation test of all canonical axes:		pseudo-F = 2.5; p = 0.0001			

*VIF: variance inflation factor

SUPPORTING INFORMATION

Environmental controls on the distribution of salt-marsh foraminifera from the southern coastline of South Africa

Kate L. Strachan, Jemma M. Finch, Trevor R. Hill, Robert L. Barnett, Craig D. Morris & Peter Frenzel

Appendix S3 A partial redundancy analysis (pRDA) accounting for spatial variability among transect locations (fitted as a covariable) and the effects of all measured environmental variables on the composition of foraminiferal species in the Knysna Estuary.

	Axis 1	Axis 2	Axis 3	Axis 4	
Eigenvalue	0.2015	0.0731	0.0595	0.0184	
Explained variation (cumulative %)	26.42	36.01	43.81	46.22	
Pseudo-canonical correlation (r)	0.8761	6766	0.7099	0.4925	
Explained fitted variation (cumulative %)	54.88	74.79	90.99	96.00	
Environmental variable	VIF*	Correlations (r)			
Elevation	79.22	-0.72	0.29	-0.09	0.04
pH	5.68	0.48	0.26	0.38	0.22
Salinity	2.88	0.00	-0.26	0.23	-0.17
Organic content	53.63	-0.59	0.37	-0.20	0.17
Clay	146.27	-0.57	0.38	-0.11	0.09
Silt	3033.32	-0.62	0.33	-0.16	0.09
Sand	3631.13	0.62	-0.34	0.17	-0.09
Permutation test of all canonical axes:		pseudo-F = 2.9; p = 0.0001			

*VIF: variance inflation factor

Appendix I: Kariega Estuary down core counts

Table I1: Count table of individual foraminiferal species found down the core, 0 cm – 20 cm

Species Name	0	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
<i>Ammonia tepida</i>	0	0	0	0	0	0	7	6	83	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Cribromoides Jeffreysii</i>	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Haynesina germanica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Jadammina macrescens</i>	128	187	207	259	259	196	103	123	132	140	150	199	137	207	164	146	66	146	123	51	55	121	
<i>Miliammina fusca</i>	66	56	46	25	45	47	29	62	8	60	25	21	25	12	37	59	39	48	0	12	36	33	
<i>Quinqueloculina spp.</i>	73	0	17	0	0	0	0	9	15	2	0	0	0	0	0	3	1	2	0	0	1	3	
<i>Scherchorella moniliform</i>	3	7	0	15	0	7	7	11		0	1	17	4	7	8	0	0	2	0	10	0	6	
<i>Trochammina inflata</i>	195	14	78	59	119	43	67	66	56	23	123	37	18	31	39	15	9	32	3	11	16	28	
<i>Trochammina ochracea</i>	14	17	41	13	21	17	46	35	17	34	16	26	26	26		11	0	16	1	23	9	37	
Total number of species	479	281	389	371	444	317	259	312	311	259	315	300	210	284	248	234	115	247	127	107	117	228	

Appendix J: Taxonomic reference list

Ammonia tepida (Cushman, 1926) = *Rotalia beccari* (Linné) var. *tepida* Cushman, 1926: p. 79, pl. 1, figs. 8a, b, c. The classification and identification of *Ammonia* species is problematic and the literature is inconsistent resulting in different studies classifying and identifying *Ammonia* differently in South Africa.

Balticammina pseudomacrescens Brönnimann, Lutze and Whittaker, 1989: p. 169, pl. 1, figs 1-5, pl. 2, figs 1-9, pl3, figs 1-4. Pls 1-3.

Brizalina pseudopunctata (Höglund, 1947) = *Bolivina pseudopunctata* Höglund: Gehrels and van de Plassche, 1999, p. 98, pl. 1, figs 6-10. Horton and Edwards, 2006, p. 63, pl. 1, figs 1a-d. Wright *et al.*, 2011, p. 58, fig. A1.

Brizalina variabilis (Williamson, 1858) = *Textularia variabilis* Williamson, 1858: p. 76, pl. 6, figs. 162, 163.

Cibicides lobatulus (Walker and Jacob, 1798) = *Nautilus lobatulus* Walker and Jacob 1798: p. 642, pl. 14, fig. 36.

Elphidium de Monfort, 1808: There at least two species of the genus, all with a rounded periphery. They belong to the group around *Elphidium articulatum* (d'Orbigny, 1839).

Glabratella milletti (Wright, 1911) = *Discorbina milletti* Wright, 1911

Helenina anderseni (Warren, 1957) = *Pseudoeponides anderseni* Warren, 1957: p. 30, pl. 4, figs, 12-15. Parker and Athearn, 1959, p. 341, pl. 50, figs. 28-31. *Helenie anderseni* (Warren): Saunders, 1957, p. 374, figs. 1, 2. Todd and Low, 1967, p. 18, text fig. 2, fig. 2.

Jadammina macrescens (Brady, 1870) = *Trochammina inflata* (Montagu) var. *macrescens* H. B. Brady, in G. S. Brady and Robertson 1870: p. 290, pl. 11, figs. 5a-c. *Jadammina polystoma* Bartenstein and Brand, 1938: p. 381, 382, pls. 1, 2.

Miliammina fusca (Brady, 1870) = *Quinqueloculina fusca* Brady in Brady and Robertson, 1870, p. 47, pl. 11, figs. 2, 3.

Quinqueloculina d'Orbigny, 1826: There is much confusion about species identification within this genus. We differentiate *Q. seminula* and keep all other species as a group here.

Quinqueloculina seminula (Linnaeus, 1758) = *Serpula seminula* Linnaeus, 1758: p. 786, pl. 2, figs. 1a-c.

Scherochorella moniliforme (Siddall, 1886) = *Reophax moniliformis* Siddall, 1886; Redois and Debenay, 1996: p. 258, pl. 1, fig. 3.

Trochammina inflata (Montagu, 1808) = *Nautilus inflatus* Montagu, 1808: p. 81, pl. 18, fig. 3. *Trochammina inflata* (Montagu): Brönnimann and Whittaker, 1984, p. 311–315, figs. 1–11 (neotype erected). *Trochammina inflata* (Montagu) var. *macrescens* Brady in Brady and Robertson, 1870, p.47, pl. 11, figs. 5 a–c.

Spirillina vivipara Ehrenberg, 1843: p. 422, pl. 3, fig. 41, sec. 7.

Spiroloculina laevigata Cushman and Todd, 1944: Haake 1975, p. 20; pl. 1, figs 11, 12

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Appendix K: Age depth model for the Kariega record

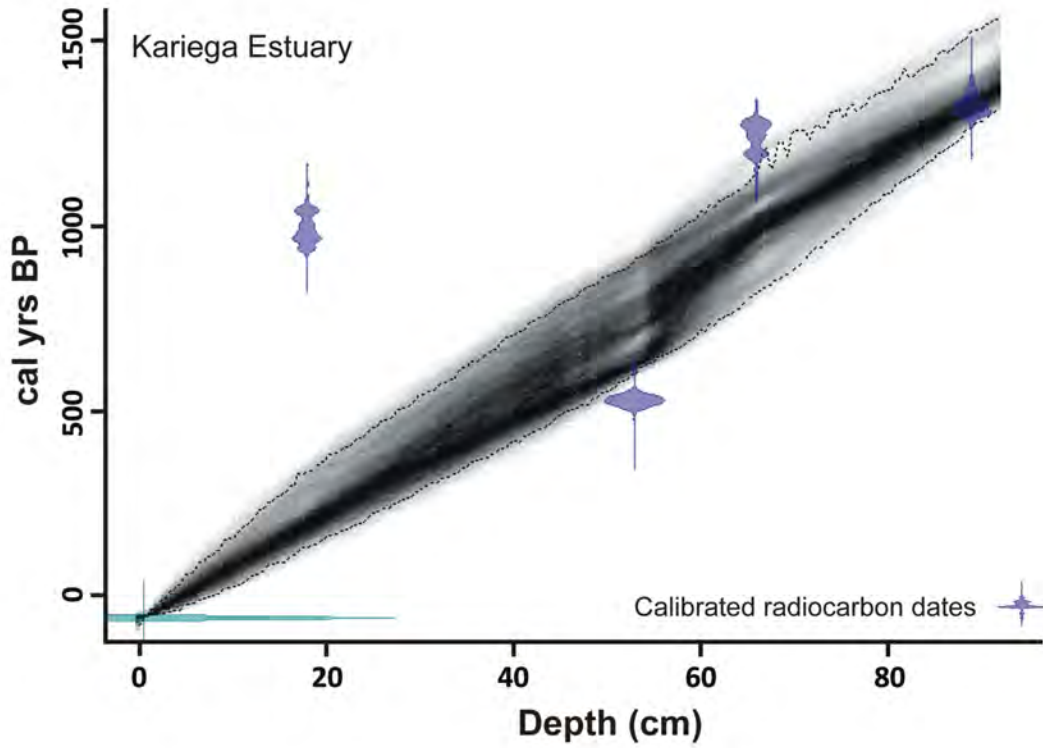


Figure K1: Age-depth model for the Kariega record based on four accelerator mass spectrometry determined ages. The surface age is assumed to represent the present day (taken from Strachan *et al.*, 2014).