Studies on the ecology and taxonomy of nematodes of Saldanha Bay, South Africa

By

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Submitted in fulfilment of the requirements for the degree

Philosophiae Doctor

In the Faculty of Natural Science

At the University of the Western Cape

September 2013

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This thesis is dedicated to the memory of my parents David (1922-1994) and Martha Hendricks (1923-2012)

DECLARATION

I declare that: **Studies on the ecology and taxonomy of nematodes of Saldanha Bay, South Africa**, is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Martin Gustav John Hendricks

May 2013

Signed: .....

Acknowledgements

This study was funded by the Royal Society and I was fortunate to conduct a study of this neglected taxonomic group in South Africa. At the onset I thank the Royal Society and the Department of Biodiversity and Conservation Biology, University of the Western Cape, for allowing me to conduct this research project.

This study was conducted as a part-time project. Although I work in a department where research opportunities abound, one seldom finds enough time to spend on your project (not with undergraduate and graduate student teaching, guiding and consultations, meetings!). This nematode journey started when I read a list Royal Society - UWC project endeavours and I was attracted to one of the few invertebrate projects simply titled *The Nematodes of Saldanha Bay*. Admittedly, there was an enticing sweetener added – a visit to The Natural History Museum (NHM), London. I thank my supervisor, Professor Mark J Gibbons for firstly introducing me to the wonderful, yet complicated ways of one of the dominant taxa on earth. Secondly, thank you for the encouragement, advice, criticism, but above all understanding and support when the project stalled or moved a snail's pace. Professor P. John Lambshead was my London teacher and advisor and I was able to learn tremendously from him, until his retirement. While I worked in the laboratories at the NHM, I was fortunate to learn from and work with Ms Nicola Debenham, Dr Timothy Ferrero, Ms Margaret Packer and Dr Natalie Barnes. Thank you for the support, advice, friendship. As part of the Darwin Initiative I was able to attend two workshops at the Plymouth Marine Laboratory, Plymouth, U.K., and I am indebted to the Royal Society for allowing me to attend these important workshops (taxonomy and statistical methodologies).

Drs Toufiek Samaai, Wayne Florence, Gordon Harkins, Messrs Goosain Isaacs, Zaahir Toefy formed a formidable team and I thank them for their sterling SCUBA work. We formed one of the best collecting teams and it remains a pleasure to work with you. I need to extend a special thank you to Dr Rashieda Toefy, who allowed me to share the problems and joys of working with nematodes with her. We still have lots of caffeine to consume for all future foraminifera-nematode endeavours.

My family and friends supported me throughout the project. A special thank you to my sister, Lorette, who has borne many of my responsibilities at home when I was away or working late hours. Thank you for all your encouragement and support. My parents told us that they could offer us all the opportunities to study and I am eternally thankful to them.

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ABSTRACT

Few studies of shallow water marine nematodes have been conducted around South Africa, and none from the west coast. Here, I analyse the composition of nematode communities from six stations along a 3 km transect in Saldanha Bay during both summer and winter, in order to describe the communities present and to explore the effects of sediment composition and heavy and trace metal concentrations on community structure. In order to put the local data into a global context, these data are analysed together with some consolidated data from elsewhere and patterns of richness and composition (at the level of genus and species) examined.

The transect in Saldanha Bay extended from below a mussel raft at one end into the bay, and six cores (35.7mm diameter) were collected at each station. All nematodes were counted and 100 randomly identified from each core. A total of 136 nominal species, 117 genera and 36 families were identified from both summer and winter stations.

Nematode abundance was highest at stations under the mussel raft, which were characterized by high mud content and high concentrations of trace and heavy metals: diversity was comparatively low and the assemblage was dominated by a few, non-selective deposit feeders (especially *Sabatieria*). Abundance decreased, but diversity increased, with an increase in distance from the mussel raft, which was coupled with an increase in the particle size of sediments and a significant reduction in metal concentrations. There were three dominant (Comesomatidae, Desmodoridae and Linhomoeidae, present in 96%, 85% and 83% of samples, respectively) and four subdominant families (Chromadoridae, Microlaimidae and Xyalidae, all in 79% of samples) that were largely responsible for determining the community structure across the bay. Multivariate analysis of the data using PRIMER indicated that copper was the single variable that best accounted for the structure ofthe communities (70.1%), and the best 2-variable combinations were copper and organic nitrogen (70.3%), followed by copper, organic nitrogen and mean grain size (69.7%). Abundance was higher at all stations in winter than summer, and the results of the PERMANOVA test on station and season indicated that the variation in between Station-Season accounted for 27% of the differences in community structure. Although these results should be treated with caution owing to limited temporal sampling, they are similar to those obtained elsewhere in the world and indicate that nematodes can be used to study anthropogenic impacts in a local context.

Despite the fact that Saldanha Bay has been subjected to industrial activities for more than thirty years, estimates of species richness for Saldanha Bay were surprisingly high: S= 136; ICE = 150; CFE= 173. As too were estimates of generic richness (S= 117; ICE = 131; CFE= 149), which were the fourth most rich of those global sites compared from similar depths. Incorporation of these data into a global dataset revealed an absence of any clear latitudinal pattern in the distribution of richness (genera or families), and there was no obvious geographic structure to global communities, based on the available data. These results suggest that genera and families are poor proxies for species (at the evolutionary level, but not at the ecological level) and they support the idea that everything is everywhere.

Comments on ways that nematode research can be advanced in South Africa are made.

INTRODUCTION

Chapter 1

Nematodes, commonly called roundworms, belong to the Phylum Nematoda. Nematodes have a pseudocoelomate body organization (Hyman, 1951), possessing an ecto-, endo- and mesoderm and although they possess a simple body plan they have complex organs (Yeates *et al.*, 2009). Nematodes possess a cuticle that moults, they are generally slender, are all circular in cross-section, most taxa are unsegmented (externally) and they have a hydrostatic skeleton (Moore, 2006). Recently nematodes were placed in the same clade as arthropods (Mallatt *et al.*, 2004). This classification is based on the study of rDNA and *Hox* gene complexes and the ability of the groups to undergo moulting. According to this system the phyla Nematoda and Arthropoda (moulting) together with Onycophora and Tardigrada (sharing of similar genes with nematodes and arthropods) are placed in the Superphylum Ecdysozoa (Mallatt *et al.*, 2006).

The classification of nematodes from taxonomic descriptions is in a constant state of revision, and recently molecular and morphological techniques have been employed to resolve the systematics and phylogenies within the phylum (Blaxter *et al.*, 1998; Sharma *et al.*, 2006; Meldal *et al.*, 2007; De Ley, 2006; Bhadury *et al.*, 2006, Neres *et al.*, 2010, Bik *et al.*, 2010). Modern molecular phylogenetic studies recognize two classes: Enoplea and Chromadorea. These classes are divided into three subclasses i.e. Enoplia, Dorylaimia (both Enoplea) and Chromadoria (Inglis, 1983; De Ley, 2006; Holterman *et al.*, 2006, Bik *et al.*, 2010): the previously recognized Class Secernentea is now nested within the Chromadoria as the order Rhabditida (De Ley, 2006; Meldal *et al.*, 2007). De Ley (2006) noted that Enoplia and Dorylaimia differ from Chromadoria in respect of their ecology and life-histories, cuticle characteristics and the structure of the pharynx.

Nematodes belonging to the subclass Enoplia are primarily marine, although there are a number of freshwater taxa present in the subclass. Most taxa are free-living and there are no extant animal parasites (De Ley, 2006). Dorylaimia are freshwater and terrestrial and get readily stressed in marine environments (Abebe *et al.*, 2008). The diversity of Dorylaimia is high and includes both free-living and parasitic taxa. The latter include both animal and plant parasites (De Ley, 2006) while free-living Dorylaimia include many predator/omnivore forms. Bik *et al.* (2010) studied the order Enoplida using small sub-unit sequences of 18S, 28S and cox1 genes and described two distinct clades within the subclass Enoplia i.e. the

terrestrial Order Triplonchida and predominantly marine Order Enoplida, with wide-scale molecular diversity. Chromadoria are represented by terrestrial, freshwater and marine species, both free-living and parasitic.Chromadoria are able to survive in extreme conditions due to their impermeable cuticles, they display a wide range of cuticular ornamentations and the bodies of free-living species are generally stouter than the other subclasses.

Nematodes are free-living or parasitic and all forms possess an alimentary canal. They are found in terrestrial, freshwater, estuarine and marine environments and they occupy most ecological niches (Nicholas, 1984). In terrestrial environments nematodes are well studied because of their importance as parasites and pests in agriculture. For this reason their taxonomy and classification is generally well resolved but the sampling methods that have been employed to study them have tended to be of a semi-quantitative nature (Higgins & Thiel, 1988). This means that our understanding of terrestrial nematode diversity is incomplete and it creates problems for comparative studies of diversity (Lambshead, 2004). On the other hand, marine nematodes are poorly understood from a taxonomic point of view but as the studies are largely based on quantitative methods our understanding of diversity is far better (Gray, 1994; Lambshead *et al.*, 2003).

The interstitial environment that most free-living nematodes occupy is also home to a number of other vermiform organisms including Loricifera, Kinorhyncha, Tardigrada, Gastrotricha, Gnathostomulida and Harpacticoida (McIntyre, 1969; Higgins & Thiel, 1988). All of these organisms are characterised by minute size, and represent members of what Mare (1942) defined as meiofauna. These are organisms that are larger than 63 μm, but that will pass through a 1 mm sieve, although Leduc *et al.* (2010) suggested 32 μm sieves for deep-sea studies. Nematodes and harpacticoid copepods are the best-known groups within the meiofauna, of which they are permanent members. This contrasts with what are considered as temporary meiofauna, which are members of the assemblage for only the early parts of their life, before growing into macrofauna. Although the size limits of macrofauna, meiofauna and microfauna are subject to debate (Higgins & Thiel, 1988), they are not totally arbitrary owing to the size-based structure of marine foodwebs (Jennnings *et al.*, 2002) and to metabolic generalities linked to size (Tita *et al.*, 1999).

Some nematodes cause physical disturbance of the sediment (Sherman *et al.*, 1983), modifying the sediment environment and then increasing the abundance of microbial organisms that could serve as a food resource (Yeates *et al.*, 2009). Nematodes specifically

are able to change the ecosystem through their feeding specialities, digestive and metabolism processes (Vanaverbeke *et al.*, 2011). They are broadly classified as either grazers / browsers or as predators. Nematodes generally release carbon and nitrogen when they feed on detritus, bacteria or kill their prey (Yeates *et al.*, 2009). Predacious nematodes may control their prey communities, but they are influenced by the sediment structure, grain size and water content within interstitial spaces (Gallucci, 2005).

The composition, biomass and diversity of interstitial meiofauna are largely dependent on sediment grain size structure, which is influenced by hydrodynamic process and local geology (Moreno *et al.*, 2007; Giere, 2009). Coarse grained sediments tend to occur in areas of considerable water movement; they are porous and generally oxygen-rich, but food poor (Thiel, 1975; Giere, 2009). Such sediments are characterised by polychaetes, nematodes and harpacticoid copepods, and harpacticoid copepods tend to be more numerous than nematodes (Willems *et al.*, 1982). By contrast, fine-grain sediments tend to be found in areas with reduced water movement and interstitial oxygen levels can be very low owing to the infilling of pores by organic-rich muds (Steyaert *et al.*, 1999; McLachlan & Turner, 1994). Such sediments are characterised by nematodes, harpacticoid copepods, turbellarians and archiannelids and harpacticoid copepods tend to be significantly less numerous than nematodes (Raffaelli, 1982).

1.1 Factors affecting nematode diversity

1.1.1 Temperature and salinity

Latitude and temperature are intimately linked (Willig *et al.*, 2003), and there is a clear relationship between latitude and diversity in marine organisms (Boucher, 1990; Boucher & Lambshead, 1995; Lambshead *et al.*, 2000, Brown *et al.*, 2001 and Gobin and Warwick, 2006) (see also Chapter 5). At the local scale, however, the influence of temperature on nematode communities is less clear. For example, seasonal peaks in abundance that could be related to the effects of temperature on generation time (Tietjen, 1969; Heip, *et al.*, 1985; Soetaert *et al.*, 1995) are confounded in estuarine environments by concurrent changes in salinity and food resources, as well as hydrodynamic processes. Like other organisms, marine nematodes have temperature (and salinity) optima at which they perform best, though few LT_{50} studies have actually been conducted (see Moens & Vincx, 2000a,b). In general an increase in temperature is linked to a reduction in generation time (Gerlach, 1971), although the generation time of some species appears to be unaffected by

temperature (Heip *et al.*, 1985). Changes in salinity affect development times and many species prefer the middle to upper range of salinity (Tietjen & Lee, 1973). Forster (1998) demonstrated that nematodes are able to osmoregulate, with upper-shore species being the most efficient osmoregulators. In hypersaline areas, such as mangroves, nematode assemblage structure is ill-defined with a high variation within and between sampling areas: diversity is significantly reduced in areas where salinity exceeds 100 ‰ (Ólafsson, 1995).

1.1.2 Sediment structure

Just as it is hard to unambiguously separate out the influence of temperature on nematodes and nematode communities in seasonal studies, so it is difficult to separate out the effect of sediment structure *per se* from the effects of other co-variant environmental factors such as organic enrichment and dissolved oxygen concentration (Rosenberg *et al.*, 2001). It should be realised too that depth can impact sediment structure through its effect on water movement (Soetaert & Heip, 1995) and hence nematode communities (Etter & Grassle, 1992). Small grains tend to limit the ability of nematodes to move or swim effectively between particles, and fine-grained sediments generally support distinct communities comprised of larger taxa (Tita *et al.*, 1999). Although coarse grained sediments have larger interstitial spaces, and support smaller species (Brown & McLachlan, 1990, Steyaert *et al.*, 1999) these taxa are also more armoured as the sediments tend to be fairly mobile (Soetaert *et al.*, 2002, Gheskiere *et al.*, 2005). Interestingly, common habitats across the world, albeit coarse sand or coastal mud, tend to be dominated by particular sets of nematode taxa (Steyaert *et al.*, 2003; Vanaverbeke *et al.*, 2011). Thus coarse sands are frequently dominated by species of the families Draconematidae and Epsilonematidae (Gourbault & Decraemer, 1992, Decraemer & Gourbault, 2000), whilst fine sands are populated largely by *Sabatieria punctata*, *Ascolaimus* spp. *Daptonema tenuispiculum*, all typical non-selective deposit feeders (Vanaverbeke *et al.*, 2011). Fine sand communities tend to exhibit communities of low diversity while diversity in coarse sediments can be significantly higher and these sediments contain all the feeding modes.

1.1.3 Organic carbon

Organic carbon in the form of detritus and associated microbes (bacteria, fungi and protists) fuels benthic production pathways. The more organic enrichment there is therefore, the greater the infaunal biomass that may be supported (Gooday & Turley, 1990, Brown *et al.*, 2001; Quijón *et al.*, 2008). Coarse sediments generally contain less detritus than fine

grained sediments (Drgas *et al.*, 1998), meaning that nematode biomass is lower in the former than the latter (Moreno *et al.*, 2008a). But diversity tends to be higher in coarse, than fine, sediments – both absolutely and in terms of trophic complexity (Gheskiere *et al.*, 2004). Taxa common in such "clean" habitats include *Paracanthonchus* (Cyatholaimidae; 2A), *Daptonema* (Xyalidae; 1B), Chromaspirinia (Desmodoridae; 2B), Oncholaimus (Oncholaimidae; 2B), Pomponema (Cyatholaimidae; 2B), Microlaimus (Microlaimidae; 2A), Epacanthion (Thoracostomopsidae), Richtersia (Selachnematidae) and taxa of family Desmoscolecidae such as *Tricoma* sp., *Desmoscolex* sp.(Mundo-Ocampo *et al.*, 2007; Moreno *et al.*, 2011). Near-shore environments rich in particulate, and dissolved, organic matter tend to support deposit-feeding communities (1A, 1B) (Gheskiere *et al.*, 2004) communities that are dominated by complexes of *Sabatieria* (1B), *Dorylaimopsis* (2A), *Terschellingia* (1A), *Microlaimus* (2A), *Parodontophora* (2A), *Cobbia* (2A), *Halalaimus* (1A), *Sphaerolaimus* (2B), *Elzalia* (1B)(De Leonardis *et al.*, 2008; Liu *et al.*, 2007; Hua *et al.*, 2009; Fu *et al.*, 2012.). The biomass, diversity and trophic structure of nematode communities not only vary spatially, but also temporally and seasonal changes have been observed that are linked to seasonal changes in organic enrichment, water depth and salinity (Fu *et al.*, 2012).

1.1.4 Oxygen

Oxygen plays a fundamental role in structuring benthic and pelagic communities (Imabayashi in Karim *et al.*, 2002). Most coastal areas are subjected to short-term low oxygen episodes, yet most benthic populations are able to tolerate these stresses (Karim *et al.*, 2002). Oxygen availability could impact on food resources and therefore the feeding strategies of benthic communities as well as abundance and diversity. For instance, in areas with high organic input and accumulation of organic matter on the seabed anaerobic conditions may develop primarily caused by microorganisms processing the organic matter (Gray *et al.*, 2002). Sediments may become oxygen stressed when available oxygen is utilized by these microorganisms (Cloern, 2001). Only those benthic taxa that are able live in oxygen-stressed environments would be able to survive, thus affecting benthic diversity and abundance (Wetzel *et al.*, 2002). Some species of nematodes and foraminifera are often the only taxa present in the high abundance (Neira *et al.*, 2001; Steyaert *et al.*, 2007) while copepods may disappear. Wetzel *et al.* (2002) further suggested that nematodes are able to migrate into the water column to escape reducing environment.

Austen and Widbom (1991) and later Van Colen *et al.* (2009) have noted that nematode assemblages show reduced diversity and within-site variability after hypoxic events, and that recovery of an impacted area may be slow or variable. Interestingly, Levin *et al.* (1991) and Cook *et al.* (2000) noted that low oxygen *per se* was not responsible for driving changes in nematode abundance at deep-sea stations but rather food resources.

Many countries need to dredge their harbours or estuaries because of silt accumulation. These dredging deposits may contain sewage waste and anoxic conditions may results from their decomposition. The sediments may contain a sulphide zone below the oxygenic zone and many organisms, permanently or temporarily, inhabit this zone (thiobios) (Powell *et al.*, 1983, Jensen, 1987a). Boyd *et al.* (2000) reported that a typical species such as *Sabatieria pulchra*, a facultative anaerobe, dominates the meiobenthic assemblage under these circumstances and it is able to tolerate limited anoxic conditions. Armenteros *et al.* (2009) showed that nematode diversity under hypoxic and polluted conditions is determined by a few cosmopolitan "tolerant species" i.e. *Daptonema oxycerca, Sabatieria pulchra, Terschellingia longicaudata and T. gourbaultae.*

1.1.5 Disturbance

Owing to their small size and rapid generation times, nematode communities, like those of other meiobenthic taxa, can show pronounced spatial variability in composition and structure at microscale levels (Moens *et al.*, 1999; Van Gaever *et al.*, 2004), and this patchiness reflects, in part, small scale changes in the physical, chemical and biological environment (Somerfield *et al.*, 2007; Schratzberger *et al.*, 2008). But it also reflects non-equilibrium processes linked to environmental disturbance (Connell, 1978; Gingold *et al.*, 2010).

In undisturbed conditions, dominant species would be expected to out-compete subordinate species through competitive exclusion (Huston, 1979; Hughes, 1984; Connell, 1979) and this would tend to reduce overall community diversity. In natural biological communities, however, equilibrium communities are rarely observed because disturbance events that reset processes of ecological succession (recovery) prevent competitive interactions from reaching their inevitable conclusion (Austen & Widdecombe, 2006). Such communities tend to exist in a non-equilibrium state, especially if disturbance events are spatially and temporally un-phased, and they tend to display relatively high diversity (Zajac & Whitlach, 1982; Lambshead & Hodda, 1994). In the context of nematodes and meiofauna,

agents of disturbance at the microscale may be linked to predator cropping (Dayton & Hessler, 1972), macrofaunal tubes and tracks, faecal piles, phytodetrital matter, mud deposits, and sediment shifts though benthic storm action (Sherman *et al.*, 1983; Levin *et al.* 2001; Somerfield *et al.*, 2007).

1.2 Disturbance events relating to dredging, eutrophication, sewage and heavy metals

Aside from natural disturbance events that modify infaunal communities, coastal habitats are constantly being altered by anthropogenic activities. These activities include the construction of harbours, the reclaiming of shorelines for urban development, sewage deposits via pipelines, industrial fallout, heavy metal contamination and many more (Boyd *et al.*, 2000; Schratzberger *et al.*, 2006; Derycke *et al.*, 2007; Santos *et al.*, 2009; Nikulina & Dullo, 2009; Fukunaga *et al.*, 2010). All of these activities not only disturb and disrupt the structure of the sediment environment (Thrush & Dayton, 2002) but their scale is generally such that they tend to homogenise (temporally and spatially) the composition and structure of associated infaunal communities (Thrush & Dayton, 2002; Cryer *et al.*, 2002). Of course, the biological response to disturbance will depend on the nature of both the disturbance (intensity, frequency, type) and the environment (Lenihan & Oliver, 1995; Occhipinti-Ambrogi& Savini, 2003). Regardless, knowledge about the effects of anthropogenic activities on biological communities is important as it plays to issues of environmental management and allows long-term plans to be developed that balance the needs of the environment against the socio-economy (Trett *et al.*, 2009). We need to understand how biological communities respond to anthropogenic disturbance and we need to understand the processes and response pathways that will take them back to a near pre-disturbance state. In order to collect this information, we tend to monitor the environment (Wolfe *et al.*, 1987; Goldberg & Bertine, 2000) and Lambshead (1986) has argued that nematodes are useful tool for measuring biological responses to disturbance in marine environments. His arguments for so doing were based on a number of their characteristics, as follows:

1) They are normally very abundant with high species diversity
2) They are ubiquitous and persistent as a taxon
3) They are easily sampled due to their small size
4) They lack a planktonic larval stage and migrant species would not impact on any studies
5) They have a high turnover rate, thus short life histories, and

6) They live in sediments (mud, sand or combinations thereof), so that any changes would be readily manifested.

Many metals (such as mercury, copper, lead, arsenic, chromium, cadmium, zinc) occur naturally in sediments at low concentrations (Clark *et al.*, 2009). They become toxic to marine organisms when anthropogenic activities introduce excess amounts into the environment. Most of these metals tend to accumulate in muddy sediments where they form complex compounds through chelation (Stronkhorst *et al.*, 2003). However, once the sediments are disturbed, metals are re-suspended and may become problematic. Heavy metals accumulate in harbour sediments and some of these (copper, mercury and lead), may lower the productivity of marine nematodes and thus affect meiofaunal populations (Vrancken & Heip 1986).

Fichet *et al.* (1999) investigated the importance of nematodes during the transfer of heavy metals (cadmium, copper, lead and zinc) to other feeding groups. Nematodes are able to sequester heavy metals through a number of processes and Fichet *et al.* (1999) demonstrated that only Zn is biologically controlled. Nematodes penetrate deeper into sediments than epibenthic copepods and the latter exhibited reduced levels of heavy metal uptake. Fichet (1998) earlier pointed out that metal-laden sediments may then become an important contamination agent in both the pelagic and benthic ecosystems since nematodes constitute a food source for juvenile fish and epibenthic macrofauna (Smith and Coull, 1987, Gee, 1989, Coull *et al.*, 1995).

Large amounts of oil are spilled into the sea by natural seepage, oil tanker discharge, shipping accidents or river effluent (Beyrem *et al.*, 2010). Oil may be crude or refined products and these may affect benthic organisms. In some cases hydrocarbon compounds may increase abundance, yet in other cases abundance, diversity and life history (Balsamo *et al.*, 2011) will be negatively affected through toxic concentrations or asphyxia (Ingole *et al.*, 2011; Lv *et al.*, 2011). Boucher (1981, 1983) noted that the abundance of nematodes and copepods, in shallow water sediments off the French coast a few months after the *Amoco Cadiz* oil spill, were not significantly different from pre-spill numbers. Shortly after the spill nematode and copepod abundance were reduced, but densities started to recover quite quickly although nematode diversity decreased significantly. Gourbault (1987) further reported that the recovery process in the Morlaix Estuary, also affected by the same oil spill, was long-term but assemblages tended to recover to pre-spill conditions. However, the spill effects

were greatest in shallow water habitats with lowered diversity even after four years. From a one year-long study along the South African coast following the Venpet/Venoil shipping disaster, Fricke *et al.* (1981) found that harpacticoid copepods were negatively affected by pollution but that nematode abundance was not significantly different from a control site. That said, however, the physical disturbance caused by mechanically removing the oil deposits on a second beach, had a greater negative impact on nematode and copepod densities. Fricke *et al.* (1981) reported that both beaches showed evidence of recovery after six months.

An important form of physical disturbance over the deeper shelf is demersal trawling. This activity is widely practised and it disturbs the benthos, removes fish and epibenthic macrofauna. In addition meiofauna tend to be dislodged and re-suspended together, with organic matter and nutrients (Schratzberger & Jennings, 2002). Schratzberger and Jennings (2002) and Liu *et al.* (2010) have reported that moderate levels of trawling may initially increase nematode abundance, and the latter authors have noted that recovery from trawling may take place within one year after the cessation of trawling activities. Liu *et al.* (2010) found that nematode diversity indices were initially higher at non-impacted sites, but that these differences were not significant over the entire study period. Nematode community structure was however altered with a preference of stout –bodied, clavate-shape tail and k-strategist taxa in non-impacted sites (Liu *et al.*, 2010) Schratzberger and Jennings (2002) conducted a Before-After-Control-Impact (BACI) experiment and concluded that meiofauna were resistant to the effects of beam trawling. Meiofauna are readily suspended during trawling activities and they also have short generation times therefore abundance, species diversity and species richness not significantly different between control sites although the community structure was moderately altered.

Cultural eutrophication is defined by the Urban Waste Water Treatment Directive of the European Commission as "the enrichment of water by nutrients especially compounds of nitrogen and phosphorus, causing an accelerated growth of algae and higher forms of plant life to produce an undesirable disturbance to the balance of organisms and the quality of the water concerned" (Bock *et al.*, 1999). Although it was originally identified in lakes (See Bennett *et al.*, 2001; Smith, 2006), it is becoming a problem in many coastal and nearshore waters of the world (Nixon, 1995; Nikulina & Dullo, 2009) and has a multitude of effects on pelagic and benthic systems (Bonsdorff *et al.*, 1997). Coastal environments are subjected to large nutrient fluxes caused by the proximity of human settlements and concomitant activities

(Yodnarasri *et al.*, 2006). High concentrations of nitrogen and phosphorus are delivered to coastal areas mainly as untreated or partially treated sewage as well as terrestrially-derived sludge that are deposited in marine environments. Chemical contamination, high levels of N and P will change the sediment characteristics and the pelagic environment. One of the consequences of excessive nutrient loading is a change in abundance and diversity of nematodes. Lorenzen *et al.* (1987) reported a mass aggregation of *Pontonema vulgare* in polluted fjords, while Mirto *et al.* (2002) reported an increase in biomass of nematodes beneath fish cages. On the other hand Duplisea & Hargrave (1996) found no significant difference in nematode biomass in a similar fish cage versus control experiment.

Like Lambshead (1986) before him, Bongers *et al.* (1991) too has advocated the use of marine nematodes as biological indicators of environmental health. These latter authors have used abundance patterns and the ratio between the Wieser feeding types (Wieser, 1953), as well as maturity indices based on the life strategies of nematodes to assess disturbance in a number of polluted and undisturbed habitats. Nematode assemblages consist of species that may include both *r*- strategists and *K*- strategists, the former being regarded as colonisers and the latter as persisters. Bongers *et al.* (1991) suggested that *r*-strategists are favoured after a pollution event (see also Warwick 1986).

1.3 Aims

Studies on marine nematodes around South Africa are few in number and with few exceptions these have been of a generally superficial nature. These studies are comprehensively reviewed in Appendix 1.1, and aside from some early taxonomic work, most of the ecological work has simply involved counting and/or weighing nematodes as a group: there has been no consideration of species identity. Further, most of these studies have been conducted on sandy shores along the SE coast of South Africa, and while their results are useful in elucidating possible patterns of energy flow within and between different components of sandy shore systems, their wider value is strictly limited.

Here, I set out to describe the nematode communities from Saldanha Bay on the west coast of South Africa. The nematodes collected are counted and identified to species level (see also APPENDICES 1.3 and 1.4) and patterns within the data are explored using a suite of concurrently collected environmental data with a view to understanding the factors that structure nematode communities in the region (Chapters 2 - 4).

An attempt is also made to place the results of this study into a global context: how similar are the communities observed in Saldanha Bay to those observed elsewhere and if indeed there are similarities, can any lessons learnt or generalisations made from those studies be carried to the present one (Chapter 5). This Chapter also investigates the impact of sampling on our observation, in order to determine whether they are broadly representative of the nematodes in Saldanha Bay.

The National Spatial Biodiversity Assessment (Driver *et al.*, 2005; 2012) has provided a framework for biodiversity management in South Africa. Most of the information used in those compilationshas been derived from macrofauna of one type or another, and meiofauna have not been considered. I conclude by exploring the possible merit and value of including meiofaunal data in future NSBAs (Chapter 6), as well making some comments on ways that research in this area can be moved forward.

CHAPTER 2

Materials and Methods

2.1 Saldanha Bay – location, history and physico-chemical environment.

Saldanha Bay (33° S, 18° E) is situated on the west coast of South Africa (Fig 1.1). It is a semi-enclosed bay, experiencing no significant freshwater input. Depths range from 20-25 m at the opening of the bay and decrease progressively towards the shore (Flemming, 1977). The general geology of Saldanha Bay is dominated by Palaeozoic granite (~500 million years old) that is overlain by calcrete sheets and sand. The latter are derived from Quaternary coastal and marine deposits (Flemming, 1977; Du Plessis & De la Cruz, 1977).

Saldanha Bay has been subject to physical alteration (see below) but was originally a semi-enclosed circular embayment divided into two sections, namely North Bay and Inner Bay (Flemming, 1977). Five islands i.e. Jutten, Malgas, Marcus, Meeuw and Schaapen form part of the Saldanha Bay system (Figure 1.1). Marcus Island is situated in the mouth of Inner Bay and it influenced (and continues to influence) the hydrology of inshore waters as well as the sediment structure in the surrounding areas (Flemming, 1977). Sediment advection and distribution is wave-driven in Saldanha Bay and tide-driven in the adjacent Langebaan Lagoon, to the south.

Flemming (1977) identified four sediment zones in the bay: a central exposed area flanked on either side by semi-exposed zones within Inner Bay, a sheltered area originally called North Bay, to the east of the modern-day Marcus Island Causeway, and lastly a transitional zone leading to Langebaan Lagoon (See Figure 2.1). An abrasion zone within the exposed zone produced sediments and most of the sediments are very coarse (1-2 mm particle diameter). Flemming (1977) further reported that the semi-exposed areas as well as the sheltered area are dominated by very fine sands (63-125 μm particle diameter).

Saldanha Bay opens into a national conservation area to the south, Langebaan Lagoon (West Coast National Park), which is an important wetland reserve for migrating waders (Hockey & Turpie, 1999). It lies within the nutrient-rich Benguela upwelling system with a characteristic western facing coastline, a narrow coastal shelf and wind driven currents at the surface flowing equatorward (Shannon, 1989).

Saldanha Bay is the only natural harbour along the west coast of South Africa (Shannon & Stander, 1977), and its name reflects the whims of colonisation history. In 1503 Admiral António de Saldanha of the Portuguese fleet sailed into the present-day Table Bay, naming it *Aquada de António de Saldanha* (Bulpin, 2001). Nearly one hundred years later, in 1601, the Dutch Captain Van Spilbergen renamed Table Bay and the original name was used for the then unnamed northern bay. Saldanha Bay was used by the French as a fur seal hunting station in the early 17th century (Bulpin, 2001), and in 1666 the Dutch East India Company established a garrison at the drinking-water springs adjacent to Langebaan Lagoon.

The harbour has been extensively modified over the years and a massive jetty to service exports of iron, copper and lead concentrates was built in 1975 that effectively now divides the bay into two sections; Big Bay to the SE and Small Bay to the NW (Figure 1.1). At the same time, a causeway running between the mainland and Marcus Island was built in order to shelter tankers and ore-carriers from the swells rolling in from the South Atlantic, and this has resulted in considerable changes to the water circulation patterns within the bay (Shannon & Stander, 1977; Weeks *et al.*, 1991a). As Saldanha Bay facilitates the off-loading of crude oil at the ore loading jetty, there is a risk of oil pollution inside the bay, and the last major oil spill was recorded in 2007 (Clark *et al.*, 2011). The area around Saldanha Bay has also been subject to extensive urban development, and many light industries (including fish canneries) have been constructed along the coastline. Two of the three fishing plants presently in the area were established at the turn of the 20th century and all are situated around the modern-day Small Bay. These canneries release organic matter into the adjacent water that results in high oxygen demand, eutrophication not linked to normal upwelling processes (Monteiro *et al.*, 1990) and this leads to the development of anoxic sediments with increased sulphides (Jackson & McGibbon, 1991). Eutrophication is especially pronounced in the areas surrounding these canneries. Using stable isotopes, Monteiro *et al.* (1997) demonstrated that the nitrogen taken up by the green macrophyte *Ulva* within the bay was derived largely from the effluent leaving fish processing plants, whilst that used by this species in control sites was derived from the Benguela Upwelling System.

A pollution-monitoring programme conducted from 1974 to 1979 showed that summer chlorophyll concentrations were variable and that long-term monitoring data often masked this variability. Chlorophyll production and changes in chlorophyll concentrations are governed by a number of factors such as temperature regime, wind forcing, available light, light penetration,

salinity and water movement (Monteiro & Largier, 1999; Lionard *et al.*, 2005). Monteiro & Brundrit (1990) reported that chlorophyll production in Saldanha Bay increased at the onset of spring-summer but during the course of the reporting period two warm-water intrusion events, with increased salinity, caused a decrease in chlorophyll production leading Monteiro & Brundrit (1990) to advocate the use of salinity changes to monitor changes in chlorophyll concentration.

Since 1984 Saldanha Bay has witnessed the development of a series of small mariculture operations, largely based on the cage and raft culture of oysters and mussels (*Mytilus galloprovincialis*). The main mussel farm (Sea Harvest Mussel Farm) is located in Small Bay and is constructed on a Spanish model that uses suspended ropes (6 m in length) on which the mussels are seeded and grown out. Mussel rafts yielded approximately 700 tonnes (wet weight) in 2008 (Clark *et al.*, 2011), resulting in the production of considerable quantities of debris in the form of carcasses, faeces and pseudofaeces.

Anthropogenic activities that resulted in changes in water circulation patterns in the bay, increased effluent disposal through canneries and urban development and mariculture activities have all impacted negatively the macrobenthic fauna of the Saldanha Bay system, through eutrophication (Jackson & McGibbon, 1991; Stenton-Dozey *et al.*, 1999). The macrofauna changed from a dominant suspension feeding community to a deposit feeding community, both in abundance and biomass. Many of the "new" species are opportunistic polychaetes while the sandprawn, *Upogebia capensis*, that was historically absent from Small Bay, has become dominant both in biomass and density.

Given that Saldanha Bay lies within the southern Benguela ecosystem, the physical characteristics of the water within the Bay are strongly influenced by changes within the parent system. Prevailing wind principally determines both the direction and magnitude of currents in Saldanha Bay (Weeks, 1991a). In summer, wind driven surface currents are especially pronounced above the thermocline (18-20° C vs. 11-13° C), at a depth of 3-6 m, while tidal effects dominate below the thermocline. Surface current speeds range from 5-20 $cm.s^{-1}$. As expected chlorophyll concentrations are variable during summer (Pitcher & Calder, 1998), but they are generally higher than during winter. In winter, there tends to be greater mixing of water: tidal effects dominate the bay's dynamics and primary production is low. Weeks *et al.* (1991b) reported on the effect of a passing cold front on the advection of water across the mouth of Small Bay inside Saldanha Bay and again noted that winds were the dominant driving force of

currents during winter storm conditions. In general, surface water tends to flow out of the Bay even during spring flood periods and these are replaced by bottom water, which can contain low concentrations of dissolved oxygen. Monteiro & Largier (1999) studied the effect of temperature and wind on the dynamics between the subtidal density driven exchange of water between the bay and coastal water from the Benguela Upwelling System. A four phase model governed by thermal stratification, wind stress and barocline dynamics were proposed: phases 1 and 2 were active periods and was characterised by colder coastal-, than bay- water resulting in a bayward barocline. The onset of an equator-directed wind event mixed water in the bay and broke down the thermocline. The same winds later drove cold water into the bay and established a strong thermocline. Surface water was warmed, but confined to a narrow layer in phases 3 and 4 (relaxation periods). During this period the barocline shifted seaward with bay water being colder than the surrounding ocean. When wind stress weakened or changed, the vertical mixing of water diminished; water was allowed to heat and cold bottom water drained from the bay. The advection of cold water enabled the influx of nutrients for phytoplankton new production while the export of new production happened during the relaxation period.

2.2 Study Site and Field Sampling.

Six stations were sampled along a transect line starting in the Sea Harvest mussel farm and proceeding in a south-easterly direction across the mouth of the Bay (Figure 1.1). Each station was 500 m from the next, and the line originated directly beneath the mussel rafts in the centre of the farm. The average depth of the study site ranged from 10 - 18 m.

Each station was sampled once during December 1998 and then again during August 1999. Seven cores were collected from each station at each sampling time using SCUBA, following the diving protocols of the University of the Western Cape. A modified *Hagge corer* (Fleeger *et al.*, 1988) was used for sampling: each corer was 30 cm in length and 3.57 cm in internal diameter (10 cm^2 surface area), and was constructed of hard plastic piping. Samples were capped underwater immediately on collection, prior to further treatment in the laboratory.

2.3 Laboratory Procedures:

On return to the laboratory all cores were emptied into suitably labelled containers, without vertical sectioning. One of these was immediately frozen for subsequent sediment

analysis, whilst the balance was fixed in 4% formaldehyde for subsequent species identification and counting.

2.3.1 Sediment Analysis.

Samples were removed from the freezer and dialysised in 63 µm filtered water overnight to remove excess salt. After dialysis, the samples were poured into a shallow dish through a series of sieves: 2 mm, 250 µm and 63 µm.

The content of each dish was then transferred to a 1*l* measuring cylinder. Care was taken to remove all the silt and suspended clay as well as transferring the correct volume. An Andreasen pipette was employed to transfer an aliquot of the suspended mud solution to a pre-weighed labelled 25 ml beaker. Since the mass and volume of water is equal, the mass of sample equated the volume of the aliquot used. The total volume of solution was determined by multiplying the dilution/ aliquot factor by 1000. All the beakers for each sample were placed in an oven at 105° C, dried overnight, and weighed. Total gravel, sand and mud fractions were determined and expressed as percentages.

The mean grain size is normally expressed in Phi units therefore each sample was converted from µm to phi (ø) units using the formula:

$$\text{Phi units } (ø) = -\log_2 D, \qquad \text{equation 1}$$

Where D = grain size in mm. The following phi units were used: 5 Phi = < 63 µm, 2 Phi = 250 µm and -1 Phi = 2 mm (Pfannkuch & Paulson, 2007). Mean grain size was then calculated from the following equation:

$$\text{Mean sediment grain size} = (ø16 + ø50 + ø84)/3, \qquad \text{equation 2}$$

(Pfannkuch & Paulson, 2007)

2.3.2 Elemental Data

Information on the metal and other elemental compositions of sediments in Saldanha Bay were taken from Monteiro *et al.* (1999). The latter biogeochemical study took place some six weeks after the summer sediment cores used in the current study were collected. Despite the temporal difference in biological and environmental sampling, the data collected by Monteiro *et al.* (1999) are unlikely to differ significantly from those noted at the time the biological samples were collected. The retention and re-mineralization of elements in sediments is dependent on the extent of natural degradation of sediment, anthropogenic activities and physical factors such as wave action, currents, bed shear stress and season (Monteiro & Roychoudhry, 2005). Metal remobilization is also driven by thermodynamic and kinetic processes and can vary from rapid to years.(Linge, 2008) Wang & Tam (2012) found that heavy metal levels in sediments showed no significant decline one year after the impact source was removed. Obee (2009) likewise reported that the remediation of sediments, subjected to fish-farming activities was variable, but that the levels of metals such as copper, zinc as well as organic carbon and sulphides remained high over time suggesting that the metals remained bound to the sediments and not released into the water column. Sampling sites 18, 12, 16, 23 and 26 of Monteiro *et al.*'s (1999) study correspond to Stations 1, 2, 3, 4 and 6, respectively (Figure 2.1). These authors collected a total of 30 cores, measuring 100 mm diameter, to a sediment depth of 400 mm. All the samples were then frozen prior to analysis. The environmental data measured by Monteiro *et al.* (1999) and used in this study include: total aluminium (Al $mg.Kg^{-1}$), total iron (Fe $mg.Kg^{-1}$), total copper (Cu $mg.Kg^{-1}$), total lead (Pb $mg.Kg^{-1}$), total cadmium (Cd $mg.Kg^{-1}$) and total zinc (Zn $mg.Kg^{-1}$), as well as organic carbon (% C) and organic nitrogen (% N). Monteiro *et al.* (1999) report that trace metals were analyzed by using an in-house digestion method (CSIR MALS 4.5) that employed a mixture of nitric acid, perchloric acid and hydrogen peroxide. This method released trace metals that were linked to silt and organic matter but not to silicates of sand fractions. Analyses were conducted by Atomic Absorption Spectrophotometry (Varian AA-1475) and the results were checked against marine sediment reference material.

2.3.3 Nematode Extraction.

The separation of nematodes from the sediment followed the three-stage protocols of the nematode research group of the Natural History Museum, London.

1) Decantation: The sample was gently washed into a 2*l* stoppered measuring cylinder using filtered tap water. The cylinder was filled, the stopper replaced and the content was inverted five times. After agitation the stopper was immediately removed and the rim of the cylinder was washed to ensure that all residual material was returned to the sample. After the sediments had been allowed to settle for ~30 seconds the water was gently decanted through a 45 µm mesh sieve. If the sieve accumulated large quantities of mud, continuous gentle taps on the lower surface of the sieve assisted the water drainage. The process was repeated a further four times.

2) Flotation: Once all the nematodes had been removed from the sample and were collected in the 45µm mesh sieve, the sieve was washed gently with Ludox-TM into a 100 ml screw-top container, according to a method described by de Jonge & Bouwman (1997). Ludox-TM is a silica-based colloidal polymer that, in the present instance, was diluted to a specific gravity of 1.15, which is considered to represent the specific gravity of marine nematodes. This was achieved by diluting two parts of Ludox-TM to three parts water, aided by a densitometer. The point of this exercise was to remove all the water from the sample and to float the nematodes in Ludox-TM. After the sample had been left for at least four hours in the Ludox-TM solution, the nematode-containing supernatant was decanted through a 45µm mesh sieve. The nematodes were then gently washed with tap water and transferred to a petri dish, prior to subsequent counting. The sample jars were refilled with Ludox-TM and the process was repeated until no further nematodes were extracted. In practise the sample was treated a maximum of six times.

3) Counting: All the extracted nematodes were manually picked from the petri-dish using a fine pointed needle, under a microscope at low magnification. Each specimen was transferred to square cavity blocks containing Seinhorst's de-hydrating solution (20 parts distilled water: 1 part glycerol: 79 parts ethanol with a few crystals of phenol to prevent bacterial and fungal growth). The cavity block was partially covered with a coverslip, and placed in a desiccator for 2-3 days in order to evaporate off the water and ethanol to leave a viscous glycerol solution. Seinhorst's S2 solution (93 parts 96% ethanol: 7 parts glycerol and a few crystals of phenol) was then added to the cavity block, which was returned to the desiccator. After a further two days, only anhydrous glycerol remained and the nematodes were ready for mounting.

A total of 100 nematodes were randomly sampled from each cavity block. A wax ring was made on a cleaned microscope slide and a small droplet of anhydrous glycerol was placed inside. Ten nematodes were placed into the glycerol droplet and arranged in the centre. A number of minute glass beads (~ 63 μm) were added to the droplet to prevent damage to the specimens when a 19 mm diameter coverslip was placed on top of the wax ring. The coverslip was fixed in position by melting the wax ring. Each slide was labelled, placed in a flat slide tray and stored prior to further examination.

2.3.4 Identification, drawing and resources

Each of the 100 specimens that was randomly selected to characterise the nematode communities in each sample was examined using a Leica microscope with x100 oil immersion lens and drawn with the aid of camera-lucida drawing tube: exemplar illustrations are shown in Figure 2.2). Specimens were identified using three pictorial guides (Platt & Warwick, 1983; Platt & Warwick, 1988; Warwick *et al.*, 1998) as well as the electronic guide provided by the Plymouth Marine Laboratory (www.pml.ac.uk/nematode/nemkey).

Owing to the very time consuming process of species identification, not all samples were examined. Abundance data (here expressed per 10 cm^2) were collected from all samples in all stations, but species were only identified from all the summer samples and stations and from all samples at three of the winter stations, stations 1, 4 and 6. All specimens were measured for length, width, tail length, amphid diameter, spicule length, oesophageal bulb diameter (if present) and oesophagus length following (Platt & Warwick (1983, 1988) and Warwick *et al.* (1998). Specimens were also categorized according to the feeding groups defined by Wieser (1953).

Wieser (1953) devised the earliest feeding group index for free living marine nematodes, based on the morphology of the buccal cavity, dividing them into four feeding groups: *1A*, *1B*, *2A* and *2B*. Nematodes in *Group 1A* have small buccal cavities and they lack teeth. They may absorb simple organic materials across their cuticles, and suck soft, perhaps bacterial-rich food into the intestine. They are regarded as selective deposit feeders and may be important in anoxic habitats. Nematodes belonging to *Group 1B* possess cup-shaped, conical or cylindrical buccal cavities also without teeth. Nematodes in this group are regarded as non-selective deposit feeders and feeding is aided by the lips and anterior part of the buccal cavity. They tend to occur in fine-sand habitats and they ingest bacteria or diatomaceous organisms. *Group 2A* nematodes possess small teeth in their buccal cavities.

These nematodes scrape surfaces or pierce cells that are subsequently sucked out. Lastly, *Group 2B* nematodes possess a large buccal cavity, armed with large teeth or stylets and they include the predatory taxa. The Wieser (1953) feeding classification is still used in studies of marine and estuarine nematodes (see modifications of Jensen (1987b), Moens & Vincx (1997) and Moens *et al.* (1999), and it is employed here to investigate spatial and temporal changes in the trophic structure of nematode communities across Saldanha Bay.

It is becoming widespread practise in studies of the effects of environmental change/disturbance on marine communities to look beyond trophic indicators alone and to also explore life-history characteristics of community members (Ferris & Bongers, 2009). Bongers (1990) proposed the use of life-history of nematofauna to ascertain the state of soil or benthic ecosystems. One such life-history characteristic is the Maturity Index (MI), which is broadly indicative of the state of the ecosystem based on the condition of the nematode assemblage. The index was first proposed by Bongers (1990) in a study of soil nematodes, and has subsequently been extended to marine and estuarine nematodes (Bongers *et al.*, 1991, Bongers & Ferris, 1999). Effectively MI is calculated by using the weighted proportion of each nematode taxon based on equation 3. Nematodes were classified as colonizers or persisters (*c-p*) based on their life history strategies. This classification approximates the ecological *r*-strategist and *K*-strategist. Disturbance or pollution events affect *K*-strategist and when they disappear as result of the disturbance the available resources would be used by elevated levels of colonizing taxa. The (*c-p*) rating ranged from 1 to 5 and was assigned at the family level. The *c-p* index was calculated using the weighted proportion of each nematode taxon based on the equation

$$MI = \sum_{i=1}^{n} v(i) \cdot f(i) \qquad \text{Equation 3}$$

Where *v(i)* is the value of taxon *i* given in a table (Bongers, 1990) and *f(i)* the frequency of taxon *i.* Bongers *et al.* (1991) applied the index to both generic and family taxonomic levels.

The five *c-p* categories range from extreme *r*- strategists (*c-p*1) to extreme *K*-strategists (*c-p*5) as follows (Ferris & Bongers, 2009):

*c-p*1 - This category includes nematodes with a short generation time and an ability to produce large numbers of small eggs. Enriched environments with large bacterial resources

are typical for these taxa and they are able to withstand chemical enrichment and elevated carbon and nitrogen levels. Nematodes in this category form dauerlarvae under unfavourable conditions.

*c-p*2 - These nematodes also have relatively short generation times, small eggs and fast growth rates. However they occur in a wide range of environments, but they do not form dauerlarvae. In contrast to *c-p*1 nematodes their response to environmental pollution is less rapid. Nematodes belonging to this category mostly feed on bacteria and fungi.

*c-p*3 - Nematodes belonging to this category are more sensitive to environmental disturbances and they have a longer generation time than the *c-p*2 nematodes. This category also includes bacterial and fungal feeders, as well as predators.

*c-p*4 - Nematodes in this category have a long generation time, they are large bodied with relatively small gonads and they are sensitive to chemical disturbance. This category includes some bacterial, omnivorous and predacious nematodes.

*c-p*5 - Nematodes that belong to the category belong to the order Dorylaimida and they are all large bodied and are long living. They produce few but large eggs; they have low metabolic rates and are generally slow movers. These nematodes are highly sensitive to chemical pollution and include large predatory and omnivorous nematodes.

2.4 Numerical and Statistical Analysis

The diversity of nematodes in each sample was calculated using Simpson's dominance index as expressed in equation 4:

$$\lambda = \sum p_i^2 \qquad \text{Equation 4}$$

Where p_1^2 is the portion of the total density derived from the *i*th species. The reciprocal value $1/\lambda$ was used in this study.

The Simpson index is more robust than the Shannon Index, especially when using small sample sizes and has the advantage that confidence limits can be fitted (Magurran, 1983). Data were jack-knifed to generate an overall index of diversity (and associated 95% confidence interval) for each station following the protocols outlined by Magurran (1983).

The data have been analysed in a number of ways. In the first instance the summer and winter data were treated separately and mean measures and assorted indices of dispersion

were calculated for each station. Within each season, patterns across stations and between measures were examined using either Pearsons or Spearmans Rank correlations (Zar, 1999) depending on whether the data were parametric or non-parametric, as determined by visual plots of normality and Levine's test (Harrad *et al.*, 2008) for homoscedasticity. To test for the effect of seasonality on univariate measures, either ANOVA or Kruskal-Wallis non-parametric ANOVA tests were employed (Zar, 1999). A post-hoc comparison of means using the Tukey Honest Significance Difference Test (HSD) was then computed to determine significant differences between the means of multiple groups (Zar, 1999). Tests were considered significant at the 95% level ($p = 0.05$) and all results were corrected for multiple testing using the Bonferroni adjustment (*a posteriori*) (Hochberg, 1988). The Bonferroni adjustment was used in order to minimize Type -1 statistical errors and only ρ-values lower than the Bonferroni values were considered as being significant. All computations were effected in Statistica v. 7 (Statsoft).

Owing to the fact that elemental data were only collected by Monteiro *et al.* (1999) during summer, their comparisons with nematode data have been limited to summer samples only. Furthermore, since Monteiro *et al.* (1999) have provided only a single datum for each elemental measure per station, it has been necessary to collapse nematode and sediment grain measures into mean values per station.

Nematode communities were identified from the samples on the basis of similarities in their numerical species composition. In the first instance, the seasonal data were treated separately; densities were root transformed and rare species (those occurring in less than 5% of the samples) were eliminated, following the arguments of Clarke & Gorley (2001). The similarity between samples in their numerical species composition was determined using the Bray Curtis measure (e.g. Field *et al.*, 1982) (Equation 5):

$$\delta_{jk} = \frac{\sum_{i=1}^{s} \left| Y_{ij} - Y_{ik} \right|}{\sum_{i=1}^{s} \left(Yi_{j} + Y_{ik} \right)} \qquad \text{Equation 5}$$

Where, Y_{ij} = score for ith species in the jth sample; Y_{ik} = score for the ith species in the kth sample; δ_{jk} = dissimilarity between the jth and kth samples summed over all s species with δ_{jk} ranging from 0 (identical scores for all species) to 1 (all species unique).

The resulting similarity matrix was visualised in both a 2-dimensional dendrogram and a 2-dimensional MDS plot. All analyses were conducted using PRIMER version 5 software (Clarke & Warwick, 1994; Clarke & Gorley, 2001).

In order to identify the species that were largely responsible for structuring the communities identified in the dendrograms and MDS plots, the SIMPER routine in PRIMER was employed, *a posteriori*. SIMPER analysis relies on Bray-Curtis similarities between samples and the routine is able to identity characteristic and discriminating aspects between two samples. In SIMPER the average dissimilarity between all pairs of samples is computed by using the contribution that each species makes towards the average dissimilarity between two groups. Abundant species will contribute more towards the dissimilarity within a group. Likewise, the average similarity between all groups are calculated and the contribution of each species to that similarity is then determined (Clarke & Warwick, 1994). Given that most nematode assemblages do not display normality, comparisons between and within groups are not tested as 1-way ANOVA. Instead a non-parametric procedure, based on a similarity matrix of the sample set, ANOSIM (analysis of similarities) was used to test for differences among samples. A global R statistic is calculated (Equation 6) to test the null hypothesis that there are no differences in community structure at the sampling sites.

$$R = \frac{\left(\bar{r}_B - \bar{r}_W\right)}{\frac{1}{2}M}, \qquad \text{equation 6}$$

Where $M = n\ (n\text{-}1)/2$ and n is total number of samples. R approximates zero if all similarities between and within samples are the same, thus accepting the null hypothesis. When R =1 all replicates within sites are similar to each other than to any other replicate from other sites (Clarke & Gorley, 2001).

Following the separate analysis of summer and winter data, all were combined to explore the effects of seasonality and station on nematode community composition and structure. Seasonality was further tested for explicitly using a two-way, fixed main effects (season, station and season x station) Permutational Analysis of Variance (PERMANOVA) in PRIMER v6 (Clarke & Gorley, 2006) with PERMANOVA add-on package (Anderson *et al.*, 2008). PERMANOVA uses permutations to test the effect of variables on a set of factors (such as season and station) in an analysis of variance. Since the winter matrix only consisted of three stations the analysis was restricted to the corresponding summer stations. Differences

in nematode structure were determined by Bray-Curtis similarity procedure using untransformed nematode abundance data with group average linkage.

In exploring the relationships between environment and nematodes, multivariate analyses have been used in addition to the bivariate ones noted above. The BIOENV procedure in PRIMER was used to explore the quantitative link between the nematode communities and their environment, Rank correlations estimates between a subset of similarities of environmental factors and similarity between samples provide an estimate of which environmental variable or combination of variables best group the samples according to their taxonomic patterns (Clarke & Warwick, 1994; Somerfield *et al.*,1994). The procedure is therefore able to explain how the abiotic factors best match the biological matrix. Owing to the fact that there was only one set of full environmental data (summer), analyses were restricted, and were further constrained because they required that all nematode samples be collapsed.

Abundance and biomass (per 10 cm^2) curves (ABCs) were constructed in order to determine the effect of environmental stress on community structure. Abundance curves correspond to the k-dominance curves described by Lambshead *et al.* (1983) while biomass was calculated according to a standard formula described by Warwick (1986) and Warwick *et al.* (1997). Biomass was determined following Wieser (1960) and Warwick & Price (1979):

$$\text{Dry mass} = 1.13 \times (L \times W^2) \times 530 \times 0.25 \qquad \text{equation 7}$$

where the 1.13 refers to the specific gravity of nematodes extracted in Ludox, L = body length (µm) and W = maximum (µm), 530 is a dimensionless conversion factor for nematodes and 0.25 is conversion factor to dry mass.

Density and dry mass of each species were plotted as cumulative percentages against species rank. When the biomass curve is well-separated from and lies above the abundance curve then the community is considered to exist in an undisturbed environment. However, when the two curves are reversed the community is considered to be subject to heavy disturbance. Intermediate levels of disturbance will be indicated by the close proximity of the two curves that may cross each other. PRIMER v5 calculates ABC plots and provides a single statistic, Warwick (W). Clarke (1990) proposed the W statistic and it is defined mathematically as:

$$W = \frac{\sum_{i=1}^{S}(B_i - A_i)}{[50(S-1)]}, \qquad \text{equation 8}$$

Where A_i = abundance and B_i = biomass and S = number of species to ith value. The W ranges from +1 for even densities between species but biomass dominated by a single species to -1 with even biomass but dominance by a single species.

CHAPTER 3

Results

3.1. Physico-Chemical Environment

3.1.1. Sediment Size Structure

Figure 3.1A shows changes in the sediment composition across the study site during summer, from which it can be seen that Gravels (-1 φ; > 2 mm) represented a generally small fraction of the sediments. Sediments at Station 1 were dominated by mud (5 φ; < 63 μm), which accounted for 94% of the sediment weight there. The mud contribution decreased across the study site, as sand (2 φ; 250 μm) tended to increase, with the transition between Station 1 and Station 2. Sediments were dominated by sand, which represented between 75-93% of sediment weight.

Effectively similar results were observed during winter (Figure 3.1B). Gravel was again uncommon and although it constituted the sub-dominant component at Station 4 (> 13.5%) it contributed < 1% to the sediment at all other Stations. As noted in the summer samples, the sediments at Station 1 were muddy (> 94%) while sands otherwise were dominant (77-89%). There was some intra-station variability in sediment composition: one sample at Station 6 was dominated by mud (>95%) whilst two samples at Station 4 yielded more than 35% gravel (See Appendix 1.2 for full details).

A two-way ANOVA (station and season) indicated that although mean particle size did not vary with season (Table 3.1), it did vary with station and it did vary at some stations on a seasonal basis. Overall, the mean sediment grain size was significantly smaller at Station 1 (4.47 φ) than at the other stations during both seasons and it tended to increase with distance across the study site (Figure 3.2). There was no consistent pattern to detailed seasonal changes in sediment size across the sampling grid, suggesting localised factors may have been responsible for the results observed at each station. The highest mean grain size was recorded at Station 4 (winter: 1.93 φ), while mean grain sizes ranged between 2.50 - 2.99 φ for all other stations (Figure 3.2). Otherwise, samples from Station 4 (winter) differed in mean grain size (significantly) from all samples except for those from Station 3 (winter), Station 5 (both seasons) and Station 6 (summer) (Table 3.2).

3.1.2. Trace Metals and Particulate Organic Carbon and Nitrogen

The concentrations of trace metals ($mg.kg^{-1}$) and percentage particulate organic Carbon and Nitrogen, corresponding to the sampling sites used by Monteiro *et al.* (1999), are presented in Table 3.3. Trace metals, organic Carbon and Nitrogen concentrations were highest at Station 1 with the transition between high and low values somewhere between Station1 and Station 2 and decreasing across the sampling transect to Station 6.

The results of Spearman Rank correlations (Table 3.4) indicate that the different environmental variables measured were significantly and highly inter-correlated. Mud and grain size exhibited a strong positive correlation with all the chemicals indicating that chemical concentrations were significantly higher in Group I samples, with chemical concentrations decreasing along the study grid. These results were corroborated by the strong negative correlations between sand and chemical concentrations. Further, all chemicals were highly inter-correlated indicating the accumulation of chemicals in mud-dominated environments.

3.1.3. Summary

In summary, sediment size generally increased along the transect grid from Stations 1 to 6, while concentrations of trace metals, organic Carbon and Organic Nitrogen decreased. Although the latter measures were only determined for summer, there is no reason to suppose that this pattern would not hold true for winter, given the general consistency in the size distribution of the sediments across the Bay (Figure 3.1), and the strength of the correlations between metals and sediment size (Table 3.4).

3.2 Nematodes

3.2.1 Abundance

Temporal and spatial changes in the abundance of nematodes in Saldanha Bay are shown in Figure 3.3. During summer there was a general decline in nematode abundance across the sampling stations, and while this trend was also apparent to a lesser extent during winter, there was a much greater variation about mean estimates of abundance per station. On average, densities during winter were higher than those observed during summer, as evidenced by the results of the two-way ANOVA (Table 3.5). The pattern observed was not a linear decrease in density with station, however, as suggested perhaps by Figure 3.3. During

winter, nematodes were significantly less common at Stations 4 and 5 than at the balance of, especially the other winter, stations (Table 3.6). The results indicate that abundance was significantly lower for Stations 5 and 6 during summer, than at most of the other stations during both seasons.

3.2.2 Sample Diversity

Temporal and spatial patterns in the diversity of nematode samples across Saldanha Bay (Simpson's reciprocal Index, $1/\lambda$) are illustrated in Figure 3.4. Species diversity was very low at Station 1, increased significantly to Station 2 and remained similarly high across the balance of the transect. Similar patterns were observed during both seasons and there was no interaction between season and station in 2-way ANOVA (Table 3.7). Except for the samples collected at Station 4, nematode diversity was by and large significantly greater during summer than winter (Table 3.8).

3.2.3 Community diversity

A plot of (pseudo)mean community diversity at each station, constructed by jack-knifing Simpson's $1/\lambda$, is shown in Figure 3.5 and, the results of a 2-way ANOVA (season and station) are presented in Table 3.9. Community diversity was significantly different between stations and between seasons and there was a significant interaction between the two. Diversity was lowest at Station 1 during both seasons (Figure 3.5) and they differed significantly from Station 4 (summer and winter) and Station 6 in winter (Table 3.10). Station 6 (winter) revealed significant differences with all stations. Station 6 summer sites yielded the highest diversity. Only Stations 1, 4 and 6 were tested for spatial and temporal interactions and the results do not portray the influence of other sampling sites on the diversity of the community across Saldanha Bay. In summary, diversity was low at Station 1; diversity increased towards the middle Stations, reaching maximum diversity at Station 6 in summer while diversity in winter showed a decrease towards the outer Station 6, to approximate values recorded at Stations 2 and 3.

3.2.4 Species Composition

Summer:

A total of 100 species were identified during summer (APPENDIX 1.3): the order Chromadorida was dominant. These 100 species were divided among 32 families and Figure

3.6illustrates changes in mean familial richness per sample across the study site. A maximum of 15 families were present at Station 1 with Comesomatidae (51.8%) as the dominant family. There was no significant difference between number of families at Station 1 and the other Stations (Table 3.11). Family representation was similar, yet variable, outside Station 1 and no family contributed in excess of 50% of individuals to the assemblage at any given site. Linhomoeidae (26%) and Leptolaimidae (22%) replaced Comesomatidae at Station 2 (maximum of 23 families) and Station 3 (maximum of 18 families), respectively. Linhomoeidae was again the dominant family at Station 4 (23 families) and Station 6 (28 families), but was replaced by Xyalidae (35%) at Station 5 (21 families).

Overall, the dominant taxa during summer were *Sabatieria* sp.1, *Microlaimus* sp. 1, *Daptonema* sp. 1, *Terschellingia* sp. 3 and *Metalinhomoeus* sp.1 (APPENDIX 1.3). These species accounted for 40% of the total nematodes sampled. A total of 19 taxa were represented as "singletons" or "doublets" in samples, and these accounted for <3% of the total numbers identified (APPENDIX 1.3).

Spatial plots of the abundance of the most common species are shown in Figure 3.6, and the results of 1-way ANOVA and Tukey tests are shown in Tables 3.12 and 3.13. All the dominant species investigated showed pronounced and significant patterns of distribution across Saldanha Bay. *Sabatieria* sp.1 was the dominant taxon at Station 1 (contributing to the low diversity observed at this site) and was significantly less abundant at Station 3, 5 and 6 (Figure 3.6A). In contrast, *Microlaimus* sp.1 exhibited a reverse trend with densities initially low at Station 1 and increasing to a maximum at Station 6 (Figure 3.6B). The abundance of *Metalinhomoeus* sp.1 was low at Station 1 and increased to a maximum at Station 4, before declining again at the outer stations (Figure 3.6C). The densities of *Chromadorella* sp.1 were low at Station 1, attained a maximum at Station 2 and then declined progressively across the balance of the study site.

Winter:

A total of 83 species were identified at Stations 1, 4 and 6 (APPENDIX 1.4), comprising 27 families. The mean familial richness of samples at Station 1 was significantly lower than the other Stations (Figure 3.6; Table 3.14). In contrast to Station 1 (summer) the winter assemblage there was represented by only 8 families, with Comesomatidae dominating (95%). Otherwise, winter assemblage composition generally followed the same trend as in

summer, with Microlaimidae (13%) and Linhomoeidae (29.3%) as the dominant families at Station 4 (23 families) and station 6 (28 families), respectively.

Sabatieria sp.1, *Microlaimus* sp.1 and *Metalinhomoeus* sp.1, *Paralinhomoeus* sp.1, and *Linhomoeus* sp. were the dominant species overall and accounted for 61% of total numbers in the winter assemblage (APPENDIX 1.4). *Sabatieria* sp.1 alone accounted for 38% of this total. Seventeen species were represented as "singletons" or "doublets" and they accounted for just over 1% of the total numbers identified during winter.

Just as noted during summer, the dominant species all showed marked spatial patterns in abundance across Saldanha Bay (Figure 3.7), and the patterns observed for each were broadly similar to those observed some six months before. *Sabatieria* sp.1 decreased significantly across the study site (Tables 3.15 and 3.16) and was absent from a number of Station 6 samples (Figure 3.7A). *Microlaimus* sp.1 was again least common at Station 1 and most abundant at Station 6 (Figure 3.7B), while *Chromadorella* sp.1 was most common mid-way along the transect (Figure 3.7D). Only *Metalinhomoeus* sp.1 showed a slightly different pattern of abundance during winter, being most common at Station 6, as opposed to Station 4 during summer (Figure 3.7C).

3.2.5 Feeding Groups

The relative importance of the different feeding types is illustrated in Figure 3.8: all four feeding types described by Wieser (1953) were present in all samples. Non-selective deposit feeders (1B) and epigrowth feeders (2A) were the dominant feeding types (50 % and 25 % respectively) during summer, whilst selective deposit-feeders (1A) accounted for 22% and omnivores/carnivores (2B) only for 3% of the assemblage. The ratio of feeding types differed across the study area during summer. The ratio of non-selective deposit feeders to epigrowth feeders was 15.6 at Station 1 and it decreased with distance from Station 1. At the middle stations non-selective deposit feeders comprised approximately 44% of the assemblage; their contribution increased again at Station 5 (63%) and then approximated the values for epigrowth feeders (26% vs. 43%) at Station 6. The ratio of non-selective deposit feeders to epigrowth feeders was 1.4 at Station 4 and 0.54 at Station 6. The winter assemblage was also dominated by non-selective deposit feeders 1B (59%) and epigrowth feeders (26%), while selective deposit feeders and omnivores/carnivores only accounted for 9% and 6% of the winter assemblage, respectively. The ratio of non-selective deposit feeders

to epigrowth feeders at Station 1 indicated a complete dominance of non-selective deposit feeders (285:1), but the ratio decreased to 1.1 and 0.8 for Stations 4 and 6, respectively.

3.2.6 Maturity Index

Maturity Indices (MI) for summer and winter assemblages are presented in Table 3.17, while the *c-p* scores for each taxon is listed in Appendices 13 and 1.4. In summer, MI values increased with distance from Station 1 (Figure 3.9) reaching a peak at Station 3 (2.47). MI values then decreased and the lowest values were recorded at Station 5 (2.18). Most nematodes belonged to the *c-p* 2 (bacterio-fungal feeders) guild at all the stations. This value was the highest at Station 1 (77.6%) and lowest at Station 6 (55.9%). Station 1 exhibited the lowest proportion of *c-p* 3 individuals (18.7%) and the contribution of these individuals increased progressively across the study grid reaching a maximum of 36.6% at Station 6. The contribution of *c-p* 4 nematodes was greatest at Stations 3 and 4, 13% and 11% respectively, but it was low at all the other stations. Stations 5 and 6 were the only stations where *c-p* 5 individuals occurred. In general *c-p* 1 values were low at all stations except for Station 5 where these nematodes accounted for 11% of the assemblage, largely due to the fact that *Thalassomonohystera* sp.1 was present in all the cores at Station 5. Station was also the only station that was significantly different from all other station (Table 3.18).

In winter, Station 1 (2.05) recorded the lowest overall MI, with values increasing away from Station 1. Station 6 exhibited the highest overall MI (2.85). The contribution of *c-p* 1 and *c-p* 4 were low and no taxa belonging to *c-p* 5 were recorded. Station 1 was dominated by *c-p* 2 (95%) nematodes and their contribution decreased across the study grid while the contribution of *c-p* 3 increased from 4% (Station 1) to 28% (Station 6).

3.2.7 Nematode Communities

3.2.7.1 Summer

A dendrogram showing the similarity in the numerical composition of the samples collected during summer is shown in Figure 3.10. Two clear clusters were apparent at the 17% level of similarity, separating samples associated with Station 1 (Group IA), from the balance (cluster Group IB). Most of the divisions in IB occurred at similarities between 38

and 43%. At the 38% level cluster Group IB was further divided into Group IIA, being generally comprised of samples from Stations 2-4, and Group IIB, associated with samples from Stations 5-6. These overall groups are conveniently clustered here as Group IA (Group 1), Group IIA (Group 2) and IIB (Group 3). Except for the majority of samples comprising Group 1, it is interesting to note that overall levels of similarities were relatively low, even between samples from the same station. This suggests considerable intra-station variability. The physical and biological attributes of these three groups are shown in Table 3.19, immediately below Figure 3.10. Moving from Groups 1 to 3, there is an apparent reduction in the amount of mud and a concomitant decrease in the concentrations of trace and heavy metals and organic Carbon and Nitrogen. Although there is a reduction in mean nematode abundance from Group 1-3, samples within Groups 2 and 3 are similar in both levels of species and feeding diversity.

The results of an *a posteriori*, 1-way ANOSIM (Table 3.20) revealed that all three groups were well separated with a global statistic of R = 0.84 at the 0.1 % level of significance. Pair-wise comparisons between cluster groups showed that Group 1 was consistently well separated from all other stations (R = 0.999). Likewise, Groups 2 and 3 were equally well separated from one another (R = 0.81).

Table 3.21 summarizes the contributions made by individual species towards the structure of the dendrogram (Figure 11) as identified by the SIMPER routine in PRIMER. Group 1 samples were very homogeneous and three species (*Sabatieria* sp.1, *Parodontophora* sp.1 and *Terschellingia* sp.3) accounted for 97% of the similarity within the Group. Group IB samples were more heterogeneous (similarity index: 31.9%): six species contributed ~ 50% of the similarity, with *Sabatieria sp.*1 (19%) being most responsible. Group 2 samples were also characterized by a high abundance of *Sabatieria sp.*1 (21%), and five other species contributed to more than 50% of the similarity (similarity index: 43.7%) within the Group. Four species accounted for ~ 50% of the similarity within Group 3 samples (similarity index: 35.4%). Interestingly, only *Sabatieria* sp.1 was held in common between these two groups.

The nematodes that were responsible for the greatest dissimilarity between assemblages as identified by the SIMPER routine are summarized in Table 3.22. From this it is clear that *Sabatieria* sp.1, which was responsible for ~34% of the dissimilarity between groups IA and IB, was characteristically more common in the former than the latter as too

were *Parodontophora* sp.1 and *Terschellingia* sp.3. Together these three taxa contributed > 50% of the dissimilarity between the two groups. It is interesting to note that no species from Group IB were selected by the SIMPER procedure at this level, indicating that communities in these latter samples were highly variable.

Groups 2 and 3 were 76% dissimilar to each other on average and 13 species were needed to account for 50% of the dissimilarity observed (Table 3.22). As noted from Table 3.19, densities of nematodes were generally higher in Group 2 than 3, and the other taxa that were at greater abundance in the latter than the former were: *Daptonema* sp.1, *Microlaimus* sp.1, *Thalassomonhystera* sp.1 and *Paramicrolaimus* sp.1.

3.2.7.2 Winter

A dendrogram showing the similarity in the numerical composition of three winter stations is given in Figure 3.11. Samples again clustered in an ordered manner and two major clusters, IA and IB, were recognized: Group IA (Group1) was distinct from the rest (10.4% similarity), while IB was divided into Group IIA (Group 2) and Group IIB (Group 3) at a similarity of 37%. Group 1 consisted entirely of Station 1 samples, Group 2 comprised all samples from Station 4 and Group 3 comprised all Station 6 samples.

The physical and biological attributes of these three groups are shown in Table 3.23, immediately below Figure 3.11. Sand fractions were low in Group 1 increasing to maximum values in Group 2 and thereafter decreasing in Group 3 samples. The mud fractions changed in a reversed manner from Group 1 to Group 3 in a similar manner to summer. However, the contribution of mud was increased in Group 3 winter samples. Gravel accounted for 9% of Group 2 sediments, but was negligible in the other Groups. Mean sediment grain size also increased across the study site with maximum values at Group 2 sites. The density of nematodes was highest at Group 1 sites and decreased across Groups 2 and 3. The order Chromadorida remained the dominant taxon throughout the study site. The family Comesomatidae was dominant in Group 1 assemblages and was replaced by the family Microlaimidae in those of Groups 2 and 3. *Sabatieria* sp.1 completely dominated the nematode fauna of Group 1 assemblages. *Microlaimus* sp.1 and *Sabatieria* sp.1 dominated Group 2 assemblages, while *Microlaimus* sp.1 and *Paralinhomoeus* sp.1 dominated those of Group 3. Species richness was lowest in Group 1 site, and increased in Groups 2 and 3 (as summer). Non-selective deposit feeders (IB) dominated Group 1 assemblages (95%) and feeding diversity was low (expressed as $H' = 0.5$). Feeding diversity was similar for Groups 2

and 3 (again as summer): Group 2 was dominated by IB feeders that were replaced by epigrowth feeders in Group 3.

The results of a 1-way ANOSIM procedure (Table 3.24) revealed that groups were separated with a global statistic of R = 0.99 at 0.1 % significance level. Pairwise comparisons revealed that Group 1 was completely separated from all other stations (R=1). Groups 2 and Group 3 were equally well separated from one another (R = 0.95).

Table 3.25 lists the results of the SIMPER analysis for the winter data. Group 1 was dominated by *Sabatieria* sp.1 (similarity index: 92.9%), while *Microlaimus* sp.1 (31%) was the major contributor to the abundance in the remaining Groups. Further analysis showed that among Group 2 samples *Microlaimus* spl. (20%), *Sabatieria* sp.1, *Parallelecoilas* sp.1 and *Thalassomonhystera* sp.1 contributed together to 50% of the similarity index of 51.5%. *Microlaimus* sp.1 (~30%) was the major contributor to similarity in Group 3 and with *Metalinhomoeus* sp.1 and *Paralinhomoeus* sp.1 accounted for 50% of the abundance.

Table 3.26 lists the species that contributed towards the dissimilarities in winter samples. As in the summer samples, *Sabatieria* sp.1 was the dominant species that caused dissimilarities between the different cluster groups. Group 1 was 94% dissimilar from the rest, with *Sabatieria* sp.1 contributing 53% of the dissimilarity. Group 1 samples were extremely homogeneous (93% similarity) while the remaining groups were more or less similar (37%). Groups 2 and 3 were 69% dissimilar. *Microlaimus* sp.1 (12%) was the dominant species in the dissimilarity index and ten species accounted for 50% of the dissimilarity. Densities of nematodes (Table 3.23) were generally higher in Group 2 than 3, yet seven taxa were at greater abundance in the latter than the former: *Microlaimus* sp.1, *Metalinhomoeus* sp.1, *Paralinhomoeus* sp.1, *Paralongicyatholaimus* sp.1, *Linhomoeus* sp.1, *Molgolaimus* sp.1and *Bolbolaimus* sp.1.

3.2.7.3 Summer and winter combined

In order to determine the effect of seasonality on assemblage composition, the winter and summer samples have been combined (Figure 3.12) and the whole dataset was re-analysed. Groups IA and IB were two distinct groups with only 14% similarity. Group IB was divided into Groups IIA and IIB that separated at 32.5% similarity level. Group IA (Group 1) represented Station 1 samples from both seasons; Group 2 was represented by Group IIA and consisted of all the middle stations in summer as well as (distantly) winter

samples from Station 6; Group 3 (Group IIB) was comprised primarily of Stations 5 and 6 and included Station 4 (winter).

Table 3.27 summarizes the sediment and biological parameters that structure the pooled data set. The sediment profile followed an orderly pattern with sand fraction increasing from Groups 1 to Group 3 while mud fractions displayed an inverse pattern. Mean sediment grain size also increased across the groups and gravel formed a small component of the overall sediment structure.

Nematode density was highest at Group 1 sites and decreased across the dendrogram from left to right. The order Chromadorida dominated throughout the study site. Comesomatidae was the dominant family in Group 1 and was replaced by the family Microlaimidae in Groups 2 and 3. *Sabatieria* sp.1 was the dominant species in Group 1, *Sabatieria* sp.1 and *Microlaimus* sp.1 dominated Group 2 while *Microlaimus* sp.1 and *Paralinhomoeus* sp.1 dominated Group 3 assemblages. Species richness was low at Group 1 sites and high in Groups 2 and 3. Non-selective deposit feeders (IB) dominated Group 1 samples and feeding diversity was low ($H' = 0.04$). Group 2 was characterised by the dominance of IB feeders and they were replaced by epigrowth feeders, while feeding diversity was similar for Groups 2 and 3.

The results of a 1-way *a posteriori* ANOSIM procedure (Table 3.28) revealed that the Groups were well separated with a global R statistic of 0.83 at 0.1 % significance level. Pair-wise comparisons of nematode communities showed that Group 1 was well separated from all other stations ($R = 0.9$). Groups 2 and 3 were also distinct ($R = 0.62$), although the lower test statistic suggests overlap between samples was evident.

Sabatieria sp.1 accounted for 94% of the similarity of Group I samples (Table 3.29). The densities of *Sabatieria* sp.1 and *Microlaimus* sp.1 alternated as the dominant contributor to the similarity indices of 38.6% and 34.8% for Groups 2 and 3, respectively.

Group IA and IB were very dissimilar (88.4%) with *Sabatieria* sp.1 and *Microlaimus* sp.1 contributing to 51% of the dissimilarity (Table 3.30). Further, the dissimilarity between Groups 2 and 3 were also high (74.2%) and 13 species contributed to 50% of the dissimilarity. Four species, *Daptonema* sp.1, *Thalassomonhystera* sp.1, *Metacyatholaimus* sp.1 and *Paramicrolaimus* sp.1, were the major contributors from Group 3 towards this dissimilarity.

3.2.8 Effects of Season and Distance

The results of distance-based PERMANOVA on Station (fixed), samples nested within stations and Season (fixed) are presented in Table 3.31. The results were derived from Bray-Curtis similarity using untransformed data showed that only 13.3% of the variation within the data was explained by differences between Seasons, while the largest percentage difference (41.6 %) occurred between Stations. The results for the variation in between Station-Season and samples accounted for 27% and 38% of the differences in community structure.

3.2.9 Abundance Biomass Comparison curves (ABC)

The species dominance curves for the summer samples are presented in Figure 3.13. It should be remembered that in undisturbed habitats the biomass curve dominates the abundance curve, and that increased levels of disturbance result in an elimination of some of the dominant species so that the two curves tend to coincide or overlap. This is reflected in the Warwick Statistic, which is a measure of stress within a sample set and ranges from 1 (undisturbed) to -1 (extremely disturbed). At Station 1, the cumulative abundance curve was higher than that for biomass, and the W statistic was -0.44, suggesting the samples were subjected to environmental stress. In the AB Curves for all other stations, the cumulative biomass curve was generally slightly above that of abundance (W = ~0.1), suggesting that these sites were also subjected to a measure of disturbance. The exception was Station 5, where the biomass curve was consistently elevated above that of abundance (W = 0.241), suggesting this site was the least affected by environmental disturbance. No meaningful k-dominance curve could be generated from Station 1 in winter since the sample site was dominated by *Sabatieria* sp.1. However, AB Curves for Stations 4 and 6, illustrated in Figure 3.14, show that the cumulative biomass curve is consistently above the abundance curve (W = 0.118) while Station 6 exhibited a variable relationship with biomass curve slightly above abundance curve (W = 0.063).

3.3 Relationships between the physical and biological data

Simple correlations between the physical and biological data are reported in Table 3.4, and these show that mean sediment grain size (and sand fractions) were strongly (but negatively) correlated with density. Diversity was positively (and significantly) correlated with the sand fraction, although the R value was low. Increased species diversity was also negatively

correlated to density. Both sand and mud fractions were strongly correlated with the abundance of the dominant species: as expected *Sabatieria* sp.1 was positively correlated with mud and negatively correlated with sand, whilst *Microlaimus* sp.1 exhibited the opposite response. These results are in agreement with previously noted changes in abundance across the study site (see Figure 3.7).

Metals, organic Carbon (C) and organic Nitrogen (N) were all strongly and positive correlated with nematode density, but negatively correlated with diversity Further, Total Cu, Total Lead (Pb), Total Cadmium (Cd), Total Zinc (Zn) and organic C correlated significantly with the dominant species i.e. *Sabatieria* sp.1 and *Microlaimus* sp.1.

In order to look at the whole suite of measured environmental variables on the structure of the nematode communities identified by cluster analysis (Figure 3.10), the data were subjected to a BIOENV procedure. The metal and other elemental data were derived from Monteiro *et al.* (1999), and were collected during summer, and represented here as mean values per station (Appendix 1.5). In order to fit the biological data to these it was necessary to collapse all nematode samples collected during summer into a single average per station, a process that has been repeated too for the sediment data. The dendrogram based on group-average sorting of the similarity matrix between samples is shown in Figure 3.15. This compares well with that shown in Figure 3.10, though the variability evident in the latter has obviously been completely lost. Station 1 separated from all other Stations. Stations 2-6 generally followed the spatial profile of the study area. With the sandy sites clustered together and the sites with mixed sediments forming one group. The outputs from the BIOENV analysis of the summer data are listed in Table 3.32. Copper (Cu) and organic nitrogen were the two variables (Spearman's $\rho = 0.703$) that "best" explained the variation in the nematode data. Cu was also the only variable included in the top four best combinations (Spearman's $\rho = 0.695$). The best three-variable combination was Cu, sediment grain size and organic nitrogen (Spearman's $\rho = 0.697$). Variables that were not included in the ten best combinations included Pb, Fe, Al, mud, grain size and gravel. Organic carbon and Cd were included in only one combination with Zn and sand in the lower six combinations.

3.4 Summary

In summary, muddy sediments characterised Station 1 samples, with high concentrations of trace elements, organic Carbon and organic Nitrogen. Nematode abundance was greatest at this station and communities were dominated by *Sabatieria* sp.1 during both seasons. There

was generally a high degree of similarity in the numerical composition of samples within and between seasons,: diversity was low and most of the species were non-selective deposit feeders. Sand fractions tended to increase progressively with distance from Station 1, although there was some seasonal and intra-station variability. Trace metals, and organic C and N, and overall nematode density significantly decreased from Stations 1-6, whilst diversity increased. The ratio of deposit feeders to epigrowth feeders also changed with distance. Coloniser species (*c-p 2*) were dominant at Station 1 during both seasons, whilst the contribution of *c-p 3* species to the community increased with increasing distance away from Station 1. This mixture of *c-p 2* and *c-p 3* indicates that the nematode community is variable and dependant on sediment structure, food resources and physical stresses such as water circulatory patterns and wind direction. *Sabatieria* sp. 1 was replaced by *Microlaimus* sp. 1 and *Paralinhomoeus* sp.1 as the dominant taxa across the study site and that season was not a major determinant of nematode community structure.

CHAPTER 4

DISCUSSION

4.1 Physical and chemical nature of sediment structure

Sediments at Saldanha Bay consisted primarily of sand and mud with small amounts of gravel for both study seasons. Mud was concentrated in the western corner of Small Bay with dominant deposits under the mussel rafts (Netto & Valgas, 2010). The transition from mud-sand through mud-gravel-sand to sand-dominated mixtures along the middle stations correspond well with the general sediment profiles described by Flemming (1977) and more recently by Monteiro *et al.* (1999).

The change in sediment grain size over distance, as well as season, can be attributed to both anthropogenic and natural events. Weeks *et al.* (1991a, b) has reported that during winter, water movement is primarily tidally-induced, and passing cold fronts associated with prevailing north-easterly winds tends to drive water movement in the Bay. The increased advection of water into the Bay during winter would serve to scour and drive sediments across the bay resulting in an increase in grain size in "exposed" areas such as Station 4. Of course, finer sediments are also deposited at more sheltered sites and there was a deposition of mud in two Station 6 samples (Flemming, 1977; Monteiro *et al.* 1999). Ships that enter the harbour use a shipping lane and they have a turning circle (~580 m diameter) on the seaward side of the loading jetty (http://www.ports.co.za/saldanha-bay.php). Stations 3 and 4 were located close to the edges of this shipping lane. The lane is periodically dredged and it is likely that this could contribute to the elevation of gravel fractions at both sites during both seasons.

4.2 Metals and organic matter

The accumulation of organic carbon, organic nitrogen and metals are commonly associated with the presence of fine sediments such as mud (Clark *et al.*, 2009) In marine sediments bacteria and micro-organisms secrete a mucus film that surround sediment particles. This biofilm may then act as a template for the uptake of metals and water. Micro-organisms (such as diatoms) also excrete waste products used by other bacteria). Organic matter and trace metals often form complex compounds and these then become readily available to organisms through chelation (Duchart *et al.*, 1973; Howarth *et al.*, 1988; Decho, 2000). This trend was

followed in the present study with the highest concentrations of organic matter and metals present under the mussel rafts at Station 1. The concentration of metals, organic carbon and nitrogen decreased significantly with increasing distance from the mussel rafts, as mud and organic matter levels declined.

4.2.1 Organic matter

Owing to its position in the Benguela Upwelling region Saldanha Bay is characterized by relatively high levels of phytoplankton primary production (3.47 g of C m^{-2} d^{-1}, Pitcher & Calder, 1998). When phytoplankton eventually dies the material sinks through the water column and settles on the seabed as phytodetritus (approximately 1g Carbon $m^{-2}d^{-1}$ for the whole bay, Monteiro *et al.*, 1998). Natural levels of primary production are driven by upwelled nitrogen and daily new primary production is ~ 1.72 g of C m^{-2} d^{-1} (Pitcher & Calder, 1998). The balance of primary production (~ 1.75 g of C m^{-2} d^{-1})is derived from regenerated organic matter or from anthropogenic activities. Two sources of increased organic matter have been noted in the area: that from the fish processing plant in Small Bay (Monteiro *et al.*, 1997) and that comprising faecal and biogenic waste from the mussel cultivation industry (Stenton-Dozey *et al.*, 1999).

4.2.1.1 Organic nitrogen

Monteiro *et al.* (1999) and Clark *et al.*, (2009, 2011) reported that organic nitrogen levels were highest in the western part of Small Bay, including the mussel rafts, it decreased across the bay and they concluded that the high levels of organic nitrogen in the sediments were derived from phytoplankton and organic input from fish processing plants, mussel farm, sewage and storm-water drainage from the waste water treatment sites and septic tanks. Recently Toefy (2011) reported mean organic nitrogen values for two sites associated with cultural eutrophication *viz.* St Helena Bay and Robben Island in Table Bay. Organic nitrogen content of control samples were respectively 0.09% and 0.05% while impacted sites contained 0.2% and 0.13% organic nitrogen. These values were lower than those recorded at Station 1 in Saldanha Bay, due to the deposition of faeces and pseudofaeces from the mussel rafts. This value was however lower than the 0.5% recorded by Bailey (1987), for the upper sediment layer at St Helena Bay. This difference could be explained in the retention of organic matter and the clearing rates due to the longer retention period (~ 25days) of organic matter in St Helena Bay (Walker & Pitcher, 1991), compared to 6 - 8 days in Saldanha Bay

(Monteiro & Largier, 1999). Dalto *et al.* (2006) reported percentage organic nitrogen ranging from 0.06 - 0.17% at New Caledonia lagoon sites in Coral Sea of South Pacific Ocean. The study area was also impacted by anthropogenic factors. Inshore stations exhibited the upper values but these were still lower than the Station 1 values at Saldanha Bay. All sites were characterized by high mud content, primarily derived from nickel mining activities, and high summer tropical rainfall run-off.

4.2.1.2 Organic carbon

Monteiro *et al.* (1999) reported that the mean organic carbon recorded for Saldanha Bay ranged from 7.5% (Station 1) to 0.3% (Station 6). This was due to changes in bay dynamics as a result of alterations of currents, reduction in wave turbulence and reduction of bed shear stress. Clark *et al.* (2009) further reported that organic carbon remained high at the mud-dominated sites in Small Bay, but that organic carbon content of Big Bay became elevated since 2005 due to an increase in muddy deposits.

A comparison of other studies revealed the following: Diz *et al.* (2006) reported organic carbon values ranging from 2 – 2.5% for outer stations to 3.5 - 4% for inner stations at Ría de Viga, an upwelling area in Spain. This area experience high upwelling pulses, high organic carbon deposition resulting from high phytoplankton production but also high clearing rates (less than 8 days) to prevent thebuildup of anoxic benthic layers. Dalto *et al.* (2006) calculated organic carbon (as % dry weights) ranging from 0.4 to 1.18 at New Caledonia lagoon, primarily derived from anthropogenic activities such as sewage discharge. Liu *et al.* (2007) reported summer values ranging from 0.65%, for sand-dominated sites, to 6.5%, for silt-clay sites, from shallow water shelf of south Yellow Sea, China.

4.2.2 Metals

The primary source of trace metals in the southern Benguela upwelling system is derived from newly upwelled South Atlantic Central Water. These trace elements become available to phytoplankton and eventually settle at the water-sediment surface when phytoplankton dies (Monteiro & Roychoudhury, 2005). Monteiro & Roychoudhury, (2005) further described a strong linear relationship between most trace metals and organic carbon and a weaker relationship between trace metals and mud in St Helena Bay, immediately north of Saldanha Bay.

Table 4.1 lists a comparison of trace metal concentrations in sediments at selected global study sites. These sites are either situated in bays or harbours or they represented shallow water environments with mining or dredging activities. Among the South African studies Saldanha Bay trace metal concentration was higher than Robben Island (Toefy 2011), an open-water upwelling area with active water advection, as well as the adjacent St Helena Bay (Toefy, 2011). Trace metals concentrations were higher in some global study sites while other sites recorded lower values. At those sites with extensive mining or metal-based activities (Somerfield *et al.*, 1994; Ward & Hutchings, 1996) the comparable values were lower at Saldanha Bay; at the Charante Maritime Harbours, with similar activities to Saldanha Bay, the comparable values were higher at Saldanha Bay. By and large this situation existed at the other sites listed.

The Monteiro *et al.* (1999) dataset used in this study reported on total metal concentrations. Although these values provide an indication of the level of sediment contamination; they provide no information about the abundance of remineralized free ions, which are perhaps of greater consequence to infauna (Somerfield *et al.*, 1994; Fichet *et al.*, 1999). Whilst biological data have been interpreted here with reference to total metal concentrations (as in many studies, e.g.Somerfield *et al.*, 1995, Gyedu-Ababio *et al.*, 1999), caution should therefore be used in their subsequent use.

4.3 Nematode community

The results presented here conform in general details to those of other studies of nematodes in shallow water environments conducted elsewhere in temperate regions of the world. Station 1 differs from all the other stations in sediment structure, chemistry and biology. It was characterised by high mud content and this decrease with distance away from the station. The sediments carried significantly high concentrations of trace metals and organic material and diversity indices indicated that the station was dominated by a small number of dominant species.

4.3.1 Abundance and diversity

Muddy sediments, as observed at Station 1, are generally characterized by high nematode abundance and biomass (Heip *et al.*, 1985; Warwick & Gee, 1994; Boucher & Lambshead, 1995; Steyaert *et al.* 1999; Vanaverbeke *et al.*, 2002; Rzeznik-Orignac *et al.*, 2003; Barnes *et al.*, 2008). Warwick & Gee (1994) for instance, noted that sediments of the

Tamar estuary (England) were predominantly muddy in character and that nematode abundances ranged from 1.41 – 6.06 x 10^6 m^{-2}. Rzeznik – Orignac *et al.* (2003) studied nematodes on the mudflats of Brouage in France, and reported nematode densities ranging from 600 – 3849 individuals 10 cm^{-2}. The upper values of both these studies agree well with those observed here.

The muddy nature of the substratum at Station 1 can be blamed in large part on the deposition of mussel faeces and associated biogenic wastes (Stenton-Dozey *et al.*, 1999; Monteiro *et al.*, 1990). The high levels of organic enrichment (over and above those associated with natural eutrophication induced by the upwelling nature of system) obviously influence the amount of food resources available to meiofauna which leads to elevated abundances. However, it can also lead to hypoxia and anaerobic processes within the sediments leading to the accumulation of hydrogen sulphide, which serves to reduce diversity (Neira *et al.*, 2001; Levin, 2003). In hypoxic or sulphide laden sediments, the abundance and diversity of nematodes may increase (or decrease) depending on the depth of the oxic layer and the intensity of the hydrogen sulphide concentration. These effects were demonstrated in a microcosm experiment from an intertidal muddy area in the Oosterschelde, Netherlands (Steyaert *et al.* (2007). This study showed that abundance in most nematode species was reduced, some negligibly and some species disappeared in these layers, while at least one taxon, *Metachromadora vivipara*, showed an increased abundance. Clark *et al.* (2009) reported that hypoxic conditions below the mussel rafts at Saldanha Bay, but it was not possible to determine these effects in the present study because only the top 10 cm was sampled.

Mirto *et al.* (2000, 2002, and 2010) investigated the effects of the biodeposition of faeces and pseudo-faeces from mussel and fish farms on the benthic environment in the Mediterranean Sea, and they noted a decrease in abundance of most meiofaunal taxa, including nematodes. They attributed this decrease to the persistence of low oxygen zones beneath the mussel rafts, in contrast to sites where mixing allowed the re-suspension of organic matter and the penetration oxygen into the sediment. The decrease in species richness was however less evident in sediments covered with seagrasses in contrast to exposed sediments.

Sediments enriched with organic matter serve to act as traps for trace metals. Copper and lead, for example, form precipitates with Fe oxides or they may adsorb to sediment

particles and organic matter, thus increasing their bioavailability to benthic organisms (Somerfield *et al.*, 1994). Many of these metals become toxic in high concentrations, which further serve to dampen diversity in affected sediments, although this is dependent on the sediment structure, interstitial water between sand grains and overlying water (Austen & McEvoy, 1997).

Copper competes with other metals for biological uptake sites, and may be consumed or absorbed via the cuticle (Somerfield *et al.*, 1994). BIOENV results (Table 4.2) showed that copper was included in the top four best combinations of variables used in the analysis and was the environmental variable that best explained nematode community structure. Other studies have also recognised copper as being one of the most important elements structuring nematode communities. Vranken & Heip (1986) studied the effects of copper and other heavy metals on the productivity of the nematode *Diplolaimella* sp. They concluded that excess copper significantly depressed nematode productivity. Production/Biomass (P/B) ratios for control animals was 22, but dropped to 15.5 in 1 mg l^{-1} Cu saturated sediments. Lee & Correa (2005) studied the effect of copper mine tailings on the beach meiofauna of northern Chile and reported that sediment grain size was not a significant factor in determining species composition but copper contamination negatively affected meiofaunal communities.

Zinc is also an important trace chemical in marine sediments, and causes different responses under different experimental and environmental conditions. Austen *et al.* (1994) were able to demonstrate, using microcosm experiments, those meiobenthic organisms reacted more negatively to zinc than to copper in muddy environments, but that this was reversed in sand. Their explanation for this was that there were fewer available sites for copper adsorption in sand (less iron oxide and organic matter) and that free copper ions were the more freely available for uptake. It seems that Zn intake is biologically controlled (Fichet *et al.*, 1999), as it is an important coenzyme constituent in the phosphorylation process in vitamin production. Elevated cadmium levels will compete with zinc for uptake sites; and cadmium would reverse the biological pathways. In the present study, zinc was highly and significantly correlated with other trace chemicals, organic matter and sediment grain size. BIOENV results (Table 4.2) showed that zinc was included in six of the "best" combinations in combination with sand.

Austen *et al.* (1994) demonstrated that Cd played an insignificant role in structuring nematode communities, even when Cd was administered at high levels. Somerfield *et al.* (1994) concluded that Cd tended to remain in solution and therefore less toxic to nematodes.

This observation was in accordance with the view adopted by Coull & Chandler (1992) that not all metals exhibit the same degree of toxicity and that low level concentrations would not adversely affect diversity and abundance. However, Howell & Smith (1985) demonstrated that Cd was actively absorbed via the cuticle through the binding properties of proteins, both in the cuticle and muscle, therefore making Cd available to the next trophic level. The results of BIOENV (Table 4.2) indicated that Cd was not one of the factors that influenced community structure.

Inter-core variability of sediments was low at Station 1. The mud fraction constituted 94.2 ± 3.8(S.D.) % of the total size fraction of sediments and it was a homogeneous habitat. Mud dominated sediments exhibit low species diversity and Station 1 is a typical example. A limited number of families dominate muddy sediments and Station 1 is once again typical. Further, muddy sediments are dominated by nematodes belonging to deposit feeding group (1A and 1B) and MI values represented by *c-p* 2 nematodes. These criteria were met by Station 1 nematodes.

In areas of high pollution, nematodes mostly dominate the meiofaunal assemblages (Sandulli & Grimaldi, 2000), and they form dense masses, thus variability between and within cores tend to be low, as evidenced here. Areas of high pollution are likewise characterized by the presence of fine-grained sediments and increased levels of organic matter and trace metals.

During summer three species dominated the assemblage at Station 1 (Table 3.24) i.e. *Sabatieria* sp.1 (71%), *Parodontophora* sp. (13.5%) and *Terschellingia* sp.3 (11.7%). In the winter analysis, Station 1 indices indicated very low diversity (λ = 1.12) and it was exemplified by the extreme dominance of *Sabatieria* sp.1.

Sabatieria sp.1 was by far the dominant species and its contribution towards the dissimilarity between stations was approximately 35%. Somerfield *et al.* (1995) reported that *Sabatieriapulchra* was especially abundant at disturbed sites with muddy sediment. Their findings were in accordance to the findings of Wieser & Kanwisher (1961) that species from *S. pulchra* complex thrive in oxygen depleted, high organic and sulphide environments. Schratzberger *et al.* (2007) investigated the combination of biological traits to identify patterns in nematode assemblages. At the mud and fine sand sites, the combination of selective deposit feeders/clavate tail shape/1-2 mm length/slender body/coloniser-persister score 2 best matched the species that dominated the site. *Sabatieria* sp.1 falls within this

category and the results of present study indicate that this condition also prevailed at Station 1. Steyaert *et al.* (1999) proposed two groups of *Sabatieria* i.e. the *S. pulchra* complex that live in muddy, depressed redox environments and *S. ornata* complex that live in well oxygenated coarse sediments. *Sabatieria* sp.1 specimens collected at Station 1 possibly belong to the *S. pulchra* complex, but species descriptions are needed to test this assumption.

Wieser & Kanwisher (1961) reported that species from the *S. pulchra* complex are able to inhabit deeper layers of the sediment. This observation was supported by Steyaert *et al.* (1999) who discovered that *S. punctata* was able to penetrate into the sediment and their distribution was regulated by the availability of food rather than the oxygen concentration in the sediment. Nematodes along the Belgian coast were very diverse in well-aerated coarse sediment, containing well-defined interstitial spaces, in contrast to finer sediment. However, seasonal changes in the oxygen content of muddy and fine sediments enabled the accumulation of fine organic matter that in turn resulted in higher diversity of nematodes, especially of non-selective deposit feeders. In the present study, the extent of faecal pellets and associated cohesive sediments provided a habitat that facilitated the dominance of *Sabatieria* sp 1.

Terschellingia sp.3 was also dominant in Station 1 samples. This species resembled the cosmopolitan species *Terschellingia longicaudata* and possessed a characteristic filiform tail as well as similar morphometrics. This taxon occurs in muddy environments (Bhadury *et al.*, 2008) and Schratzberger *et al.* (2007) reported that organisms with this tail morphology were closely linked to mud/silt dominated environments.

The high organic content in muddy environments provides excellent feeding opportunities for deposit-feeding nematodes (*Groups 1A and 1B*). *Group 1A* represents nematodes with small, toothless buccal cavities. Organisms selectively feed on food deposits by sucking small, soft particles through the oesophagus. Included in *Group 1B* are nematodes with cup-shaped, conical or cylindrical buccal cavities, all lacking teeth. Organisms do not select their food items and feeding is aided by the lips as well as the anterior part of the buccal cavity.Studies at other global sites with muddy habitats revealed that Groups *1A* and *1B* tended to dominate the nematode assemblages. Warwick *et al.* (1997) reported that *Sabatieria* sp. (*1B*), *Terschellingia* sp. (*1A*), *Molgolaimus* sp. (*1A*) were the dominant nematodes within beds of the mussel, *Atrina zelandica* in Mahurangi harbour, Australia. *Leptolaimus* sp. (*1A*), *Sabatieria* sp. (*1B*), *Terschellingia* sp. (*1A*), *Daptonema* sp. (*1B*),

Metalinhomoeus sp. (*1B*) were the dominant taxa at the muddy stations in Takamatsu coastal area of Sea Inland Sea, Japan (Yodnarasri *et al.*, 2006). Moreno *et al.* (2008a) found that *Paracomesoma* sp. (*1B*) and *T. longicaudata* (*1A*) comprised 60% of population in the inner harbour of Genoa-Voltri, Italy (52% fine silt). The same situation persisted in a study conducted by Liu *et al.* (2007) from the shallow off-shore sites along the Shandong Peninsula, Yellow Sea, China, where the assemblage was dominated by *Dorylaimopsis* sp., *Microlaimus* sp. (*2A*), *Leptolaimus* sp. (*1A*), *Parasphaerolaimus* sp. (*1B*) were the dominant taxa.

The life history characteristics of nematode communities, as indicated by MI, are often determined by the nature of sediments. Muddy, shallow-water sediments are commonly associated with disturbed environments caused by chemical pollution, eutrophication, nematodes associated with these sediments are normally opportunistic colonizers with low *c-p* values. A number of examples illustrate this condition: Gyedu-Ababio *et al.* (1999) found that the MI (1.70) and diversity was the lowest at the mud dominated station in their study of the Swartkops Estuary, South Africa. This was typical of a stressed environment contaminated by heavy metals. Soetaert *et al.* (1995) studied a number of European estuaries and calculated MI values ranging from 2.1 – 2.8. One station was dominated by a typical opportunistic freshwater nematode and MI values of 1.6 were recorded for this very muddy site. Schratzberger *et al.* (2006) studied four recharge sites in Orwell Estuary, southeast England. The sites consisted of dredged sediments that were deposited into excavations along the estuary. The deposited sediments were primarily muddy exceeding 70% of the sediment composition. Schratzberger *et al.* (2006) and they recorded mean MI value of 2.48 for all sites. The dominant feeding group was non-selective feeders and >89% of nematodes attained *c-p* values between 2 and 3. These values are indicative of environment under stress although the increase in *c-p* values temporally indicated that habitat was in the process of recovering.

As sediments become coarser nematode abundance tends to decrease and diversity increases (Mundo-Ocampo *et al.*, 2007). Increased grain size allows for greater heterogeneity in habitat (Gheskiere *et al.*, 2004) and an increased potential for microhabitat diversity. Well-sorted sediments are likely to be subjected to water movement and bed shear stress. Nematodes are thus allowed to become suspended and many may select microhabitats (Wetzel *et al.*, 2002), while others are passively transported (Warwick & Gee, 1984). Food resources and food partitioning play a further role in structuring the community. Species will compete for food resources but they may also be subjected by disturbance vectors that will

prevent domination. Urban-Malinga *et al.* (2005) reported that nematode and other meiofaunal abundances at Norwegian beaches were generally low, but that average abundances were higher at medium grain sized (903 individuals 10 cm^{-2}) sheltered sites compared to exposed sites with coarse sediments (50 individuals 10 cm^{-2}). Since elevated *c-p* 1 values are characteristic of enriched environments; the results of Station 5, occurring outside the enriched environment, is surprising.

4.3.2 Influence of disturbance

Stenton-Dozey *et al.* (1999) determined that the macrofaunal communities, present under the mussel rafts at Saldanha Bay, were affected by the disturbance caused by bio-deposition from mussels. The degree of disturbance was shown by ABC plots and cluster analyses and was most prevalent in the middle of the mussel farm. Raft 28 (Stenton-Dozey *et al.*, 1999) coincided with Station 1 of the present study. A Warwick Statistic of -0.044 indicated that Station 1 nematodes were disturbed and this value compared well with W = -0.057 calculated for macrofauna from raft 28 (Stenton-Dozey *et al.*, 1999).

In addition, other forms of biological disturbance caused by burrowing macrofauna and predatory fish could create suitable environments for nematode colonisers, while anthropogenic disturbances caused by mariculture, dredging, eutrophication also influenced nematode community structure. Dredging activities probably disturbed the sediment sufficiently to create new niches for nematodes to occupy, in accordance to the *intermediate disturbance hypothesis* (Connell, 1979) as well as *the habitat heterogeneity hypothesis* (MacArthur & Wilson in Gingold *et al.*, 2010). Moreover, according to the dynamic equilibrium hypothesis (Huston, 1994), the combination of intermediate disturbance events coupled with intermediate productivity levels experienced during upwelling and downwelling may result in increased species richness. Station 4 was also distinct from other sites in terms of sediment structure and it was adjacent to the shipping lane. Anecdotal evidence revealed that the lane was dredged at least once between the two seasons and this increase in coarse sediment content was evident at Station 4 sites during winter (Hendricks & Gibbons, 2010). Interestingly, the results from ABC cumulative curves indicate that Stations 4 (winter) was not adversely affected by disturbance events, such as dredging but Station 6 showed signs of disturbance during both seasons.

In summer the combination of water circulatory patterns, thermal profiles, wind-induced dynamics related to water mixing, sediment movement through bed shear stress and production could create a heterogeneous sediment profile that may influence the community structure of nematodes. Only summer data were available for trace chemicals and organic C and N and the intervening period between summer and winter sampling exercises was nine months apart. Although upwelling events were decreased during winter (Monteiro & Largier, 1999; Weeks *et al.*, 1991b) winter storms played a role in advecting water into the bay and thereby changing the sediment structure. This was evident in the sediment structure of Group 2 samples with a partial increase in gravel fractions and sediment grain size while Group 3 samples showed increase in mud fractions. When the pooled samples were compared, winter samples clustered differently from their summer counterparts. Similar abundances caused winter Group 2 samples to align with summer Group 3 while winter Group 3 aligned with summer Group 2. Similarities in sediment structure accounted for most of these variabilities in samples. The high similarity in Group 1 was indicative of a disturbed environment and it was manifested in the low diversity values recorded. Whilst it is tempting to interpret some of the seasonal changes in nematode communities in terms of seasonality *per se*, we should remember the very limited nature of the time series, so that differences may simply reflect stochastic environmental changes de-coupled from time of year. Such is not unlikely given the generally rapid life-cycles of most free-living taxa (Thorson, 1950, Allan, 1976) and more work in this area is clearly needed.

In heterogeneous and well-sorted sediments with low levels of potential toxic metals communities would be able to diversify. These assumptions are evident in the current study with diversity changing with increase in sediment grain size, decreasing sediment metal content, changes in feeding strategies by nematodes and changes from *colonizer community* to a *colonizer-persister* community.

The presence of high levels food resources in Saldanha Bay should play a major role in the structuring of nematode assemblages. The C: N ratio for particulate organic matter is 6.6 (Kähler & Koeve (2001). C: N ratios in excess of 7 would indicate that organic nitrogen was derived from an external source such as phytoplankton or other nitrogen depleted sources. Monteiro *et al.* (1999) found that the high C: N ratio at Small Bay was influenced by the deposition of faeces from the mussel rafts and fish waste products that originated in Small Bay. Further, they reported that C: N ratio in Big Bay was lower than in Small Bay and they concluded that the particulate nitrogen was derived from decomposing phytoplankton. The

presence of available food and the relatively stable environment at Station 1 resulted in the aggregation of large numbers of non-selective deposit feeders, belonging to a few dominant species. Lorenzen *et al.* (1987) reported the same phenomenon for *Pontonema vulgare* from organically polluted waters in Germany. Mirto *et al.* (2002) also reported the dominance of non-selective deposit feeders in the sediments beneath the fish farm cages in their study.

In the present study the proportion of non-selective deposit feeders, during summer, remained high throughout the study area, but was the lowest at Station 6. Epigrowth feeders formed a small proportion of feeding types at Station 1. Their contribution increased across the study and comprised nearly 50% of the feeding type composition at Station 6. This situation was agreement with the increased amount of phyto-organic matter available in Big Bay, especially in summer (Pitcher & Calder, 1998). Winter feeding type groupings were less pronounced with non-selective deposit feeders and epigrowth feeders comprising 83% (Station 4) and 81% (Station 6) of the feeding assemblage. Station 6 however maintained a dominant epigrowth feeding regime, indicating that the surface sediments carry adequate amounts of phytodetritus. Coarse sediments, in well oxygenated water, allowed for the penetration of plankton detritus especially when it is coupled to water movement (Rusch & Huettel, 2000). This accumulation would favour abundance of epigrowth feeders. Omnivore or predator populations remained low throughout the study.

In summary, nematode diversity increased across the bay from the highly impacted mussel farm (Station1), with a dominance of cohesive sediments, to the sand-dominated stations in Big Bay. At Station 1, the nematode assemblage was dominated by few species in summer, while *Sabatieria* sp. 1 was the dominant species in the winter samples. Statistical analyses indicated that Station 1 differed significantly from all other Stations in respect of sediment composition, species richness, total abundance, accumulation of carbon and nitrogen and the accumulation of trace metals. Eutrophication was evident at Station 1 and the effect of Cu and organic nitrogen on nematode community composition was evident from the results of BIOENV.

Diversity patterns across the other Stations indicated that the rest of the Stations exhibited diversity indices that were similarly high and equally distributed. Nematode assemblage was orderly clustered across the study area and multivariate analyses illustrated that environmental factors influenced the nematode community structure. ABC cumulative

curves suggested that nematode communities outside Station 1were not adversely affected by the environment and Warwick Statistic for all the Stations was positive.

The presence of the dominant nematode families and species across the study area conforms to global patterns as reported by Heip *et al.* (1985), Steyaert *et al.* (1999), Somerfield *et al.*(2007), Liu *et al.*, (2007), Mundo-Ocampo *et al.*, (2007) and recently Hua *et al.*, (2009) and will be further discussed in the following chapter.

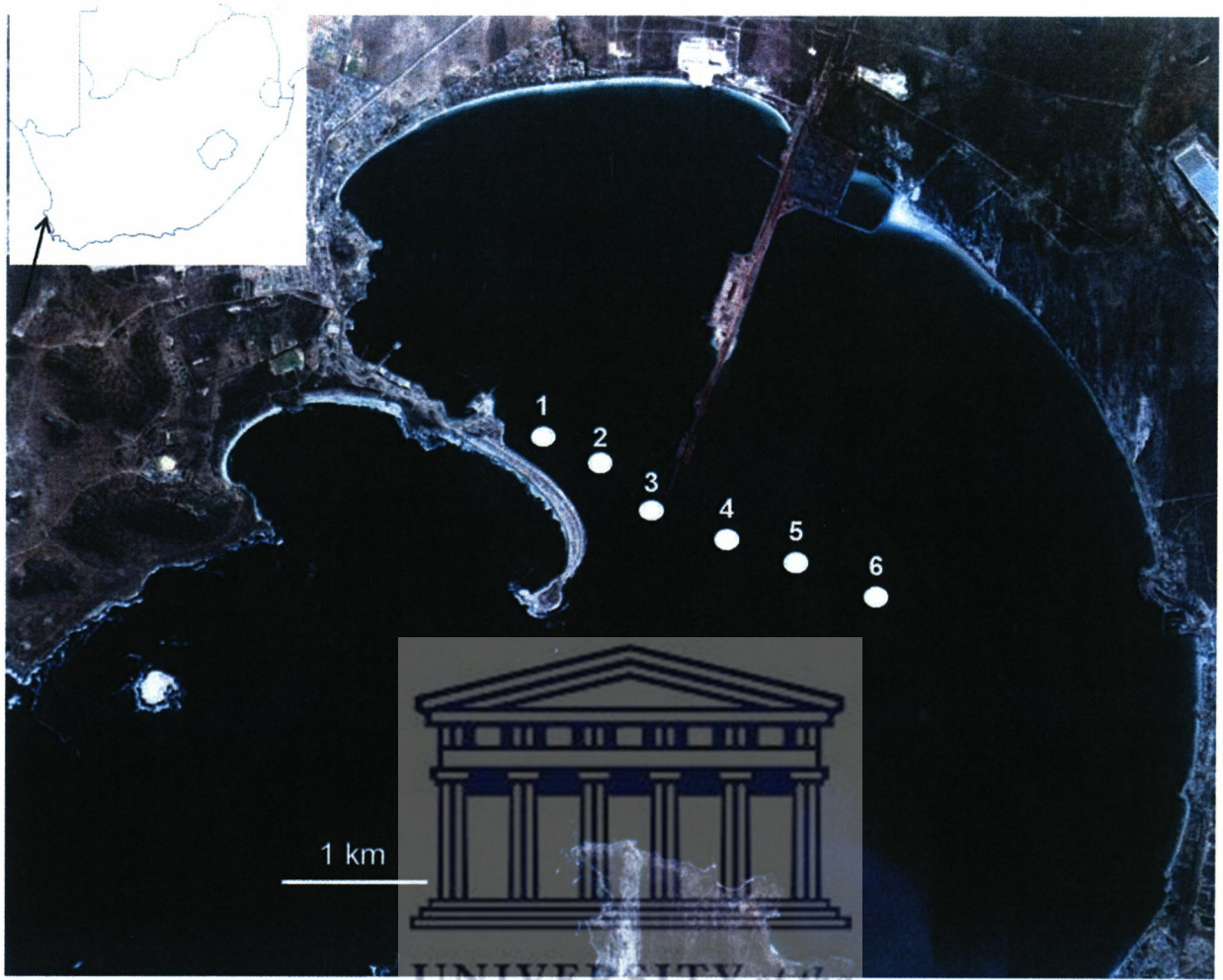

Figure 1.1: Sampling stations at Saldanha Bay in December 1998. The same transect was used to sample in August 1999. (Google map)

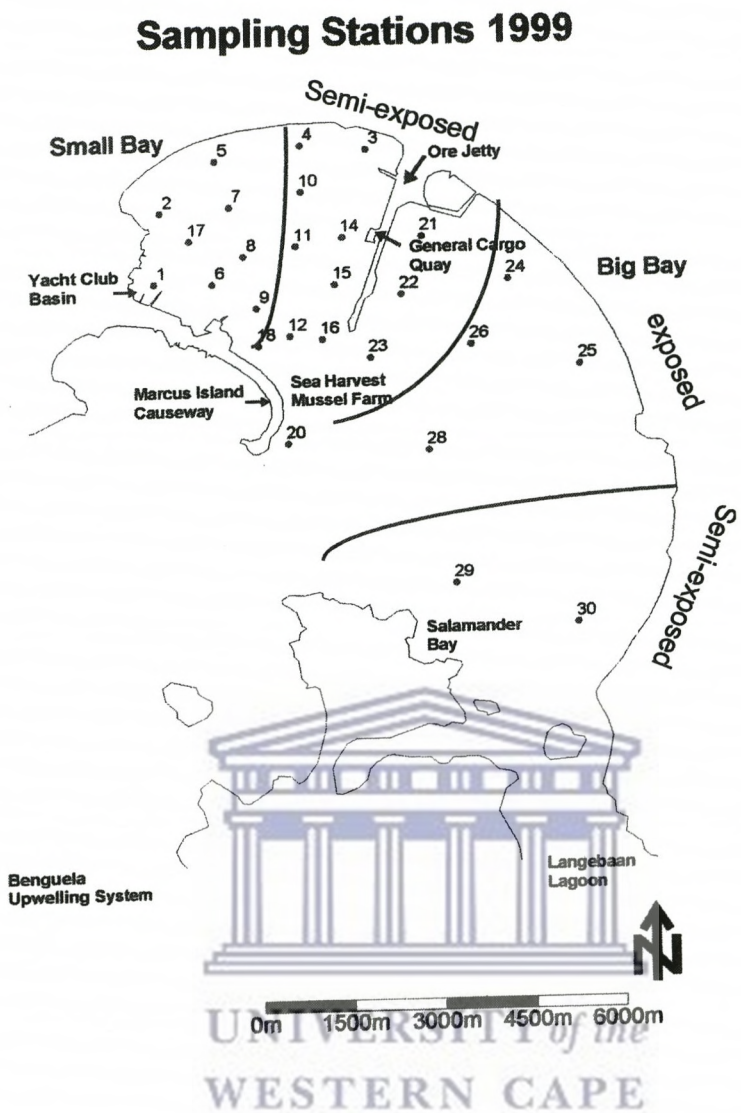

Figure 2.1: A map of Saldanha Bay indicating all sediment sampling stations in February 1999 by Monteiro et al. Stations 18, 12 16, 23 and 26 corresponded to nematode stations 1-4 and 6 respectively.(Reproduced from Monteiro et al, 1999). Also included are the energy zonations explained by Flemming (1977) prior to the construction of harbour facilities and Marcus Island Causeway.

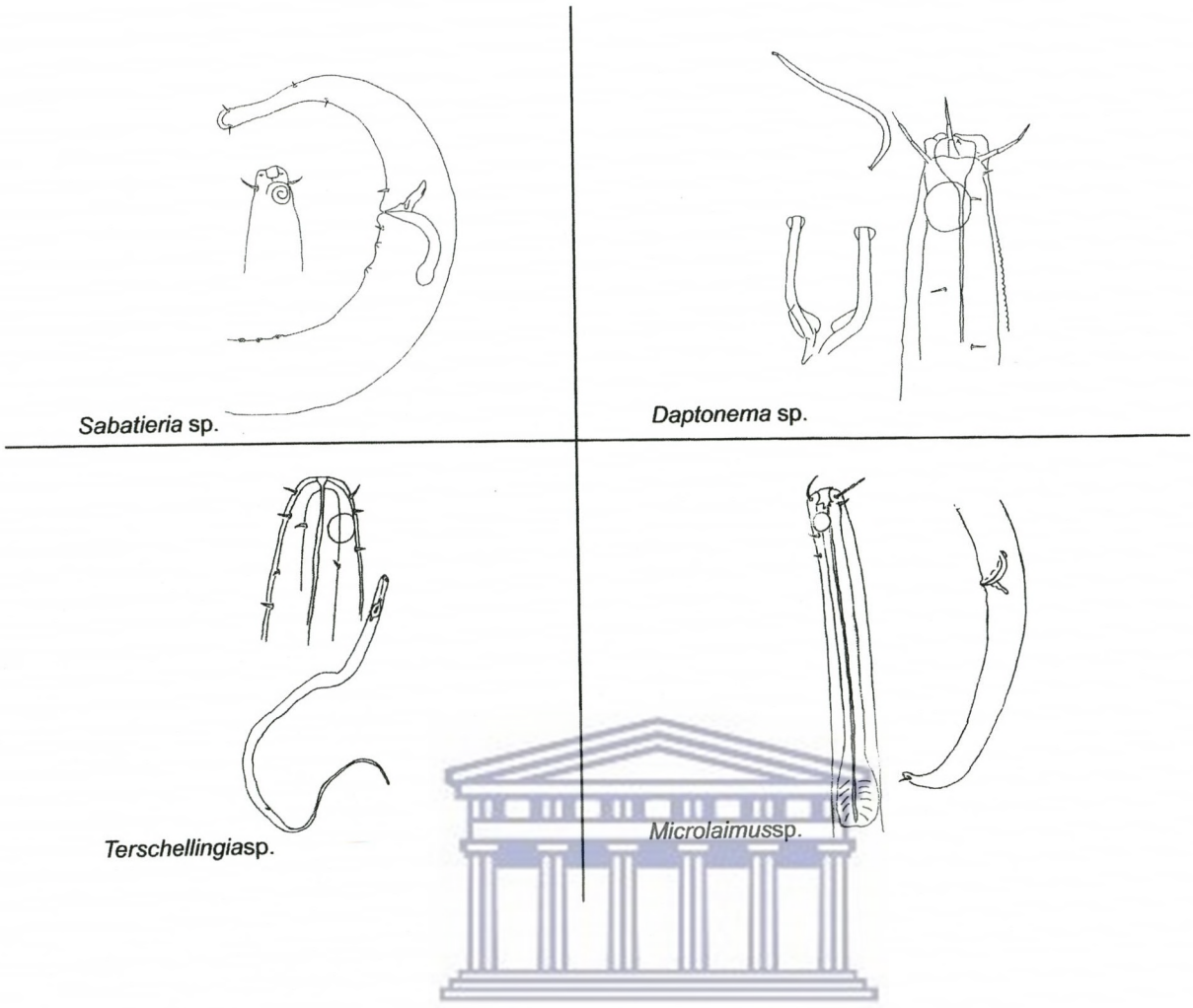

Figure 2.2: Examples of line drawings depicting some of the dominant taxa found in Saldanha Bay: *Sabatieria* sp., *Daptonema* sp., *Terschellingia* sp. and *Microlaimus* sp. Drawings are not presented to scale.

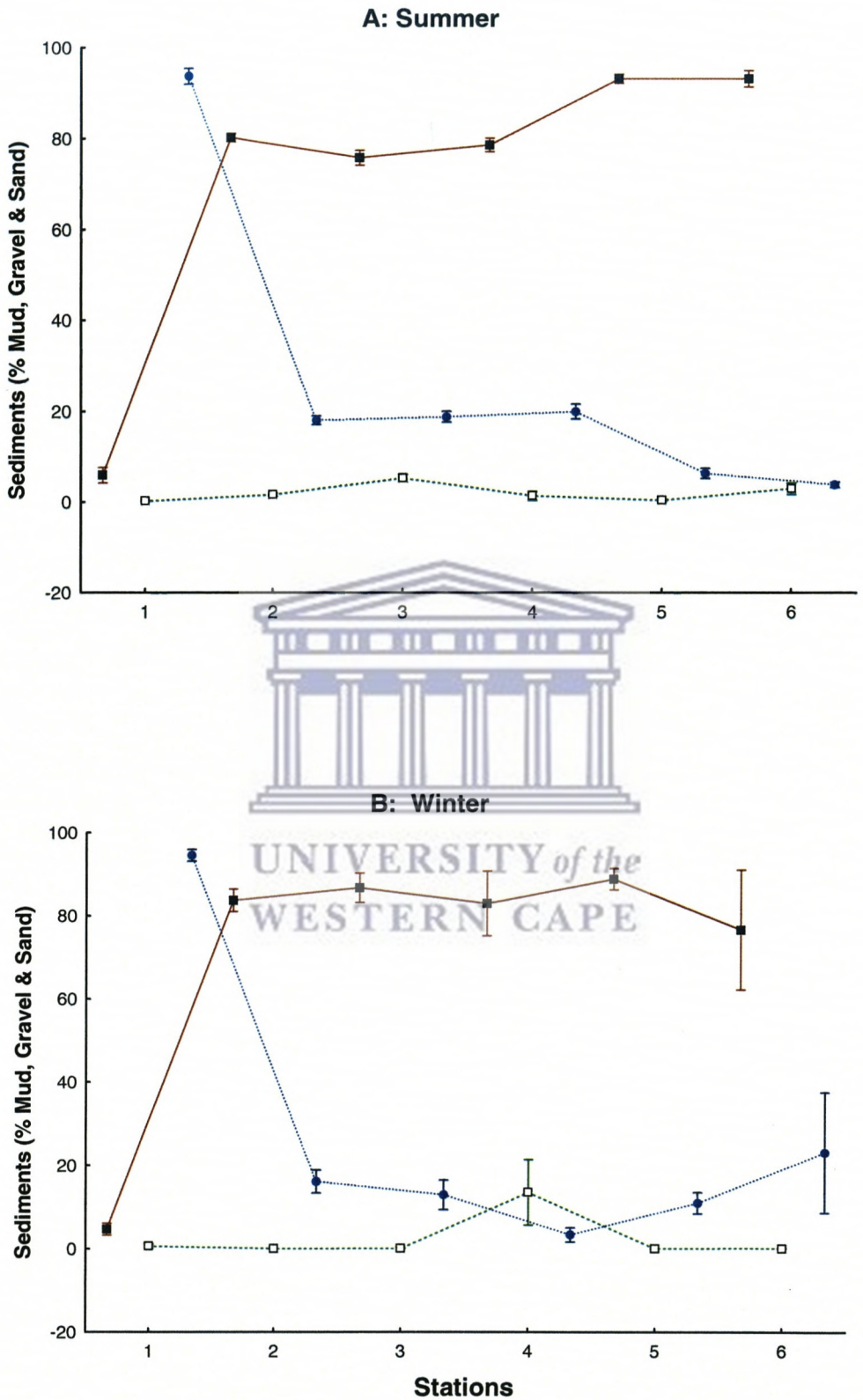

Figure 3.1: Spatial changes in the fractional size composition of sediment samples at six sites across a transect in Saldanha Bay during A) summer and B) winter.

(Mud●, Sand■ and Gravel□). Also shown are SE bars.

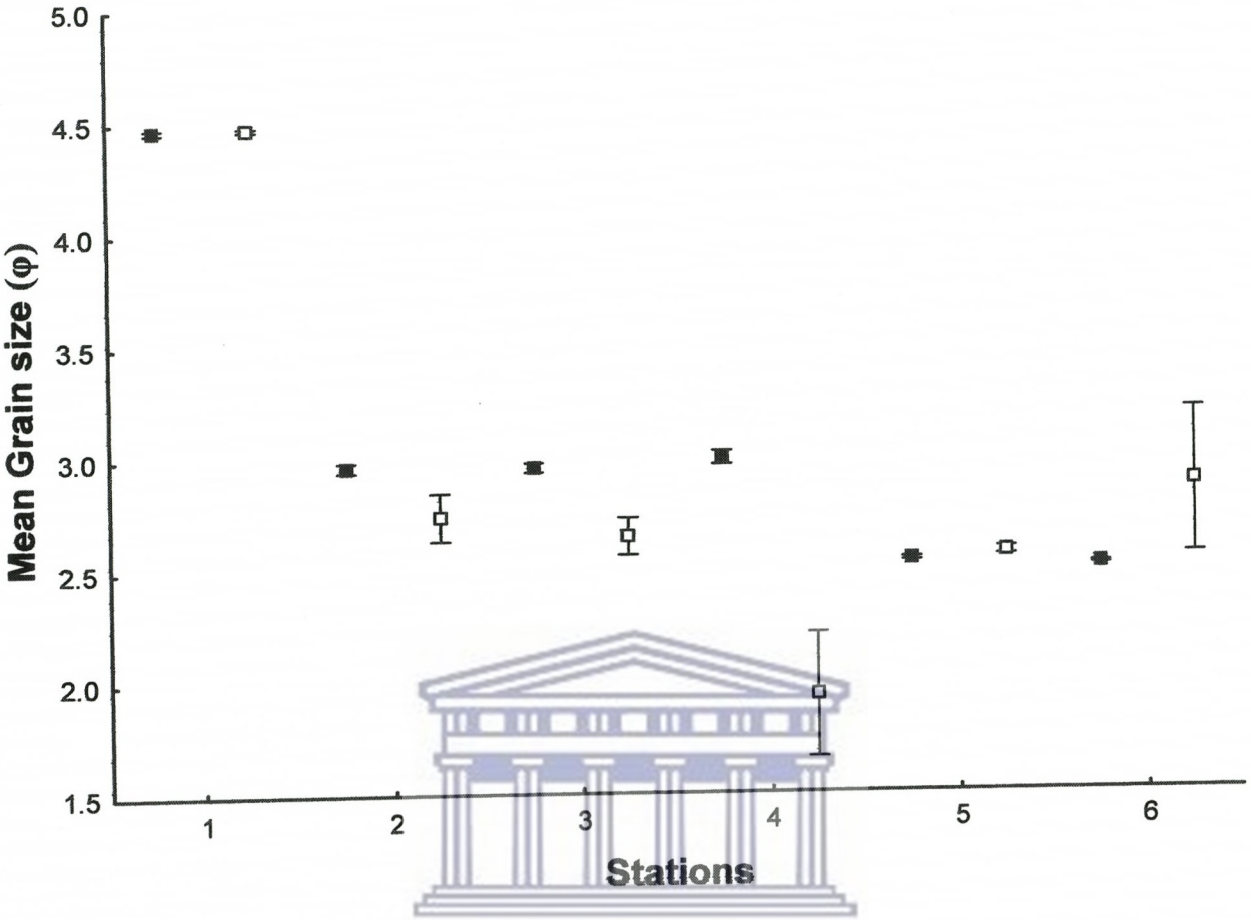

Figure 3.2: Spatial changes in the mean Grain Size composition of sediment samples at six sites across a transect in Saldanha Bay during A) summer ■ and B) winter □. Also shown are SE bars.

Table 3.1: Results for 2-way ANOVA to determine the effect of Season and Distance, and their interaction on Mean Sediment Grain Size in Saldanha Bay. Significance at $\rho < 0.05$ after the Bonferroni adjustment.

Source	Degrees of Freedom	Sum of Squares	Mean sum of Squares	F	ρ - value
Station	5	33.6493	6.7299	67.155	0.00001*
Season	1	0.7126	0.7216	7.111	0.0098
Station*Season	5	3.5016	0.7003	6.988	0.00003*
Error	60	6.0128	0.1002		
Total	71				

Table 3.2: Results for *post hoc* Tukey Honest Significant Difference (HSD) for effect of mean GRAIN SIZE on distance and season. Reported is mean sediment grain size (Phi) for each sampling station. * Significant at 0.05 level after the Bonferroni adjustment.

Mean grain size (Phi)	Station 1 Summer (4.47)	Station 1 Winter (4.47)	Station 2 Summer (2.96)	Station 2 Winter (2.74)	Station 3 Summer (2.96)	Station 3 Winter (2.65)	Station 4 Summer (2.99)	Station 4 Winter (1.93)	Station 5 Summer (2.53)	Station 5 Winter (2.56)	Station 6 Summer (2.50)	Station 6 Winter (2.87)
Station 1 Summer												
Station 1 Winter	1.00											
Station 2 Summer	0.0001*	0.0001*										
Station 2 Winter	0.0001*	0.0001*	0.98									
Station 3 Summer	0.0001*	0.0001*	1.00	0.99								
Station 3 Winter	0.0001*	0.0001*	0.85	1.00	0.87							
Station 4 Summer	0.0001*	0.0001*	1.00	0.96	1.00	0.75						
Station 4 Winter	0.0001*	0.0001*	0.0002*	0.002*	0.0002*	0.012	0.0001*					
Station 5 Summer	0.0001*	0.0001*	0.46	0.99	0.48	1.00	0.35	0.07				
Station 5 Winter	0.0001*	0.0001*	0.58	1.00	0.59	1.00	0.45	0.04	1.00			
Station 6 Summer	0.0001*	0.0001*	0.36	0.98	0.38	1.00	0.26	1.00	1.00	1.00		
Station 6 Winter	0.0001*	0.0001*	1.00	1.00	1.00	1.00	1.00	0.001*	0.79	0.87	0.69	

Table3.3: Trace metal concentrations determined by Monteiro *et al.* (1999) at selected sites in Saldanha Bay. Sites respectively correspond to Stations 1, 2, 3, 4 and 6 of present study (see Materials & Methods). Station 5 was calculated as the mean values between Stations 4 and 6.

	Total Al ($mg.Kg^{-1}$)	Total Fe ($mg.Kg^{-1}$)	Total Ni ($mg.Kg^{-1}$)	Total Cu ($mg.Kg^{-1}$)	Total Zn ($mg.Kg^{-1}$)	Total Cd ($mg.Kg^{-1}$)	Total Pb ($mg.Kg^{-1}$)	Organic C (%)	Organic N (%)
Station 8	17338.06	13888.89	28.97	12.73	76.07	6.68	53.75	7.54	0.42
Station 12	3937.01	3393.68	20.00	4.00	13.60	4.32	48.75	1.98	0.05
Station 16	2902.16	2762.11	15.88	4.00	8.00	3.47	37.50	0.7	0.01
Station 23	3968.25	2964.21	18.24	3.43	10.40	3.79	35.00	0.64	0.04
Station 26	2945.11	2282.11	12.35	2.86	5.50	3.05	30.00	0.26	0.02

Table 3.4: Results of the Non-parametric Spearman Rank Order Correlation analyses of nematode SUMMER abundance with sediment structure, chemical composition, diversity indices and dominant species. Results show R values with significant R - values* at the 0.05 level after Bonferroni adjustments.

	Density	Sand	Gravel	Mud	GrainS	Al	Fe	Cu	Pb	Cd	Zn
A: physical/ chemical											
Density											
Sand	-0.69*										
Gravel	-0.07	-0.02									
Mud	0.73*	-0.96*	-0.17								
Grain Size (Phi)	0.78*	-0.91*	-0.25	0.96*							
Total Al	0.60*	-0.47	-0.61*	0.62*	0.64*						
Total Fe	0.84*	-0.79*	-0.21	0.83*	0.86*	0.78*					
Total Cu	0.78*	-0.87*	0.01	0.82*	0.84*	0.46	0.89*				
Total Pb	0.71*	-0.73*	0.07	0.66*	0.69*	0.40	0.82*	0.93*			
Total Cd	0.84*	-0.79*	-0.21	0.83*	0.86*	0.78*	1.00	0.89*	0.82*		
Total Zn	0.84*	-0.79*	-0.21	0.83*	0.86*	0.78*	1.00	0.89*	0.82*	1.00	
Organic Carbon	0.80*	-0.83*	-0.02	0.80*	0.83*	0.54*	0.94*	0.98*	0.95*	0.94*	0.94*
Organic Nitrogen	0.63*	-0.45	-0.49	0.57*	0.61*	0.94*	0.84*	0.55*	0.59*	0.84*	0.84*
B: Biological											
Simpson's (1/λ)	-0.27	0.36	0.14	-0.28	-0.30	-0.13	-0.28	-0.48	-0.50*	-0.28	-0.28
Number spp. (S)	0.03	0.21	0.05	-0.16	-0.12	-0.05	-0.07	-0.24	-0.32	-0.07	-0.07
Sabatieria sp.	0.57*	-0.58*	0.02	0.54*	0.56*	0.23	0.56*	0.66*	0.65*	0.56*	0.56*
Microlaimus sp.	-0.26	0.54*	0.00	-0.45	-0.44	-0.18	-0.44	-0.63*	-0.60*	-0.44	-0.44
Metalinhomoeus sp.	0.40	-0.29	0.10	0.34	0.34	0.17	0.31	0.23	0.04	0.31	0.31
Chromadorella sp.	0.01	-0.04	0.34	0.06	-0.01	-0.17	0.05	0.03	-0.02	0.05	0.05

Table 3.4 (continued): Spearman correlation analyses of nematode SUMMER abundance with sediment structure, chemical composition, diversity indices and dominant species. * Correlation is significant at $\rho < 0.05$ level.

	Organic Carbon	Organic Nitrogen	1/λ	S	*Sabatieria* sp.	*Microlaimus* sp.	*Metalinhomoeus* sp.
A: physical/ chemical							
Organic Carbon							
Organic Nitrogen	0.66*						
B: Biological							
Simpson's (1/λ)	-0.43	-0.19					
Number spp. (S)	-0.19	-0.09	0.56*				
Sabatieria sp.	0.65*	0.31	-0.53*	-0.17			
Microlaimus sp.	-0.58*	-0.25	0.56*	0.66*	-0.43		
Metalinhomoeus sp.	0.23	0.09	0.36	0.52*	-0.01	0.09	
Chromadorella sp.	0.05	-0.11	0.34	0.45	0.19	0.11	0.38

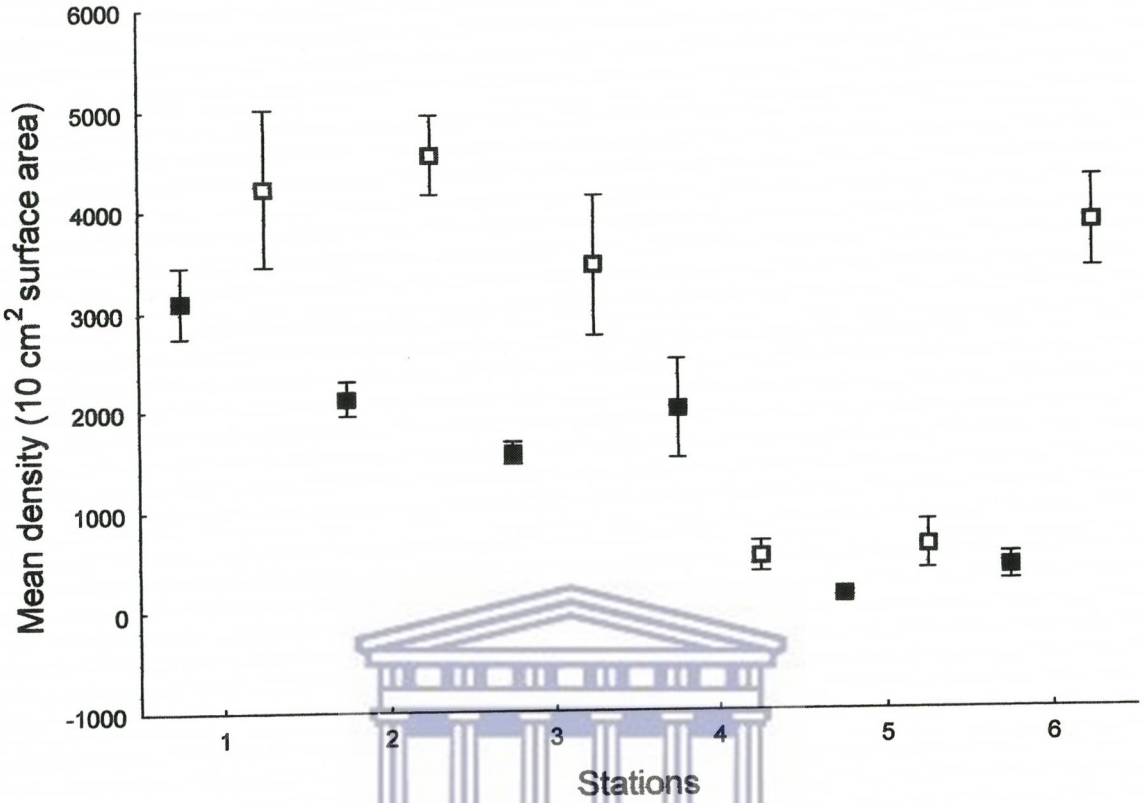

Figure 3.3: Spatial changes per mean sample density (10 cm² surface area) across a transect in Saldanha Bay during a) summer ■ and b) winter □. Species level input only provided for Stations 1, 4 and 6 during winter (See Materials and Methods). Also shown are SE bars.

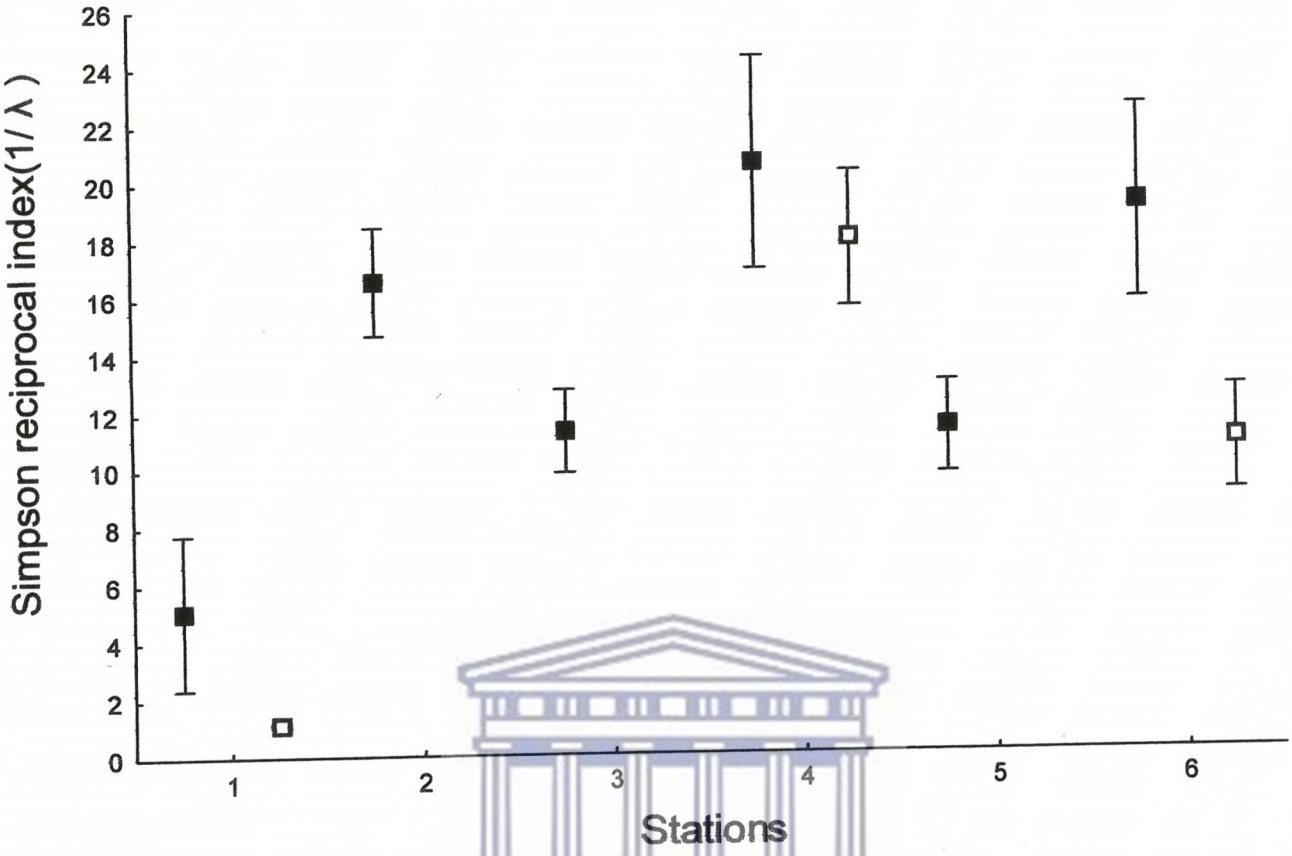

Figure 3.4: Spatial changes per mean sample Simpsons's reciprocal (1/λ) species richness index across a transect in Saldanha Bay during a) summer ■ and b) winter □. Species level input only provided for Stations 1, 4 and 6 during winter (See Materials and Methods). Also shown are SE bars.

Table 3.5: Results for two-way ANOVA to determine the effect of Season and Distance, and their interaction on nematode densities in Saldanha Bay.

Source	Degrees of Freedom	Sum of Squares	Mean sum of Squares	*F*	ρ - value
Station	5	849999885	16999977	16.9043	0.0001
Season	1	29735350	29735350	29.5679	0.0001
Station*Season	5	43187458	8637492	8.5889	0.0001
Error	58	58328420	1005662		
Total	69	9812511130			

Table 3.6: Results of a *post hoc* Tukey Honest Significant Difference (HSD) test for differences in nematode densities between sampling stations and seasons.* Significant at 0.05 level after the Bonferroni adjustment. Reported is mean densities for each sampling station.

	Station1 Summer (3098.0)	Station 1 Winter (4224.3)	Station 2 Summer (2125.8)	Station 2 Winter (4544.3)	Station 3 Summer (1568.8)	Station 3 Winter (3441.2)	Station 4 Summer (2013.2)	Station 4 Winter (529.0)	Station 5 Summer (148.4)	Station 5 Winter (635.6)	Station 6 Summer (413.8)
Station 1 Summer											
Station 1 Winter	0.726										
Station 2 Summer	0.870	0.028*									
Station 2 Winter	0.362	1.00	0.005*								
Station 3 Summer	0.282	0.002*	0.998	0.0003*							
Station 3 Winter	1.000	0.968	0.507	0.751	0.078						
Station 4 Summer	0.770	0.016*	1.00	0.003*	0.999	0.381					
Station 4 Winter	0.002*	0.0001*	0.226	0.0001*	0.814	0.0004*	0.324				
Station 5 Summer	0.001*	0.0001*	0.0733	0.0001*	0.462	0.0002*	0.115	1.0000			
Station 5 Winter	0.008*	0.0001*	0.389	0.0001*	0.924	0.001*	0.510	1.0000	0.999		
Station 6 Summer	0.001*	0.0001*	0.149	0.0001*	0.695	0.0003*	0.224	1.0000	1.001	1.0000	
Station 6 Winter (3832.8)	0.980	0.999	0.152	0.984	0.012	0.999	0.097	0.0001*	0.0001*	0.0002*	0.0001*

Table 3.7: Results for two-way ANOVA to determine the effect of Season and Distance, and their interaction on sample species diversity (1/λ) in Saldanha Bay.

Source	Sum of SquareS	Degrees of Freedom	Mean sum of Squares	*F*	ρ - value
Stations	1657.25	2	828.63	19.545	0.0001*
Season	207.85	1	207.85	4.903	0.035
Stations*Season	44.87	2	22.44	0.529	0.595
Error	1229.47	29	41.231		

Table 3.8: Results of a *post hoc* Tukey Honest Significant Difference (HSD) test identifying differences in Simpsons's reciprocal index between selected stations and seasons. * Significant at $\rho < 0.05$ level after the Bonferroni adjustment. Reported is mean index for each sampling station.

	Station1 Summer (5.0843)	Station 1 Winter (1.121)	Station 4 Summer (20.539)	Station 4 Winter (17.897)	Station 6 Summer (18.817)	Station 6 Winter (10.768)
Station 1 Summer						
Station 1 Winter	0.895					
Station 4 Summer	0.004*	0.0003*				
Station 4 Winter	0.022*	0.002*	0.980			
Station 6 Summer	0.018*	0.001*	0.998	0.999		
Station 6 Winter	0.659	0.138	0.130	0.424	0.345	

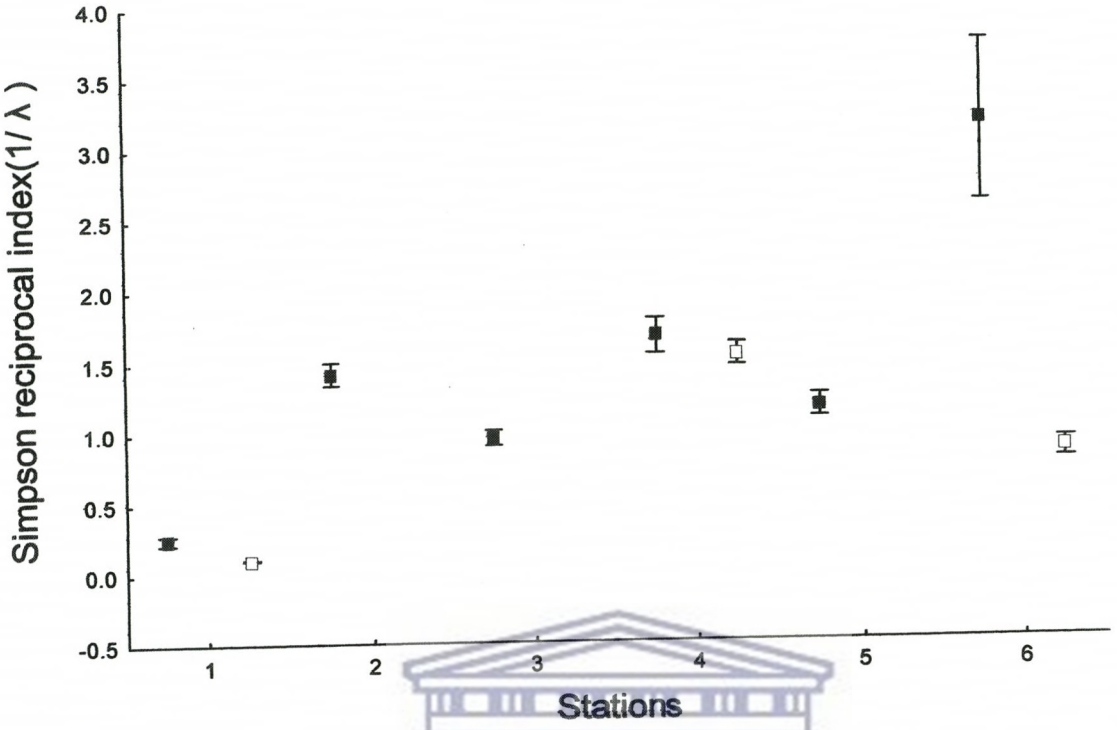

Figure 3.5: Spatial changes of community Simpson's diversity index at six sites across a transect in Saldanha Bay during a) SUMMER ■ and b) WINTER □. Species level input only provided for Stations 1, 4 and 6 during winter. Also shown are SE bars.

Table 3.9: Results for two-way ANOVA to determine the effect of Season and Distance, and their interaction on pseudo nematode community diversity (1/λ) in Saldanha Bay. * significant at 0.05 level

Source	Degrees of Freedom	Sum of Squares	Mean sum of Squares	*F*	ρ - value
Stations	8.37087	2	4.18544	10.6948	0.0001*
Season	10.32427	1	10.32427	26.381	0.0003*
Stations*Season	8.09458	2	4.04729	10.3418	0.0004*
Error	11.34922	29	0.39135		
Levene's	0.013				

Table 3.10: Results of a *post hoc* Tukey Honest Significant Difference (HSD) test identifying differences in community diversity (1/λ) between seasons and selected stations.
*** Significant at $\rho < 0.05$ level after the Bonferroni adjustment. Reported is mean index for each sampling station.**

	Station 1 Summer 0.25123	Station 4 Summer 1.4115	Station 6 Summer 0.99973	Station 1 Winter 1.5210	Station 4 Winter 1.2352	Station 6 Winter 3.1725
Station 1 Summer						
Station 4 Summer	0.034*					
Station 6 Summer	0.380	0.883				
Station 1 Winter	0.017*	0.999	0.741			
Station 4 Winter	0.101	0.996	0.988	0.967		
Station 6 Winter	0.0001*	0.0006*	0.0002*	0.001*	0.0002*	

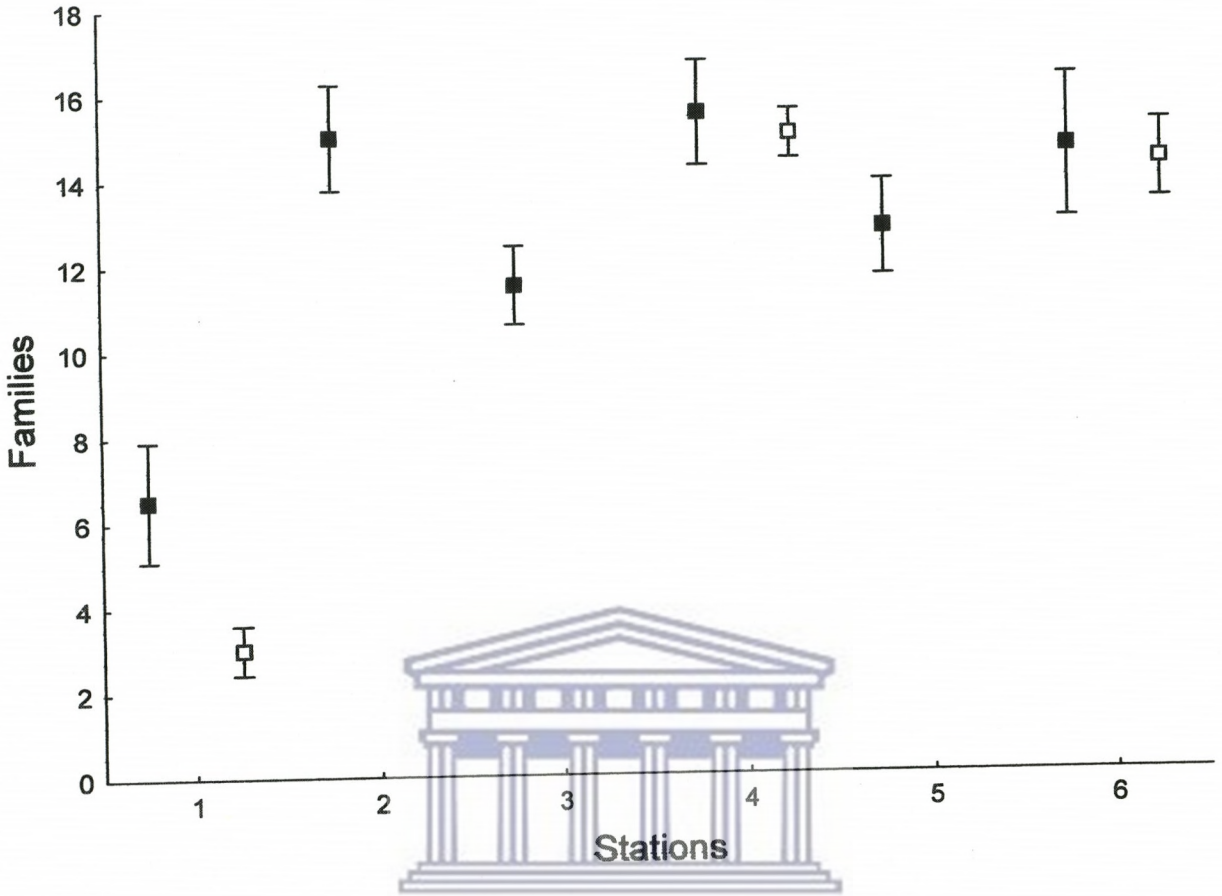

Figure 3.6: Spatial variation in number of nematode families at Saldanha Bay during a) SUMMER■ and b) WINTER□. Shown are means and SE bars. Reported are only families for Stations 1, 4 and 6 during winter.

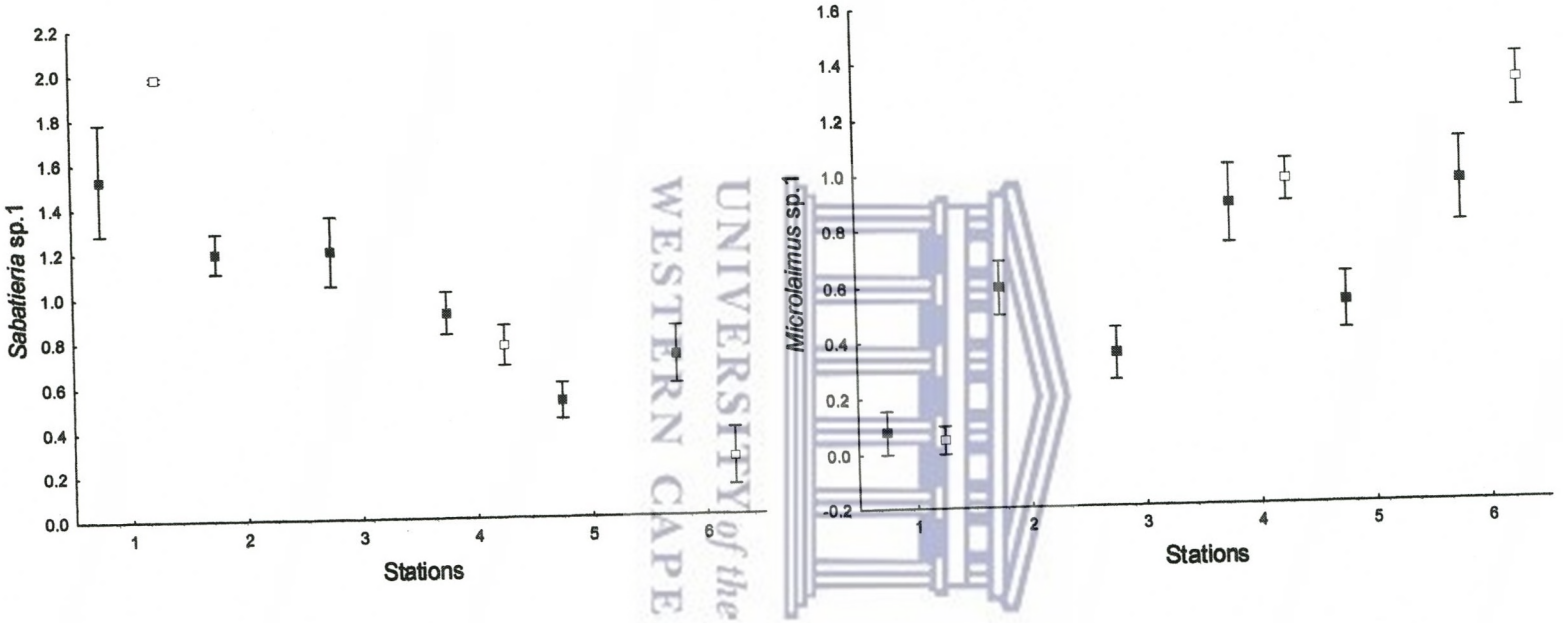

Figure 3.7: Spatial variation in abundance of selected species collected at Saldanha Bay during a) SUMMER ■ and b) WINTER □. Shown are the means and SE bars. Species level input only provided for Stations 1, 4 and 6 during winter.

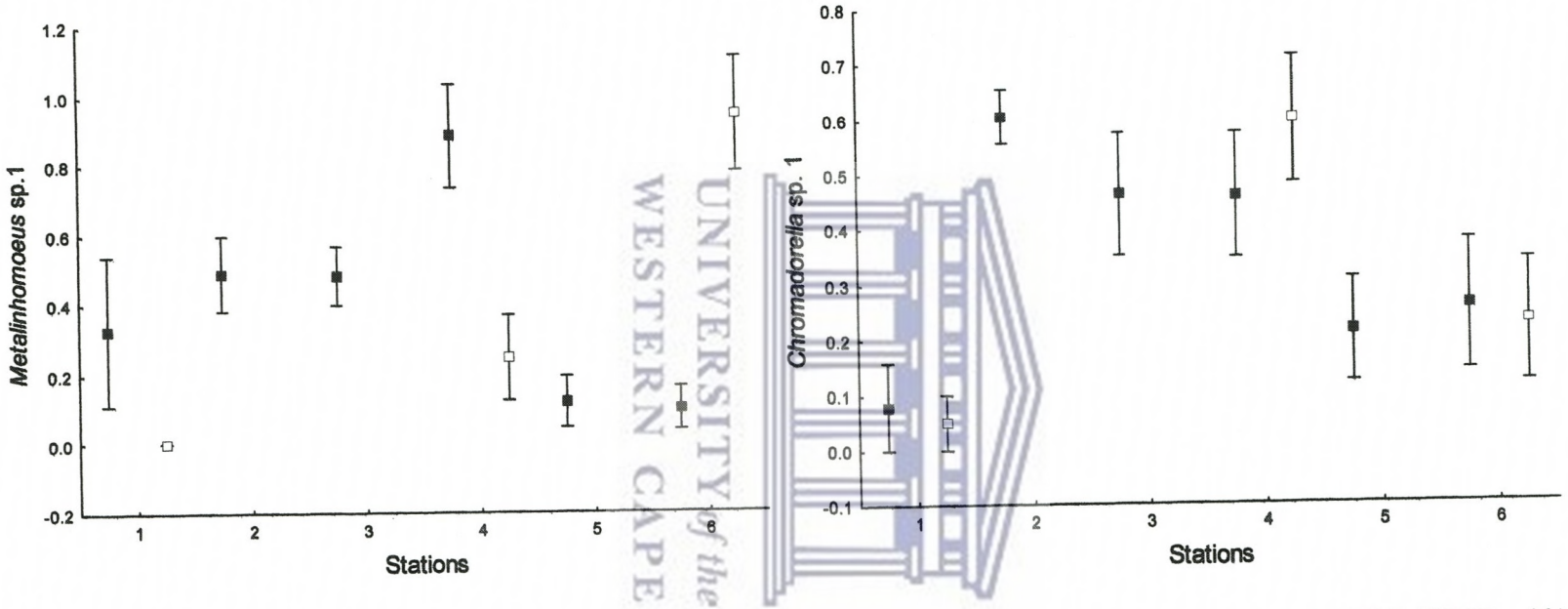

Figure 3.7 (continued): Spatial variation in abundance of selected species collected at Saldanha Bay during a) SUMMER ■ and b) WINTER □. Shown are the means and SE bars. Species level input only provided for Stations 1, 4 and 6 during winter.

Table 3.11: *post hoc* Multi-comparison results of non-parametric Kruskal-Wallis ANOVA for FAMILIES in SUMMER assemblage. Reported is mean Kruskal-Wallis rank, z'-score and ρ-value (italized) for each sampling station. $H = H_{(5,36)} = 16.05$, $p = 0.007$.
*** Significant at 0.05 level after Bonferroni adjustment.**

	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
	5.50	23.67	13.75	25.17	17.50	22.33
Station 1						
Station 2	3.07					
	0.03					
Station 3	1.39	1.68				
	1.00	*1.00*				
Station 4	3.32	0.25	1.93			
	0.013	*1.00*	*0.80*			
Station 5	1.93	0.99	0.60	1.24		
	0.80	*1.00*	*1.00*	*1.00*		
Station 6	2.85	0.23	1.45	0.48	0.78	
	0.07	*1.00*	*1.00*	*1.00*	*1.00*	

Table 3.12: Results for 1-way ANOVA to determine the effect of Distance on the distribution of four dominant (>5% of assemblage) nematode species collected in SUMMER. Reported is Levene's statistic for transformed (Log + 1) data.

Source of variation	*Sabatieria* sp. 1					*Microlaimus* sp. 1				*Metalinhomoeus* sp. 1				*Chromadorella* sp.1			
	SS	DF	MS	*F*	ρ	SS	MS	*F*	ρ	SS	MS	*F*	ρ	SS	MS	*F*	ρ
Between groups	3.74	5	0.75	5.87	<0.01	3.21	0.64	8.51	<0.01	2.45	0.49	5.05	<0.01	1.12	0.49	4.06	<0.01
Within groups	3.696	29	0.13			2.19	0.08			2.81	0.09			1.601	0.06		
Total	160.87	34				56.89				60.20				74.16			
Levene's statistic	0.327					0.241				0.01*				0.169			

Table 3.13:Results of a *post hoc* Tukey Honest Significant Difference (HSD) test identifying differences between dominant species in SUMMER assemblages.
*** Significant at ρ < 0.05 level after the Bonferroni adjustment.**

	Station 1	Station 2	Station 3	Station 4	Station 5
		Sabatieria sp. 1			
Station 1					
Station 2	0.59				
Station 3	0.61	1.00			
Station 4	0.06	0.76	0.75		
Station 5	0.00*	0.05	0.04*	0.47	
Station 6	0.01*	0.23	0.22	0.93	0.94
		Microlaimus sp. 1			
Station 1					
Station 2	0.033*				
Station 3	0.535	0.653			
Station 4	0.00*	0.469	0.025*		
Station 5	0.108	0.999	0.894	0.300	
Station 6	0.000*	0.235	0.008*	0.997	0.138
		Metalinhomoeus sp. 1			
Station 1					
Station 2	0.94				
Station 3	0.95	1.00			
Station 4	0.04*	0.27	0.25		
Station 5	0.88	0.39	0.42	0.00*	
Station 6	0.81	0.29	0.31	0.00*	1.00
		Chromadorella sp. 1			
Station 1					
Station 2	0.01*				
Station 3	0.08	0.90			
Station 4	0.09	0.89	1.00		
Station 5	0.93	0.10	0.52	0.53	
Station 6	0.77	0.14	0.67	0.68	1.00

Table 3.14: *post hoc* Multi-comparison results of non-parametric Kruskal-Wallis ANOVA for FAMILIES in WINTER assemblage. Reported is mean Kruskal-Wallis rank, z′-score and ρ-value (italized) for each sampling station. $H = H_{(2,18)} = 11.69$, $p = 0.003$. * Significant at 0.05 level after Bonferroni adjustment.

	Station 1	Station 4	Station 6
	3.5	13.12	11.83
Station 1			
Station 4	3.14		
	*0.005**		
Station 6	2.70	0.43	
	0.02	*1.00*	

Table 3.15: Results for 1-way ANOVA to determine the effect of Distance on the distribution of four dominant (>5% of assemblage) nematode species collected in WINTER. Reported is Levene's statistic for transformed (Log + 1) data.

Source of variation	*Sabatieria* sp. 1					*Microlaimus* sp. 1				*Metalinhomoeus* sp. 1				*Chromadorella* sp. 1			
	SS	DF	MS	*F*	ρ	SS	MS	*F*	ρ	SS	MS	*F*	ρ	SS	MS	*F*	ρ
Between groups	9.28	2	4.64	91.6	<0.01	5.05	2.54	73.6	<0.01	2.86	1.43	17.3	<0.01	0.94	0.47	8.42	<0.01
Within groups	0.76	15	0.05			0.52	0.03			1.24	0.08			0.83	0.06		
Total	160.87	34				56.89				60.20				74.16			
Levene's statistic	0.01*					0.435				<0.01				0.07			

Table 3.16: Results of a *post hoc* Tukey Honest Significant Difference (HSD) test identifying differences between dominant species in SUMMER assemblages.
*** Significant at $\rho < 0.05$ level after the Bonferroni adjustment.**

	Station 1	Station 4
	Sabatieria sp. 1	
Station 1		
Station 4	0.00*	
Station 6	0.00*	0.00*
	Microlaimus sp. 1	
Station 1		
Station 4	0.00*	
Station 6	0.00*	0.02*
	Metalinhomoeus sp. 1	
Station 1		
Station 4	0.33	
Station 6	0.00*	0.00*
	Chromadorella sp. 1	
Station 1		
Station 4	0.00*	
Station 6	0.41	0.04*

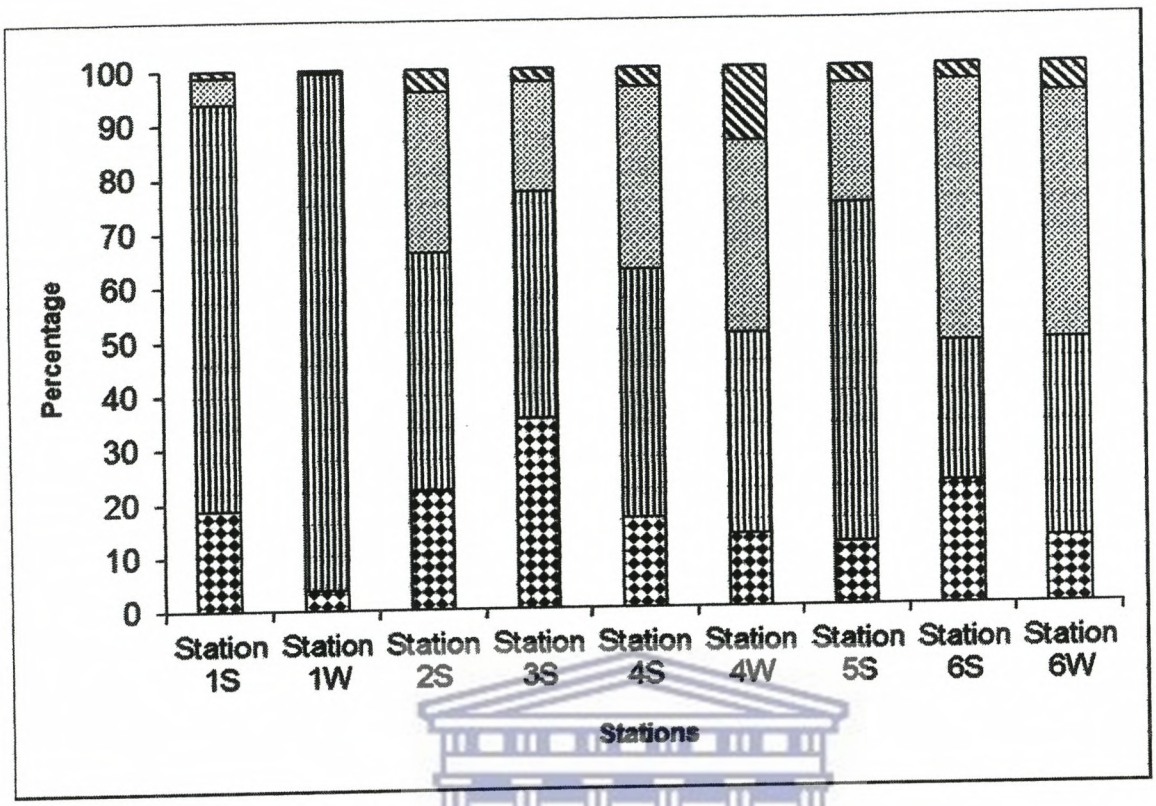

Figure 3.8: Proportions (%) of nematode feeding groups (Wieser, 1953) across a transect from station 1 to 6. S = Summer and W = Winter. ▩ = selective deposit feeder (Gr. 1A); ▥ = non-selective deposit feeder (Gr. 1B); ▩ = epigrowth feeder (Gr. 2A); ▩ = omnivore/ carnivore (Gr. 2B).

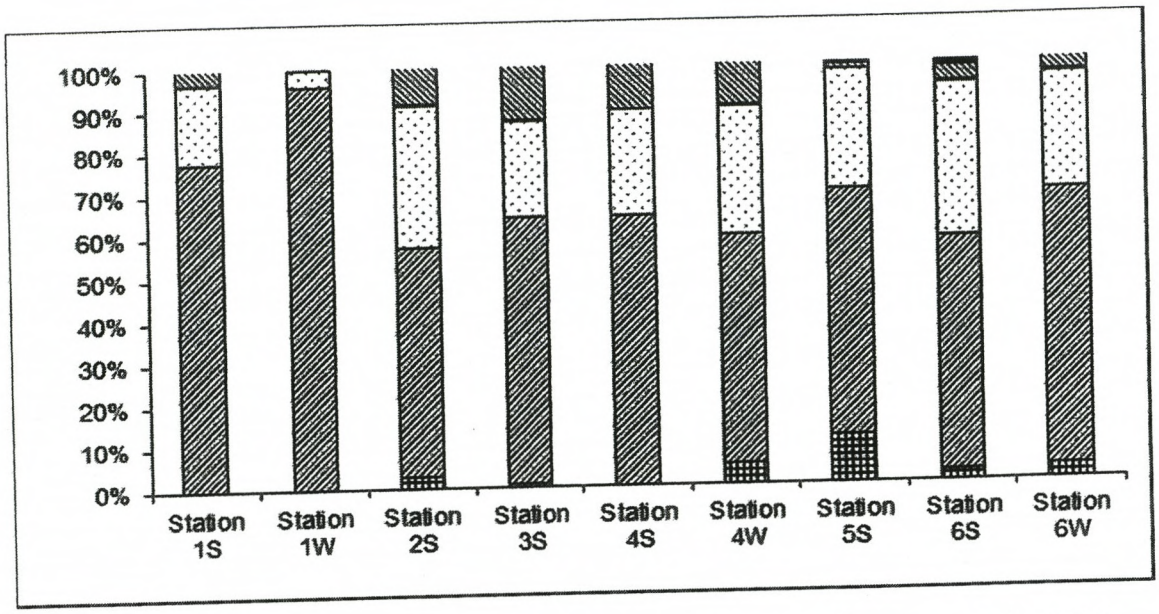

Figure 3.9: Proportions (%) of nematode Maturity Index groups (Bongers *et al.*, 1989) across a transect from station 1 to 6. S = Summer and W = Winter. ## = *c-p 1*; ▨ = *c-p 2*; ⊡ = *c-p 3*; ▧ = *c-p 4*; ■ = *c-p 5*.

Table 3.17: Results for the number of nematode per MI (*c-p*) scores at six stations in SUMMER and three stations in WINTER. Also indicated is the MI value for each station.

	Station 1 (2.25)	Station 2 (2.45)	Station 3 (2.47)	Station 4 (2.40)	Station 5 (2.18)	Station 6 (2.32)	Station 1 winter (2.05)	Station 4 winter (2.45)	Station 6 winter (2.85)
c-p 1	1	16	3	2	37	9	0	20	18
c-p 2	451	309	338	320	194	189	571	228	371
c-p 3	109	197	125	134	94	138	25	129	161
c-p 4	20	51	70	54	4	14	1	43	19
c-p 5	0	0	0	0	2	6	0	0	0

Table 3.18: Results of the Non-parametric Spearman Rank Order Correlation analyses of nematode SUMMER sites with Maturity Index scores. Results show R values with significant R - values* at the 0.05 level after Bonferroni adjustments.

	c-p	Station 1	Station 2	Station 3	Station 4	Station 5
Station 1	-0.40					
Station 2	-0.40	1.00				
Station 3	-0.40	1.00	1.00			
Station 4	-0.40	1.00	1.00	1.00		
Station 5	-0.70	0.90*	0.90*	0.90*	0.90*	
Station 6	-0.40	1.00	1.00	1.00	1.00	0.90*

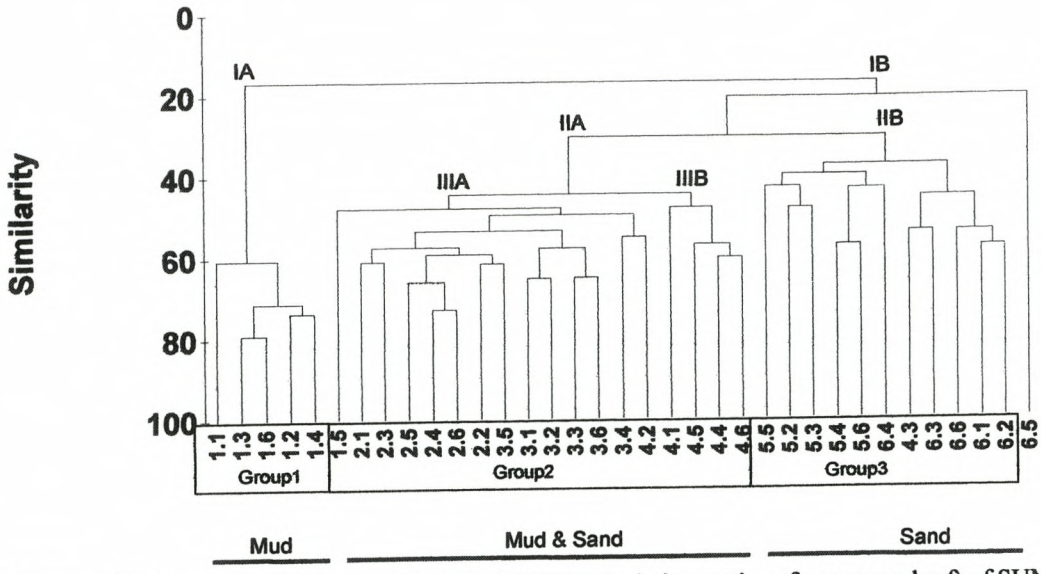

Figure 3.10: Hierarchical cluster analysis in GROUPS depicting stations from mussel raft of SUMMER samples with square root transformation using Bray-Curtis similarity index. The samples are labelled 1-6 from mussel farm in Small Bay (Station 1) to Big Bay (Station 6) (See Figure 1.1).

Table 3.19: Summary of selected variables corresponding to three cluster groups for SUMMER samples.

	SUMMER		
	Group 1	Group 2	Group 3
Variable	IA (N = 5) Mean (STD)	IIA (N = 18) Mean (STD)	IIB (N = 11) Mean (STD)
Sand	6.8 (4.1)	74.0 (18.4)	92.5 (5.3)
Gravel	0.3 (0.4)	2.5 (2.5)	1.0 (1.8)
Mud	92.9 (4.1)	23.5 (18.9)	6.5 (5.6)
Grain size (φ)	4.46 (0.02)	3.05 (0.36)	2.57 (0.16)
Cu	12.7	4.3 (2.1)	3.04 (.19)
Pb	53.8	40.1 (8.4)	30.0
Cd	6.7	4.0 (0.8)	3.3 (0.3)
Organic C	7.5	1.5 (1.6)	0.4 (0.1)
Organic N	0.43	0.1 (0.1)	0.03 (0.01)
Mean no. spp.	8	30	26
Dominant order	Chromadorida (64%)	Chromadorida (48%)	Chromadorida (56%)
Dominant family	Comesomatidae	Comesomatidae	Xyalidae
Dominant spp.	*Sabatieria* sp. 1; *Parodontophora*	*Sabatieria* sp. 1; *Leptolaimus*	*Daptonema*; *Microlaimus*
Dominant feeding group	Non-selective deposit (1B) (75%)	Non-selective deposit (1B) (44%)	Non-selective deposit (1B) (44.5)
Mean density	3035	2068	329
Simpsons (1/λ)	2.37	15.76	11.6
Feeding index (H')	0.88	1.12	1.07
Maturity index (H')	0.52	0.92	0.94

Table 3.20: SUMMER results of pairwise tests from ANOSIM for significant differences in nematode communities between hierarchical cluster groups. Data square root transformed and 999 permutations

Univariate measures	Nematodes	
	R	ρ
Cluster Group IA, IB	0.842	0.001
Cluster Group IA, IIA	0.997	0.001
Cluster Group IA,IIB	0.999	0.001
Cluster Group 2A,2B	0.807	0.001

Table 3.21: List of dominant nematode genera identified by SIMPER, responsible for similarity in structure of cluster Groups (by Level) in SUMMER as illustrated in Figure 3.10.

Level	Genus	Ave. abundance	Contribution (%)	Genus	Ave. abundance	Contribution (%)
	CLUSTER A			CLUSTER B		
I(A&B)	*Sabatieria* sp.1	16.6	71.8	Sabatieriasp.1	10.3	19.3
	Parodontophora	15.2	13.5	*Microlaimus*	5.4	9.5
	Terschellingia sp. 3	12.2	11.7	*Daptonema*	5.2	8.8
				Paralinhomoeus sp.1	3.1	5.1
				Metalinhomoeus	3.4	3.9
				Chromadorella	1.9	3.8
II (A & B)	*Sabatieria* sp.1	14.0	20.7	*Daptonema*	9.0	17.2
	Paralinhomoeus sp.1	4.8	8.1	*Microlaimus*	7.3	13.0
	Leptolaimus	6.2	6.5	Sabatieriasp.1	4.9	10.5
	Cobbia sp.3	3.9	6.0	*Thalassomonhystera*	4.2	8.0
	Metalinhomoeus	5.3	5.9	*Theristus*	2.7	7.0
	Terschellingia sp 3	5.2	5.8			

Table 3.22: List of dominant nematode genera identified by SIMPER, responsible for differences in structure of cluster Groups (by Level) in SUMMER as illustrated in Figure 3.10.

Level	Genus	Average Abundance		Contribution (%)
		Cluster A	Cluster B	
I (A & B) (84.01%)	*Sabatieria* sp.1	60	10.27	34.23
	Parodontophora	15.2	0.37	10.14
	Terschellingia sp 3	12.2	3.20	6.80
II (A & B) (75.96%)	*Sabatieria*	14.00	4.91	8.63
	Daptonema	3.11	9.00	5.85
	Leptolaimus	6.22	0.18	5.05
	Microlaimus	4.50	7.27	4.96
	Terschellingia sp 3	5.17	0.27	4.08
	Metalinhomoeus	5.33	0.64	4.04
	Paralinhomoeus sp.1	4.78	0.64	3.46
	Cobbia sp.3	3.89	0.00	3.18
	Thalassomonhystera	1.06	4.18	2.98
	Linhomoeus	3.22	0.36	2.42
	Halalaimus sp.4	2.61	0.09	2.19
	Paramicrolaimus	1.33	3.09	2.18
	Paralinhomoeus sp.2	2.83	0.55	2.16

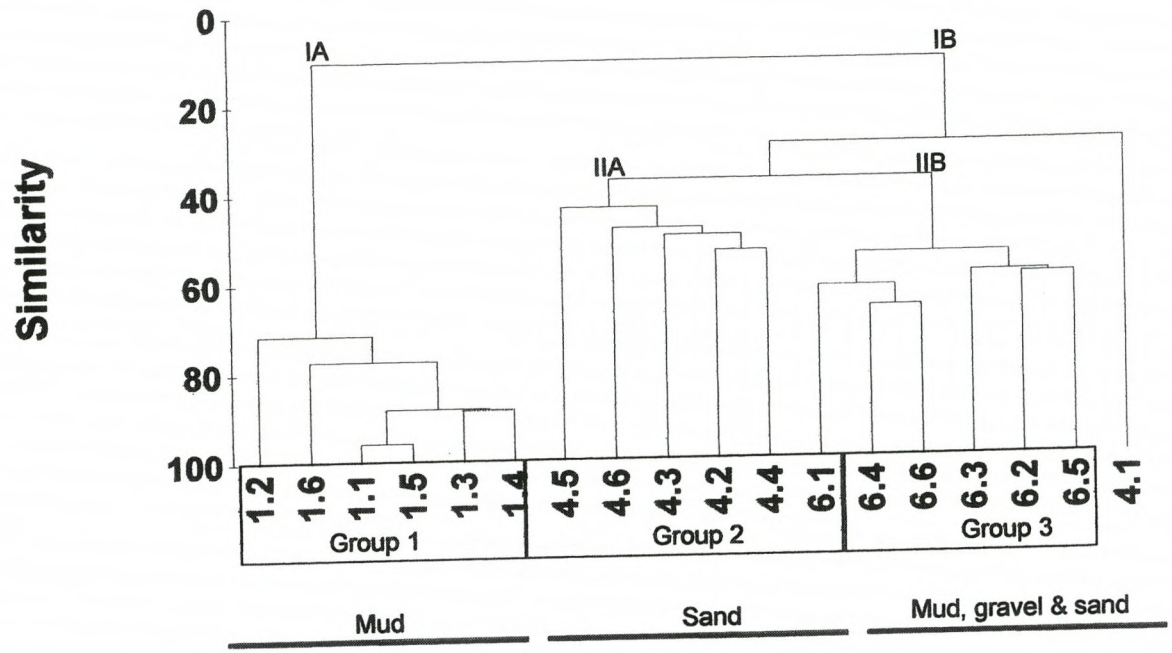

Figure 3.11: Hierarchical cluster analysis in GROUPS depicting stations from mussel raft of WINTER samples with square root transformation using Bray-Curtis similarity index. The samples are labelled 1-6 from mussel farm in Small Bay (Station 1) to Big Bay (Station 6).

Table 3.23: Summary of selected variables corresponding to three cluster groups for WINTER samples.

	WINTER		
	Group 1	Group 2	Group 3
Variable	IA (N = 6) Mean (STD)	IIA (N = 5) Mean (STD)	IIB (N = 6) Mean (STD)
Sand	4.7 (3.5)	87.9 (16.5)	76.7 (35.3)
Gravel	0.7 (1.1)	9.2 (17.8)	0.1 (0.3)
Mud	94.6 (3.5)	2.9 (4.4)	23.2 (35.4)
Grain size (φ)	4.47 (0.02)	2.08 (0.63)	2.87 (0.79)
Mean no. spp.	4	27	28
Dominant order	Chromadorida (99%)	Chromadorida (64%)	Chromadorida (54%)
Dominant family	Comesomatidae	Microlaimidae	Microlaimidae
Dominant spp.	*Sabatieria* sp. 1	*Microlaimus*; *Sabatieria* sp. 1	*Microlaimus*; *Paralinhomoeus* sp. 1
Dominant feeding group	Non-selective deposit (1B) (95.5%)	Non-selective deposit (1B) (37%)	Epigrowth feeder (2A) (46%)
Mean density	4449	2998	2399
Simpsons (1/λ)	1.13	14.31	9.30
Feeding index(H')	0.18	1.23	1.08
Maturity Index (H')	0.27	0.74	0.62

Table 3.24: WINTER results of pairwise tests from ANOSIM for significant differences in nematode communities between hierarchical cluster groups. Data square root transformed and 999 permutations

Univariate measures	Nematodes	
	R	ρ
Cluster Group IA,IB	0.989	0.001
Cluster Group IA,IIA	1.0	0.002
Cluster Group IA,IIB	1.0	0.002
Cluster Group IIA,IIB	0.949	0.002

Table 3.25: List of dominant nematode genera identified by SIMPER, responsible for similarity in structure of cluster Groups (by Level) in WINTER as illustrated in Figure 3.11.

Level	Genus	Ave. abundance	Contribution (%)	Genus	Ave. abundance	Contribution (%)
	CLUSTER A			CLUSTER B		
I(A&B)	*Sabatieria* sp.1	94.3	98.9	*Microlaimus*	15.4	30.5
				Linhomoeus	3.9	6.7
				Thalassomonhystera	3.2	6.4
				Paralinhomoeus sp.1	5.3	6.1
II(A & B)	*Microlaimus*	8.4	19.9	*Microlaimus*	22.0	29.5
	Sabatieria sp.1	6.4	14.8	*Metalinhomoeus*sp.1	11.2	10.3
	Parallelecoilas	5.2	7.7	*Paralinhomoeus* sp.1	8.5	9.6
	Thalassomonhystera	3.6	5.8			

Table 3.26: List of dominant nematode genera identified by SIMPER, responsible for differences in structure of cluster Groups (by Level) in WINTER as illustrated in Figure 3.11.

Level	Genus	Average Abundance		Contribution (%)
		Cluster A	Cluster B	
I (A & B) (94.19%)	*Sabatieria* sp.1	94.33	3.50	53.18
II (A & B) (68.72%)	*Microlaimus*	8.40	22.00	12.34
	Metalinhomoeus sp.1	1.40	11.17	8.60
	Paralinhomoeus sp.1	2.20	8.50	6.42
	Parallelecoilas	5.20	0.00	4.36
	Sabatieria	6.40	1.33	4.33
	Paralongicyatholaimus	1.40	4.83	3.40
	Linhomoeus	2.4	5.83	3.25
	Molgolaimus	0.00	3.33	2.87
	Bolbolaimus sp.1	0.20	3.00	2.52
	Parodontophora	2.60	0.00	2.31

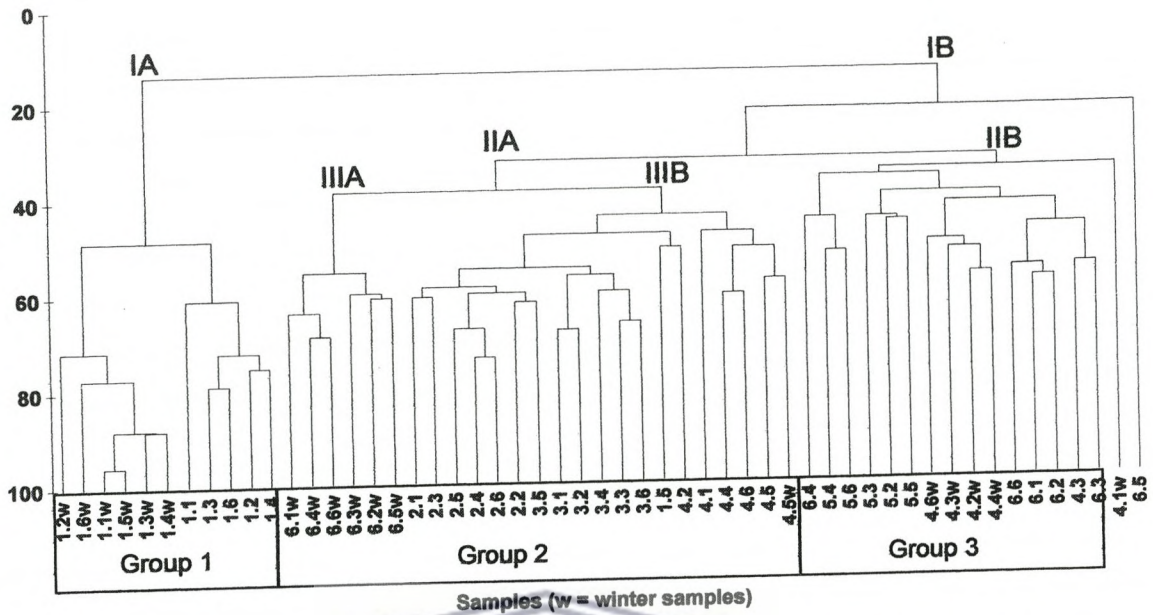

Figure 3.12: Hierarchical cluster analysis in GROUPS depicting stations from mussel raft of ALL samples with square root transformation using Bray-Curtis similarity index. The samples are labelled 1-6 from mussel farm in Small Bay (Station 1) to Big Bay (Station 6). Samples marked w = winter samples.

Table 3.27: Summary of selected variables corresponding to three cluster groups for ALL samples.

	ALL		
	Group 1	Group 2	Group 3
Variable	IA (N = 5) Mean (STD)	IIA (N = 25) Mean (STD)	IIB (N = 11) Mean (STD)
Sand	5.6 (3.7)	74.0 (22.6)	93.2 (5.0)
Gravel	0.5 (0.9)	3.4 (8.1)	1.1 (1.9)
Mud	93.8 (3.7)	22.5 (23.1)	5.7 (5.4)
Grain size (φ)	4.46 (0.02)	2.93 (0.61)	2.5 (0.4)
Dominant order	Chromadorida (83.4%)	Chromadorida (49%)	Chromadorida (60%)
Dominant family	Comesomatidae	Microlaimidae	Microlaimidae
Dominant spp.	*Sabatieria* sp. 1	*Microlaimus*; *Sabatieria* sp. 1	*Microlaimus*; *Paralinhomoeus* sp. 1
Dominant feeding group	Non-selective deposit (1B)	Non-selective deposit (1B)	Epigrowth feeder (2A)
Mean density	3684	2420	429
Simpsons (1/λ)	1.71	14.18	17.58
Feeding index(H')	0.5	1.11	1.12
Maturity Index (H')	0.33	0.90	0.96

Table 3.28: Pairwise tests from ANOSIM of COMBINED summer and winter samples for significant differences in nematode communities between hierarchical cluster groups. Data square root transformed and 999 permutations

Univariate measures	Nematodes	
	R	ρ
Cluster Group IA,IB	0.932	0.001
Cluster Group IA,IIA	0.989	0.001
Cluster Group IA,IIB	1.0	0.001
Cluster Group IIA,IIB	0.622	0.001
Cluster Group IIIA, IIIB	0.77	0.001

Table 3.29: List of dominant nematode genera identified by SIMPER, responsible for similarity in structure of cluster Groups (by Level) in COMBINED summer and winter as illustrated in Figure 3.12.

Level	Genus	Ave. abundance	Contribution (%)	Genus	Ave. abundance	Contribution (%)
	CLUSTER A			CLUSTER B		
I(A&B)	*Sabatieria* sp.1	79.0	94.2	Sabatieriasp.1	8.2	15.4
				Microlaimus	8.1	15.3
				Daptonema	3.9	6.9
				Paralinhomoeus sp.1	3.7	5.8
				Metalinhomoeus	4.2	4.7
				Thalassomonhystera	2.4	4.6
II (A & B)	*Sabatieria* sp.1	10.6	14.2	*Sabatieria* sp.1	14.0	20.8
	Paralinhomoeus sp.1	5.8	10.5	*Paralinhomoeus* sp.1	4.8	8.1
	Microlaimus	8.7	10.0	*Leptolaimus*	6.2	6.5
	Metalinhomoeus	6.7	8.6	*Cobbia* sp,3	3.9	6.0
	Linhomoeus	3.9	6.5	*Metalinhomoeus*	5.3	5.9
				Terschellingia sp, 3	5.2	5.8

Table 3.30: List of dominant nematode genera identified by SIMPER, responsible for differences in structure of cluster Groups (by Level) in COMBINED summer and winter samples as illustrated in Figure 3.12.

Level	Genus	Average Abundance		Contribution (%)
		Cluster A	Cluster B	
I(A&B) (88.4)	*Sabatieria* sp.1	79.0	8.2	46.1
	Microlaimus	0.1	8.1	5.0
II(A&B) (74.2)	*Sabatieria* sp.1	10.6	5.2	7.6
	Microlaimus	8.7	7.3	7.3
	Metalinhomoeus sp.1	7.7	0.6	5.5
	Daptonema	2.7	6.5	4.7
	Paralinhomoeus sp.1	5.8	0.6	4.7
	Leptolaimus	4.5	0.1	4.0
	Terschellingia sp. 3	3.8	0.2	3.3
	Linhomoeus	3.9	0.7	3.1
	Thalassomonhystera	1.6	4.1	2.9
	Cobbia sp.3	2.8	0.3	2.4
	Paralinhomoeus sp.1	2.4	0.4	2.0
	Metacyatholaimus	1.8	2.1	2.0
	Paramicrolaimus	1.2	2.2	2.0

Table 3.31: Results of the PERMANOVA based on Bray-Curtis similarity of nematode assemblage at Saldanha Bay. Data were untransformed. Each test was conducted using 998 permutations.

	df	SS	MS	*F*	*p*	% variation
Season	1	4641.8	4641.8	3.15	0.022	13.26
Station	1	44588	22294	15.1	0.001	41.65
Season vs. Station	2	11975	5987.7	4.06	0.001	27.42
Residual (cores)	30	44269	1475.6			38.41

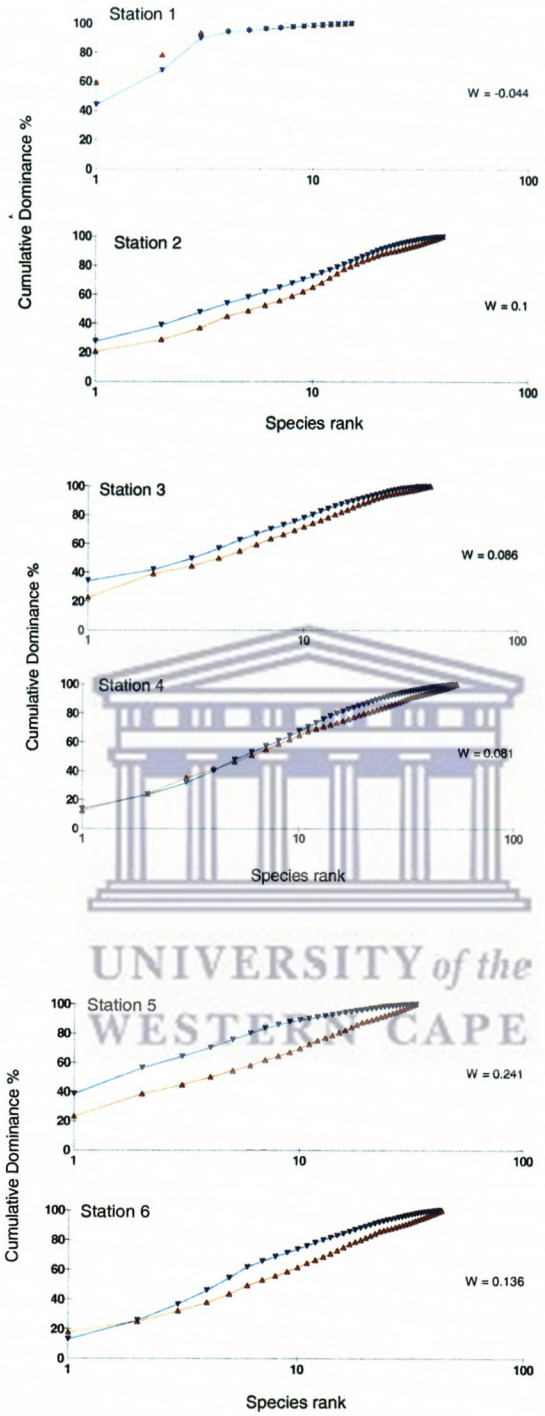

Figure 3.13: Results of cumulative Abundance (▲)-Biomass (▼) curves (ABC) for marine nematodes collected in SUMMER at Saldanha Bay. Warwick Statistic (W) is also given.

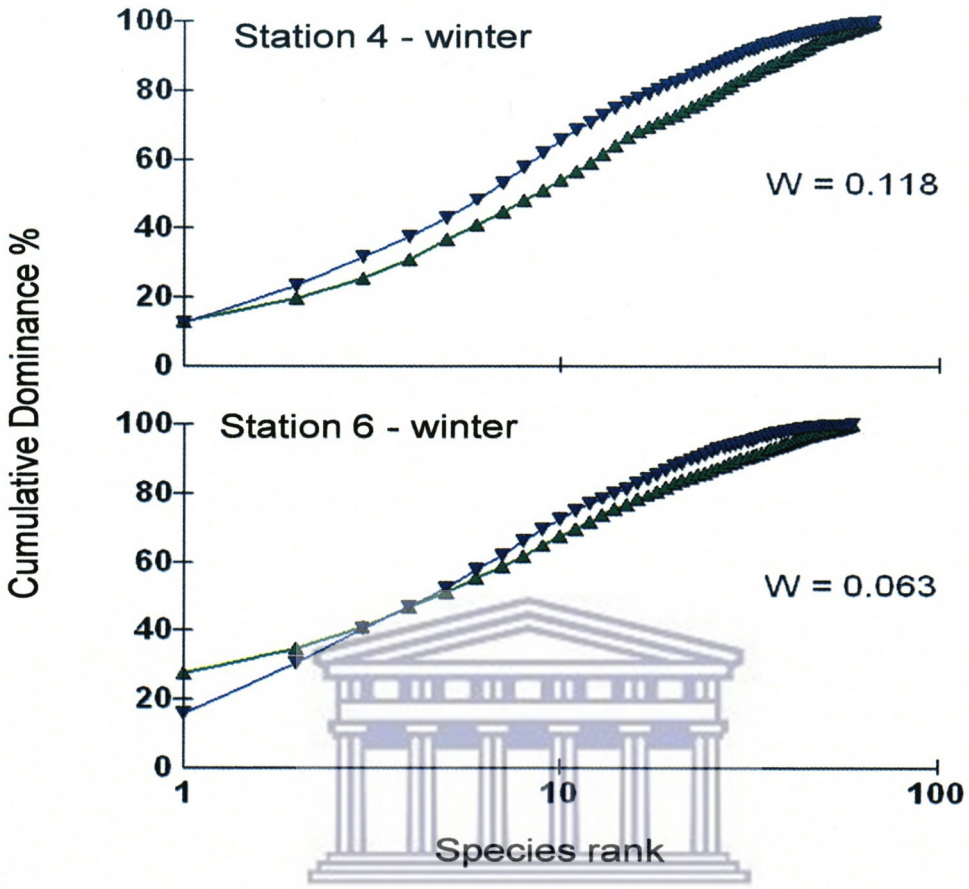

Figure 3.14: Results of cumulative Abundance (▲)-Biomass (▼) curves (ABC) for marine nematodes collected in WINTER at Saldanha Bay. Warwick Statistic (W) is also given.

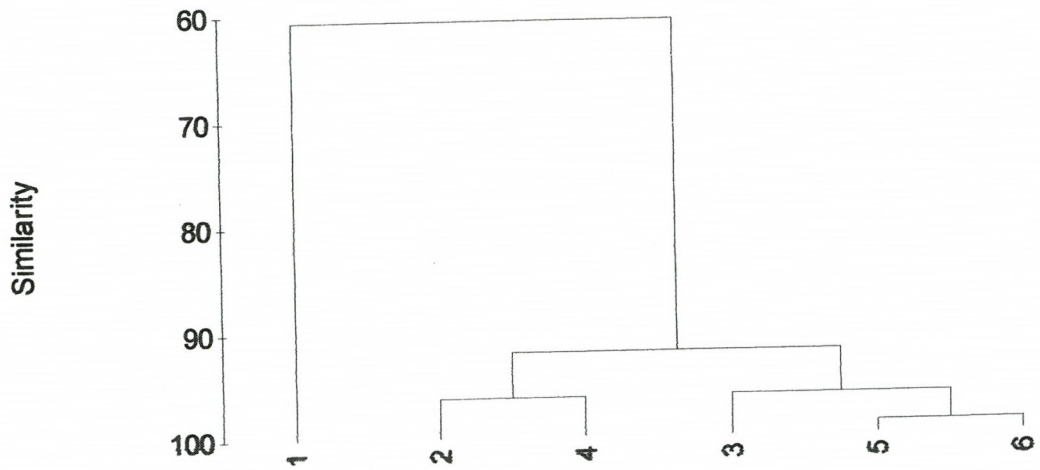

Figure 3.15: Dendrogram depicting the relationship of sediment structure and environmental chemicals on diversity at Saldanha Bay.

Table 3.32: Summary of BIOENV results. Environmental variables (√) contributing to subsets providing the ten "best" matches (ρ = Spearman's rank correlation) with root-root transformed averaged nematode SUMMER abundance across sites.

ρ	Sand (%)	Gravel (%)	Mud (%)	Grain size (µm)	Al	Fe	Cu	Pb	Cd	Zn	Org C (%)	Org N (%)
0.703							√					√
0.701							√					
0.697				√			√					√
0.695				√			√					
0.661	√									√		
0.661	√			√						√		
0.661	√						√			√		
0.661	√								√	√		
0.661	√									√	√	
0.661	√									√		√

Table 4.1: A comparison of major trace metal concentrations between Saldanha Bay and selected global sites. Values are reported as µg/g (= mg/kg). [1] (Monteiro *et al.*, 1999), [2 & 3] (Toefy, 2011), [4] Lee *et al.*, 2008), [5] (Kontas, 2008) [6] (Boyd *et al.*, 2000) [7] Fichet *et al.*, 1999), [8] (Somerfield *et al.*, 1994) [9] (Ward & Hutchings, 1996) and [10] (Rzeznik-Orignac *et al.*, 2003). Also included are the major activities that may contribute to trace metal content.

	Saldanha Bay[1]	Robben Island[2]	St Helena Bay[3]	Youngil Bay[4]	Izmir Bay, Turkey[5]	Tees Bay, N.E England[6]	Charente–Maritime harbours[7]	Restronguet Creek, Fal Estuary[8]	Port Pirie, Spencer Gulf[9]	Brouage mudflat, France[10]
Al	2945 - 17338	N.A.	N.A.	6	38226 - 91532	N.A.	N.A.	N.A.	N.A.	N.A.
Fe	2282 - 13889	847 - 1820	1470 - 3587	2.5	12404 - 76899	N.A.	N.A.	55845	N.A.	N.A.
Ni	12.35 - 29	N.A.	N.A.	N.A.	15 - 127	31	N.A.	30	N.A.	N.A.
Cu	2.86 - 13	1.2 - 4.1	2.3 - 22.7	115	4 - 70.8	67	46 - 97	2532	8 - 390	10.7
Zn	5.5 - 76	4.4 - 10.9	7.4 - 64	371	26 - 295	158	190 - 430	3814	270 - 16700	108.9
Cd	3.05 - 7	0.03 - 0.09	0.4 - 0.7	3.7	N.A.	0.21	0.3 - 1.9	2.75	9 - 267	0.2
Pb	30 - 54	3.7 - 7	1.6 - 8	49	N.A.	102	45 - 106	209	110 - 5270	30.1
Activities	Mussel farm, iron ore loading, fish factories	Sewage pipeline	Fish factory, cultural		Industrial water waste	Dredging	Oyster farm, industrial, cultural	Mining	Mining	Mudflats

CHAPTER 5

The nematode assemblage at Saldanha Bay: Biodiversity and species richness

5.1 Introduction

5.1.1 Marine biological diversity and biogeography

The marine environment covers approximately 71% of the surface of the earth (Smith & Jakubowska, 2000) and hosts a large number of species (Hessler & Sanders, 1967; Sanders, 1968; Jones & Sanders, 1972; Sanders & Hessler, 1969; Grassle & Maciolek, 1992; Gray *et al.*, 1997). Quite how many species are found in the sea, however, is a question of some debate (May, 1992; Gray *et al.*, 1997; Lambshead *et al.*, 2000; Kotwicki *et al.*, 2005; Miljutin *et al.*, 2010).

Grassle & Maciolek (1992) collected box-core samples from along a 176 km transect off the New Jersey and Delaware coast, U. S. A., and identified 798 macro-faunal species from a total sampling area of 21m². Using species-accumulation curves these authors calculated that for each square kilometre of deep-sea environment, one new species is added to the accumulation curve. Given the estimated size of the deep-sea at their study sites (occurring at a depth of 1500-2100 m), these authors then estimated that $1x10^7$macro-faunal species could be found in the global ocean. May & Godfrey (1994), and a number of others (May, 1994; Gray, 1994; Lambshead & Boucher, 2003), have questioned Grassle and Maciolek's (1992) estimate by preferring to use a direct method of calculation. May & Godfrey (1994), for instance, using the 200000 marine macrofaunal species known at the time (May 1992), argued that this number may be closer to $5x10^5$.

Grassle & Maciolek's (1992) estimate of species richness was derived from deep-water samples, and Gray (2001) has subsequently suggested, from work off Australia, that shallow water environments may be equally species rich, with sediment of similar structure exhibiting comparable species richness. Gray *et al.* (1997) previously revealed that shallow water species richness, for macrofauna, is as high as or higher than that

observed in deep-sea stations and that they exhibit similar species: area relationships. The latter authors argue that shallow water landscapes may consist of a great diversity of habitats or microhabitats, and because many species only occur in a limited number of these habitats, species richness in shallow water could be higher than in the deep sea, which, bar the occasional whale-fall are generally considered to be fairly uniform.

Gray (2002) later reviewed species richness in marine soft sediments and summarised four patterns: 1) in deep-sea environments, species occur at a lower abundance than in shallow waters due to a decrease in a particulate organic matter. 2) The deep-sea fauna, in general, is more species dense (i.e. the number of species per unit area) at a local scale, than in coastal areas due to an increase in dominance at shallower sites. The heterogeneous nature of shallow water environments, caused by differences in sediment structure, however, results in a similar species richness on a regional scale. 3) Species richness increases from the edge of the continental shelf to the bathyal and then decreases to the abyssal because food resources are limited at abyssal depths (Levin *et al.*, 2001) 4) Species richness declines from the subtropics to the poles due, in part. to a decrease in productivity levels resulting from a decline in "the coupling between primary and secondary production" (Gray 2002) but that the pattern is not present in the Southern Hemisphere, possibly due to a paucity of knowledge, especially from Africa. Since the publication of (Gray 2002), a number of macroecological studies have been conducted on marine organisms along the South American coast: molluscs (Valdovinos *et al.*, 2003), algae (Santelices & Meneses, 2000), peracarid crustaceans (Rivadeneira *et al.*, 2011) and nematodes (Lee & Riveros, 2012)

Latitudinal patterns in the distribution of species richness are widespread across marine, freshwater and terrestrial environments, and the decrease from the tropics to the poles is regarded as one of the global ecological rules, for which a very large number of explanations have been proposed (Willig *et al.*, 2003; Gray, 2002, Mittelbach *et al.*, 2007; Fernandez *et al.*, 2009; Freestone *et al.*, 2011). Latitudinal gradients in the marine realm have been comprehensively reviewed by Hillebrand (2004), although variations in the strength of the pattern appear to vary with body size and trophic position, as well as habit and habitat. Whilst some authors have suggested that patterns in the Northern and

Southern Hemispheres may differ (Rex *et al.*, 1993; Willig *et al.*, 2003), Hillebrand's (2004) meta-analysis of 198 marine data sets indicates that this is not true, and that a significant negative gradient exists regardless of regions, habitats or taxonomic groups.

Patterns in the distribution of richness are closely linked to patterns in marine biogeography. Ekman (1953) divided the shallow-water marine faunal environment into a number of distinct regions. These regions were governed by temperature regimes, allopatric vicariance and evolutionary time, and were divided into warm-water, temperate, boreal and Arctic regions for the Northern Hemisphere. Ekman (1953) pointed out that most of the land masses were found in the North. In the South, faunal regions were largely within the warm temperate regions of Africa, Australasia and South America, antiboreal and Antarctic regions. In a more recent attempt to partition the global ocean into biogeographic regions, Longhurst (1998) used a combination of ocean currents and fronts, as well as chlorophyll profiles (as an indication of production). Longhurst's (1998) biogeography was based on regional functionality rather than distribution *per-se*, and reflects geography rather than biogeography. His classification seems to work well for the pelagic realm, but is of limited use in shallow-water environments because the satellite sensors used in classification process were only able to investigate the upper layers of the pelagos. Spalding *et al.* (2007) classified the coastal and shelf areas, by using 230 digital maps of biogeographic regions, and they recognised 12 realms, 62 provinces and 232 eco-regions. Spalding *et al.* (2007) pointed out that the provinces (in their system) serve as well-defined evolutionary units and that temperature, latitude and vicariant events leading to isolation have each contributed to the formation of the Marine Ecoregions of the World.

5.1.2 Marine nematode diversity and biogeography

Nematodes are the most abundant of the Eumetazoa (Heip *et al.*, 1985), and free-living marine species frequently dominate benthic samples, both numerically and in terms of species richness (May, 1988; Wilson, 2000; Lambshead, 2004). Estimates of species

richness have received considerable attention (e.g. Gray, 2002; Lambshead and Boucher, 2003; Gingold *et al.*, 2010).

On the basis of an estimated macro-faunal species richness of $1x10^7$ species by Grassle & Maciolek (1992), Lambshead (1993) estimated that there were as many as $1x10^8$ species of nematodes in the deep sea. Lambshead (1993) recalculated the Grassle and Maciolek estimates by using the earth's deep-sea area ($3x10^8 km^2$) and then adding one new species per km^2 (the same multiplier used by Grassle & Maciolek, 1992). This estimate was accepted for a long time, but it could not be fully tested due to the lack of adequate data. Lambshead & Boucher (2003) subsequently revised this number downwards to $1x10^5$ species, on the grounds of limitations posed by availability of heterogeneous habitats (such as found in shallow-water environments), or the lack of dispersal barriers. Their calculations were supported by large-scale experiments conducted by Brown *et al.* (2001) and Lambshead *et al.* (2003). Mokievsky & Azovsky (2002) argued that in many regional or large-scale (λ) diversity studies, workers tended to use local (α) datasets that were often incomplete, and these authors proposed that when such local datasets are used then the species termination curves should be expanded as data become available. Mokievsky & Azovsky (2002) predicted that there were only between 10000 and 20000 species worldwide.

Just as estimates of macrofaunal richness are dependent on the vagaries of the methods used to obtain them, so too are those for nematodes. Indeed, given their very small size, and the large number of factors that can influence communities and diversity even at the microscale (Leduc *et al.*, 2012), the total seabed currently sampled for benthic organisms, in general, and nematodes, in particular, is negligible in comparison to the total area of marine sediment (Gage, 1996) and this significantly adds to the complexity of estimating of species richness and diversity.

Perhaps in part because surface production, oxygen availability, sediment structure and disturbance can all impact the richness and diversity of nematode assemblages at the local scale, and that different micro-habitats host different species (Vanreusel *et al.*, 2010), clear and consistent patterns in the distribution of nematode richness are hard to identify. Boucher (1990) and Boucher & Lambshead (1995) have

noted that a non-linear relation existed between depth and diversity; the ecological diversity of marine nematodes from the abyssal and bathyal depths was higher than from shallower areas or from tropical and temperate areas, which were subjected to physical disturbance.

Studies on the latitudinal gradients in nematode diversity are scarce, by comparison with those on macro-fauna. Boucher (1990) observed that temperate communities were generally more species rich than those from the tropics. This observation was supported by Lambshead *et al.* (2002) in the North Pacific: a fact that that the latter authors attributed to latitudinal patterns in surface production. In the North Atlantic, Lambshead *et al.* (2000) have suggested that richness is greater at higher than lower latitudes, although Rex *et al.* (2001) suggested that after their (Lambshead *et al.* 2000) data had been corrected for depth-related impacts, there was no clear latitudinal change in richness, a conclusion in part supported by Lambshead *et al*'s (2001) response. Most of the data on latitudinal diversity gradients in nematode communities has been derived from studies in the deep sea, but using artificial substrata in a series of subtidal experiments, Gobin & Warwick (2006) concluded that even in shallow water nematodes, latitudinal patterns in richness were unclear.

Part of the reason perhaps for the lack of any clear latitudinal trend in nematode diversity reflects their small size, which impacts on population size and opportunities for dispersal both of which are considered to increase with decreasing body size (Hillebrand, 2004, Fontaneto & Brodie, 2011). The "everything is everywhere" hypothesis (Fenchel 1993; Finlay *et al.*, 1996) implies that small organisms are widely dispersed and as a consequence should show weak patterns of richness at the global level. In their meta-analytical review of the impact of body size on the strength of latitudinal gradients in species richness, Hillebrand & Azovsky (2001) noted that meiofaunal taxa tended to display weak gradients, and Hillebrand (2004) in his wider meta-analysis of marine taxa attributed part of this at least to their infaunal nature, as well as to their small size. Thorson (1957) has suggested that infauna occur in a spatially and temporally (rather) homogeneous habitat, and that this sameness may limit the development of strong latitudinal gradients. That said, habitat heterogeneity has largely been discounted as an

explanation for gradients (Roy *et al.*, 2000). Indeed, Vanreusel *et al.* (2010) found that deep-sea cold water seeps were colonized by shallow-water related taxa, while deep-sea vents showed similar assemblages to those of adjacent sediments.

Just as the jury is still clearly out on whether free-living marine nematodes display strong latitudinal gradients in species richness, so too it is on whether there are marked patterns of global biogeography. If the "everything is everywhere" hypothesis holds true for nematodes, we might expect patterns to be unclear, and in their study of species lists from global freshwater and soil environments Artois *et al.* (2011) concluded that well defined biogeographic patterns were not obvious for free-living nematodes. This is in agreement with some of the observations of Decraemer *et al.* (2001), who reviewed the cosmopolitan nature of marine nematodes in the family Epsilonematidae. These latter authors concluded that whilst some species, such as *Metepsilonema bermudae*, were indeed very widely distributed others were restricted in their distribution. Part of the reason for the absence of a clear biogeography reflects a paucity of knowledge in most areas of the world (Artois *et al.*, 2011), as well as problem with species identification as the morphologies of many taxa are poorly known and the taxonomic relationship of many taxa are very complex. For example, Ingels *et al.* (2006) studied the distribution pattern of two species of nematodes in the family Desmodoridae around Antarctica and concluded that extensive morphological and molecular studies were needed to ascertain their distributions.

Invertebrate faunas contain many undescribed species, and new species are constantly being described, and to get around this problem ecological studies often use higher order proxies (genus, family) (Lovell *et al.*, 2007). Grelle (2002) investigated the relationships between species, generic and familial richness in four orders of mammals from the Amazon and Central America. Familial richness was related to species richness in primates, but not in any of the other orders. There was, however, a significant and positive correlation between genus and species richness in all the orders examined and Grelle (2002) proposed that the genus may serve as a good proxy for species. Working on spiders in Portugal, Cardoso *et al.* (2004) found that there too, the genus was a good proxy for species, provided sampling effort, geography, and type of habitat was duly

considered. Rosser & Eggleton (2012) asked whether higher taxa were good proxies for species in soil-dwelling insects. These authors worked with datasets from five tropical and two temperate countries and used Coleoptera and Formicidae as study groups, finding that genus could be used as a good proxy for species in the former, but not for the (smaller) latter. They also found that at the family level the relationship was poor, and that the results depended on the availability of taxonomic information, sampling effort and equitability, and in general advised against the use of higher level proxies.

Nematodes are small and their abundance is high and many ecological studies are conducted in deep-sea environments or require SCUBA assisted coring. Nematodes are usually reported on at the genus level, since many are not described to species level. Abebe *et al.* (2004) reported that most ecological studies use arbitrary species names (e.g. species 1, species 2 etc) to designate separate morphospecies, but that this approach presents problems when comparing datasets. They too noted that the genus was a good proxy for species in their study of the nematodes from Gulf of Maine.

The aim of this study is to place the nematodes of Saldanha Bay in a global context and to contribute to the debate about patterns of species richness and biogeography. As noted above, the literature generally describes a declining species richness declines with increasing latitude (Willig *et al.*, 2003) and here I test whether similar patterns are observed at the genus (and family) level using available data sets. In addition, I explore global biogeography to determine if there is a match between patterns generated by nematodes (again at the genus and family) and those produced by others (Ekman, 1953, Longhurst, 1998; Spalding *et al.*, 2007).. Information on free-living marine nematodes from the Southern Hemisphere is comparatively uncommon, and from Africa decidedly rare. Comparative data from the global literature have been used and, where possible, information on sampling and environment has been included in order to try and account for the effects of same on the results.

5.2 Materials and methods

Nematodes were sampled from six cores at each of six stations along a transect in Saldanha Bay during summer 1998, and from four stations in winter 1999, as outlined in Chapter 2: In order to derive overall estimates of species, generic and familial richness in Saldanha Bay, and to ascertain whether the sampling effort was adequate, accumulation curves were generated using Colwell's *EstimateS* (version 8: http://viceroy.eeb.uconn.edu/estimates): species data were collapsed by both genus and family. This method uses a random sample from the dataset, and calculates species (and in this case also generic and familial) density. Thereafter, a new (random) sample is analysed and each new species (genus/family) is added, in a "species" accumulation curve (Chao, A. 1987, Colwell & Coddington, 1994, Lee & Chao, 1994, Butler and Chazdon, 1998, Chazdon *et al.*, 1998 and Colwell *et al.*, 2004). This process was repeated 50 times and *CurveExpert1.3* (http://flu.org.cn/en/download-79.html) was then employed to fit a Morgan – Mercer - Flodin (MMF) sigmoidal model to the curves, from which the asymptote was determined.

A number of other estimates of richness were computed for Saldanha Bay using *EstimateS*. These estimators needed to be independent of sample size, patchiness effects and sample order (Chazdon *et al.*, 1998). The ones used here are the Abundance-based Coverage Estimator (ACE), that takes samples with less than ten individuals into account and the Incidence-based Coverage Estimator (ICE), which accounts for studies with less than ten sampling units (Lee & Chao, 1994). Chao 2 Incidence-based estimators and second-order Jackknife estimators (Jackknife 2) both calculate richness by utilizing samples with only one or two species (Chao, 1987), while Jackknife 2 also takes the number of samples into consideration (Chazdon, *et al.*, 1998). These methods also take effects of patchiness into account (Chazdon *et al.*, 1998; Lambshead *et al.*, 2003). Gray (2000) warned that Chao 2 tends to over-estimate species richness in samples with mostly one or two individuals.

In order to place the Saldanha Bay data into a global context, it has been necessary to use similar datasets from the literature. Unfortunately, surprisingly few published studies provide comprehensive lists (Nicholas & Hodda, 1999; Vanhove *et al.*,

2004), either in the body of the manuscript, or as appendices or supporting, on-line information. All too often only the dominant taxa are reported, and a minority provide sample specific data – both of which make direct comparisons with our data difficult. Perhaps more alarming though is a general lack of adequate information on the (quantitative) environment (Pastor de Ward, 1998), or sampling meta-data (Gambi *et al.*, 2003).

A thorough review of the literature generated a total of 22 useable shallow-water (thereby removing depth as a confounding variable, as per Rex *et al.* (2001)) datasets (Figure 5.1), which were carefully consolidated, corrected (synonymies and misspellings) and collapsed (all species per genus and all genera per family, summed). Salient environmental (grain size, latitude, depth), sampling (number, volume and area of samples, total number of individuals counted and identified) and community data (alpha richness, diversity and equitability, and density) were similarly brought together for each site. It should be stressed that owing to vagaries in the identification of free-living marine nematodes, all data used here are based on the genus (or family – see below) level and not on the species, though as noted previously this is not uncommon in the nematode literature (Muthumbi *et al.*, 2004; Netto & Valgas, 2010; Moreno *et al.*, 2011; Gingold *et al.*, 2011).

Estimates for generic/familial richness at each global study site were computed as for Saldanha Bay, using *EstimateS* and *CurveExpert1.3.* In order to explore the effects of latitude, sediment grain size and depth, as well as the various sampling (volume, number and areal extent) and community (diversity, evenness and abundance) attributes on species richness, multiple regression analyses (forward selection) have been used in a two phased approach. In the first instance, observed richness was tested against all predictors (environmental and sampling) and in the second, estimated richness was tested against only environmental predictors: the theory being that the accumulation curve takes into consideration the vagaries of sampling. Data were tested for normality visually in Statistica v7, and log transformation was not necessary. Significance levels ($p<0.05$) were adjusted to account for multiple testing using the Bonferroni correction (Hochberg, 1998).

In order to see the relationships between richness of the different taxonomic levels and thereby explore issues of taxonomic surrogacy, Pearson correlations (Zar, 1999) were computed between the observed number of species, genera and families in all samples from Saldanha Bay: data were not transformed and normality was confirmed visually using Statistica v7. Subsequently, the distribution of nematodes in the Saldanha Bay samples was examined at the species, generic and familial levels and similarities between each were tested. This was done in order to check the observations of Clarke and Warwick (1998) that higher taxonomic levels can be useful and robust proxies for lower ones. The Bray-Curtis similarity index was computed between samples using PRIMER v6 (Clarke & Gorley, 2006) and comparisons between the three matrices (species-genus/family and genus-family) were evaluated using the RELATE routine in PRIMER. The RELATE routine tests the null hypothesis that there is no relationship between the two matrices ($\rho = 0$) and the matching coefficient ρ reflects the similarity (Spearman Rank) of multiple random permutations around zero (Clarke & Gorley, 2001).

In exploring patterns of global biogeography, all the data for each site were pooled (by genus/family), and the similarity between sites was again computed using the Bray-Curtis Index in PRIMER v6 (Clarke & Gorley, 2006). The RELATE routine was also then used to test the null hypothesis that there was no relationship between the two matrices and the similarity matrices were visualised in both a 1-dimensional dendrogram (following group-average linkage) and a 2-dimensional nMMDS plot.

The relationship between the nematode data and the environmental and sampling data was investigated using a Distance Based Linear Model (DISTLM) in PERMANOVA+ (Anderson *et al.*, 2008). At first, DISTLM conducts a marginal test, which determines how much of the variance in the nematode resemblance matrix can be explained by each predictor variable. DISTLM then partitions the variation in data distribution according to a best fit multiple regression model, which provides a best solution (adjusted R^2) for a combination of the available predictors. The distance-based redundancy analysis (dbRDA) routine used in DISTLM then examines the available variables and predicts the best linear combinations of variables that then explain the greatest variation (Anderson *et al.*, 2008).

5.3 Results

5.3.1 Patterns in Saldanha Bay.

As noted in Chapter 3, a total of 4 488 specimens were identified from the 53 samples collected in Saldanha Bay, representing 36 families, 117 genera and 136 nominal species. Richness and diversity varied across the transect (Table 5.1) as did the dominant families (Table 5.2) and genera (Table 5.3). Overall, assemblages were dominated by the families Comesomatidae and Linhomoeidae and to a slightly lesser extent by Xyalidae and Microlaimidae. The genus *Sabatieria* was predominant throughout and indeed overall it accounted for c. 27% of all specimens identified.

Accumulation curves for the Saldanha Bay fauna are illustrated in Figures 5.2 (genus) and 5.3 (family). Both curves indicate an increase with increasing sample size and both approach asymptotes. The standard deviations of the primary estimators i.e. ACE, ICE, Chao 2, and Jackknife 2 all decreased as sample size increased (APPENDIX 5.1).

Richness estimates for Saldanha Bay are presented in Table 5.4. In the case of genera, the Incidence Coverage Estimator (ICE) index became stable at 127 genera after only 37 sample simulations (data not shown). Other genus richness estimators produced similar results with Chao 2 (126 genera) and Jackknife 2 (140 genera) both approaching asymptote after 33 simulations. The maximum genus richness was generally similar in all estimators with second order Jackknife recording the highest value (140 genera) followed by ICE (131 genera) and Chao 2 (122 genera). The fitted genus accumulation curve, from the Morgan-Mecer-Flodin model (MMF), yielded the maximum number of 149 genera and the regression equation is expressed in Table 5.5.

In the case of the family data (Table 5.4), ICE values became stable at 39 families after only 30 sample simulations: Chao 2 (44 families) and Jackknife 2 (42 families) both approached asymptote after 33 and 30 simulations, respectively. The maximum family richness was similar in all estimators with Jackknife 2 recording the highest value (47 families) followed by ICE (44 families) and Chao 2 (43 families). The fitted family

accumulation curve, from the MMF model, yielded the maximum number of 91 families and the regression equation is expressed in Table 5.6.

There are very strong positive correlations between the numbers of species, genera and families in samples collected from Saldanha Bay (Table 5.7). This suggests that families and genera are good surrogates for species, in this context. The results of the RELATE routine (Table 5.8) comparing the structure of communities in Saldanha Bay, as defined using species, genera and families are similarly convincing: $\rho = 0.99$ (species-genus, $p = 0.001$), $\rho = 0.966$ (species and family, $p = 0.001$) and $\rho = 0.96$ (genus and family, $p = 0.001$). This too indicates that both genus and family may serve as good proxies for species – in ecological studies.

5.3.2 Global Patterns

APPENDICES 5.2 and 5.3 show comparable information for genera and families (respectively) from the global data set assembled. A total of 264 genera were identified, the five most widely distributed being *Daptonema* (95%), *Viscosia* (91%) and *Sabatieria* (86%), as well as *Terschellingia* and *Theristus* (both 77% of sites). A total of 51 families were identified: Chromadoridae, Linhomoeidae, Oncholaimidae and Xyalidae were present at all the sites, followed by Desmodoridae (95% of sites), Axonolaimidae and Selachnematidae (both at 91% of sites).

Estimates of overall richness for each site in the global data set, as derived by ACE, ICE, Chao 2 and Jackknife 2 are shown in Tables 5.9 and 5.10 (genus and family, respectively). In the genus dataset ACE, ICE, Chao 2 and Jackknife 2 estimates were close to each other for individual stations. Saldanha Bay recorded the highest ICE value (131), followed by St Martin's Flats (114), Italian Marine Protected Areas (113) and St Martin Flats (99). The lowest ICE value was calculated for Baltic Sea (29). The highest ICE value for the family data was once again recorded for Saldanha Bay (44), followed by Martin Bay (34), Italian Marine Protected Areas (31) and the Gulf of Maine (30). The lowest values were recorded for Cienfuegos Bay and Bothnian Bay (15 and 14 families, respectively). It should be noted that during the computation process Chao estimated CV

values greater than 0.5 for some of the study sites. In those cases the values were re-computed and the classical Chao instead of bias correlated estimates were used. The larger of Chao 2 and ICE were then recommended as the best estimate of incidence-based richness.

The estimates of generic richness derived from the MMF model, illustrated as Curve-Fit Estimates (CFE), for each of the 22 global study sites available to us here are shown in Table 5.11 and Figures 5,3A and 5.3B. The table also includes the environmental, physical and community variables used in the analysis. The generic richness indices indicate that the communities in Saldanha Bay are the fourth most rich of those occurring at similar depths. The results for Figures 5.3A and 5.3B showed a weak relationship between both genus CFE (r^2: 0.164) and family CFE (r^2: 0.057) against latitude. When only the Northern Hemisphere samples were plotted, the genus CFE-latitude (r^2: 0.213) and family CFE-latitude (r^2: 0.037) relationships remained weak .

The results of the MRAs to explain the variation in observed genus richness against environmental, sampling and biological variables revealed that only the number of nematodes counted and identified and family richness contributed significantly to the overall analysis (Table 5.12). The MRA for observed family richness against the same variables revealed that all predictors contributed significantly to the explained variation in family composition (Table 5.12). The MRA estimated (CFE) richness of genera and families against environmental predictors showed that neither latitude, depth nor sediment grain size could be used as predictors (Tables 5.12).

The dendrograms and nMMDS plots for the genus and family data are shown in Figures 5.4 and 5.5 (respectively), on which no clear geographic pattern is discernible. For example, Saldanha Bay clusters with the Celtic and NW Irish seas as well as the Gulf of Maine in both genus and family datasets, whilst the other South African datasets (Gamtoos and Swartkops estuaries) cluster with the North Sea and Manfredonia (Mediterranean Sea) in the genus and family datasets, respectively. The results of RELATE analysis between the global genus- and family-based similarity matrices were similar ($\rho = 0.68$, $p = 0.001$).

In the case of the generic data, Table 5.13 shows that of the three environmental variables examined, only Depth was significant ($p = 0.013$) in the marginal tests and that it explained a mere 11% of the observed variation in the distribution pattern. All three variables were needed to construct the best-fitting model (though only two, Depth and Latitude, were significant) and together they accounted for 28% of the total variation: note the low overall adjusted R^2 value (0.118) .The dbRDA plot is shown in Figure 5.6, which separates samples on the basis of depth along the x-axis (explaining c. 55% of fitted variation) and latitude and substratum along the y-axis.

Table 5.14 shows comparable results for the family dataset, from which it can be seen that only latitude is significant ($p = 0.023$), though it explained less than 10% of distribution pattern. Again all three predictors were needed to construct the best-fitting model (adjusted $R^2 = 0.16$), and though none were significant, in combination they accounted for c. 30% of the variation. The dbRDA plot is shown in Figure 5.7. The first two vectors only accounted for 94.6% of the fitted variation and this was 29.7% of the total variation. The third vector explained 100% of the fitted variation.

5.4 Discussion

The results presented here indicate quite clearly that the sampling programme undertaken in Saldanha Bay was adequate to define species richness: 136 observed species from 53 samples and 4488 individuals examined, as oppose to estimates of 173 species using Curve-Fit Estimators or between 145 and 156 species from a suite of non-parametric species estimators. This gives confidence in the data collected.

The results of the MRAs indicate that sampling (area, number, number of individuals examined etc) does have an impact on observed richness, and that this influence is stronger than any environmental signal (Tables 5.12). These observations are not novel (e.g. Boucher & Lambshead, 1995), hence the need to account for sampling bias using standardisation methods such as e.g. accumulation curves. Interestingly, the estimates for generic and family richness in Saldanha Bay (Tables 5.9 and 5.10), are higher than those for all other areas examined here. That said, the CFE estimate (Table 5.11) ranks Saldanha Bay fourth behind the studies from Indian mangroves (Chinnadurai & Fernando, 2007), Italian MPAs (Moreno *et al.*, 2008a) and Cienfuegos Bay in the Caribbean (Armenteros *et al.*, 2009), in terms of genera, but first in terms of family.

It is hard to explain this observation, given that Saldanha Bay lies in a cold-temperate upwelling area, though the relationship between latitude and richness (generic or familial) is not clear (Table 5.13). The paucity of adequate datasets for the Southern Hemisphere restrict the interpretation of data, but based on the available evidence, the absence of any significant latitudinal influence on richness is in agreement with Rex *et al.*'s (2001) observations on the Lambshead *et al.* (2000) data collected in the deep North Atlantic, and on the experimental findings of Gobin & Warwick (2006). It also agrees with the observations of Kotwicki *et al.* (2005) on true meiofauna and it can be interpreted in either of two ways. Firstly, the richness of genera (and families) may not be a useful proxy for species, and secondly, should everything be everywhere (Fenchel & Finlay, 2004); we might not then expect to see pronounced latitudinal gradients (Hillebrand & Azovsky, 2001).

Although the results of the MRA indicate that there is a relationship between the number of families and genera (Table 5.12), their significance as predictors of each other is not pronounced. Similar results have been observed for the family-species relationship by a number of groups working on diverse organisms from arthropods to mammals, though the genus-species relationship seems to be, understandably, better (Grelle, 2002; Cardoso *et al.*, 2004; Rosser & Eggleton, 2012). That said, it is important to distinguish between evolutionary relationships as oppose to ecological relationships, because whilst genera may be good proxies for species at the ecological level that does not imply they should be good proxies at the evolutionary one. The data for Saldanha Bay, for example, suggest that genera are excellent proxies for species at the ecological level (as Clarke and Warwick, 1998; Abebe *et al.*, 2004), in terms both of richness (Table 5.7) and distribution (see RELATE statistics in 5.3.1, above). But the global data suggest otherwise, and perhaps it is then premature to try and explore relationships between diversity and latitude until such stage as more rigorous, consistent and definitive species data become available (as Lee & Riveros, 2012). Holterman *et al.* (2008) analysed 128 near full length small subunit rDNA sequences of nematodes belonging to the major marine orders Chromadorida, Desmodorida, Monhysterida, Araeolaimida and Plectida. The phylum nematode is placed at the base of Superphylum Ecdysozoa and Holterman *et al.* (2006) placed Chromadorida at the base of nematodes. Holterman *et al.* (2008) hypothesized that at family and genus levels nematodes are taxonomically very similar and that they are able to make transitions (termed "lifestyle changes" in habitat transitions by Bik, 2010) and diversify (species) based on morphological and physiological changes. The basal Chromadorida included taxa that are able to live in different environments and the transition from marine to other habitats occurred at least 16 times in their evolutionary history.

The Everything is Everywhere argument (*sensu* Fenchel, 1993; Finlay *et al.*, 1996) is difficult to counter using conventionally collected information from genera (and especially families), and the results of the global dataset suggest that most nematode genera are widely spread, and that many are cosmopolitan by nature. A total of 265 genera were identified (Appendix 5.2): *Daptonema* was present in 95% of the 22 study sites, while *Viscosia* (90%), *Sabatieria* (86%), *Terschellingia* and *Theristus* (both 77%)

were also widespread. Similar observations on the distribution of genera have been noted by Derycke *et al.* (2005), Bhadury *et al.* (2008), as well as Bik *et al.* (2010), and, as noted earlier Vanreusel *et al.* (2010) found that deep-sea cold water seeps were colonized by shallow-water related taxa, while deep-sea vents showed similar assemblages to those of adjacent sediments. Derycke *et al.* (2013) attributed this "homogenisation" (own emphasis) to the influences of vicariant events linked to continental drift, sea level fluctuations and glacial cycles, which must obviously be facilitated by their small size. Indeed, dispersal is influenced by a large number of biological and environmental factors (body shape, body size, ability to swim, hydrodynamic forces, sediment structure) and life-histories (presence of dauer larvae, parasitism), while the genetic structure would be determined not only by the geographic distance or life history of populations but also by water current and ecological characteristics of the habitat (Derycke *et al.*, 2013).

Whilst it is difficult to argue against the everything is everywhere hypothesis at the generic level, Bik *et al.* (2010) have provided evidence that even at the species level, some are indeed widely distributed. Using molecular data, these authors noted that nematode endemism was low, especially at deep-sea sites, and that both deep-sea and shallow water taxa were widely distributed. Molecular studies have shown that both shallow water and deep-sea environments have been independently colonized a number of times (as implied by Holterman *et al.* (2008) and that there was very little divergence in genetic lineages (< 1% in the family Oncholaimidae) (Bik *et al.*, 2010). Oncholaimidae are able to disperse in a number of ways: passive floating, drifting along with sediments after/during storms, biological transport vectors such as drifting algae, birds, humans and other mammals (Palmer, 1988; Ullberg & Ólafsson, 2003).

Interestingly, when the data are pooled and CFEs are derived (as previously) for each region (Table 5.15 and Figure 5.8), South Africa would appear to be particularly rich in nematode families. Tempting though it is to interpret this in terms of artefacts, it likely reflects the fact that the samples comprising the pool are derived from both different environments and from different biogeographic provinces, albeit at similar depths. The samples from Saldanha Bay are marine and were collected from the cold temperate, Namaqua province (sensu Emanuel *et al.*, 1992), whilst those of Gyedu-

Ababio *et al.*, (1999) and Gyedu-Ababio (2011) were collected from estuarine systems along the warm temperate south coast. This emphasises the fact that any attempt to explore patterns of richness with latitude need to take account of variations in habitat (Gobin & Warwick, 2006), because both sets of studies were conducted at essentially similar latitudes (Table 5.11).

Given the lack of any clear pattern in the distribution of richness, the lack of a clear biogeographic signal to the global dataset comes as no surprise, and supports the Everything is Everywhere hypothesis. Interestingly though, whilst latitude, depth and sediment structure played no part in influencing patterns of richness, they do (in various combinations depending on taxon unit) influence structure at the community level (Figures 5.6 and 5.7). This is perhaps not surprising given habitat (etc) specificities (as above highlighted by Emanuel *et al.*, 1992), and again is not at odds with the Everything is Everywhere hypothesis, which assumes that the species assemblage found in one habitat would also be present globally in similar habitats.

Whilst genera and families may be good proxies for species in an ecological context, it is less clear that they are suitable proxies for species at the evolutionary level. The data presented above suggest that there are no clear latitudinal patterns in the richness of shallow-water nematodes as measured using genera, which is both the most frequently reported taxonomic unit and the highest basic unit that can be compared across studies. This relationship is even poorer when examined using families. Unfortunately then, until such time as a global standard is established in this regard, the only way it will be possible to examine large scale patterns in richness will be through dedicated research by single workers (or perhaps networked groups working to common standards), as exemplified by the recent work of Lee & Riveros (2012). Given that sampling effort significantly impacts on estimates of point diversity, relationships need to be established using correction methods (as here), and even then we need to take cognisance of differences in habitat sampled.

Vandepitte *et al.* (2009) recently reported on an integrated database for meiofauna funded by the European Union Network of Excellence on Marine Biodiversity and Ecosystem Functioning. In total 83 datasets were recorded that included those from deep-

sea to coastal sites, from Arctic to the Antarctic but mostly from European marine waters. The MANUELA (Meiobenthic and Nematode biodiversity: Unravelling Ecological and Latitudinal Aspects) database include 1283 unique stations with approximately 140 000 records. MANUELA would allow the analysis of datasets that are standardized for species list and contain meta-data that would permit researchers to conduct studies over a large temporal and spatial scale. MANUELA however reveals a paucity of information from African environments, particularly from western marine environments south of the equator, and work to redress this gap is needed.

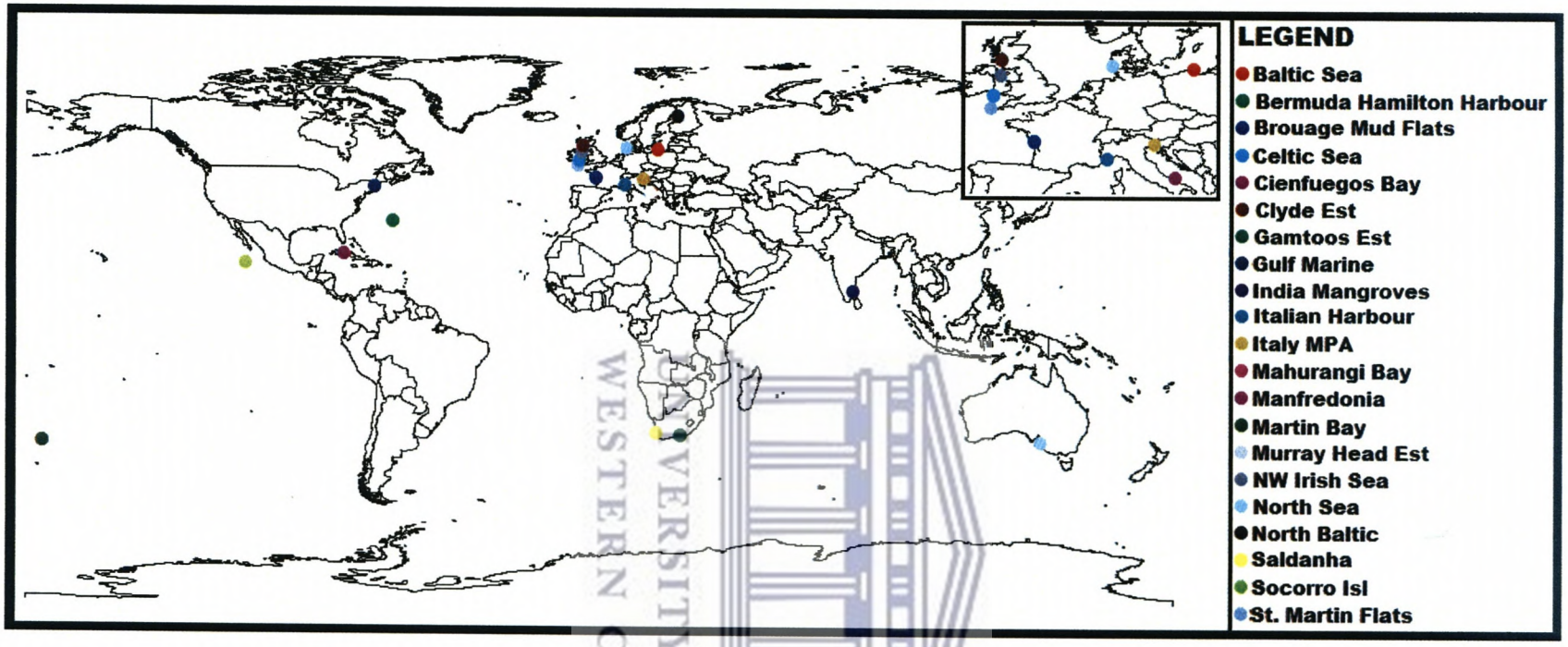

Figure 5.1: Global distribution of marine nematodes from 22 fully reported sites. The list of authors is presented in Table5.11. Note that Celtic Sea and St Martin Flats, Scilly Island data points overlap.

Table 5.1: The mean number of species, mean abundance and jack-knife alpha diversity indices for all nematodes in Saldanha Bay from six stations (six cores (10 cm²) per station). S, mean number of species recorded per station; 1/λ (= inverse Simpson's index), species diversity index per station, J' (=Pielou's), measure of equitability.

Station	Mean abundance of specimens per station	Mean number of species per station(S) ± S.E.	Total number of species per station	Simpson index (1/λ') ± S.E.	Pielou's index of equitability (J')
1	3661.17 ± 443.12	7 ± 2.13	44	1.73 ± 0.38	0.39 ± 0.08
2	2125.83 ± 179.65	32 ± 1.84	65	18.2 ± 2.31	0.88 ± 0.02
3	1568.83 ± 109.16	27 ± 2.11	57	12.1 ± 2.31	0.84 ± 0.02
4	1271.08 ± 331.45	30 ± 1.68	100	28.1 ± 3.15	0.89 ± 0.01
5	148.4 ± 29.26	23 ± 2.82	59	12.5 ± 2.15	0.86 ± 0.02
6	2123.33 ± 561.91	26 ± 1.6	100	16.7 ±3.5	0.86 ± 0.02
Total number of spp.	136				

Table 5.2: Dominant and subdominant of nematode families at six stations in Saldanha Bay. Percentage contributions presented in brackets.

Stations	Dominant family	Subdominant families	Habitat
1	Comesomatidae (73.4%)	Linhomoeidae (10.6%), Axonolaimidae (6.8%)	Muddy
2	Linhomoeidae (26.1%)	Comesomatidae (17.9%), Xyalidae (14.6%)	Sand, mud
3	Leptolaimidae (22.1%)	Comesomatidae (21.2%), Linhomoeidae (19.3%)	Sand, mud
4	Linhomoeidae (18.2%)	Microlaimidae (11.5%), Comesomatidae (11.3%)	Sand, gravel
5	Xyalidae (35%)	Monhysteridae (13.9%), Cyatholaimidae (6.9%)	Sand
6	Microlaimidae (20.6%)	Linhomoeidae (15.4%), Xyalidae (11.2%)	Sand

Table 5.3: Composition of dominant (> 5%) and subdominant (> 1%) of nematode genera present at six stations in Saldanha Bay

Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
*Sabatieria*sp.1 73.8%	*Sabatieria* sp.1 16.7%	*Sabatieria* sp.1 20.5%	*Microlaimus* 11.2 %	*Daptonema* 23.0%	*Microlaimus* 20.3%
Parodontophora 6.5%	*Terschellingia* sp.3 10.1%	*Leptolaimus* sp 1 14.8%	*Sabatieria* sp.1 8.7%	*Thalassomonohystera* 12.0%	*Paralinhomoeus* sp. 1 5.6%
Terschellingia sp 4 5.2%	*Cobbia* sp. 3 5.6%	*Terschellingia* sp.3 5.51%	*Metalinhomoeus* sp. 1 6.6%	*Odontophora* 5.3%	*Sabatieria* sp.1 4.2%
Molgolaimus 1.7%	*Leptolaimus* sp 1 4.6%	*Halalaimus* sp.4 5.4%	*Paralinhomoeus* sp. 1 4.4%	*Theristus* 4.7%	*Linhomoeus* sp. 1 3.9%
Metalinhomoeus sp. 2 1.6%	*Linhomoeus* sp. 1 4.1%	*Camacolaimus* 5.4%	*Chromadorella* 3.9%	*Microlaimus* 4.3%	*Paralongicyatholaimus* 3.5%
	Paralinhomoeus sp. 1 3.9%	*Paralinhomoeus* sp. 1 4.6%	*Linhomoeus* sp. 1 3.5%	*Sabatieria sp.*1 4.0%	*Paramicrolaimus* 3.3%
	Microlaimus 3.6%	*Cobbia* sp. 3 4.4%	*Parallelecoilas* 2.7%	*Promonhystera* 3.7%	*Thalassomonohystera* 2.8%
	Chromadorella 3.2%	*Daptonema* 3.1%	*Aegialoalaimus* 2.6%	*Metadasynemoides* 2.7%	*Theristus* 2.7%
	Daptonema 3.2%	*Chromadorella* 2.6%	*Theristus* 2.4%	*Metacyatholaimus* 2.3%	*Molgolaimus* 2.6%
	Paralinhomoeus sp. 2 3.1%	*Metalinhomoeus* sp. 1 2.6%	*Thalassomonohystera* 2.3%	*Diplopeltoides* 2.3%	*Bolbolaimus* sp. 1 2.5%
	Paralongicyatholaimus 3.1%	*Linhomoeus* sp. 1 2.2%	*Paralinhomoeus* sp. 2 2.2%	*Dasynemoides* 2.0%	*Daptonema* 2.5%
	Halalaimus sp.4 2.6%	*Halalaimus* sp.1 1.9 %	*Parodontophora* 2.0%	*Longicyatholaimus* 2.0%	*Polysigma* 2.3%
	Metalinhomoeus sp. 1 2.6%	*Metalinhomoeus* sp. 2 1.7%	*Cobbia* sp. 3 1.5%	*Paralinhomoeus* sp. 1 1.7%	*Metadasynemoides* 2.0%
	Thalassomonohystera 2.4%	*Microlaimus* 1.7%	*Paralongicyatholaimus* 1.5%	*Paralongicyatholaimus* 1.7%	*Pselionema* sp. 1 2.0%
	Metacyatholaimus 2.4%	*Paralinhomoeus* sp. 2 1.5%	*Paramicrolaimus* 1.5%	*Spirinia* 1.7%	*Cobbia* sp.1 2.0%
	Calyptronema 2.4%	*Halalaimus* sp.3 1.5%	*Siphonolaimus* 1.5%	*Camacolaimus* 1.3%	*Dasynemoides* 1.7%
	Theristus 2.1%	*Valvaelaimus* 1.3%	*Chromadorina* 1.3%	*Chromadora* 1.3%	*Metacyatholaimus* 1.7%
	Paramicrolaimus 1.9%	*Theristus* 1.1%	*Metalinhomoeus* sp. 2 1.3%	*Paramicrolaimus* 1.3%	*Odontophora* 1.5%
	Tubolaimoides 1.5%	*Metacyatholaimus* 1.1%	*Viscosia* 1.3%	*Siphonolaimus* 1.3%	*Leptonemella* 1.2%
	Chromadorina 1.4%	*Aegialoalaimus* 1.1%	*Dasynemoides* 1.2%	*Chromadorella* 1.0%	
	Valvaelaimus 1.2%	*Amphimonhystrella* 1.1%	*Trochamus* 1.1%	*Chromadorina* 1.0%	
	Oncholaimus 1.2%	*Leptolaimus* sp.2 1.1%		*Neotonchus* 1.0%	
	Halalaimus sp 1 1.2%			*Paracyatholaimus* 1.0%	
				Retrotheristus 1.0%	
				Stylotheristus 1.0%	

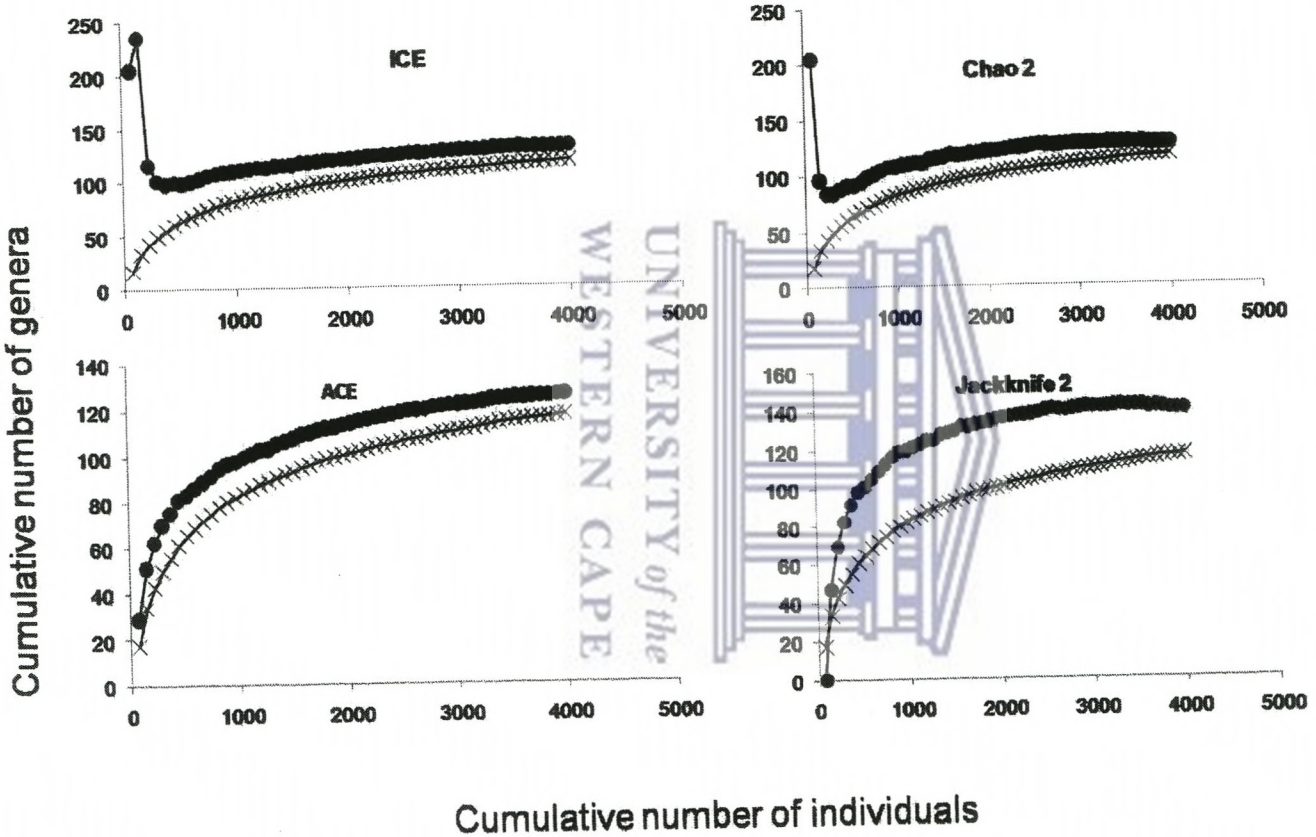

Figure 5.2: Four genus richness estimators for marine nematodes in Saldanha Bay. The upper curves represent the individual genus richness indices and the lower curve is a plot of the number of genera in pooled samples versus the number of individuals in the study area.

Table 5.4: Non-parametric estimators of species, genus and family richness using *EstimateS* software for Saldanha Bay.

Samples	ACE	ICE	Chao 2	Jackknife 2
Species richness	145	150	145	156
Genus richness	126	131	127	142
Family richness	43	44	43	46

Table 5.5: Estimations of species and genus richness of marine nematodes at Saldanha Bay using Morgan-Mecer-Flodin Model plots of species and genus accumulations per sample.

	Sigmoidal curve parameters	r	Standard Error	Estimated Richness	Observed Richness
Saldanha Bay species	a = -4.75943 b = 148.273 c = 173.438 d = 0.75426	0.9998	0.427	173	136
Saldanha Bay genus	a = -1.10637 b = 157.9925 c = 148.8741 d = 0.765669	0.9997	0.706	149	117

Table 5.6: Estimations of family richness of marine nematodes at Saldanha Bay using Morgan-Mecer-Flodin Model of a plot of family accumulation per sample.

	Sigmoidal curve parameters	r	Standard Error	Estimated Family Richness	Observed Family Richness
Saldanha Bay	a = -70.9646 b = 1.771405 c = 90.87385 d = 0.153072	0.9997	0.706	91	35

Table 5.7: Results of the Pearson Rank Order Correlation analyses of nematode species, genera and families at Saldanha Bay. Results show R values with significant R - values* at the 0.05 level.

Variable	S-species	S-genus
S -species		
S-genus	0.939*	
S-family	0.863*	0.897*

Table 5.8: Results of RELATE statistic in PRIMER v6 correlating nematode species, genera and families in Saldanha Bay. Presented are Rho values. All ρ-values were statistically not significant

	Species	Genus
Species		
Genus	0.99	
Family	0.966	0.96

Table 5.9: Non-parametric indicators of genus richness using *EstimateS* software for 22 global sites.

Sites	ACE	ICE	Chao 2	Jack-knife 2
Mahurangi Harbour, New Zealand	68	74	71	80
Martin Bay, New Zealand	77	83	82	91
Murray River Estuary, Australia	47	61	62	67
Swartkops Estuary, South Africa	55	64	59	67
Gamtoos Estuary, South Africa	37	50	39	51
Saldanha Bay, South Africa	126	131	127	142
Mangroves, India	44	74	54	66
Socorro Island, Mexico	27	60	47	47
Cienfuegos Bay, Caribbean Sea, Cuba	80	88	88	97
Hamilton Harbour, Bermuda	58	60	95	69
Manfredonia, Italy	60	84	84	77
Gulf of Maine	82	83	77	88
Genoa-Voltri Harbour, Italy	76	86	84	95
Brouage Mud flats, France	38	42	52	43
Marine Protected Areas, Italy	83	114	79	85
St. Martin Flats, England	91	99	93	101
Celtic Sea	52	52	53	53
North West Irish Sea	60	63	68	72
Baltic Sea	28	29	39	31
North Sea	66	80	74	84
Clyde estuary, England	67	74	71	79
Bothnian Bay, North Baltic Sea	49	40	42	45

Table 5.10: Non-parametric indicators of family richness using *EstimateS* software for 22 global sites.

Sites	ACE	ICE	Chao 2	Jack-knife 2
Mahurangi Harbour, New Zealand	27	28	28	30
Martin Bay, New Zealand	32	34	34	38
Murray River Estuary, Australia	26	30	30	34
Swartkops Estuary, South Africa	19	20	20	22
Gamtoos Estuary, South Africa	21	24	24	28
Saldanha Bay, South Africa	43	44	43	46
Mangroves, India	21	29	24	30
Socorro Island, Mexico	17	25	22	25
Cienfuegos Bay, Caribbean Sea, Cuba	15	15	15	16
Hamilton Harbour, Bermuda	29	29	35	34
Manfredonia, Italy	19	21	19	22
Gulf of Maine	29	30	29	31
Genoa-Voltri Harbour, Italy	29	29	31	31
Brouage Mud flats, France	23	22	21	23
Marine Protected Areas, Italy	27	31	25	30
St. Martin Flats, England	25	26	25	27
Celtic Sea	21	21	21	21
North West Irish Sea	23	23	23	25
Baltic Sea	15	14	14	15
North Sea	24	23	23	23
Clyde estuary, England	27	28	27	30
Bothnian Bay, North Baltic Sea	15	15	15	16

Table 5.11: Environmental data for 22 global sites. The table includes genus and family richness as indicated by Curve-Fit Estimators, environmental, sampling and community indicators. S = genus or family richness. Southern hemisphere locations are listed from south towards equator followed by northern hemisphere locations from equator towards Arctic region. List of authors appear at the end of the table.

			Environmental				Sampling			Community			
	CFE Genus	CFE Family	Depth (m)	Latitude	Substrate (Φ)	Area (m²)	Number Samples	Sample Depth (cm)	Sample Volume (cm³)	N counted	S Density - Genera	S - Genera	S - Families
Mahurangi Harbouri[1]	91	31	4	-37	216.95	85	16	10	849	4145	0.01568154	65	27
Martin Bay[1]	99	36	7	-37	803	80	15	10	796	6930	0.01212121	84	31
Murray River Estuary, Australia[2]	75	35	1	-36	1514	4712	240	5	23562	1824	0.02357456	43	21
Swartkops Estuary, South Africa[3]	84	20	1	-34	1047.327	3982	120	10	39820	16761	0.00292345	49	19
Gamtoos Estuary, South Africa[4]	58	53	1	-34	186.951	4778	144	10	47784	5101	0.01039012	53	21
Saldanha Bay, South Africa[5]	149	91	15	-33	227.842	530	53	10	5300	4488	0.02606952	117	36
Mangroves, India[6]	218	41	3	11	500	141	20	10	1414	2174	0.01655934	36	20
Socorro Island, Mexico[7]	50	20	2	19		393	20	10	3927	156	0.16025641	25	15
Cienfuegos Bay, Cuba[8]	177	17	14	22	33.2	191	36	6	1145	13806	0.00478053	66	9
Hamilton Harbour, Bermuda [9]	75	32	10	32	262.66	109	24	10	1086	2400	0.02166667	52	25
Manfredonia, Italy[10]	82	26	55	42	63	130	21	5	651	697	0.06743185	47	18
Gulf of Maine[11]	99	34	54	43	214					1072	0.06436567	69	28
Genoa-Voltri Harbour, Italy[12]	95	47	7	44	173.667	336	33	2	672	1100	0.06272727	69	28
Brouage Mud flats, France[13]	53	31	0	46		407	36	5	2034	3597	0.00973033	35	19
Marine Protected Areas, Italy[14]	193	36	4	46	378.5602	223	36	10	2232	3784	0.01427061	54	23
St. Martin Flats, England[15]	100	29	0	50	575	188	15	15	2827	11995	0.00525219	63	24
Celtic Sea[16]	55	21	110	51	69	450	45	5	2250	1813	0.02151131	39	21
North West Irish Sea[16]	64	23	78	54	46	450	45	5	2250	1923	0.02444098	47	23
Baltic Sea, [17]	32	31	2	55	302.3	122	12	15	1832	2888	0.01038781	30	16
North Sea [17]	106	24	2	55	327	122	12	15	1832	11217	0.00588393	66	23
Clyde estuary, England [18]	91	28	1	56	173.833	61	16			9367	0.00704601	66	27
Bothnian Bay, North Baltic Sea [19]	63	16	25	65	113.344					877	0.02622577	23	13

Authors of studies used in Table 5.11:

1) Warwick *et al.*, 1997.
2) Nicholas *et al.*, 1992.
3) Gyedu-Ababio *et al.*, 1999.
4) Gyedu-Ababio, 2011.
5) Present study.
6) Chinnadurai & Fernando, 2007.
7) Jesús-Navarette, 2007
8) Armenteros *et al.*, 2009.
9) Warwick *et al.*, 1990
10) De Leonardis *et al.*, 2008.
11) Abebe *et al.*, 2004
12) Moreno *et al.*, 2008a
13) Rzeznik-Orignac *et al.*, 2003.
14) Sandulli *et al.*, 2010.
15) Somerfield *et al.*, 2007.
16) Schratzberger *et al.*, 2008.
17) Urban-Malinga *et al.*, 2005.
18) Lambshead, 1986.
19) Schiemer *et al.*, 1983.

Table 5.12: Results of a Multiple Regression Analysis of Genus, Family richness (S), CFE-Genus and CFE-Family against environmental and sampling variables. * denotes the variables that tested significantly. S/CFE: for instance, S denotes coefficient of S genus against S family, CFE denotes coefficient of CFE family against CFE genus. N/A Not available

Model	Number of cases	Regression coefficients ± S. E.								Adjusted Squared multiple correlation (R^2)	F statistic
		Depth	Latitude	Substrate	Area	N counted	No. of samples	Sample volume	S/CFE		
S Genus	21	Not included				0.0027±0.0007 (0.002)	Not included		3.024±0.495 (0.0001)	0.75	F(8,12) 8.515
S Family	21	Not included	0.1403±0.053 (0.0188)	0.0084±0.003 (0.0054)	Not included	-0.001±0.0002 (0.0005)	-0.07±0.025 (0.0199)	0.0002±0.0001 (0.043)	0.256±0.333 (0.0001)	0.768	F(6,14) 12.057
CFE genus	21	N/A	-1.49±0.854 (0.097)	N/A	N/A	N/A	N/A	N/A	Not included	0.093	F(1,19) 3.045
CFE family	21	N/A	Not included	N/A	N/A	N/A	N/A	N/A	0.079±0.072 (0.287)	0.0097	F(1,19) 1.197

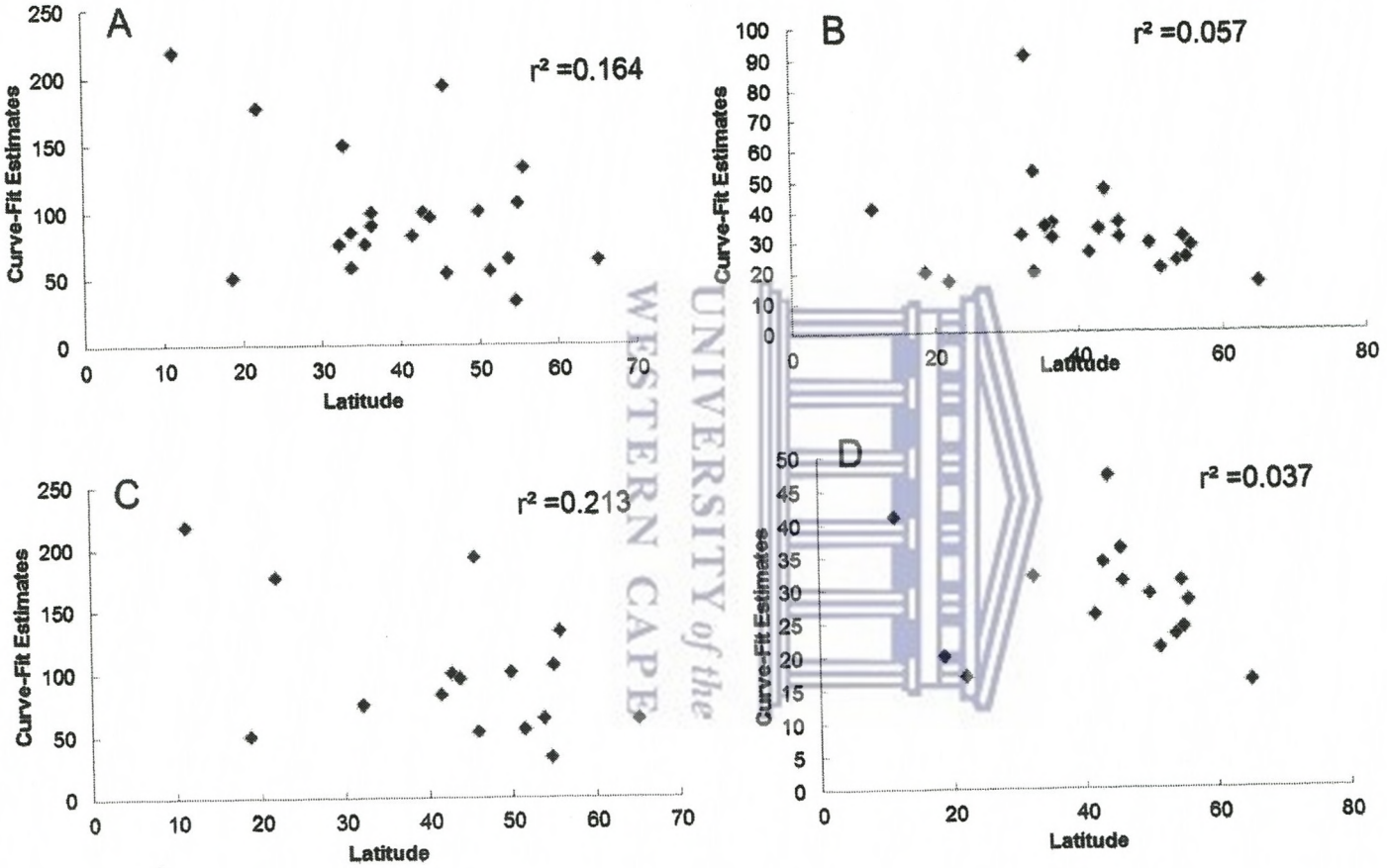

Figure 5.3: Global genus richness (A) and global family richness (B) of marine nematodes at 22 sites based on CFE estimates and across latitudinal space. Genus richness (C) and family richness (D) of Northern Hemisphere sites as well as are r^2 values are shown.

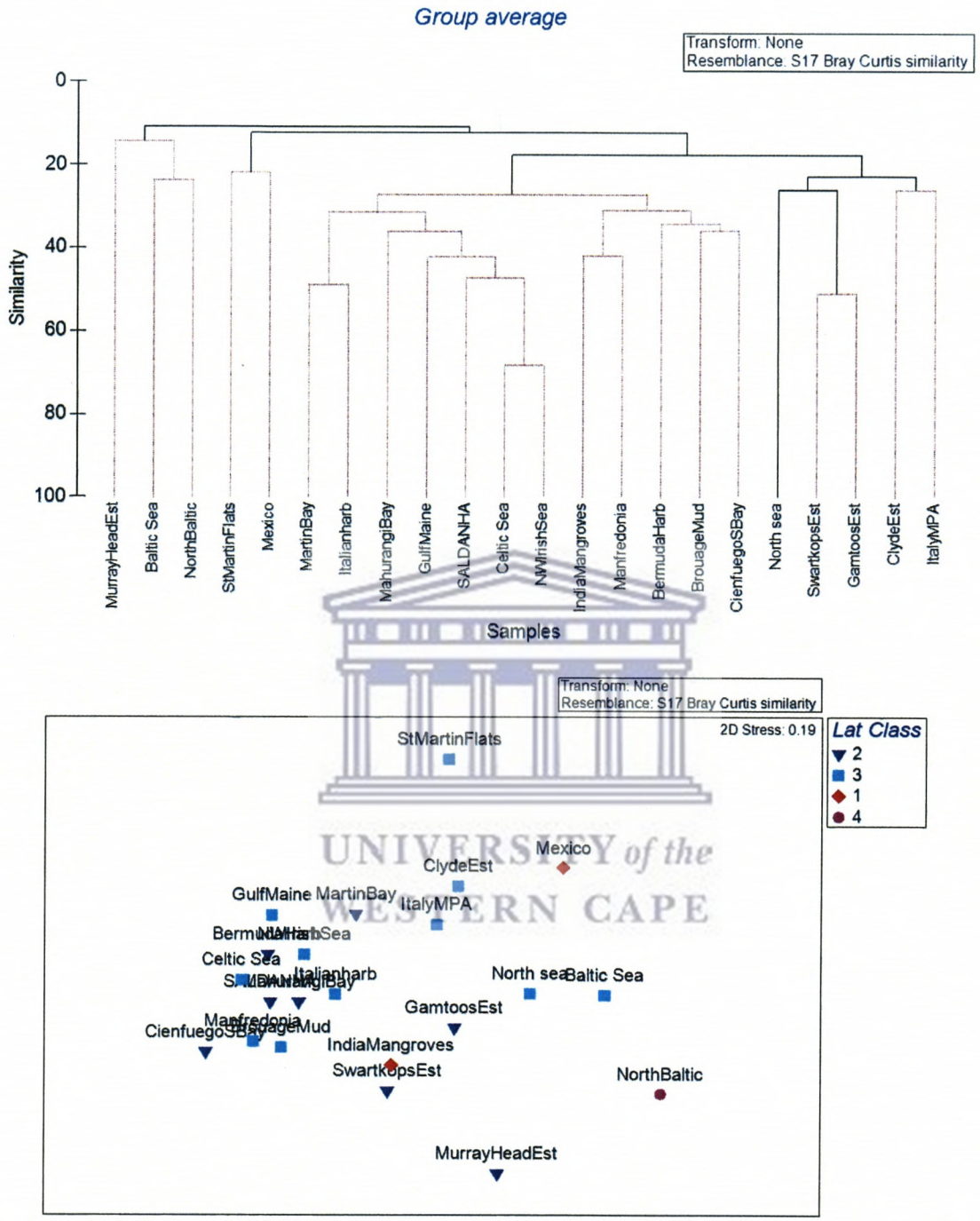

Figure 5.4: Similarity matrices visualised in both a 1-dimensional dendrogram (following group-average linkage) and a 2-dimensional nMMDS plot of nematode genus distribution at 22 global study sites using Bray-Curtis similarity and no transformations.

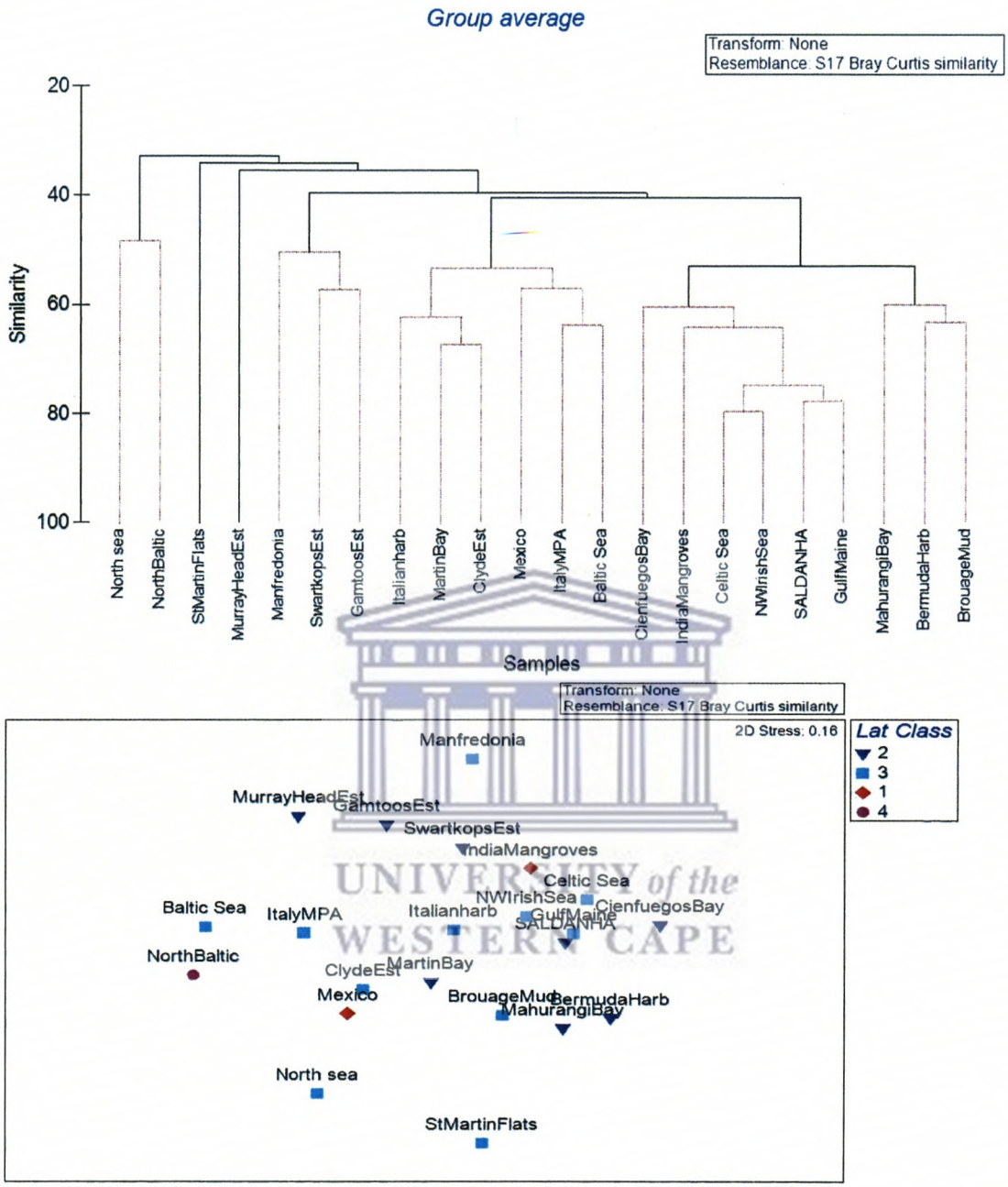

Figure 5.5: Similarity matrices visualised in both a 1-dimensional dendrogram (following group-average linkage) and a 2-dimensional nMMDS plot of nematode family distribution at 22 global study sites using Bray-Curtis similarity and no transformations.

Table 5.13: Results of Distance-based linear model (DISTLM) for global genera composition and selected environmental variables. Variables: selected to construct optimal model. Marginal tests: explaining variation for each variable. Sequential tests: tests to determine whether each variable contributes significantly to explained variation. Prop.: % variation explained. Cumul.: cumulative variation explained. * significant at $\rho<0.05$ after Bonferroni adjustment.

Marginal tests

Variables		Variable	SS(trace)	Pseudo-F	P	Prop.
1	Depth	Depth	5575.8	1.8578	0.013*	0.1102
2	Latitude	Latitude	3939.6	1.2666	0.19	0.0779
3	Substratum	Substratum	4886.7	1.6036	0.049	0.0966

Sequential tests

Variable	Adjusted R^2	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+Depth	0.0509	5575.8	1.858	0.011	0.1102	0.1102	15
+Lat	0.1018	5257.1	1.851	0.007	0.1039	0.2141	14
+Substratum	0.118	3504.6	1.257	0.223	0.0693	0.2834	13

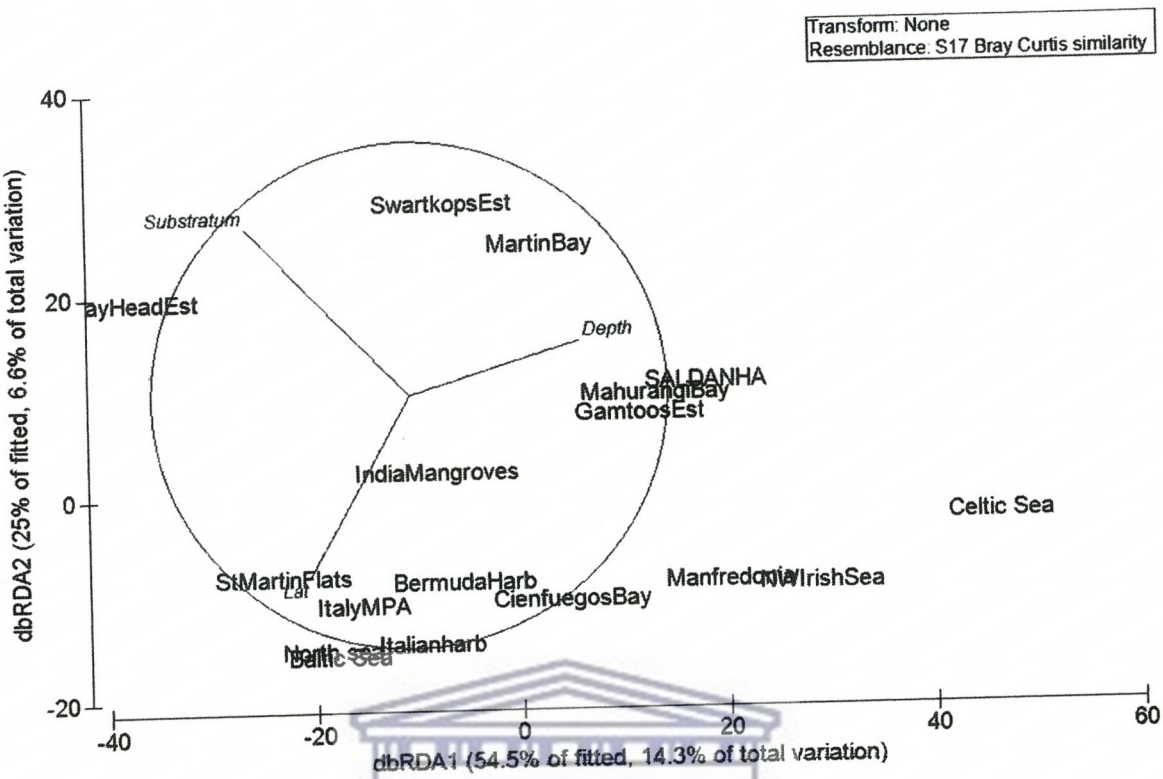

Figure 5.6: Distance-based redundancy analysis of genus data for global sites from Distance-based linear model with three environmental variables (latitude, substratum, depth).

Table 5.14: Results of Distance-based linear model (DISTLM) for global family composition and selected environmental variables. Variables: selected to construct optimal model. Marginal tests: explaining variation for each variable. Sequential tests: tests to determine whether each variable contributes significantly to explained variation. Prop.: % variation explained. Cumul.: cumulative variation explained. * significant at $\rho<0.05$ after Bonferroni adjustment.

Variables		Marginal tests Variable	SS(trace)	Pseudo-F	P	Prop.
1	Depth	Depth	2509.2	1.435	0.159	0.087
2	Latitude	Latitude	2310.9	1.311	0.023	0.084
3	Substratum	Substratum	2335.9	1.327	0.243	0.081

Sequential tests

Variable	Adjusted R^2	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+Depth	0.024	2509.2	1.435	0.18	0.087	0.0.87	15
+Lat	0.128	2310.9	1.311	0.11	0.15	0.237	14
+Substratum	0.155	2335.9	1.327	0.184	0.076	0.313	13

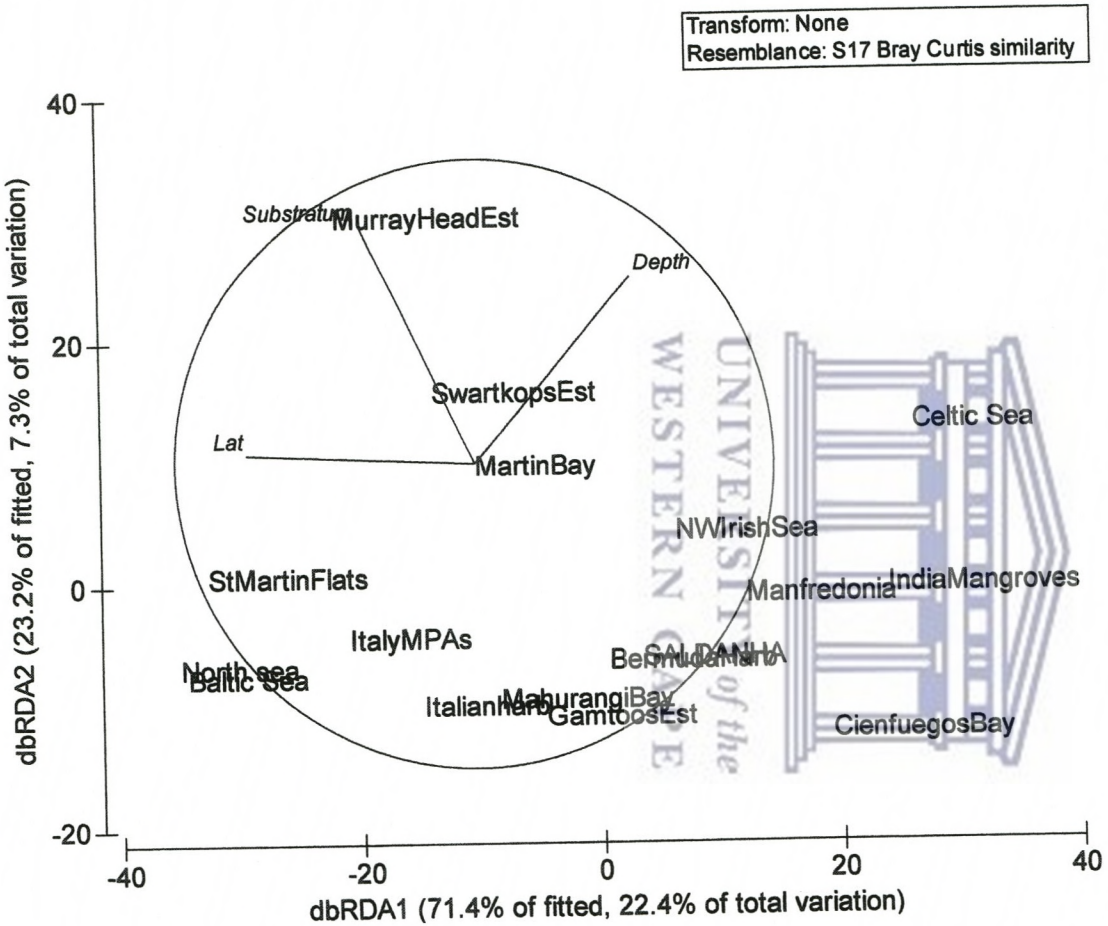

Figure 5.7: Distance-based redundancy analysis of family data for global sites from Distance-based linear model with three environmental variables (Latitude, depth and substratum).

Table 5.15: Curve-fit Estimators based on Morgan-Mecer-Flodin Model of a plot of genus and family accumulation curves for selected regions originally reported in identified in Table 5.11. Authors follow those of Table 5.11.

Sites	Genus Curve-fit Estimates	Family Curve-fit Estimate
Australasia[1, 2]	162.1	37.25
Indian mangrove [6]	218.18	41.27
South Africa [3, 4, 5]	186.3	87.59
N. E. Atlantic [15, 17, 18, 19]	167.66	41.9
Mediterranean [10, 12, 14]	184.1	37.9
N. W. Atlantic [11]	98.57	28.31
Tropical N.W. Atlantic [8,9]	138.22	34.05
Pacific [7]	50.07	20.21

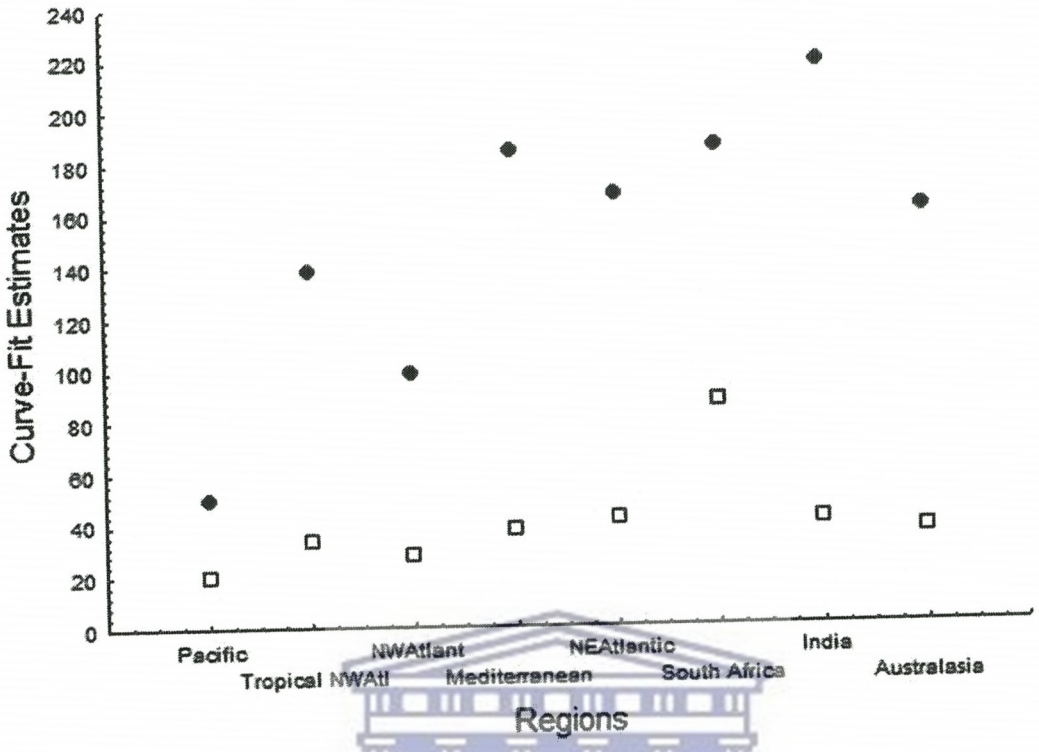

Figure 5.8: Distribution of Curve-Fit Estimates for eight global regions compiled from study sites used in Table 5.15. Graph depicts Estimates for genera (●) and families (□).

CHAPTER 6

6.1 General conclusions

The present thesis set out to describe the free-living nematode communities in Saldanha Bay and to explore the relationships between nematode communities and the environment there. It additionally attempted to explore how the nematode communities of Saldanha Bay fit in globally, with respect to richness and biogeography.

The present study represents the first quantitative examination of the nematode fauna from along the west coast of South Africa, and contributes new data to the regional databases for biodiversity (e.g. GBIF, OBIS). A total of 53 core samples collected across two seasons and six sites along a transect in Saldanha Bay, and together they revealed a total of 136 species from 117 genera and 36 families. Of these 136 species, two new species were described (APPENDIX 6.1), which, given that 134 others could not be unambiguously identified (APPENDIX 1.3), suggests that we have barely scratched the surface for this taxon in the region – especially given that South African west coast communities are generally accepted as having a lesser number of species than south coast and, especially, east coast communities (Bustamante & Branch, 1996; Griffiths *et al.*, 2010).

Sampling of the study was more than adequate, and species accumulation curves stabilised within the number of units actually examined. This lends credible support for the conclusions reached. As in many other ecological studies (e.g. Moreno *et al.*, 2008b; Lee *et al.*, 2008) the abundance and diversity of nematodes in Saldanha Bay is strongly influenced by the psammal environment, and heavy metals, organic loading and sediment grain structure all influenced community structure. Diversity was typically suppressed in areas with high levels of carbon and metal enrichment, and these communities were considered as disturbed. The ABC curves for all other sites studied indicated that they were not disturbed. The results of distance-based PERMANOVA on Station and Season, derived from Bray-Curtis similarity, showed that the differences between Seasons only

explained 13.3% of the variation within the data while the variation between Station-Season accounted for 27% of the differences in community structure.

In their comprehensive spatial biodiversity assessment for South Africa, Lombard *et al.* (2004) highlighted ten crises facing the South African marine environment. These crises covered a range of management issues, and only three indirectly have implications for infauna: shallow-water mining operations, demersal trawling and the effects of coastal developments and their associated impacts such as dredging, storm-water run-off, sewage waste disposal, industrial waste disposal. This situation has not changed, and the most recent biodiversity assessment report (Driver *et al.*, 2012) continues to identify mining, fishing and anthropogenic development as risks and Sink *et al.* (2012) recommends that a number of marine taxa need priority attention in order to address knowledge gaps. This list includes nematodes.

During the mid-1980's the United Kingdom formulated a legal framework for ecological impact assessment, and this lead to the incorporation of nematodes as important components in biological surveys (Trett *et al.*, 2009). Communities are generally patchily distributed and seasonal variability and food availability can lead to the inaccurate assessment of contamination events (Moens *et al.*, 1999; Clarke & Warwick, 1999; Bremner *et al.*, 2006; Monthum & Aryutaka, 2006). Meiofauna assemblages provide a higher resolution in impact assessments than the more conventionally used macrofauna, in addition to requiring smaller samples. For this reason meiofauna in general, and nematodes in particular, are used extensively in molecular, ecological and ecosystem management studies (see reviews by Yeates *et al.*, 2009; Neilson *et al.*, 2009), and a large number of studies demonstrating their utility in such studies now exist (e.g. Somerfield *et al.*, 1995, Muthumbi *et al.*, 2004, Gyedu-Ababio & Baird, 2006, Fraschetti *et al.*, 2006).

The attributes of nematodes that lend themselves to studies of ecological assessment include:

Nematodes are present in abundance and they are more easily sampled than most macrofauna (Maria *et al.*, 2008).

Nematodes are found in virtually all marine environments, including contaminated substrata.

Nematodes exhibit high species richness compared to other phyla (Boucher & Lambshead, 1995).

Nematodes have wide and variable tolerance and sensitivity ranges; some are opportunistic and are highly tolerant to the physico-chemical environment, whilst others are more restricted and sensitive.

Nematodes have a low mobility which means that their residence reflects the environment in which they are sampled (Soetaert *et al.*, 2002).

Nematodes have relatively short life cycle times therefore the effects of stresses will be reflected in the structure of communities within one or a few life cycles (Hopper & Meyers, 1966; Vranken *et al.*, 1984; Bongers, 1990).

Nematodes spend the major part of their life in the interstitial spaces between sediments. They are thus in direct contact with the interstitial pore water (Willems *et al.*, 1982; Soetaert & Heip, 1989; Wang *et al.*, 2011). This exposure to any contaminant may be an important factor in determining their survival.

In order for nematodes to be usefully employed in any studies (impact or otherwise), baselines need to be established against which change can be measured. Unfortunately, nematodes are difficult to unambiguously identify to species level, so that costs saved in sampling at sea are likely to be more than compensated for by analysis in the laboratory. That said, the results suggest that the identification of material to genus, and even family, level can be a useful proxy for species (as Clarke & Warwick, 1998), which means that identification time can be reduced though the efficacy of this (as oppose to macrofauna) would need to be rigorously tested.

Whilst genera and families may be good proxies for species in an ecological context, it is less clear that they are suitable proxies for species at the evolutionary level. The data presented here indicate that there are no clear latitudinal patterns in the richness of shallow-water nematodes as measured using genera, which is both the most frequently

reported taxonomic unit and the highest basic unit that can be compared across studies. This relationship is even poorer when examined using families. Unfortunately then, until such time as a global standard is established in this regard, the only way it will be possible to examine large scale patterns in richness will be through dedicated research by single workers (or perhaps networked groups working to common standards), as exemplified by the recent work of Lee & Riveros (2012). Given that sampling effort significantly impacts on estimates of point diversity, relationships need to be established using correction methods (as here), and even then we need to take cognisance of differences in habitat sampled. Such standardisations are, I fear, a long way off.

The lack of a significant latitudinal signal to patterns of generic richness recalls the *Everything is Everywhere* hypothesis (Fenchel, 1993; Finlay *et al.*, 1996; Artois *et al.*, 2011), and this is reflected very strongly in the complete lack of structure observed in the biogeographies constructed here. While this may partly reflect a lack of species-level data, evidence is beginning to mount (Artois *et al.*, 2011; Guill, 2011) that minute interstitial metazoans, such as nematodes, tardigrades, rotifers, gastrotrichs, may be subject to the same lack of constraints as protists, on which the hypothesis is based. Clearly much more work is needed in this regard.

6.2 General recommendations

In a local and regional context, the following recommendations for future work are made:

Funding agencies in the region need to provide more, and perhaps dedicated, grants focussed on meiofauna, especially nematodes. At present, there are no centres for the study of meiofauna in the region, and this niche could be capitalised upon with funding resources. Although the National Research Foundation (NRF), working through the Southern African Network for Oceanic and Coastal Research (SANCOR) has recognised studies of pollution to be sorely needed (NRF, *et al.*, 2011), and dedicated monies to try and redress this accordingly, the call did not receive widespread support from the community and it has been discontinued.

A database of all recorded nematode taxa should be constructed. This database should preferably be held at a central facility, such as the Iziko South African Museum's Marine Invertebrate database, Iziko Biodiversity Explorer, (www.iziko.org.za); and it should be remotely accessible. Gibbons *et al.* (1999) reported 338 nematode species from around South Africa and this list could serve as an important starting point, although it likely needs updating and verification.

An identification guide (again on-line) would be useful as a training tool, to assist potential and current researchers. The guide could be similar to those published by Platt & Warwick (1983, 1988) and Warwick *et al.* (1998) especially those sections that include the star taxa as well as the major habitats.

Voucher collections need to be established so that independent studies can work to the same, standardised units (morphospecies 1, 2, 3 etc).

DNA barcoding of all new samples should be conducted. This process was initiated by Bik *et al.* (2010) where a sample of South African sandy shore nematodes *was* used to investigate the relationship between deep-sea and shallow water nematodes.

All new coastal developments should include a sediment ecological assessment for meiofauna or nematodes. This would be useful as a baseline in especially relatively undeveloped coastal areas. Marine reserves are well established along the South African coast (Turpie *et al.*, 2000; Majiedt *et al.*, 2013) and should be useful in determining baseline criteria. Further, proposed off-shore mining explorations should include meiofaunal surveys.

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APPENDIX 1.1

Marine nematode literature in South Africa

Studies of South African marine nematodes are limited. The first recorded investigation of nematodes along the coast of South Africa was a description of three species of *Euchromadora, Oncholaimus and Enoplus* by Von Linstow (1908) from Lüderitzbucht, Namibia. Few papers exist that deal directly with nematodes, either as part of meiofaunal communities or through taxonomic descriptions. Dinet (1973) presented a quantitative account of deep-sea meiofauna off Walvis Bay, Namibia, while Vitiello (1975) described two new species of the family Leptosomatidae in Lamberts Bay, north of Saldanha Bay. Prior to the publication of Day *et al.* (1970), Inglis (1961, 1963 and 1966) described 23 new species (including five new genera from the coast off South Africa. The descriptions were based on specimens collected from University of Cape Town Ecological Surveys and the National Institute for Water Research along the east and west coasts off South Africa. Coles (1977) then identified 32 species of nematodes (belonging to 19 genera and eight families) and including seven new species (Order: Enoplida) collected along the South African coast. He also provided the most detailed inventory of nematodes along the South African coast.

The first overview of marine nematology in South Africa was conducted by Furstenberg and Dye (1982). They recognized that marine meiofauna studies were neglected in Africa although a number of ecological and taxonomic studies were conducted. Most of the earlier ecological work relevant to meiofauna was conducted on sandy beaches along the South African coast. One of the first publications related to a study of the vertical and horizontal distribution of sub-littoral meiofauna in Algoa Bay, along the south coast of South Africa (McLachlan, 1977; McLachlan & Furstenberg, 2007; McLachlan *et al.*, 1977). The study reported on the correlation between nematode abundance and dominance along unpolluted and sewerage exposed beaches. However, none of the specimens were described, therefore no information is available about the nematode diversity within the assemblage. Other studies included those of unpolluted sandy beaches along the west, south and southwestern coastline of South Africa (Hennig *et al.*, 1982, Hennig *et al.*, 1983, Fricke & Flemming, 1983, Warwick, 1984), vertical profiles of meiofauna in sandy subtidal environments (Malan &McLachlan, 1985) and

studies on a large artificial reef (Fricke *et al.*, 1986). Dye (1978) reported on the ecophysiological parameters that affect meiofauna in the Swartkops estuary on the East Coast, while Gibbons and Griffiths (1986) made a comparison of macrofauna and meiofauna across a rocky shore in False Bay. More recently, Gyedu-Ababio *et al.* (1999) reported on the first full-scale study of nematode as pollution indicators in South Africa with a study conducted along the Swartkops estuarine system in Port Elizabeth, South Africa. They studied the effects biogeochemical factors such grain size, phytoplankton production, organic carbon, salinity and heavy metal pollutants on nematode abundance and community structure. In addition Gyedu-Ababio *et al.* (1999) also identified possible indicator taxa for sediments polluted by heavy metals. Gyedu-Ababio and Baird (2006) followed this study with a microcosm experiment of effect of heavy metals on nematode abundance and community structure. They identified a group of nematodes that are tolerant to heavy metal pollutants reported that nematode communities exhibit different responses to pollution treatments. Gyedu-Ababio (2011) expanded the investigation of the Swartkops and Gamtoos estuarine systems and concluded that effects of some of the metals and organic carbon could not distinguish between the nematode communities. He further argued for extensive studies along the South African coast in order to enhance the use of nematodes as biological indicators. Hendricks and Gibbons (2010; see Appendix 6.1) recently described *Perepsilonema benguelae* and *Leptepsilonema saldanhae* from Saldanha Bay and these were the first marine nematode descriptions in more than a decade. Currently, Vosloo and Hendricks (submitted) presented an overview of marine nematode research in Southern Africa.

Examples of nematode research in Africa

Nematode research in Africa was primarily restricted to the east coast off Africa. A number of papers dealt with taxonomy of deep sea and shallow water nematodes. These include the description of four new species in the family Epsilonematidae by Verschelde and Vincx (1992, 1993). Muthumbi and Vincx (1997) described seven species of the genus *Oncholaimus* that co-exist in the deep sea. They discussed the ability to share available food resources due to the diversity of the buccal cavity. Muthumbi *et al.* (1997) further described 12 new and known species of the family Comesomatidae from both shallow water and deep-sea sediments. These papers were in essence the first serious

attempts to redress the lack of taxonomic knowledge about marine meiofauna in general and marine nematode research in particular occurring in Africa.

In South Africa, Day *et al.* (1970) undertook a scientific account of the diversity of marine life in False Bay, Cape Town. They provided an inventory of a rich and diverse fauna from databases provided by Eyre (1939), Broekhuysen (1940), Bokenham and Stephenson (1938), yet they purposely dismissed the few records available for microscopic taxa, such as Nematoda, Ostracoda or Protozoa, due to the lack of sufficient data. South Africa is considered as the third most biologically rich country in the world (Driver *et al.*, 2005), yet its marine diversity is largely unknown. The South African marine environment contains a large number of endemic species (Awad *et al.*, 2002), but the distribution patterns are very patchy due to insufficient sampling efforts. Benthic communities are largely unknown or under-represented due to a lack of trained staff and funding (Gibbons *et al.*, 1999). Gibbons (1991) undertook a review of meiofauna work on rocky shore environments in South Africa. Most of the work was carried out in False Bay and related to relationship between meiofaunal and algal communities, algae and sediment accumulation (that in turn shelter meiofauna), the dietary component of intertidal fish. No information was available about nematode or foraminifera. Recently, this paucity of knowledge was addressed by Toefy *et al.* (2003, 2005), on Foraminifera present in sediments accumulated by *Gelidium pristoides*, and later Toefy (2011) studied Foraminifera from Table Bay and St Helena Bay along the southwest coast of South Africa.

Appendix 1.2: Sediment structure at Saldanha Bay for Summer and Winter. Indicated is percentage composition as well as sediment grain size (Φ) for each sampling station.

Sample number	Sand (%)	Gravel (%)	Mud (%)	Phi (Φ)	Sand (%)	Gravel (%)	Mud (%)	Phi (Φ)
1.1	8.54	0.38	91.08	4.45	4.00	0.00	96.00	4.48
1.2	11.55	0.00	88.45	4.43	3.09	2.84	94.07	4.47
1.3	3.42	0.00	96.16	4.48	9.60	0.00	90.40	4.45
1.4	8.66	0.93	90.42	4.45	8.00	0.90	91.10	4.45
1.5	1.69	0.12	98.19	4.49	3.40	0.40	96.20	4.48
1.6	1.69	0.12	98.19	4.49	0.15	0.00	99.85	4.50
2.1	82.73	3.12	14.14	2.86	72.89	0.00	27.11	3.11
2.2	77.67	2.04	20.30	3.00	77.84	0.00	22.16	3.04
2.3	80.46	0.66	18.89	2.99	88.04	0.00	11.96	2.57
2.4	77.63	1.93	20.45	3.01	87.93	0.00	12.07	2.57
2.5	80.76	1.10	18.14	2.97	87.38	0.38	12.24	2.57
2.6	82.08	1.25	16.67	2.94	88.14	0.00	11.86	2.57
3.1	80.26	4.16	15.59	2.90	89.40	0.73	9.87	2.55
3.2	72.28	6.16	21.57	3.00	85.88	0.00	14.12	2.58
3.2	79.19	1.77	19.05	2.98	77.03	0.23	22.74	3.05
3.4	75.31	6.41	18.29	2.94	95.90	0.00	4.10	2.52
3.5	70.09	7.21	22.69	3.01	76.60	0.00	23.40	2.65
3.6	77.72	6.26	16.03	2.90	95.90	0.10	4.00	2.52
4.1	78.49	0.94	20.57	3.01	58.10	35.65	6.25	1.18
4.2	80.72	0.11	19.17	2.99	95.54	0.00	4.46	1.80
4.3	78.58	0.00	21.42	3.03	95.07	4.93	0.00	2.47
4.4	72.50	0.64	26.85	3.10	100.00	0.00	0.00	2.50
4.5	83.63	0.31	16.07	2.93	59.21	40.79	0.00	1.09
4.6	77.72	6.26	16.03	2.90	89.77	0.23	10.00	2.55
5.1	93.63	0.05	6.32	2.53	93.13	0.00	6.83	2.54
5.2	94.01	0.10	5.89	2.53	94.10	0.00	5.90	2.53
5.3	93.59	0.34	6.07	2.53	93.74	0.00	6.26	2.53
5.4	95.35	0.09	4.57	2.52	90.30	0.52	9.18	2.55
5.5	94.40	1.67	3.94	2.51	80.27	0.00	19.73	2.62
5.6	88.38	0.00	11.62	2.57	81.70	0.00	18.30	2.61
6.1	94.65	0.92	4.42	2.52	4.76	0.00	95.24	4.48
6.2	96.65	1.58	1.78	2.50	88.98	0.79	10.23	2.55
6.3	96.74	0.37	2.91	2.51	95.40	0.00	4.60	2.52
6.4	89.60	5.98	4.41	2.49	91.64	0.00	8.36	2.55
5.5	86.04	7.79	6.17	2.49	88.07	0.00	11.93	2.57
6.6	95.68	0.97	3.36	2.51	91.10	0.00	8.90	2.55

Appendix 1.3: Abundance of nematodes in SUMMER; highlighted taxa indicate those used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	Feeding gr	c-p value	1.1	1.2	1.3	1.4	1.5	1.6	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4
Aegialoalaimus	1A	4	0	0	0	0	3	0	1	0	0	0	0	0	2	1	1	1
Ammotheristus	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Amphimonhystrella	1B	2	0	0	0	0	2	0	2	1	0	2	0	1	2	0	2	1
Anticyathus	1B	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Antomicron	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0
Araeolaimus	1A	3	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Axonolaimus	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bodonema	1A		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Bolbolaimus* sp.1**	2B	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
***Bolbolaimus* sp.2**	2B	3	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Calyptronema	1B	4	0	0	0	0	0	0	0	5	1	0	5	3	0	1	0	0
Camacolaimus	2A	3	0	0	0	0	1	0	1	0	1	1	0	2	10	7	5	5
Campylaimus	1B	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Catanema	2A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceramonema	2A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cervonema	1A	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chromadora	2A	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Chromadorella	2A	3	0	2	0	0	0	0	2	4	2	3	5	3	0	2	4	4
Chromadorina	2A	3	0	0	0	0	0	0	2	0	0	1	1	4	0	0	0	1
Chromaspirinia	2B	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Cobbia* sp.1**	2A	3	0	0	0	0	1	0	0	0	2	1	1	1	0	0	0	1
***Cobbia* sp.2**	2A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Cobbia* sp.3**	2A	3	0	0	0	0	3	0	11	5	3	2	8	4	4	4	2	2
Comesa	1B	3	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0
Cyartonema	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1.3 (continued): Abundance of nematodes in SUMMER; highlighted taxa indicate those used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	3.5	3.6	4.1	4.2	4.3	4.4	4.5	4.6	5.2	5.3	5.4	5.5	5.6	6.1	6.2	6.3	6.4	6.5	6.6	> 5% Contribution
Aegialoalaimus	0	1	0	2	1	2	4	7	1	0	0	1	0	1	0	1	0	0	0	45.71
Ammotheristus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	8.57
Amphimonhystrella	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	31.43
Anticyathus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8.57
Antomicron	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	14.29
Araeolaimus	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	11.43
Axonolaimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2.86
Bodonema	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2.86
***Bolbolaimus* sp.1**	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	0	0	0	14.29
***Bolbolaimus* sp.2**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5.71
Calyptronema	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	28.57
Camacolaimus	0	2	0	1	0	0	0	0	0	4	0	0	0	0	0	1	1	1	0	42.86
Campylaimus	0	1	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	17.14
Catanema	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2.86
Ceramonema	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2.86
Cervonema	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	2.86
Chromadora	0	0	0	0	1	1	1	0	0	1	3	0	1	0	0	0	0	0	0	20.00
Chromadorella	3	1	1	0	2	3	3	5	0	0	1	2	1	2	0	2	0	3	0	65.71
Chromadorina	0	0	3	1	2	0	3	2	0	1	0	2	0	0	0	2	0	0	0	37.14
Chromaspirinia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	5.71
***Cobbia* sp.1**	0	0	0	2	1	0	0	0	1	0	0	0	0	3	4	1	1	0	1	40.00
***Cobbia* sp.2**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	4	5.71
***Cobbia* sp.3**	8	4	1	5	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	51.43
Comesa	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	11.43
Cyartonema	0	0	0	0	0	1	0	1	0	0	0	0	0	3	0	0	0	0	1	11.43

Appendix 1.3 (continued): Abundance of nematodes in SUMMER; highlighted taxa indicate those used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	Feeding gr	c-p value	1.1	1.2	1.3	1.4	1.5	1.6	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4
Cyatholaimus	2A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Daptonema	1B	2	0	0	0	0	7	0	2	3	7	3	2	2	0	0	3	2
Dasynemoides	1A	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Desmolaimus	1B	2	0	0	0	0	0	0	3	1	0	0	0	0	0	0	1	1
Desmolorenzia	1A	4	0	0	0	0	0	0	3	1	0	0	0	0	0	0	2	1
Desmoscolex	1A	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Diplolaimella	1B	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Diplopeltoides	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplopeltula	1A	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Disconema	1A	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Doliolaimus	1B	3	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Echinotheristus	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eleutherolaimus	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Elzalia	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumorpholaimus	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eurystomina	2B	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Filitonchus	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Filoncholaimus	1B	4	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
***Halalaimus* sp.1**	1A	4	0	0	0	0	3	0	1	1	2	0	3	0	3	0	2	0
***Halalaimus* sp.2**	1A	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
***Halalaimus* sp.3**	1A	4	0	0	0	0	0	0	0	1	2	0	0	0	1	2	1	1
***Halalaimus* sp.4**	1A	4	0	0	0	0	2	0	0	0	5	2	3	5	14	8	3	2
***Halalaimus* sp.6**	1A	4	1	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0
***Halalaimus* sp.7**	1A	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
***Halalaimus* sp.8**	1A	4	0	0	0	0	2	0	1	0	0	0	0	0	3	0	0	0

Appendix 1.3 (continued): Abundance of nematodes in SUMMER; highlighted taxa indicate those used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	3.5	3.6	4.1	4.2	4.3	4.4	4.5	4.6	5.2	5.3	5.4	5.5	5.6	6.1	6.2	6.3	6.4	6.5	6.6	> 5% Contribution
Cyatholaimus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5.71
Daptonema	4	8	0	2	4	6	3	2	22	26	10	15	9	2	1	5	2	0	3	74.29
Dasynemoides	0	0	0	0	2	0	0	1	0	1	1	2	2	7	5	0	0	0	2	28.57
Desmolaimus	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	17.14
Desmolorenzia	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	17.14
Desmoscolex	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8.57
Diplolaimella	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	5.71
Diplopeltoides	0	0	0	1	1	0	0	0	2	3	2	2	0	1	0	1	1	0	0	25.71
Diplopeltula	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	1	0	0	1	20.00
Disconema	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	5.71
Doliolaimus	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	11.43
Echinotheristus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	2.86
Eleutherolaimus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	5.71
Elzalia	0	0	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	11.43
Eumorpholaimus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	5.71
Eurystomina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	5.71
Filitonchus	0	0	0	0	1	1	0	0	0	0	2	0	1	1	1	0	0	0	0	17.14
Filoncholaimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.86
***Halalaimus* sp.1**	4	1	0	3	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	34.29
***Halalaimus* sp.2**	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5.71
***Halalaimus* sp.3**	1	2	2	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	34.29
***Halalaimus* sp.4**	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34.29
***Halalaimus* sp.6**	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	17.14
***Halalaimus* sp.7**	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	11.43
***Halalaimus* sp.8**	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	14.29

Appendix 1.3 (continued): Abundance of nematodes in SUMMER; highlighted taxa indicate those used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	Feeding gr	c-p value	1.1	1.2	1.3	1.4	1.5	1.6	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4
***Halalaimus* sp.9**	1A	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Karkinochromadora	2A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lauratonema	1B	[illegible]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Leptolaimus* sp.1**	1A	2	0	0	0	0	2	0	1	5	1	9	2	9	12	7	23	0
***Leptolaimus* sp.2**	1A	2	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	8
Leptonemella	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linhomoeus	2A	2	0	0	0	0	2	0	3	12	3	3	2	1	2	1	2	0
Longicyatholaimus	2A	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Manunema	1A	[illegible]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Metachromadora	2B	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Metacyatholaimus	2A	3	0	0	0	0	3	0	3	2	0	5	2	2	0	0	0	0
Metadasynemella	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Metadasynemoides	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Metalinhomoeus* sp.1**	1B	2	5	0	0	0	14	0	2	5	3	2	0	3	1	1	3	0
***Metalinhomoeus* sp.2**	1B	2	0	0	0	0	4	0	1	2	2	0	0	0	1	1	3	5
Microlaimus	2A	2	0	0	0	0	2	0	3	2	9	2	4	1	3	3	0	0
Minolaimus	2A	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Molgolaimus	1A	3	0	0	0	0	7	0	1	0	1	0	1	0	0	0	0	0
Nemanema	1A	*4*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Neotonchus	2A	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontophora	1B	2	1	0	0	0	0	0	4	1	2	0	0	0	0	0	0	0
Oncholiamus	2B	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Oxystomina	1A	4	3	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0
Pandolaimus	2B	[illegible]	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Paracomesoma	2A	2	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0

Appendix 1.3 (continued): Abundance of nematodes in SUMMER; highlighted taxa indicate those used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	3.5	3.6	4.1	4.2	4.3	4.4	4.5	4.6	5.2	5.3	5.4	5.5	5.6	6.1	6.2	6.3	6.4	6.5	6.6	> 5% Contribution
***Halalaimus* sp.9**	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8.57
Karkinochromadora	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5.71
Lauratonema	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2.86
***Leptolaimus* sp.1**	13	17	0	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	45.71
***Leptolaimus* sp.2**	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5.71
Leptonemella	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2.86
Linhomoeus	6	0	7	2	1	3	1	7	0	0	0	0	1	2	0	0	0	0	0	57.14
Longicyatholaimus	0	0	0	0	1	0	0	1	2	1	0	0	3	1	0	1	0	0	0	22.86
Manunema	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	8.57
Metachromadora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2.86
Metacyatholaimus	6	0	1	0	5	4	3	1	3	0	0	4	0	1	1	0	0	0	5	48.57
Metadasynemella	0	0	0	0	0	1	0	1	0	0	1	0	1	2	1	0	0	0	1	20.00
Metadasynemoides	0	0	0	0	0	1	0	1	0	2	0	5	1	3	6	0	0	0	11	22.86
***Metalinhomoeus* sp.1**	3	1	21	5	3	2	20	5	0	0	0	1	0	1	0	1	0	0	0	65.71
***Metalinhomoeus* sp.2**	4	0	4	0	0	1	5	0	0	0	0	1	0	0	0	0	0	0	0	34.29
Microlaimus	1	1	3	8	4	19	2	17	2	1	2	7	2	11	7	22	3	2	19	82.86
Minolaimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5.71
Molgolaimus	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	3	0	1	0	34.29
Nemanema	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2.86
Neotonchus	0	0	1	0	1	1	0	0	1	3	0	0	0	1	1	2	0	0	0	22.86
Odontophora	0	0	0	0	0	1	1	1	2	0	2	13	1	2	3	1	2	2	2	48.57
Oncholiamus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5.71
Oxystomina	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	20.00
Pandolaimus	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	11.43
Paracomesoma	0	0	2	0	0	1	2	0	0	0	0	1	0	0	4	0	0	0	1	25.71

Appendix 1.3 (continued): Abundance of nematodes in SUMMER; highlighted taxa indicate those used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	Feeding gr	c-p value	1.1	1.2	1.3	1.4	1.5	1.6	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4
Paracyatholaimus	2A	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Paralinhomoeus* sp.1**	1B	2	0	0	0	0	9	0	1	4	6	3	3	6	3	6	8	2
***Paralinhomoeus* sp.2**	1B	2	0	0	0	0	8	0	4	5	2	1	2	4	2	1	0	2
Parallelecoilas	2B	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paralongicyatholaimus	2A	3	0	0	0	0	1	0	1	3	2	4	4	4	1	0	0	0
Paramicrolaimus	2A	[illegible]	0	0	0	0	0	0	2	1	2	1	1	4	1	1	1	0
Paramonohystera	1B	2	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0
Parodontophora	2A	2	29	20	10	12	0	5	0	1	0	0	0	1	0	0	0	0
Perepsilonema	1A	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platycomopsis	1A	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygastrophora	2B	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polysigma	2A	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pomponema	2B	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prochromadorella	2A	2	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	1
Promonhystera	1B	2	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	2
Prorhynconema	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
***Pselionema* sp.1**	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Pselionema* sp.2**	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pterygonema	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Retrotheristus	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Rhynchonema	1B	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
***Sabatieria* sp.1**	1B	2	40	54	60	63	1	86	31	6	18	15	16	12	2	23	22	17
***Sabatieria* sp.2**	1B	2	0	0	0	0	0	0	1	1	3	0	0	0	1	2	0	0
Setoplectus	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Setosabatieria	1B	2	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1

Appendix 1.3 (continued): Abundance of nematodes in SUMMER; highlighted taxa indicate those used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	3.5	3.6	4.1	4.2	4.3	4.4	4.5	4.6	5.2	5.3	5.4	5.5	5.6	6.1	6.2	6.3	6.4	6.5	6.6	> 5% Contribution
Paracyatholaimus	0	0	0	2	0	0	2	0	0	0	1	0	2	0	0	0	2	1	2	20.00
***Paralinhomoeus* sp.1**	6	0	6	2	1	7	7	7	1	0	0	2	2	0	1	0	0	0	0	62.86
***Paralinhomoeus* sp.2**	2	1	6	0	4	3	6	2	0	0	0	1	1	0	0	0	0	0	0	54.29
Parallelecoilas	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2.86
Paralongicyatholaimus	0	0	1	0	4	0	0	2	0	5	0	2	0	3	1	1	0	0	3	48.57
Paramicrolaimus	0	1	0	3	5	3	0	3	2	0	1	0	1	6	9	6	0	0	4	60.00
Paramonohystera	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	0	14.29
Parodontophora	0	0	0	0	3	0	2	0	1	0	0	0	0	1	0	0	1	0	1	37.14
Perepsilonema	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2.86
Platycomopsis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	4	2	11.43
Polygastrophora	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	5.71
Polysigma	0	0	0	0	1	0	0	0	0	0	0	0	0	9	6	4	0	1	6	17.14
Pomponema	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5.71
Prochromadorella	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	22.86
Promonhystera	1	0	2	1	0	0	0	0	7	0	3	0	2	0	0	0	1	0	0	31.43
Prorhynconema	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	5.71
***Pselionema* sp.1**	0	0	0	1	0	0	0	2	1	0	0	0	1	1	0	0	0	0	2	17.14
***Pselionema* sp.2**	0	0	0	0	0	0	0	0	1	0	0	0	0	6	2	0	0	0	1	11.43
Pterygonema	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	8.57
Retrotheristus	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	11.43
Rhynchonema	0	0	0	1	2	0	0	0	1	0	0	1	0	2	1	1	0	0	0	22.86
***Sabatieria* sp.1**	14	35	9	2	9	13	7	9	2	2	5	1	3	10	2	14	2	2	4	100.00
***Sabatieria* sp.2**	0	0	4	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	22.86
Setoplectus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2.86
Setosabatieria	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11.43

Appendix 1.3 (continued): Abundance of nematodes in SUMMER; highlighted taxa indicate those used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	Feeding gr	c-p value	1.1	1.2	1.3	1.4	1.5	1.6	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4
Sigmophoranema	2B	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siphonolaimus	2B	3	0	0	0	0	1	0	0	0	1	0	3	0	0	0	0	0
Southernia	1A	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spirinia	2A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stephanolaimus	1A	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Stylotheristus	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synonema	2A		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syringolaimus	2B	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Terschellingia* sp.1**	1A	3	0	4	3	1	0	3	0	0	0	0	0	0	0	0	0	0
***Terschellingia* sp.2**	1A	3	0	0	5	0	0	2	0	1	0	0	1	0	0	1	0	0
***Terschellingia* sp.3**	1A	3	7	17	19	14	0	4	7	10	5	17	15	5	7	10	5	2
***Terschellingia* sp.4**	1A	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassoalaimus	1A	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassomonhystera	1B	1	0	0	0	0	1	0	1	2	1	2	4	4	0	1	0	1
Theristus	1B	2	0	0	0	0	0	0	2	1	1	1	4	3	0	0	1	1
Trichotheristus	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Tripyloides	1B	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Trochamus	2A	3	2	0	0	3	0	0	0	1	0	4	0	0	0	0	0	0
Tubolaimoides	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Valvaelaimus	2B	2	0	0	0	0	3	0	0	0	1	6	1	1	1	0	3	0
Viscosia	2B	3	1	0	0	3	0	0	2	0	4	0	1	0	0	2	0	0

Appendix 1.3 (continued): Abundance of nematodes in SUMMER; highlighted taxa indicate those used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	3.5	3.6	4.1	4.2	4.3	4.4	4.5	4.6	5.2	5.3	5.4	5.5	5.6	6.1	6.2	6.3	6.4	6.5	6.6	> 5% Contribution
Sigmophoranema	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2.86
Siphonolaimus	0	0	0	0	0	0	3	1	0	3	0	0	2	0	0	1	0	0	1	25.71
Southernia	0	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5.71
Spirinia	0	0	0	0	0	0	1	1	0	9	0	0	0	0	0	3	0	1	3	17.14
Stephanolaimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.86
Stylotheristus	0	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	5.71
Synonema	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2.86
Syringolaimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2.86
***Terschellingia* sp.1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11.43
***Terschellingia* sp.2**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14.29
***Terschellingia* sp.3**	4	2	0	2	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	62.86
***Terschellingia* sp.4**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.86
Thalassoalaimus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.86
Thalassomonhystera	0	1	0	1	1	0	0	0	7	3	5	8	13	1	0	5	1	0	2	60.00
Theristus	3	1	0	1	4	1	1	4	2	6	0	4	4	3	1	2	2	0	2	68.57
Trichotheristus	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	8.57
Tripyloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.86
Trochamus	1	2	1	0	1	2	2	0	0	0	2	0	0	0	0	0	1	0	0	34.29
Tubolaimoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.86
Valvaelaimus	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	25.71
Viscosia	1	2	0	0	3	0	2	5	0	0	1	0	1	1	0	1	1	2	0	48.57

Appendix 1.4: Abundance of nematodes in WINTER; all taxa listed were used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	Feeding group	c-p value	1.1	1.2	1.3	1.4	1.5	1.6	4.1	4.2	4.3	4.4	4.5	4.6	6.1	6.2	6.3	6.4	6.5	6.6	> 5% contribution
Aegialoalaimus	1A	4	0	0	0	0	0	0	1	2	1	0	5	0	0	0	0	1	0	0	33.33
Ammotheristus	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5.56
Amphimonhystrella	1B	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	16.67
Antomicron	1A	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5.56
Bolbolaimus sp.1	2B	3	0	0	0	0	0	0	0	0	0	1	0	0	2	3	0	4	2	7	38.89
Calyptronema	1B	4	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	22.22
Camacolaimus	2A	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	11.11
Campylaimus	1B	3	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	22.22
Catanema	2A	3	0	0	0	0	0	0	0	0	4	0	1	1	0	0	0	0	0	0	22.22
Choniolaimus	2A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	11.11
Chromadora	2A	2	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	16.67
Chromadorella	2A	3	0	1	0	0	0	0	11	2	5	2	2	1	1	3	2	0	0	0	61.11
Chromadorina	2A	3	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	0	1	0	27.78
Chromaspirinia	2B	4	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	22.22
Cobbia sp.1	2A	3	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	4	2	0	27.78
Cobbia sp.3	2A	3	0	0	0	0	0	0	0	0	1	1	0	2	0	0	1	0	0	0	27.78
Comesa	1B	3	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	27.78
Comesoma	1B	2	0	0	0	0	0	0	0	4	1	5	3	1	0	0	0	1	0	0	38.89
Cyartonema	1A	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	11.11
Cyatholaimus	2A	3	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1	1	2	27.78
Daptonema	1B	2	0	0	0	0	0	0	0	6	0	1	0	6	2	1	1	4	2	2	55.56
Dasynemoides	1A	3	0	0	0	0	0	0	2	3	1	2	0	0	0	1	1	0	0	0	38.89
Desmolaimus	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	3	0	16.67
Dichromadora	2A	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	5.56

Appendix 1.4 (continued): Abundance of nematodes in WINTER; all taxa listed were used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	Feeding group	c-p value	1.1	1.2	1.3	1.4	1.5	1.6	4.1	4.2	4.3	4.4	4.5	4.6	6.1	6.2	6.3	6.4	6.5	6.6	> 5% contribution
Diplopeltoides	1A	4	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	2	22.22
Diplopeltula	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5.56
Doliolaimus	1B	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	11.11
Draconema	1A	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5.56
Eleutherolaimus	1B	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	16.67
Enoplolaimus	2B	2	0	0	0	0	0	0	0	2	0	0	1	2	0	0	0	1	0	0	27.78
Eurystomina	2B	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5.56
Gonionchus	2A	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	11.11
Halalaimus sp.1	1A	4	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	16.67
Halalaimus sp.3	1A	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5.56
Halalaimus sp.5	1A	4	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	16.67
Halalaimus sp.8	1A	4	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	1	1	4	33.33
Halalaimus sp.9	1A	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	5.56
Haliplectus	1A	3	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	5.56
Lauratonema	1B	[illegible]	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	5.56
Leptepsilonema	1A	4	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	16.67
Leptonemella	1A	3	1	6	0	1	1	0	0	0	1	0	0	1	1	0	5	3	0	2	61.11
Linhomoeus	2A	2	0	0	0	0	0	0	0	0	4	1	5	2	2	10	6	7	4	6	61.11
Longicyatholaimus	2A	2	0	0	0	0	0	0	0	3	0	1	0	1	0	0	0	0	0	0	22.22
Metachromadora	2B	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5.56
Metacyatholaimus	2A	3	0	0	0	0	0	0	1	6	2	6	3	0	5	1	0	3	1	1	61.11
Metadasynemella	1A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	11.11
Metadasynemoides	1A	3	0	0	0	0	0	0	0	3	1	1	0	0	1	0	0	1	0	0	33.33
Metalinhomoeus sp.1	1B	2	0	0	0	0	0	0	0	0	0	2	4	1	4	27	13	2	18	3	55.56
Metalinhomoeus sp.2	1B	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	16.67

Appendix 1.4 (continued): Abundance of nematodes in WINTER; all taxa listed were used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	Feeding group	c-p value	1.1	1.2	1.3	1.4	1.5	1.6	4.1	4.2	4.3	4.4	4.5	4.6	6.1	6.2	6.3	6.4	6.5	6.6	> 5% contribution
Microlaimus	2A	2	0	0	0	0	0	1	11	9	4	13	5	11	46	8	16	24	21	17	77.78
Molgolaimus	1A	3	0	5	0	2	0	6	0	0	0	0	0	0	2	2	6	5	1	4	50.00
Nannolaimus	1A	3	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	16.67
Neotonchus	2A	2	0	0	0	0	0	0	1	0	0	0	0	0	1	1	2	0	1	0	33.33
Odontophora	1B	2	0	0	0	0	0	0	0	0	0	0	0	3	1	0	1	0	0	0	22.22
Oxystomina	1A	4	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	22.22
Paracanthonchus	2A	2	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	16.67
Paracomesoma	1B	2	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	27.78
Paracyatholaimus	2A	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	16.67
Paralinhomoeus sp.1	1B	2	0	0	0	0	0	0	1	0	0	2	9	0	3	17	12	1	11	7	55.56
Paralinhomoeus sp.2	1B	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	5	1	22.22
Parallelecoilas	2B	3	0	0	0	0	0	0	0	4	7	12	0	3	0	0	0	0	0	0	27.78
Paralongicyatholaimus	2A	3	0	0	0	0	0	0	0	1	2	2	0	2	4	3	3	10	0	9	55.56
Paramicrolaimus	2A	[illegible]	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	27.78
Parodontophora	1B	2	0	1	0	0	0	0	1	1	3	0	9	0	0	0	0	0	0	0	33.33
Perepsilonema	1A	4	0	0	0	0	0	0	2	0	4	0	0	0	0	0	0	0	0	0	16.67
Polysigma	2A	2	0	0	0	0	0	0	1	3	1	0	0	1	0	0	0	2	0	0	33.33
Pomponema	2B	4	0	0	0	0	0	0	0	1	4	1	0	0	0	2	1	0	0	0	33.33
Promonhystera	1B	2	0	0	0	0	0	0	0	0	2	1	0	0	2	0	1	1	0	2	38.89
Pselionema sp.1	1A	3	0	0	0	0	0	0	0	1	0	1	0	0	4	0	2	4	2	4	44.44
Pseudonchus	2B	3	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	27.78
Retrotheristus	1B	2	0	2	0	0	0	0	1	8	0	0	0	0	0	1	0	0	0	0	27.78
Rhynchonema	1B	2	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	16.67
Sabatieria sp.1	1B	2	97	85	100	96	96	92	2	4	5	13	4	6	0	0	3	1	4	0	88.89
Scaptrella	2B	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	27.78

Appendix 1.4 (continued): Abundance of nematodes in WINTER; all taxa listed were used in data analysis, percentage contribution per taxon, feeding group and Maturity Index (c-p value).

	Feeding gr	c-p value	1.1	1.2	1.3	1.4	1.5	1.6	4.1	4.2	4.3	4.4	4.5	4.6	6.1	6.2	6.3	6.4	6.5	6.6	> 5% contribution
Siphonolaimus	2B	3	0	0	0	0	0	0	0	2	0	2	3	3	0	0	0	0	0	0	27.78
Spirinia	2A	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	5.56
Stephanolaimus	1A	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	5.56
Tarvaia	1A	[illegible]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5.56
Terschellingia sp.3	1A	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5.56
Thalassomonhystera	1B	1	0	0	0	0	0	0	2	10	2	1	2	3	5	3	2	2	1	5	72.22
Theristus	1B	2	0	0	0	0	0	0	0	3	5	1	2	1	2	1	4	5	3	2	66.67
Tricoma	1A	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5.56
Trochamus	2A	3	0	0	0	0	0	0	2	0	1	1	0	0	0	1	0	0	0	0	27.78
Viscosia	2B	3	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	1	1	44.44

APPENDIX 1.5: Mean values of metals and other environmental data from Monteiro *et al.* (1999) and present study

	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
Sand	5.92	80.22	75.81	78.77	93.15	93.18
Gravel	0.26	1.68	5.33	0.41	0.44	2.80
Mud	93.75	18.098	18.87	20.81	6.42	4.03
GrainS	4.47	2.96	2.96	2.99	2.53	2.50
Al	17338.06	3939.01	2902.16	3968.25	3456.68	2945.11
Fe	13888.89	3393.68	2762.11	2964.21	2623.16	2282.11
Cu	12.73	4	4	3.43	3.145	2.86
Pb	53.75	48.75	37.5	30	30	30
Cd	6.68	4.32	3.47	3.79	3.42	3.05
Zn	76.07	13.6	8	10.4	7.95	5.5
OrgC	7.54	1.98	0.7	0.64	0.45	0.26
OrgN	0.42	0.05	0.01	0.04	0.03	0.02

APPENDIX 5.1: The observed and estimated species richness output for nematode diversity at Saldanha Bay using *EstimateS* (Version 8.0.0). The table reports results for Abundance-basedCoverage Estimator (ACE), Incidence-based Coverage Estimator(ICE), Chao 2 and Jackknife 2 estimators

Samples	Individuals (computed)	Sobs Mean (runs)	ACE Mean	ICE Mean	Chao 2 Mean	Jack 2 Mean
1	84.68	24.44	41.87	353.34	353.34	0
2	169.36	37.42	56.16	259.3	116.26	52.19
3	254.04	49.06	70.59	150.04	104.8	79.87
4	338.72	58.98	81.28	122.13	100.73	98.28
5	423.4	66.42	88.71	117.6	103.19	109.03
6	508.08	72.06	94.72	119.7	109.26	117.29
7	592.75	76.12	98.67	119.68	111.37	121.48
8	677.43	80.28	101.96	120.8	113.35	125.29
9	762.11	84.06	105.41	123.11	115.74	129.42
10	846.79	87.56	107.71	125.16	118.05	132.78
11	931.47	91	111.21	126.44	121.28	136.47
12	1016.15	94.16	114.22	128.42	124.05	139.56
13	1100.83	96.58	116.33	130.05	125.87	141.78
14	1185.51	99.1	118.49	131.96	128.68	144.53
15	1270.19	101.5	120.64	133.85	130.77	147.43
16	1354.87	103.92	123.19	136.18	134.78	150.72
17	1439.55	105.64	124.33	136.42	134.93	151.36
18	1524.23	107.34	125.63	137.26	135.95	152.81
19	1608.91	109.26	127.15	138.43	136.97	153.95
20	1693.58	110.8	128.69	139.49	138.45	155.66
21	1778.26	112.2	129.39	139.5	138.17	155.17
22	1862.94	113.64	130.32	140.18	139	156.09
23	1947.62	114.9	130.79	140.57	139.33	156.35
24	2032.3	115.96	131.37	141.1	139.91	156.8
25	2116.98	117.14	132.32	141.94	140.66	157.71
26	2201.66	118.54	133.49	142.73	140.99	158.06
27	2286.34	119.74	134.35	143.5	141.62	158.76
28	2371.02	120.86	135.52	144.52	142.24	159.68

APPENDIX 5.1 (continued): The observed and estimated species richness output for nematode diversity at Saldanha Bay using *EstimateS* (Version 8.0.0). The table reports results for Abundance-based Coverage Estimator (ACE), Incidence-based Coverage Estimator(ICE), Chao 2 and Jackknife 2 estimators

Samples	Individuals (computed)	Sobs Mean (runs)	ACE means	ICE Mean	Chao 2 Mean	Jack 2 Mean
29	2455.7	121.7	136.28	144.79	142.62	160.04
30	2540.38	122.42	136.77	145.13	143.2	160.37
31	2625.06	123.56	137.61	146.02	144.18	161.11
32	2709.74	124.22	137.9	146.24	144.42	161.41
33	2794.42	125.04	138.5	146.68	144.86	161.93
34	2879.09	125.76	139.14	147.25	145.67	162.64
35	2963.77	126.24	139.25	147.27	145.42	162.14
36	3048.45	127.1	139.83	147.72	145.17	161.81
37	3133.13	127.76	140.32	148.2	145.73	162.29
38	3217.81	128.46	140.66	148.45	145.95	162.3
39	3302.49	129.12	141.09	148.7	145.92	162.12
40	3387.17	129.66	141.32	148.75	145.88	161.52
41	3471.85	130.38	141.65	148.9	145.71	161.03
42	3556.53	131.42	142.61	150.08	146.67	161.95
43	3641.21	132.22	143.33	150.72	147.47	162.77
44	3725.89	132.7	143.47	150.89	147.53	162.75
45	3810.57	133.18	143.63	150.79	147.03	161.82
46	3895.25	133.84	144.12	151.22	147.27	162.01
47	3979.92	134.16	144.16	151.01	146.93	161.15
48	4064.6	134.48	144.35	151.02	146.84	160.8
49	4149.28	134.92	144.63	151.12	146.76	160.4
50	4233.96	135.2	144.5	150.63	146	158.82
51	4318.64	135.44	144.56	150.43	145.64	157.98
52	4403.32	135.76	144.57	150.11	145.23	156.83
53	4488	136	144.65	150	144.96	156.05

Appendix 5.2: Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Genus	SaldanhaBay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	ItalianH	StMartinFlats	SwartkopsEst	GamtoosEst
Acantholaimus	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acanthonchus	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Acanthopharynx	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
Actinonema	0.0	0.8	0.0	0.0	0.2	1.7	0.0	0.6	0.0	0.0
Adoncholaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	2.6
Aegialoalaimus	0.9	0.1	1.2	0.1	0.0	0.0	0.0	0.0	0.2	0.7
Alaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alaimella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ammotheristus	0.9	0.0	0.0	0.1	0.0	0.7	0.0	0.0	0.0	0.0
Amphimonhystera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Amphimonhystrella	0.4	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Anomonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0
Anoplostoma	0.0	0.0	0.6	0.0	0.0	0.0	0.3	0.0	0.8	1.6
Anticoma	0.0	0.4	0.3	0.0	0.0	0.1	2.3	0.1	0.0	0.0
Anticyathus	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Antomicron	0.2	0.4	0.8	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Aphanolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aponema	0.0	0.0	0.0	0.6	1.3	0.0	0.0	0.0	0.0	0.6
Araeolaimus	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ascolaimus	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Astomonema	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.7	0.0	0.0
Atrochromadora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Axonolaimus	0.7	0.0	3.3	0.0	1.3	0.4	0.2	1.3	0.7	3.3
Bathyeurystomina	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Bathylaimus	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0
Belbolla	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Bodonema	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bolbolaimus	0.6	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Bolbonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calomicrolaimus	0.0	0.0	0.0	0.0	0.0	0.3	0.0	1.7	0.2	0.0

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists.

Genus	ClydeEst	ItalyMPAs	CelticSea	NWIrishSea	Indiamangroves	MurrayHeadEst	Baltic Sea	NorthSea	Gulf Main	Mexico
Acantholaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Acanthonchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acanthopharynx	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Actinonema	0.3	0.0	1.6	1.6	0.0	0.0	0.0	0.0	1.6	0.0
Adoncholaimus	0.2	0.0	0.0	0.0	2.5	0.0	2.7	0.0	0.0	0.0
Aegialoalaimus	0.5	0.0	0.4	0.0	0.0	0.0	0.0	0.0	3.2	0.0
Alaimus	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Alaimella	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	1.0	0.0
Ammotheristus	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphimonhystera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Amphimonhystrella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anomonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anoplostoma	0.0	7.7	0.0	0.0	0.6	0.3	0.0	0.0	0.0	0.0
Anticoma	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anticyathus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Antomicron	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aphanolaimus	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Aponema	0.0	0.0	4.0	2.9	0.0	0.0	0.0	0.0	1.0	0.0
Araeolaimus	0.0	0.3	0.0	0.0	0.2	0.0	0.0	0.0	1.0	0.0
Ascolaimus	0.2	0.0	0.0	0.0	0.0	0.0	24.3	2.2	1.0	0.0
Astomonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Atrochromadora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Axonolaimus	0.0	0.0	0.8	2.2	0.0	0.2	7.9	1.8	0.9	0.0
Bathyeurystomina	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bathylaimus	0.8	0.3	0.0	0.0	0.0	0.0	1.5	6.6	0.0	0.0
Belbolla	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.5	0.0
Bodonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bolbolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
Bolbonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calomicrolaimus	2.2	0.3	0.7	0.4	0.0	0.0	0.3	0.5	0.2	0.0

Appendix 5.2 (continued)

Genus	NorthBaltic	Manfredonia
Acantholaimus	0.0	0.0
Acanthonchus	0.0	0.0
Acanthopharynx	0.0	0.0
Actinonema	0.0	0.0
Adoncholaimus	15.2	0.1
Aegialoalaimus	0.0	0.0
Alaimus	0.0	0.0
Alaimella	0.0	0.0
Ammotheristus	0.0	0.0
Amphimonhystera	0.0	0.0
Amphimonhystrella	0.0	0.0
Anomonema	0.0	0.0
Anoplostoma	0.0	0.0
Anticoma	0.0	0.1
Anticyathus	0.0	0.0
Antomicron	0.0	0.0
Aphanolaimus	0.0	0.0
Aponema	0.0	0.0
Araeolaimus	0.0	0.1
Ascolaimus	0.0	0.0
Astomonema	0.0	0.4
Atrochromadora	0.0	0.0
Axonolaimus	2.6	0.0
Bathyeurystomina	0.0	0.0
Bathylaimus	0.0	0.0
Belbolla	0.0	0.0
Bodonema	0.0	0.0
Bolbolaimus	0.0	0.0
Bolbonema	0.0	0.0
Calomicrolaimus	0.0	0.0

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Genus	SaldanhaBay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	ItalianHarb	StMartinFlats	SwartkopsEst	GamtoosEst
Calyptronema	0.5	0.0	1.5	0.0	0.0	0.0	0.3	0.0	0.8	0.0
Camacolaimus	1.5	0.4	0.0	0.0	0.0	1.2	0.0	0.4	0.0	0.0
Campylaimus	0.2	0.2	0.0	0.0	0.5	0.0	0.3	0.0	0.0	0.0
Catanema	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cephalochaetosoma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ceramonema	0.2	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Cervonema	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetonema	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Cheironchus	0.0	0.3	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0
Chitwoodia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Choniolaimus	0.9	0.0	0.0	0.2	0.2	0.4	0.0	0.0	0.0	0.0
Chromadora	0.2	0.0	8.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Chromadorella	2.0	0.0	0.0	0.3	0.2	0.0	0.9	0.0	3.7	0.2
Chromadorina	0.7	0.0	0.0	0.0	0.5	0.2	0.6	0.0	0.6	0.0
Chromadorita	0.0	0.2	0.0	0.3	1.7	1.2	0.4	2.7	0.0	0.0
Chromaspirinia	0.2	0.0	0.0	0.6	0.1	0.0	0.0	1.3	0.0	0.0
Cienfuegia	0.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0
Cobbia	2.5	0.0	0.0	0.0	0.2	0.7	0.0	0.0	0.6	0.1
Comesa	0.3	0.0	0.0	0.6	0.2	0.2	0.8	0.3	0.0	0.0
Comesoma	0.3	1.3	0.0	0.7	0.5	0.9	0.2	0.0	0.0	0.2
Comesomoides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coninckia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crestanema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cricolaimus	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Croconema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cruznema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyartonema	0.1	0.2	0.8	0.4	0.1	0.4	0.0	0.8	0.0	0.0
Cyatholaimus	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cytolaimium	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Dagda	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Genus	ClydeEst	ItalyMPAs	CelticSea	NWIrishSea	Indiamangroves	MurrayHeadEst	Baltic Sea	NorthSea	Gulf Main	Mexico
Calyptronema	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Camacolaimus	0.0	0.3	0.0	0.0	0.9	0.3	0.0	0.6	0.9	0.0
Campylaimus	0.2	0.0	1.1	0.4	0.0	0.0	0.0	0.0	0.5	0.0
Catanema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cephalochaetosoma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ceramonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cervonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Chaetonema	0.7	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cheironchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3
Chitwoodia	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Choniolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Chromadora	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.5	0.3	0.0
Chromadorella	0.0	0.3	0.0	0.0	0.0	0.0	0.1	0.3	0.0	0.0
Chromadorina	0.0	2.3	0.0	0.0	0.0	0.0	0.5	0.4	0.3	0.0
Chromadorita	0.0	5.0	0.0	0.3	0.2	0.0	5.5	0.7	0.0	0.0
Chromaspirinia	2.3	0.7	0.0	0.0	0.0	0.0	0.0	4.1	0.0	0.0
Cienfuegia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cobbia	0.1	3.0	4.3	5.6	0.0	0.0	0.0	0.4	0.0	0.0
Comesa	0.0	0.0	6.1	5.0	0.0	0.0	0.0	0.7	0.5	0.0
Comesoma	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3
Comesomoides	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0
Coninckia	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crestanema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cricolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Croconema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cruznema	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Cyartonema	1.7	0.0	0.3	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Cyatholaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Cytolaimium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0
Dagda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 5.2 (continued)

Genus	NorthBaltic	Manfredonia
Calyptronema	0.0	0.0
Camacolaimus	0.0	0.0
Campylaimus	0.0	0.0
Catanema	0.0	0.0
Cephalochaetosoma	0.0	0.0
Ceramonema	0.0	0.0
Cervonema	0.0	0.1
Chaetonema	0.0	0.0
Cheironchus	0.0	0.0
Chitwoodia	0.0	0.0
Choniolaimus	0.0	0.0
Chromadora	0.0	0.1
Chromadorella	0.0	0.0
Chromadorina	0.1	0.3
Chromadorita	23.5	0.1
Chromaspirinia	0.0	0.0
Cienfuegia	0.0	0.0
Cobbia	0.0	0.0
Comesa	0.0	0.4
Comesoma	0.0	0.0
Comesomoides	0.0	0.0
Coninckia	0.0	0.0
Crestanema	0.0	0.0
Cricolaimus	0.0	0.0
Croconema	0.0	0.0
Cruznema	0.0	0.0
Cyartonema	0.0	0.0
Cyatholaimus	0.0	0.0
Cytolaimium	0.0	0.0
Dagda	0.0	0.0

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Genus	SaldanhaBay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	ItalianH	StMartinFlats	SwartkopsEst	GamtoosEst
Daptonema	3.7	5.2	6.9	2.8	6.0	21.5	2.3	0.2	2.4	5.6
Dasynemella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dasynemoides	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Desmodora	0.0	17.7	0.0	0.7	0.5	0.8	3.4	34.9	0.0	0.0
Desmolaimus	0.4	0.0	2.4	0.7	0.0	0.0	0.0	0.0	0.0	0.0
Desmolorenzia	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Desmoscolex	0.9	0.3	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0
Dichromadora	0.4	0.0	0.0	0.1	5.7	2.0	0.3	0.0	0.0	0.3
Diodontolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diplolaimella	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.9
Diplolaimelloides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diplopeltoides	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0
Diplopeltula	0.3	0.1	0.0	0.0	0.1	0.9	0.0	0.0	0.0	0.0
Disconema	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0
Ditlevsenella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dolicholaimus	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
Doliolaimus	0.2	0.0	0.0	0.7	0.0	0.0	0.0	0.0	3.1	0.0
Dorylaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dorylaimopsis	0.0	1.8	0.0	0.7	0.7	0.0	0.0	0.0	4.8	1.4
Draconema	0.2	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
Echinodesmodora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Echinotheristus	0.7	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0
Eleutherolaimus	0.9	0.0	0.0	0.2	0.2	0.0	0.4	0.6	0.0	0.0
Elzalia	0.9	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.3	0.3
Enoploides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0
Enoplolaimus	0.1	0.0	0.0	0.0	0.0	0.4	0.0	0.6	0.0	0.0
Enoplus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epacanthion	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epsilonema	0.0	0.4	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Ethmolaimus	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	2.5	0.2

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists.

Genus	ClydeEst	ItalyMPAs	CelticSea	NWIrishSea	Indiamangroves	MurrayHeadEst	Baltic Sea	NorthSea	Gulf Main	Mexico
Daptonema	4.3	14.0	5.2	8.7	6.3	0.6	21.9	3.1	2.8	0.0
Dasynemella	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dasynemoides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Desmodora	0.0	2.0	0.0	3.7	2.7	0.3	0.0	0.0	6.6	1.3
Desmolaimus	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6
Desmolorenzia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Desmoscolex	0.0	0.0	0.3	0.6	1.4	0.3	0.0	0.0	1.0	0.6
Dichromadora	1.6	2.3	0.0	0.0	0.0	13.0	11.1	3.3	1.0	1.3
Diodontolaimus	0.0	0.3	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Diplolaimella	0.0	0.0	0.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0
Diplolaimelloides	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0
Diplopeltoides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Diplopeltula	0.5	0.0	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Disconema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ditlevsenella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Dolicholaimus	0.0	0.0	0.7	1.4	0.0	0.0	0.0	0.0	0.0	0.0
Doliolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dorylaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dorylaimopsis	0.0	0.0	6.8	1.4	16.1	0.0	0.0	0.0	1.3	0.0
Draconema	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
Echinodesmodora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Echinotheristus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eleutherolaimus	0.8	0.0	0.0	0.0	0.0	0.1	0.0	0.5	0.0	0.0
Elzalia	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Enoploides	1.4	3.7	0.0	0.0	0.0	0.1	0.0	0.1	0.6	0.0
Enoplolaimus	0.0	0.0	0.0	0.0	0.0	0.0	15.5	0.2	0.0	12.8
Enoplus	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epacanthion	0.0	0.3	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epsilonema	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ethmolaimus	0.0	0.0	0.0	0.0	0.0	32.2	0.0	0.0	0.0	0.0

Appendix 5.2 (continued)

Genus	NorthBaltic	Manfredonia
Daptonema	0.8	6.7
Dasynemella	0.0	0.0
Dasynemoides	0.0	0.0
Desmodora	0.0	0.6
Desmolaimus	0.0	0.0
Desmolorenzia	0.0	0.0
Desmoscolex	0.0	0.3
Dichromadora	1.9	0.0
Diodontolaimus	0.0	0.0
Diplolaimella	0.0	0.0
Diplolaimelloides	0.0	0.0
Diplopeltoides	0.0	0.0
Diplopeltula	0.0	0.0
Disconema	0.0	0.0
Ditlevsenella	0.0	0.0
Dolicholaimus	0.0	0.0
Doliolaimus	0.0	0.4
Dorylaimus	0.1	0.0
Dorylaimopsis	0.0	29.0
Draconema	0.0	0.0
Echinodesmodora	0.0	0.0
Echinotheristus	0.0	0.0
Eleutherolaimus	1.3	0.0
Elzalia	0.0	1.4
Enoploides	0.0	0.0
Enoplolaimus	1.3	0.0
Enoplus	0.0	0.0
Epacanthion	0.0	0.0
Epsilonema	0.0	0.0
Ethmolaimus	0.6	0.0

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Genus	SaldanhaBay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	ItalianH	StMartinFlats	SwartkopsEst	GamtoosEst
Eubostrichus	0.0	0.4	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.0
Euchromadora	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.3	0.2	0.4
Eumorpholaimus	0.4	0.0	0.0	0.1	0.5	0.1	0.0	0.0	0.0	0.0
Eurystomina	0.7	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.3	0.0
Eutobrilus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fenestrolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Filitonchus	0.9	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
Filoncholaimus	0.2	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Gammanema	0.0	0.0	0.0	0.1	0.0	0.4	0.0	0.0	0.0	3.4
Gammarinema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.9	0.0
Geomonhystera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gomphionema	0.0	4.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Gonionchus	0.7	0.0	0.0	0.0	0.0	0.4	0.0	0.0	1.2	0.8
Graphonema	0.0	0.1	0.0	0.7	0.0	0.0	0.3	0.0	0.0	0.0
Guitartia	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Halalaimus	3.5	0.5	0.8	0.2	0.3	0.1	0.9	0.0	0.4	1.2
Halanonchus	0.0	0.0	0.0	0.0	0.5	0.0	0.5	0.0	0.0	0.0
Halaphanolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Halichoanolaimus	0.0	0.2	0.0	0.1	0.1	0.3	0.7	0.0	0.0	0.0
Haliplectus	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4
Hofmaenneria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hopperia	0.0	0.0	0.0	0.7	0.4	0.0	0.0	0.0	0.0	0.0
Hypodontolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Innocuonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ironus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ixonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0
Karkinochromadora	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Laimella	0.0	0.0	0.0	0.1	0.0	0.4	0.2	0.0	0.0	0.0
Latronema	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Lauratonema	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists.

Genus	ClydeEst	ItalyMPAs	CelticSea	NWIrishSea	Indiamangroves	MurrayHeadEst	Baltic Sea	NorthSea	Gulf Main	Mexico
Eubostrichus	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3
Euchromadora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	1.3
Eumorpholaimus	0.0	0.3	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
Eurystomina	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.3	0.0	0.0
Eutobrilus	0.0	0.0	0.0	0.0	0.0	13.4	0.0	0.0	0.0	0.0
Fenestrolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Filitonchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4	0.0
Filoncholaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gammanema	0.4	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Gammarinema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Geomonhystera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gomphionema	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Gonionchus	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Graphonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Guitartia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halalaimus	0.8	1.3	3.1	1.2	0.0	0.0	0.0	0.0	1.9	0.0
Halanonchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halaphanolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Halichoanolaimus	0.0	0.0	1.3	0.4	5.3	0.0	0.0	0.0	1.0	0.0
Haliplectus	0.0	0.0	0.0	0.0	0.6	1.8	0.0	0.0	0.0	0.0
Hofmaenneria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hopperia	0.0	0.0	0.0	0.0	9.3	0.0	0.0	0.0	0.6	0.0
Hypodontolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Innocuonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ironus	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Ixonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Karkinochromadora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.2	0.0	0.0
Laimella	0.0	0.0	1.8	1.9	0.0	0.0	0.0	0.0	0.2	0.0
Latronema	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lauratonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 5.2 (continued)

Genus	NorthBaltic	Manfredonia
Eubostrichus	0.0	0.0
Euchromadora	0.0	0.1
Eumorpholaimus	0.0	0.0
Eurystomina	0.0	0.0
Eutobrilus	0.0	0.0
Fenestrolaimus	0.0	0.0
Filitonchus	0.0	0.0
Filoncholaimus	0.0	0.0
Gammanema	0.0	0.0
Gammarinema	0.0	0.0
Geomonhystera	0.0	0.0
Gomphionema	0.0	1.3
Gonionchus	0.0	0.0
Graphonema	0.0	0.0
Guitartia	0.0	0.0
Halalaimus	0.0	1.4
Halanonchus	0.0	0.0
Halaphanolaimus	0.0	0.0
Halichoanolaimus	0.0	0.1
Haliplectus	0.0	0.0
Hofmaenneria	0.2	0.0
Hopperia	0.0	1.1
Hypodontolaimus	0.0	0.0
Innocuonema	0.0	0.1
Ironus	5.4	0.0
Ixonema	0.0	0.0
Karkinochromadora	0.0	0.0
Laimella	0.0	0.3
Latronema	0.0	0.0
Lauratonema	0.0	0.0

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Genus	SaldanhaBay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	ItalianH	StMartinFlats	SwartkopsEst	GamtoosEst
Leptepsilonema	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leptolaimoides	0.0	0.0	0.0	0.0	0.1	0.3	0.0	0.0	0.0	0.0
Leptolaimus	2.7	0.2	0.0	0.7	0.3	0.3	0.5	0.3	0.0	0.0
Leptonemella	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Linhomoeus	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Linhystera	0.0	0.0	0.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0
Longicyatholaimus	0.4	0.0	0.0	0.6	0.0	0.0	0.2	0.0	0.0	0.2
Macrodontium	0.0	0.0	0.0	8.1	0.0	0.0	0.0	0.0	0.0	0.0
Manunema	0.4	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0
Marylynnia	0.0	0.2	0.0	0.9	0.4	2.6	2.3	0.0	0.7	0.2
Megadesmolaimus	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Mesacanthion	0.0	0.4	0.0	0.0	0.1	0.9	0.1	0.6	0.5	0.0
Mesodorylaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Metachromadora	0.7	1.8	24.6	2.6	0.7	0.3	0.9	0.9	0.0	0.4
Metacomesoma	0.0	0.4	1.3	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Metacyatholaimus	1.7	0.0	0.0	3.9	0.0	0.0	0.0	0.0	0.0	0.2
Metadasynemella	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metadasynemoides	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metadesmolaimus	0.0	0.0	0.0	0.2	0.0	0.0	0.4	0.4	0.0	0.0
Metalinhomoeus	4.7	0.0	3.1	2.6	0.1	5.2	2.4	0.2	5.7	1.3
Metoncholaimus	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0
Microlaimus	7.6	3.0	0.0	0.0	2.7	1.7	0.7	0.5	1.7	1.8
Minolaimus	0.4	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
Molgolaimus	1.2	0.0	0.0	0.7	2.3	18.2	1.7	0.0	0.0	0.0
Monhystera	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	12.0	2.5
Monhystrella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mononcholaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mononchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8
Monoposthia	0.0	0.4	0.0	0.0	0.0	1.3	0.0	0.2	0.0	0.0
Morlaixia	0.0	0.0	0.0	0.0	1.0	0.7	0.0	0.0	0.0	0.0

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists.

Genus	ClydeEst	ItalyMPAs	CelticSea	NWIrishSea	Indiamangroves	MurrayHeadEst	Baltic Sea	NorthSea	Gulf Main	Mexico
Leptepsilonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leptolaimoides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Leptolaimus	5.7	0.0	4.8	2.3	0.0	0.9	0.0	0.2	2.3	0.0
Leptonemella	6.4	0.7	0.5	0.6	0.0	0.0	0.0	0.2	0.0	0.0
Linhomoeus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0
Linhystera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Longicyatholaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macrodontium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Manunema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Marylynnia	0.0	4.7	5.7	6.0	0.0	0.0	0.0	0.0	0.0	0.0
Megadesmolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mesacanthion	0.0	12.0	0.0	0.7	0.0	0.6	0.0	0.0	0.0	0.0
Mesodorylaimus	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metachromadora	3.6	0.3	0.0	0.0	1.8	0.0	0.5	4.2	0.0	12.2
Metacomesoma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metacyatholaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metadasynemella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metadasynemoides	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metadesmolaimus	2.5	0.0	0.0	1.4	0.0	0.3	0.0	0.0	0.0	0.0
Metalinhomoeus	0.0	0.0	3.9	3.7	1.5	0.8	0.0	0.0	6.1	0.0
Metoncholaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microlaimus	3.6	1.3	0.0	2.5	0.0	0.0	0.2	2.6	4.7	0.0
Minolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Molgolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.9	0.0
Monhystera	3.3	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Monhystrella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mononcholaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mononchus	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Monoposthia	1.9	0.7	0.0	0.0	0.0	0.0	0.1	9.2	0.0	0.0
Morlaixia	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0

Appendix 5.2 (continued)

Genus	NorthBaltic	Manfredonia
Leptepsilonema	0.0	0.0
Leptolaimoides	0.0	0.0
Leptolaimus	4.2	0.0
Leptonemella	0.0	0.0
Linhomoeus	0.0	0.0
Linhystera	0.0	1.1
Longicyatholaimus	0.0	0.0
Macrodontium	0.0	0.0
Manunema	0.0	0.0
Marylynnia	0.0	0.0
Megadesmolaimus	0.0	0.0
Mesacanthion	0.0	0.0
Mesodorylaimus	0.0	0.0
Metachromadora	0.0	0.0
Metacomesoma	0.0	0.0
Metacyatholaimus	0.0	1.4
Metadasynemella	0.0	0.0
Metadasynemoides	0.0	0.0
Metadesmolaimus	0.0	0.0
Metalinhomoeus	0.0	0.4
Metoncholaimus	0.0	0.0
Microlaimus	3.4	0.0
Minolaimus	0.0	0.0
Molgolaimus	0.0	0.0
Monhystera	0.1	0.6
Monhystrella	0.0	0.0
Mononcholaimus	0.0	0.1
Mononchus	0.0	0.0
Monoposthia	0.0	0.0
Morlaixia	0.0	0.0

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Genus	SaldanhaBay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	ItalianHb	StMartinFlats	SwartkopsEst	GamtoosEst
Mylonchulus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nannolaimoides	0.0	5.3	0.0	0.0	0.0	0.6	0.0	0.0	0.7	1.8
Nannolaimus	0.7	0.0	0.0	0.0	1.0	0.6	0.1	0.2	0.0	0.0
Nemanema	0.2	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Neochromadora	0.0	0.7	0.0	0.0	1.9	0.3	0.5	3.2	0.0	2.7
Neotonchoides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Neotonchus	0.3	0.7	0.0	0.0	0.0	9.2	1.8	0.0	0.0	0.0
Nudora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Odontophora	1.0	0.7	1.9	0.0	0.4	3.9	0.7	0.7	0.0	0.0
Odontophoroides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Onchium	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Oncholaimellus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4
Oncholaimus	0.4	0.0	0.0	0.2	0.0	0.1	0.2	0.0	0.2	0.3
Onyx	0.0	0.0	0.0	0.0	0.4	0.7	0.0	0.3	0.2	0.0
Oxyonchus	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Oxystomina	0.3	0.0	0.8	0.0	0.0	0.1	0.3	0.0	0.0	0.0
Pandolaimus	0.9	0.0	0.3	0.0	0.7	0.3	0.0	0.0	0.0	0.0
Paracanthonchus	0.9	0.0	0.0	0.7	0.2	0.1	0.7	0.5	0.3	1.0
Parachromadorita	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paracomesoma	0.4	0.0	0.1	0.4	3.1	0.1	8.0	0.0	0.5	1.4
Paracyatholaimus	0.3	0.0	0.0	0.0	0.0	0.2	0.2	2.2	0.8	1.8
Paradesmodora	0.0	0.5	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
Paraethmolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paralinhomoeus	4.9	0.7	0.0	0.3	0.6	0.9	1.6	0.9	0.0	0.0
Parallelecoilas	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paralongicyatholaimus	1.6	0.0	0.0	0.4	0.0	0.0	11.3	0.2	0.0	0.0
Paramesacanthion	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paramesonchium	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.3	0.0	0.0
Paramicrolaimus	1.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paramonohystera	0.1	4.8	0.3	0.6	0.0	0.0	0.2	0.1	7.8	8.7

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists.

Genus	ClydeEst	ItalyMPAs	CelticSea	NWIrishSea	Indiamangroves	MurrayHeadEst	Baltic Sea	North ea	Gulf Main	Mexico
Mylonchulus	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Nannolaimoides	3.1	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nannolaimus	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Nemanema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Neochromadora	19.7	1.0	0.0	0.0	0.2	0.0	2.6	0.3	0.0	0.0
Neotonchoides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Neotonchus	0.9	0.0	1.4	1.5	0.0	0.0	0.0	0.1	1.2	0.0
Nudora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Odontophora	2.0	3.0	0.1	4.8	0.0	0.0	0.0	0.3	4.5	0.0
Odontophoroides	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Onchium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oncholaimellus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oncholaimus	0.0	0.0	0.0	0.8	0.0	1.7	0.9	1.9	0.5	0.0
Onyx	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Oxyonchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oxystomina	0.9	0.0	0.9	0.4	0.0	0.0	0.0	0.2	0.0	0.0
Pandolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paracanthonchus	0.1	0.3	0.0	0.4	0.0	4.2	0.7	3.6	1.0	0.0
Parachromadorita	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.3	0.0	0.0
Paracomesoma	0.0	0.7	0.0	0.0	0.2	0.0	0.0	0.0	1.0	0.0
Paracyatholaimus	1.5	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0	3.8
Paradesmodora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Paraethmolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paralinhomoeus	0.0	0.0	5.0	4.0	0.7	0.0	0.0	0.3	0.3	0.0
Parallelecoilas	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Paralongicyatholaimus	0.0	0.0	0.1	0.5	0.5	0.0	0.0	0.0	2.0	0.0
Paramesacanthion	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.9	0.0
Paramesonchium	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Paramicrolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paramonohystera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.9

Appendix 5.2 (continued)

Genus	NorthBaltic	Manfredonia
Mylonchulus	0.0	0.0
Nannolaimoides	0.0	0.3
Nannolaimus	0.0	0.0
Nemanema	0.0	0.0
Neochromadora	1.3	0.4
Neotonchoides	0.0	0.3
Neotonchus	0.0	0.0
Nudora	0.0	0.0
Odontophora	0.0	0.0
Odontophoroides	0.0	0.0
Onchium	0.0	0.0
Oncholaimellus	0.0	0.0
Oncholaimus	1.6	0.0
Onyx	0.0	0.0
Oxyonchus	0.0	0.0
Oxystomina	0.0	0.0
Pandolaimus	0.0	0.0
Paracanthonchus	11.6	0.0
Parachromadorita	0.0	0.0
Paracomesoma	0.0	0.0
Paracyatholaimus	0.0	0.0
Paradesmodora	0.0	0.0
Paraethmolaimus	0.0	0.0
Paralinhomoeus	0.0	0.0
Parallelecoilas	0.0	0.0
Paralongicyatholaimus	0.0	0.1
Paramesacanthion	0.0	0.0
Paramesonchium	0.0	0.1
Paramicrolaimus	0.0	0.0
Paramonohystera	0.0	0.3

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

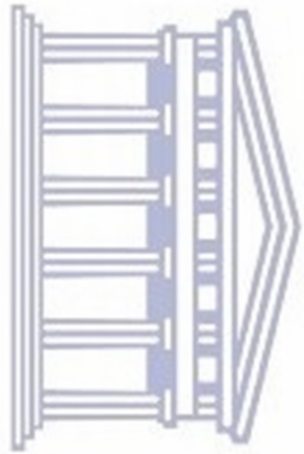
Genus	SaldanhaBay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	ItalianH	StMartinFlats	SwartkopsEst	GamtoosEst
Paranticoma	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Parasphaerolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pareurystomina	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parironus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parodontophora	2.3	1.9	0.7	1.2	0.0	0.3	2.8	0.0	1.1	4.0
Perepsilonema	0.2	0.0	0.0	0.0	0.0	0.0	0.0	26.9	0.0	0.0
Phanoderma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phanodermopsis	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pierrickia	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Platycomopsis	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plectus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polygastrophora	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2
Polysigma	0.6	0.2	0.0	0.0	0.2	0.0	0.9	0.0	0.0	0.0
Pomponema	0.3	0.0	0.0	0.7	0.5	0.0	0.3	0.0	1.7	1.2
Pontonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Praeacanthonchus	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.3	0.0	1.4
Procamacolaimus	0.0	0.0	0.0	0.0	0.7	0.2	0.0	0.0	0.0	0.0
Prochromadora	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
Prochromadorella	0.2	0.0	0.0	0.0	0.4	8.7	5.7	2.9	0.0	0.0
Prochromadorita	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Promonhystera	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prooncholaimus	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Prorhynchonema	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pselionema	0.7	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Pseudolella	0.0	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudochromadora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.5
Pseudonchus	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudoterschellingia	0.0	0.0	0.0	3.5	0.0	0.0	0.0	0.0	0.0	0.0
Pseudotheristus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pterygonema	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists.

Genus	ClydeEst	ItalyMPAs	CelticSea	NWIrishSea	Indiamangroves	MurrayHeadEst	Baltic Sea	North Sea	Gulf Maine	Mexico
Paranticoma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parasphaerolaimus	0.0	0.0	1.9	1.0	0.0	0.0	0.0	0.0	0.4	0.0
Pareurystomina	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.3	0.0
Parironus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parodontophora	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0
Perepsilonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.6
Phanoderma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0
Phanodermopsis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pierrickia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Platycomopsis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plectus	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Polygastrophora	0.0	0.0	0.0	0.0	0.0	0.0	0.1	3.2	0.0	0.0
Polysigma	0.4	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0
Pomponema	6.5	1.0	2.3	0.8	0.0	0.0	0.0	0.0	0.0	0.0
Pontonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Praeacanthonchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Procamacolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prochromadora	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.5	0.0	0.0
Prochromadorella	0.6	2.3	2.7	1.9	0.0	0.0	0.0	1.3	0.0	2.6
Prochromadorita	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Promonhystera	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Prooncholaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prorhynchonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pselionema	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.3
Pseudolella	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Pseudochromadora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudonchus	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Pseudoterschellingia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudotheristus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pterygonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 5.2 (continued)

Genus	NorthBaltic	Manfredonia
Paranticoma	0.0	0.0
Parasphaerolaimus	0.0	0.0
Pareurystomina	0.0	0.0
Parironus	0.0	0.0
Parodontophora	0.0	1.3
Perepsilonema	0.0	0.0
Phanoderma	0.0	0.0
Phanodermopsis	0.0	0.0
Pierrickia	0.0	0.6
Platycomopsis	0.0	0.0
Plectus	0.0	0.0
Polygastrophora	0.0	0.0
Polysigma	0.0	0.0
Pomponema	0.0	0.4
Pontonema	0.0	0.0
Praeacanthonchus	0.0	0.0
Procamacolaimus	0.0	0.0
Prochromadora	0.0	0.0
Prochromadorella	0.0	0.0
Prochromadorita	0.0	0.0
Promonhystera	0.0	0.3
Prooncholaimus	0.0	0.0
Prorhynchonema	0.0	0.0
Pselionema	0.0	0.0
Pseudolella	0.0	0.0
Pseudochromadora	0.0	0.0
Pseudonchus	0.0	0.0
Pseudoterschellingia	0.0	0.0
Pseudotheristus	0.0	0.0
Pterygonema	0.0	0.0



Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Genus	SaldanhaBay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	ItalianH	StMartinFlats	SwartkopsEst	GamtoosEst
Ptycholaimellus	0.0	0.2	1.6	0.0	2.0	2.3	3.2	0.0	0.0	0.0
Quadricoma	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Retrotheristus	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhabditis	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	6.4
Rhabdocoma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
Rhabdodemania	0.0	0.2	0.0	0.0	0.0	0.3	0.0	0.0	0.2	0.0
Rhips	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Rhynchonema	0.3	0.0	0.0	0.0	0.0	0.7	0.0	2.2	0.0	0.8
Richtersia	0.0	4.5	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
Sabatieria	27.5	13.3	12.7	2.9	37.5	4.3	5.6	1.5	3.8	0.2
Scaptrella	0.9	0.0	0.0	0.0	0.0	0.4	0.0	0.0	1.7	0.6
Setoplectus	0.2	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Setosabatieria	0.9	0.0	0.8	0.4	0.0	1.7	0.5	0.0	0.0	0.0
Sigmophoranema	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Siphonolaimus	0.6	0.0	0.0	0.0	0.7	0.6	0.5	0.8	0.0	0.0
Southernia	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Southerniella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sphaerolaimus	0.0	0.0	2.2	0.2	0.1	0.4	0.2	0.0	1.7	0.0
Spiliphera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spilophorella	0.0	0.0	0.3	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Spirinia	0.3	13.5	0.0	2.8	0.0	0.1	0.2	2.2	0.3	0.0
Steineria	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Steineridora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stephanolaimus	0.7	0.4	0.0	0.0	1.0	0.1	0.0	0.1	0.0	0.0
Stylotheristus	0.7	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0
Subsphaerolaimus	0.0	0.0	0.0	0.0	0.2	0.1	0.0	0.0	0.0	0.0
Symplocostoma	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Synodontium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Synonchiella	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0
Synonchium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.5

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists.

Genus	ClydeEst	ItalyMPAs	CelticSea	NWIrishSea	Indiamangroves	MurrayHeadEst	Baltic Sea	NorthSea	Gulf Main	Mexico
Ptycholaimellus	0.0	0.0	0.0	0.0	4.9	0.0	0.0	0.2	0.0	0.0
Quadricoma	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.9	0.0
Retrotheristus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhabditis	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Rhabdocoma	1.0	0.0	0.4	0.6	0.0	0.0	0.0	0.1	0.0	0.0
Rhabdodemania	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0
Rhips	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Rhynchonema	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Richtersia	0.4	0.0	4.8	1.9	0.0	0.0	0.0	0.0	7.2	0.0
Sabatieria	1.5	0.3	16.4	23.2	0.7	0.0	0.0	0.4	12.9	3.8
Scaptrella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Setoplectus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Setosabatieria	0.0	0.0	0.6	0.4	0.0	0.0	0.0	0.0	12.7	0.0
Sigmophoranema	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Siphonolaimus	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.9	0.0
Southernia	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Southerniella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Sphaerolaimus	0.0	0.0	1.8	1.9	3.5	0.3	0.0	0.1	0.7	0.0
Spiliphera	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spilophorella	0.3	1.3	0.4	0.0	0.0	0.0	0.0	0.0	0.0	3.3
Spirinia	0.2	0.7	0.0	0.6	0.7	0.0	0.0	3.5	0.0	0.0
Steineria	0.0	0.0	0.0	0.0	3.9	0.0	0.0	0.0	0.4	0.0
Steineridora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stephanolaimus	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Stylotheristus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Subsphaerolaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6
Symplocostoma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Synodontium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Synonchiella	0.0	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Synonchium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 5.2 (continued)

Genus	NorthBaltic	Manfredonia
Ptycholaimellus	0.0	0.0
Quadricoma	0.0	0.0
Retrotheristus	0.0	0.0
Rhabditis	0.0	0.0
Rhabdocoma	0.0	0.0
Rhabdodemania	0.0	0.0
Rhips	0.0	0.0
Rhynchonema	0.0	0.0
Richtersia	0.0	0.4
Sabatieria	0.0	14.9
Scaptrella	0.0	0.0
Setoplectus	0.0	0.0
Setosabatieria	0.0	7.7
Sigmophoranema	0.0	0.1
Siphonolaimus	0.0	0.0
Southernia	0.0	0.0
Southerniella	0.0	0.0
Sphaerolaimus	0.1	5.6
Spiliphera	0.0	0.0
Spilophorella	0.0	0.0
Spirinia	0.0	0.0
Steineria	0.0	0.0
Steineridora	0.0	0.0
Stephanolaimus	0.0	0.0
Stylotheristus	0.0	0.0
Subsphaerolaimus	0.0	0.1
Symplocostoma	0.0	0.0
Synodontium	0.0	0.0
Synonchiella	0.0	0.3
Synonchium	0.0	0.1

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Genus	SaldanhaBay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	ItalianH	StMartinFlats	SwartkopsEst	GamtoosEst
Synonchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Synonema	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Syringolaimus	0.2	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tarvaia	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0
Terschellingia	4.2	11.2	13.4	36.9	4.3	1.7	9.8	0.0	3.6	2.7
Thalassironus	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0
Thalassoalaimus	0.2	0.0	0.2	0.2	0.0	0.0	0.3	0.0	0.0	0.0
Thalassomonhystera	2.3	0.0	0.0	0.0	0.4	1.0	0.0	0.5	0.0	0.0
Theristus	1.8	0.4	0.0	0.0	0.0	0.3	0.2	2.8	4.9	14.2
Tobrilus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trefusia	0.0	0.0	0.0	0.0	0.6	0.2	0.0	0.0	0.0	0.0
Trichotheristus	0.1	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
Tricoma	0.2	0.9	0.0	0.0	0.0	0.0	0.4	0.1	0.0	0.0
Trileptium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tripyla	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tripyloides	0.2	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Trissonchulus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trochamus	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tubolaimoides	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Valvaelaimus	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vasostoma	0.0	0.0	0.0	0.7	0.7	0.3	0.0	0.0	0.0	0.0
Viscosia	0.9	0.2	0.6	1.0	0.3	0.4	1.6	0.5	13.9	19.4
Wieseria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Xyala	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.6

Appendix 5.2 (continued): Global genus composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Genus	ClydeEst	ItalyMPAs	CelticSea	NWIrishSea	Indiamangroves	MurrayHeadEst	Baltic Sea	NorthSea	GulfMaine	Mexico
Synonchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Synonema	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Syringolaimus	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	1.3
Tarvaia	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Terschellingia	0.2	0.7	5.4	1.4	7.8	7.3	0.0	0.0	1.7	0.0
Thalassironus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8
Thalassoalaimus	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Thalassomonhystera	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.4	0.0
Theristus	9.5	5.0	0.0	0.0	1.9	7.4	0.4	0.3	0.3	12.8
Tobrilus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trefusia	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.3	0.0
Trichotheristus	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0
Tricoma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	0.0
Trileptium	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tripyla	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0
Tripyloides	0.0	0.0	0.0	1.4	0.6	0.5	1.4	0.3	0.0	0.0
Trissonchulus	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0
Trochamus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tubolaimoides	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0
Valvaelaimus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vasostoma	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Viscosia	1.7	5.0	0.7	0.9	1.7	0.5	0.0	36.0	0.6	5.8
Wieseria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Xyala	1.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6

Appendix 5.2 (continued)

Genus	NorthBaltic	Manfredonia
Synonchus	0.0	0.0
Synonema	0.0	0.0
Syringolaimus	0.0	0.0
Tarvaia	0.0	0.0
Terschellingia	0.0	13.9
Thalassironus	0.0	0.0
Thalassoalaimus	0.0	0.0
Thalassomonhystera	0.0	0.0
Theristus	1.8	2.6
Tobrilus	1.3	0.0
Trefusia	0.0	0.0
Trichotheristus	0.0	0.0
Tricoma	0.0	0.0
Trileptium	0.0	0.0
Tripyla	4.7	0.0
Tripyloides	0.1	0.0
Trissonchulus	0.0	0.0
Trochamus	0.0	0.0
Tubolaimoides	0.0	0.0
Valvaelaimus	0.0	0.0
Vasostoma	0.0	1.4
Viscosia	0.0	0.6
Wieseria	0.0	0.0
Xyala	0.0	0.0

Appendix 5.3: Global family composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Families	Saldanha Bay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	Italian harb	StmartinsFlats	SwartkopsEst	GamtoosEst
Aegialoalaimidae	1.5	0.3	1.3	0.1	0.1	0.4	0.0	0.1	1.0	0.7
Alaimidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anoplostomatidae	0.0	0.0	0.1	0.0	0.0	0.3	0.3	0.0	0.8	1.6
Anticomidae	0.0	0.0	0.0	0.0	0.2	0.0	2.3	0.1	0.0	0.0
Aponchidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Axonolaimidae	1.2	0.1	5.9	1.2	1.7	4.4	2.8	2.0	8.5	7.4
Ceramonematidae	2.6	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Chromadoridae	4.0	2.0	18.6	0.4	11.1	16.4	12.3	8.5	4.5	3.5
Comesomatidae	28.3	16.4	14.9	23.9	40.6	6.3	13.8	1.7	9.1	3.3
Coninckiidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyatholaimidae	3.7	4.9	0.7	5.4	1.3	3.6	14.6	2.5	3.8	5.9
Desmodoridae	8.0	33.6	24.6	5.4	21.0	19.4	5.8	38.1	2.8	1.0
Desmoscolecidae	0.4	1.2	0.0	0.0	0.0	0.0	0.9	0.1	0.0	0.0
Diplopeltidae	0.5	0.3	0.0	0.0	0.3	0.2	0.3	0.0	0.0	0.0
Dorylaimidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Draconematidae	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Enchelidiidae	0.6	4.9	1.5	0.0	0.4	0.4	0.1	0.0	1.5	0.2
Enoplidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epsilonematidae	0.2	0.0	0.0	0.0	0.0	0.0	0.0	25.4	0.0	0.0
Ethmolaimidae	0.3	0.0	0.0	0.1	0.2	0.2	0.5	0.0	2.5	0.2
Haliplectidae	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	2.4
Ironidae	0.0	0.0	0.6	0.0	1.4	0.0	0.0	0.0	0.0	0.0
Lauratonematidae	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leptolaimidae	3.9	0.3	0.1	0.0	0.6	1.8	0.5	3.4	0.0	0.0

Appendix 5.3 (continued)

Families	NorthBaltic	Manfredonia
Aegialoalaimidae	0.0	0.0
Alaimidae	0.0	0.0
Anoplostomatidae	0.0	0.0
Anticomidae	0.0	0.1
Aponchidae	0.0	0.0
Axonolaimidae	20.9	0.1
Ceramonematidae	0.0	0.0
Chromadoridae	27.1	3.0
Comesomatidae	0.0	4.2
Coninckiidae	0.0	0.0
Cyatholaimidae	11.2	1.9
Desmodoridae	0.0	0.7
Desmoscolecidae	0.0	0.3
Diplopeltidae	0.0	0.1
Dorylaimidae	0.0	0.0
Draconematidae	0.0	0.0
Enchelidiidae	0.0	0.0
Enoplidae	0.0	0.0
Epsilonematidae	0.0	0.0
Ethmolaimidae	0.6	0.4
Haliplectidae	0.0	0.0
Ironidae	5.4	0.0
Lauratonematidae	0.0	0.0
Leptolaimidae	4.3	0.0

Appendix 5.3 (continued): Global family composition (%) for 22 selected sites.

Families	Saldanha Bay	BermudaH	BrouageMud	Cienfuegos	MahurangiBay	MartinBay	Italian harb
Leptsomatidae	0.1	3.1	0.0	0.0	0.1	0.0	0.0
Linhomoeidae	14.0	12.3	18.9	42.8	4.9	7.3	13.9
Microlaimidae	8.2	3.2	0.0	8.6	3.8	1.8	0.1
Monhysteridae	2.3	0.0	0.0	0.0	3.0	1.3	0.0
Mononchidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Monoposthiidae	0.0	0.4	0.0	0.0	0.0	1.0	0.0
Neotonchidae	0.3	4.9	0.0	0.2	0.0	9.2	1.8
Oncholaimidae	1.0	0.2	0.6	1.0	0.3	0.6	4.0
Oxystominidae	3.4	0.5	1.0	0.3	0.3	0.3	1.4
Pandolaimidae	0.1	0.0	0.0	0.0	0.7	0.0	0.0
Paramicrolaimidae	1.6	0.0	0.0	0.0	0.0	0.0	0.0
Peresianidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plectidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phanodermatidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhabditidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhabdodemaniidae	0.0	0.2	0.0	0.0	0.0	0.3	0.0
Selachnematidae	0.2	5.1	0.1	1.5	1.0	0.1	0.5
Siphonolaimidae	0.6	0.0	0.0	0.0	0.1	0.6	0.0
Sphaerolaimidae	0.2	0.0	2.2	0.0	0.1	0.5	0.2
Tarvaiidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thoracostomopsidae	0.1	0.0	0.0	0.0	0.1	0.5	0.2
Tripylidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trefusiidae	0.0	0.0	0.0	0.0	0.6	0.3	0.0
Tripyloididae	0.0	0.0	1.5	0.0	0.0	0.2	0.8
Tubolaimoididae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tylenchidae	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Xyalidae	12.1	5.8	7.6	9.0	5.8	22.6	22.7

Appendix 5.3 (continued): Global family composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Families	StmartinsFlats	SwartkopsEst	GamtoosEst	ClydeEst	ItalyMPAs	CelticSea	NWIrishSea
Leptsomatidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Linhomoeidae	0.4	10.6	3.9	0.1	1.0	14.2	9.0
Microlaimidae	4.7	1.9	1.9	4.2	1.7	4.7	5.0
Monhysteridae	0.0	21.1	3.4	3.5	0.0	0.0	0.0
Mononchidae	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Monoposthiidae	0.2	0.0	0.0	2.0	0.7	0.0	0.0
Neotonchidae	0.0	0.0	0.0	0.9	0.0	1.4	1.5
Oncholaimidae	0.5	16.4	22.2	1.8	5.0	0.7	1.7
Oxystominidae	0.7	0.4	1.2	1.0	1.3	4.1	1.6
Pandolaimidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paramicrolaimidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Peresianidae	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Plectidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phanodermatidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhabditidae	0.0	0.0	6.4	0.0	0.0	0.0	0.0
Rhabdodemaniidae	0.0	0.0	0.0	0.6	0.0	0.0	0.0
Selachnematidae	0.1	0.4	3.9	0.4	1.0	5.7	1.9
Siphonolaimidae	0.8	0.0	0.0	2.2	0.0	0.0	0.0
Sphaerolaimidae	0.0	4.8	0.0	0.0	0.0	3.7	2.1
Tarvaiidae	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Thoracostomopsidae	1.3	0.1	0.0	1.4	16.0	0.8	0.7
Tripylidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trefusiidae	0.0	0.0	0.0	0.1	0.0	0.4	0.6
Tripyloididae	0.0	0.0	0.2	0.1	0.3	0.0	1.0
Tubolaimoididae	0.0	0.0	0.0	2.0	0.0	0.0	0.0
Tylenchidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Xyalidae	8.2	9.9	30.7	19.3	28.3	9.2	15.3

Appendix 5.3 (continued): Global family composition (%) for 22 selected sites reporting full genus lists. Authors are listed in Table 5.11.

Families	IndiaMangroves	Murrayhead	BalticSea	NorthSea	GulfMaine	Mexico	NorthBaltic	Manfredonia
Leptsomatidae	0.2	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Linhomoeidae	10.0	8.8	0.9	0.0	9.5	0.6	1.0	7.2
Microlaimidae	0.0	0.0	0.5	3.1	5.1	0.0	3.3	0.0
Monhysteridae	0.2	5.0	0.1	0.0	0.4	0.0	0.3	0.6
Mononchidae	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0
Monoposthiidae	0.0	0.0	0.2	9.0	0.0	0.0	0.0	0.0
Neotonchidae	0.5	0.0	0.0	0.1	1.0	0.0	0.0	0.6
Oncholaimidae	15.0	2.4	3.5	40.4	1.0	5.8	17.0	15.8
Oxystominidae	0.0	0.0	0.0	0.7	1.2	0.0	0.0	29.0
Pandolaimidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paramicrolaimidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Peresianidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plectidae	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Phanodermatidae	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0
Rhabditidae	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0
Rhabdodemaniidae	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0
Selachnematidae	5.0	0.0	0.1	0.3	7.2	3.2	0.0	14.5
Siphonolaimidae	0.0	0.0	0.0	0.4	1.9	0.0	0.0	0.1
Sphaerolaimidae	3.5	0.3	0.0	0.1	1.0	0.6	0.1	1.6
Tarvaiidae	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
Thoracostomopsidae	0.0	0.2	15.5	0.7	0.6	12.8	1.3	0.0
Tripylidae	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0
Trefusiidae	0.0	0.8	0.0	0.1	0.5	0.0	0.0	0.0
Tripyloididae	0.6	0.5	2.4	6.3	0.0	0.0	4.8	0.0
Tubolaimoididae	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Tylenchidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Xyalidae	21.1	9.1	22.3	4.4	10.5	15.4	2.7	19.8

Appendix 6.1: Two new nematode species from Saldanha Bay, South Africa: *Perepsilonema benguelae* sp. nov. and *Leptepsilonema saldanhae* sp. nov. (Desmodorida, Epsilonematidae).

Pre-publication version of the published article: Hendricks, M. G. J. & Gibbons, M. J., 2010. Two new nematode species from Saldanha Bay, South Africa: *Perepsilonema benguelae* sp. nov. and *Leptepsilonema saldanhae* sp. nov. (Desmodorida, Epsilonematidae). *Zootaxa* **2504**: 20-30.

Abstract

Perepsilonema benguelae sp. nov. and *Leptepsilonema saldanhae* sp. nov. are described and illustrated from coarse sand sediments in Saldanha Bay, along the west coast of South Africa. *Perepsilonema benguelae* sp. nov. is characterised by a large swollen body in the genital region, the annuli are not clearly orientated into anteriorly and posteriorly directed margins and copulatory thorns are restricted to three pairs in the precloacal region. In *Leptepsilonema saldanhae* sp. nov. the somatic setae in the oesophageal region are very long and the first ambulatory setae of the external subventral row are short. Other distinguishing features include the shape of the amphidial fovea and the copulatory apparatus, and the presence of six ventro-lateral copulatory thorns, around the cloaca. These descriptions are the first for the family Epsilonematidae from the west coast of South Africa.

Keywords: Description, morphology, Africa, Benguela Current, marine, Nematoda, taxonomy

Introduction

Although a substantial body of work has been conducted on the ecology of sandy shores around South Africa (see e.g. Brown & McLachlan 1990), our understanding of the diversity of meiofauna, especially nematodes, is extremely limited. Inglis (1963, 1964) described a collection of nematodes from muddy environments along the west coast of South Africa, including 26 new species, and Coles (1977) described a further nine species from Saldanha Bay. This study reports on two new species of marine nematodes collected from soft sediments in Saldanha Bay.

Both species described here belong to the family Epsilonematidae, first established by Steiner (1927) and revised by Lorenzen (1973). The family currently comprises 13 genera and 96 species (Neira et al 2005), distributed across the globe in shallow and deep waters. Both species are in the subfamily Epsilonematinae, which are typically associated with coarse sediments (Vanreusel & Vincx 1986).

The genus *Perepsilonema* was erected by Lorenzen (1973) who described *Perepsilonema papulosum* on the basis of the distinguishing features of the genus. *Perepsilonema* is characterised by four subcephalic setae, one pair of setae close to the amphids, the absence of dorsal thorns posterior to the cephalic capsule and the absence of ambulatory setae (Verschelde & Vincx 1993). Thirteen species are recognized (Gourbault & Decraemer 1996):

Type species:

Perepsilonema papulosum Lorenzen, 1973 [Clasing, 1984]

Other species:

Perepsilonema bahiae (Gerlach, 1957) Lorenzen, 1973 syn. *Bathepsilonema bahiae* Gerlach, 1957

P. crassum Lorenzen, 1973

P. trauci Lorenzen, 1973

P. conifer Lorenzen, 1973 *syn. P. conifer lissum* (Lorenzen, 1973) op. Gourbault & Decraemer 1988

P. corsicum Vanreusel & Vincx, 1986

P. mediterraneum Vanreusel & Vincx, 1986

P. longispiculosum Vanreusel & Vincx, 1986

P. coomansi Vanreusel & Vincx, 1986

P. tubuligerum Gourbault & Decraemer 1988

P. kellyae Gourbault & Decraemer, 1988 [Verschelde & Vincx 1994]

P. moineaui Gourbault & Decraemer, 1992

P. ritae Verschelde & Vincx, 1994

The genus *Leptepsilonema* is characterised by eight subcephalic setae, body lacks dorsal thorns posterior to the cephalic capsule, five rows of ambulatory setae positioned anterior to the vulva and six of the eight subcephalic setae are anterior to amphidial fovea (Clasing, 1983). Ten species recognised (Decraemer & Gourbault, 2000).

Type species:

Leptepsilonema procerum Clasing, 1983

Other species:

L. macrum Clasing, 1983

L. exile Clasing, 1983

L. parafiliforme Gourbault & Decraemer 1987

L. filiforme Clasing, 1984 [Gourbault & Decraemer, 1987, 1995]

L. santii Gourbault & Decraemer, 1995

L. richardi Verschelde & Vincx 1992

L. antonioi Decraemer & Gourbault, 2000

L. dauvini Decraemer & Gourbault, 2000

L. horridum Decraemer & Gourbault, 2000

Materials and methods

Samples were collected at a depth of 20 m in Saldanha Bay (33° S, 18° E) from a sediment of sand and coarse gravel (gravel> 35%; sand >35%), using hand-held corers (10 cm^2 surface area). Nematodes were extracted from the upper 10 cm. Nematodes were separated by elutriation and washing techniques and mounted in anhydrous glycerine on microscope slides (as Warwick *et al.* 1998). Drawings were made using an Olympus-BH2 compound microscope with Nomarski Differential Interference Contrast Illumination and a camera lucida. Morphometric nomenclature (Table 1) used in this manuscript follows Gourbault and Decraemer (1988; 1994). Holotype male and one paratype female of each species are deposited in the nematode collection of the Department of Zoology, Natural History Museum (NHM), London, while other paratypes are deposited at Iziko South African Museum, Cape Town.

TABLE 1. Abbreviations for morphometric analyses, following according to Gourbault & Decraemer (1988, 1994). Measurements in µm.

abd	body diameter at level of anus
amph (%)	diameter of amphid as a percentage of the corresponding head diameter
A sl	length of anteriormost ambulatory seta of external subventral row
cs	length of cephalic setae
gub	length of gubernaculum
hl	length of head
hw	maximum head width
L	body length
mbd	maximum body diameter posterior body region
(mbd)	minimum body diameter
mbd ph	maximum body diameter in pharyngeal region
mbd/(mbd)	maximum body diameter related to minimum body diameter
N	number of body rings
ph	length of pharynx
spic	length of spicules measured along the median line

SS	length of anteriormost supporting seta
SSph	length of subdorsal somatic seta in pharyngeal region
subc s	length of subcephalic seta
t	length of tail
tmr	length of non-annulated tail region
tmr/t	non-annulated tail region related to tail length
V	position of vulva as a percentage of body length from the anterior
v	distance of vulva from anterior end
a	body length divided by maximum body diameter
b	body length divided by pharynx length
c	body length divided by tail lenghth
c′	tail length related to body width at anus or cloaca.

Description of taxon

Genus *Perepsilonema* Lorenzen, 1973

Perepsilonema benguelae **sp. nov.**

(Figs 1, 2)

Measurements Table 2.

TABLE 2. Morphometric measurements (µm)(mean, standard deviation, range) of *Perepsilonema benguelae* **sp. nov.** from Saldanha Bay. See Table 1 for abbreviations.

	Holotype Male	Females (n = 6)		
	NHM 2008:860	Mean	SD	Range
L	350.8	321	26.5	266-334
N	118	124	7	112-131
amph	3	3	0.63	-
%	37.5	29	5	-
ph	56	56.4	2.9	52.-58.7
mbd ph	32.9	30	2.9	27.7-35.5
mbd	39.4	39	3	33.6-41.9
(mbd)	13.6	15	2.2	12.3-18.7
abd	15.5	16	1.5	14.8-18.7
t	20.7	27.4	1.8	29.03-25.2
tmr	9.7	11	1.9	8.4-14.2
spic	48.4	-	-	-

gub	7	-	-	-
a	8.9	8.0	0.2	-
b	6.3	5.5	0.3	-
c	17	11.4	0.9	-
c'	1.3	1.7	0.2	-
V	-	68		-
mbd/(mbd)	2.9	2.6	0.5	3.3-2.2

Material examined. Holotype male: SOUTH AFRICA, Saldanha Bay, -33.04800°, 17.98350°, coarse sand in shipping channel, sublittoral (20 m), August 1999 by Hendricks (SCUBA-assisted handheld corers), NHM accession No. 2008:860. (Figs 1A, 1C, 2A). Paratype: six females. NHM accession No. 2008:861 (Figs 1B, 1D, 2B), Iziko South African Museum accession No. SAM A29471.

Description. Male. Total body length 352 µm. Body ε-shaped (Fig. 1A), swollen in cloacal, testis and pharyngeal regions. Cephalic capsule tapering anteriorly, truncated posteriorly; tail short, conical. Body with 118 pronounced annulations (Table 2), not clearly orientated either anteriorly or posteriorly, with prominent box-like vacuoles in swollen portions of body. External layer of cuticle thickened ventrally in testis region, with fine longitudinal markings. Somatic setae (10.3 µm) regularly spaced in six rows, anterior to the first curvature. Tail short; one ventrally directed seta (2.6 µm) on non-annulated section and two short setae (2 µm) on the last two annulated segments. Three pairs of small, conical, pre-cloacal thorns present.

Cephalic capsule conical, 14 µm wide at the broader base and 9 µm long (Fig. 2A). Labial papillae could not be detected because lip region is retracted in specimen observed. Four cephalic setae of equal length (5 µm), not at same level; dorso-lateral pair more anterior to ventro-lateral pair. Eight subcephalic setae on cephalic capsule; one pair present at base of amphidial fovea, longer (6.5 µm) than others (3 µm).

Amphidial fovea at base of cephalic capsule, extending to c. 38% of corresponding body diameter, comprising a dorso-ventrally wound loop; canalis situated in centre of spiral fovea. Buccal cavity indistinct, with small tooth; pharynx muscular, 56 µm in length with cuticularised lumen and prominent terminal bulb. Cardia 2.6 µm long, opening into bulbous intestine.

Single outstretched testis ventral to alimentary canal, extending posterior to the narrow middle section of the body (Fig. 1C); vas deferens well defined. Spicules 48 µm long, curved with well-developed "hammer-like" capitulum; velum not observed. Gubernaculum short (7 µm), parallel to spicules. Two ventral rows of small thorn-like structures present on 7th, 8th and 9th annuli anterior to cloacal opening. Prominent laterally placed somatic setae (6 µm) present on 2nd (not shown in Fig. 1C) and 6th annuli anterior to cloaca.

Female. Females (Fig. 1B) broadly similar to male in general form, shorter (Table 2). Body wide at cloaca, ovary and pharyngeal region. Number and ornamentation of annuli similar to males, but change in orientation pronounced at 88th annulation in the region of the vulva. Cephalic capsule narrower than male, 12 µm wide, 9.5 µm long (Fig. 2B), with amphidial fovea at base. Amphidial fovea, sexually dimorphic, single coil with canalis situated in centre of spiral fovea; extending to c. 29% of corresponding body diameter. Buccal cavity small, one specimen with a minute tooth; pharynx muscular, 56.4 (± 3 µm) in length with prominent terminal bulb.

Reproductive system didelphic, amphidelphic; reflexed ovaries with tips bent to opposite sides of the intestine (anterior ovary to the right, posterior to the left). Ovarian system ventral to alimentary canal (Fig. 1D). Uterine chamber medially situated, containing a number of sperm cells. Vagina sclerotinized along entire length, terminating at uterus, surrounded by constrictor muscle.

Locality and habitat. Holotype and six paratypes from course grained sediments in Saldanha Bay, at a depth of 20 m.

Diagnosis. *Perepsilonema benguelae* **sp. nov.** is a medium sized nematode with short spicules and gubernaculum; eight subcephalic setae; annulations not clearly orientated either anteriorly or posteriorly in the male; annulations with boxlike vacuoles; tail short, c = 17; copulatory thorns absent from mid-body region at level of testis; three pairs of copulatory thorns in precloacal region.

Etymology. The species is named after the Benguela Current, flowing along the west coast of southern Africa.

General remarks. A revised taxonomic key to males of the species of the genus is provided: modified from Gourbault and Decraemer (1988).

1 - Six subcephalic setae,..... 2
Eight subcephalic setae..... 3

2 - Male with two fields of poorly developed copulatory thorn-like structures, one in ventral fold, second at level of testis; a few small spines in cloacal region; spicule = 68-77 µm..... *P. tubuligerum*
Male with two fields of well-developed copulatory thorn-like structures, one at level of testis, second as precloacal thorns; spicule = 31-32 µm ..... *P. conifer*

3 - Six subcephalic setae present on cephalic capsule anterior to amphid; two setae at base of amphid inserted on first annulus..... 4
Eight subcephalic setae anterior to amphid, ... 7

4 - Copulatory thorns absent..... 5
Copulatory thorns present at level of testis or in cloacal region..... 6

5 – Annulations with numerous small vacuoles..... *P. papulosum*
Annulations with minute vacuoles with additional dorso-longitudinal striations ..... *P. moineaui*

6 - Annulations plain; one pair of large copulatory thorn-like structures plus 4 pairs small copulatory thorns in mid-body region ..... *P. kellyae*
Annulation with regular vacuoles; three pairs of copulatory thorn-like structures in precloacal region..... ..... *P. benguelae*

7 - No copulatory thorn-like structures at the enlargement of the median body ..... *P. bahiae*
Copulatory thorn-like structures at the enlargement of the median body.....8

8 - Two rows of small thorns subdorsally on caudal annulations 9
Two fields of small spines subdorsally on caudal annulations..... 11

9 - Body annulations ornamented with tiny, barely visible vacuoles.... *P. crassum*
Body annulations a single row of with large vacuoles..... 10

10 - Two fields of subventral copulatory thorn-like structures: 5 pairs at level of testis, and 3 pairs in precloacal region..... *P. trauci*
Ventral field of tiny small spines in region between dorsal and ventral body curvature; two pairs large copulatory thorns at level of testis..... *P. ritae*

11 - Single field of three pairs of subventral copulatory thorn-like structures at level of testis; no precloacal thornlike structures..... 12
Two fields of copulatory thorn-like structures at level of testis and in precloacal region..... 13

12 - Copulatory thorn-like structures well developed; spicule = 64 µm
..... *P. longispiculosum*
Copulatory thorn-like structures poorly developed; spicule = 39 µm
..... *P. corsicum*

13 Six to seven pairs of subventral copulatory thorn-like structures in testis region; two pairs copulatory thorns in precloacal region; cephalic capsule as wide as long
..... *P. mediterraneum*
Three pairs of subventral copulatory thorn-like structures in the testis region, followed by subventral pair and a single thorn in ventral region anterior to vas deferens, another two pairs subventrally in precloacal region; cephalic capsule longer than wide
..... *P. coomansi*

Genus *Leptepsilonema* Clasing, 1983

Leptepsilonema saldanhae **sp. nov.**

(Figs 3, 4)

Measurements. Table 3.

Table 3. Morphometric analysis (µm, mean and standard deviations) for *Leptepsilonema saldanhae* **sp. nov.** from Saldanha Bay. (Abbreviations listed in Materials and Methods)

	Holotype (2008:858)	Female (2008:859)	Female(SAMA29472)
L	324.6	339	406
N	119	114	126
amph	4.5	3.2	3.9
%	35	21.7	30
cs	7	9	9
subcs	12.3	13	13
hw	14	13	13.6
hl	14.8	13	14.8
phs	32.4		
ss1	31.6	21.3	23.2
ss2	33.6	13	42.7
ss3	23.9	14.7	23.9
ss4	29	22.6	28.7
A sl 1	5.8	11.6	13.6

ph	74	71	85.8
mbd ph	27	27	27
mbd	24.6	18	24.5
(mbd)	16.4	14.8	20
abd	19.4	14.2	15.5
t	29	31	34
tmr	9	12.3	14.8
spic	27		
gub or v	5.9	259	265.6
a	13	16.6	18.8
b	4.4	4.7	4.8
c	11.2	11	12
c'	1.5	2.2	2.2
V		63.7	78.3
mbd/(mbd)	1.5	1.2	1.2

Material examined. Holotype male: SOUTH AFRICA, Saldanha Bay, -33.04800°; 17.98350°, coarse sand in shipping channel, sublittoral (20 m), August 1999 by Hendricks (SCUBA-assisted handheld corers), NHM accession No. 2008:858. (Figs 3 A-C). Paratype: two females. NHM

accession No. 2008:859. (Figs 4 A-C), Iziko South African Museum accession No. SAM A29472.

Description. Male. Body round in cross-section, 324 µm long, ε -shape having swollen pharyngeal and posterior regions (Fig. 3A), with 114 annulations (Table 3) possessing well-developed hyaline outer layer. Annuli anteriorly directed behind cephalic capsule, change orientation ventrally at annule 13 (anteriorly to posteriorly), annule 24 (posteriorly to anteriorly) and annule 51 (anteriorly to posteriorly); anteriorly directed annuli change orientation dorsally at annule 23. Size and distribution of vacuoles on annuli variable, indistinct in first annule, of irregular size on anterior swelling, small and distributed as longitudinal bands in narrow middle region, and as a single row on tail; absent between ambulatory setae. Somatic setae fine, very long (24-34 µm), arranged particularly in pharyngeal and posterior regions of body. Five longitudinal rows of six to 13 ambulatory setae having hooked tips; first seta on annule 69; left external sub-ventral row with 13 collared ambulatory setae (7.4 µm); left inner sub-ventral row with six setae (6.6 µm); middle row with 7 setae (6.6 µm); right inner sub-ventral row with six setae (8.8 µm); right external sub-ventral row with 13 setae (9.6 µm). Five, thick, ventrally-directed supporting setae occur posterior to the ambulatory setae, arranged as two pairs and a singlet plus a row of three stout lateral supporting setae (3.2 µm) on the same level as external sub-ventral setae.

Cephalic capsule truncated, 14.8µm long, 14.2 µm wide (Fig. 3B), labial region partially extended; with four cephalic setae (7 µm); with six, collared subcephalic setae (14 µm), anterior to the amphids. Amphidial fovea dorso-laterally situated, dorsally looped in an inverted open U-shape, dorsal arm stretching into the first annule, extending to c. 35% maximum corresponding body diameter. Buccal cavity lacking teeth or denticles; oesophagus 74 µm long, terminating in rounded muscular bulb with strongly cuticularized lumen walls. Tail conical, with 8 annuli; three caudal setae present; no setae on non-annulated region; caudal glands not seen.

Single, outstretched testis with large sperm cells opens into short granular vas deferens (Fig. 3C), ventral and partly to left of intestine in thickened posterior region of the body, behind ventral body curve. Spicules paired, arcuate (27 µm long), relatively slender with enlarged proximal ends forming a capitulum. Gubernaculum short, straight, 5.8 µm long. A field of four ventro-lateral copulatory thorns present on annuli surrounding the cloaca, with short supporting setae; two small subventral precloacal thorns.

Female. Females similar to males in habitus (Fig. 4A), 339-406 µm in length. Cuticle with 114 annuli; vacuolar ornamentation generally as males but dorsal spiny projections more pronounced posteriorly. Amphids sexually dimorphic, exhibiting a ventrally wound spiral (Fig. 4B), with 1.5 turns, extending c. 30 % of maximum corresponding body diameter. Reproductive system didelphic, amphidelphic; reflexed ovaries (anterior ovary bent to left side, posterior ovary to right side) ventral to intestine (Fig. 4C). Vagina 12.5 µm long, ending in cuticularized outer part (2 µm long) and larger, weakly cuticularized inner part. Vulva situated ventrally in posterior body half, c. 64-78% of total body length from anterior.

Diagnosis. *Leptepsilonema saldanhae* **sp. nov.** is characterised by the following combination of characters. In the male, the shape of the amphid is a dorsally looped inverted U-shape with dorsal arm overlapping the first body annule, whilst in the female it is smaller, and spiral. The anteriormost ambulatory setae of external subventral row (A sl1) are short in the male, longer in the female. The ambulatory setae are bent, in contrast to the diagnostic key proposed by Verschelde and Vincx (1993). *Leptepsilonema saldanhae* **sp. nov.** has six prominent subcephalic setae anterior to, and two setae posterior, to the amphidial fovea, all embedded in a marked collar. *Leptepsilonema saldanhae* **sp. nov.** can be distinguished by the shape of the copulatory apparatus, by the six ventro-lateral copulatory thorns on both sides of the cloaca and the presence of two small postcloacal thorns and a short supporting seta/spine present at the cloacal opening. The long subdorsal somatic setae in the pharyngeal region are also diagnostic.

Etymology. The species is named after the type locality, Saldanha Bay, on the west coast of South Africa.

General remarks. A revised taxonomic key to the males of the species of the genus is provided: modified from Gourbault and Decraemer (1987).

1 - Spines present behind cephalic capsule, dorsally..... *L. macrum*
Dorsal spines absent..... 2

2 – Short (< 400 µm); spicules < 30 µm..... 3
Large sized body (> 400 µm); spicules > 30 µm..... 6

3 - Amphid similar in males and females 4

Amphid sexually dimorphic..... 5

4 - Amphid as curved arch; annulations with heterogeneous vacuoles, rectangular anteriorly, elongated in mid-body region and large and irregular posteriorly; 2 pairs of small copulatory thorns at posterior region of ambulatory setae; without precloacal thorns..... *L. parafiliforme*

Amphid spiral with flap; annulations with numerous fine vacuoles; field of 5 copulatory thorns at posterior region of ambulatory setae; 5 minute precloacal thorns present ..... *L. dauvini*

5 – Annulations with double row of irregularly shaped vacuoles; anteriormost annulations with a single row of vacuoles; a pair of enormous copulatory thorns at level of ambulatory setae; 3 pairs of small pre-cloacal thorns; without post-cloacal thorns..... *L. filiforme*

Annulations with single row of irregularly shaped vacuoles; vacuoles indistinct in anteriormost annulations; field of 5 copulatory thorns and 3 spines at level of ambulatory setae; 4 subventral thorns flanking cloaca; 2 small subventral precloacal thorns ..... *L. saldanhae*

6 – Copulatory thorns in one field..... 7

Copulatory thorns in two or more fields..... 9

7 - Annulations with one row of vacuoles..... 8

Annulations with more than one row of vacuoles;..... *L. exile*

8 – Annulations with vacuoles of variable size; 2-5 large copulatory spines at level of ambulatory setae..... *L. procerum*

Annulations with large vacuoles; 7-9 copulatory thorns at level of ambulatory setae ..... *L. antonioi*

9 – Copulatory thorns in two fields..... 10

Copulatory thorns in three fields..... *L. santii*

10 – Annulations with small rectangular vacuoles; 4-5 copulatory thorns in 4 rows at level of ambulatory setae comprising first field; 1 precoacal, 2 post-cloacal thorns present in second field ..... *L. richardi*

Annulations with large rectangular vacuoles; 16 - 30 copulatory thorns in 4 rows at level of ambulatory setae comprising first field; 1-2 copulatory thorns posterior to ambulatory setae in second field; without post=cloacal thorns .....*L. horridum*

Acknowledgements

Thanks to Prof. John Lambshead, Natural History Museum, London, for his constant support and encouragement. The authors thank Drs. Natalie Barnes and Tim Ferrero at the Natural History Museum, London, for their support and valuable critique on an earlier draft of the manuscript. The project was funded by the National Research Foundation (R.S.A.) and the Royal Society (London).

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Figure 1. *Perepsilonema benguelae* sp.nov. A. Holotype habitus. B. Paratype habitus.

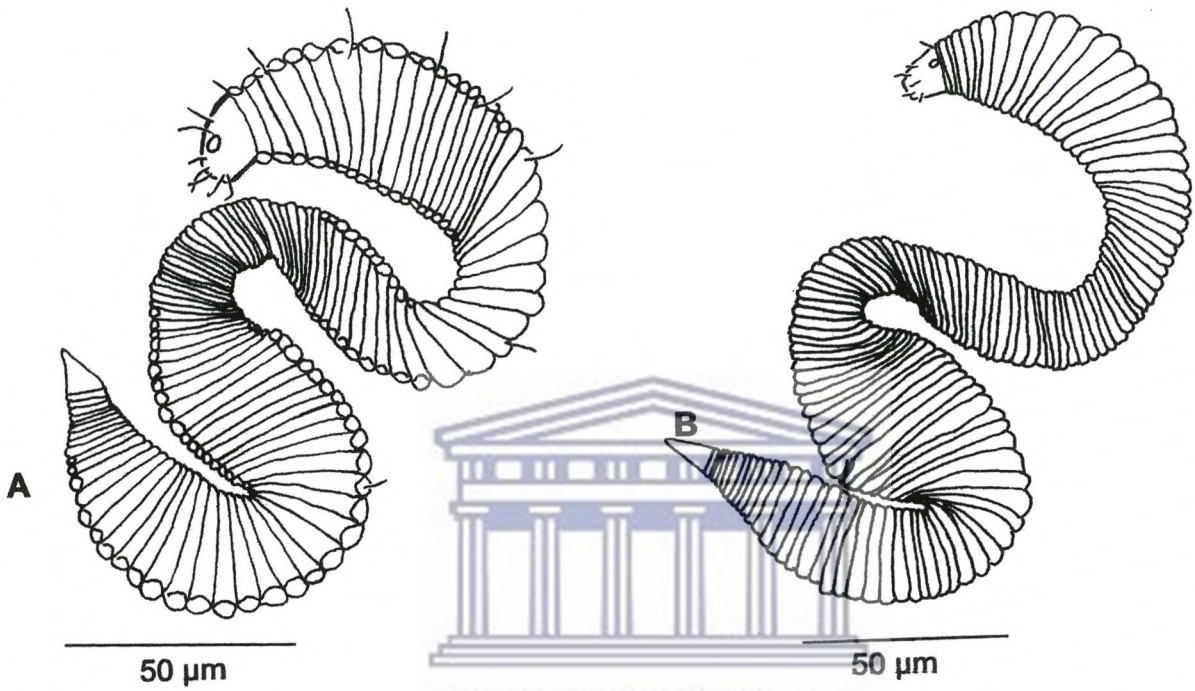


Figure 1. *Perepsilonema benguelae* sp.nov. C. Holotype male. Posterior body region with reproductive system.

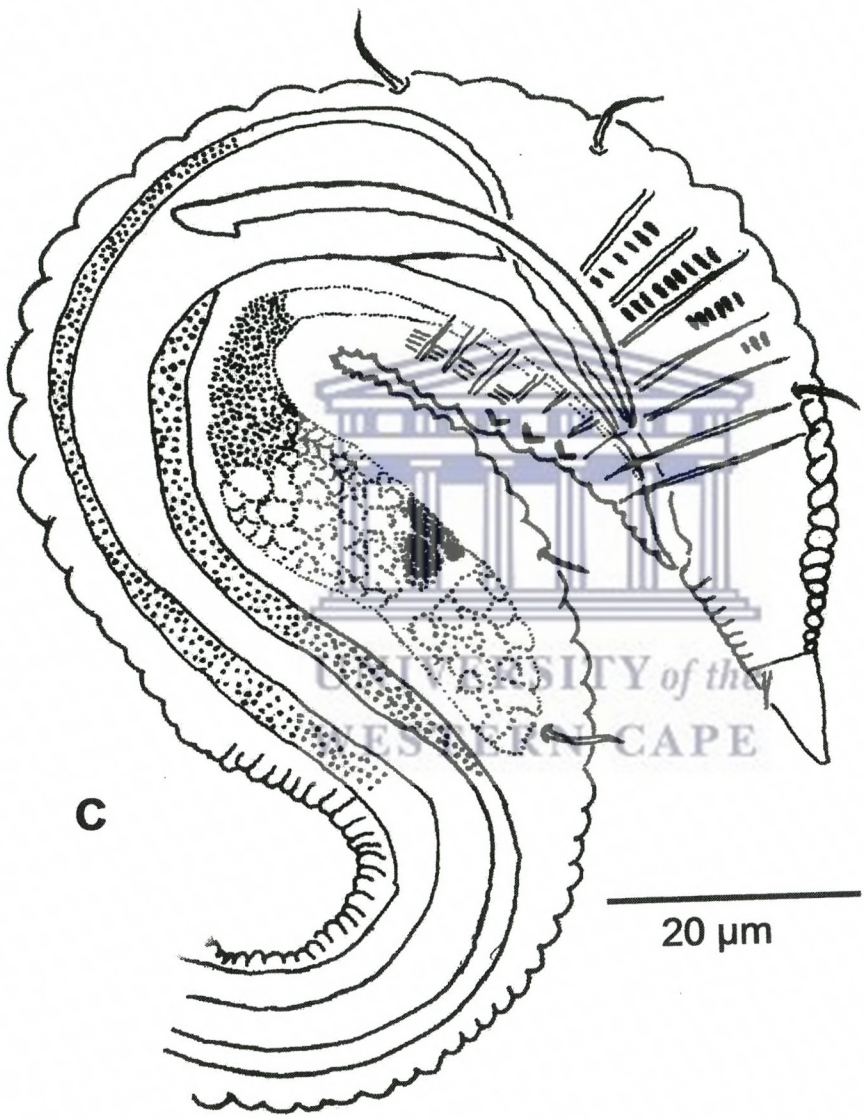
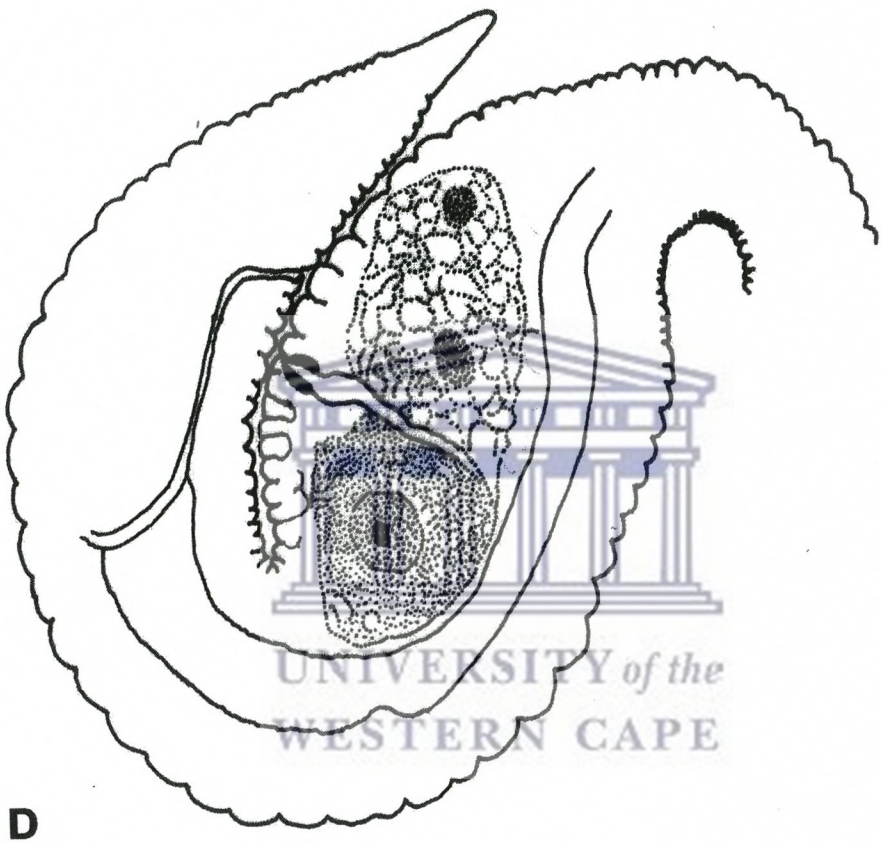


Figure 1. *Perepsilonema benguelae* sp.nov. D. Paratype female. Posterior body region with reproductive system.



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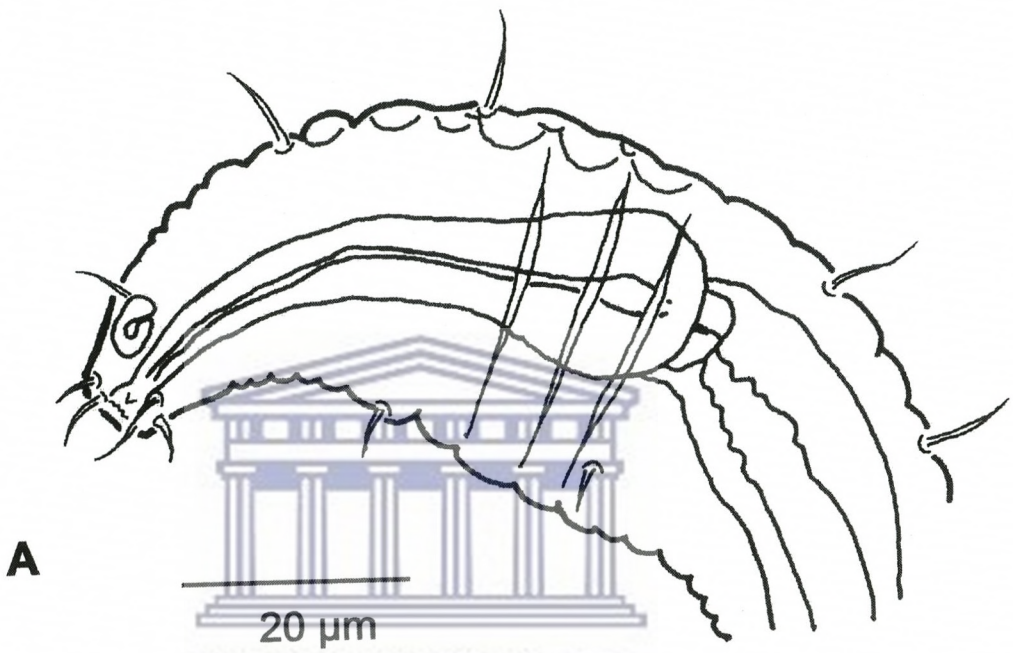

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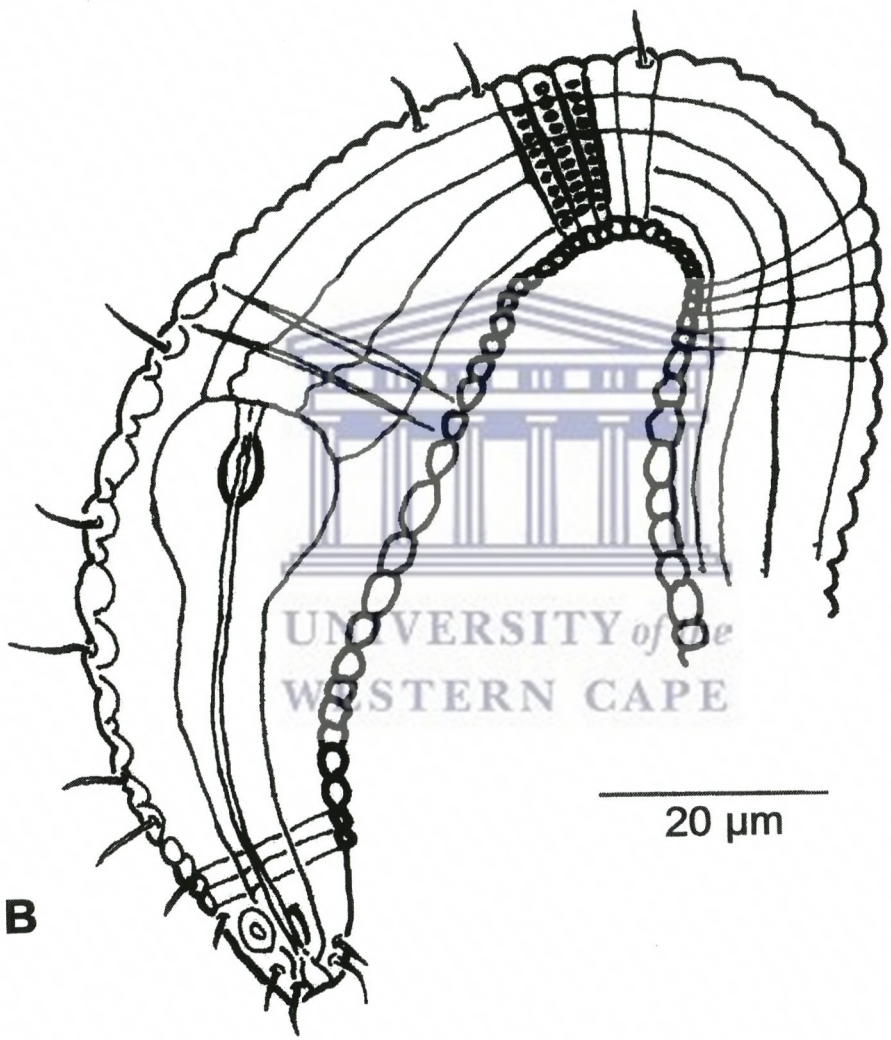

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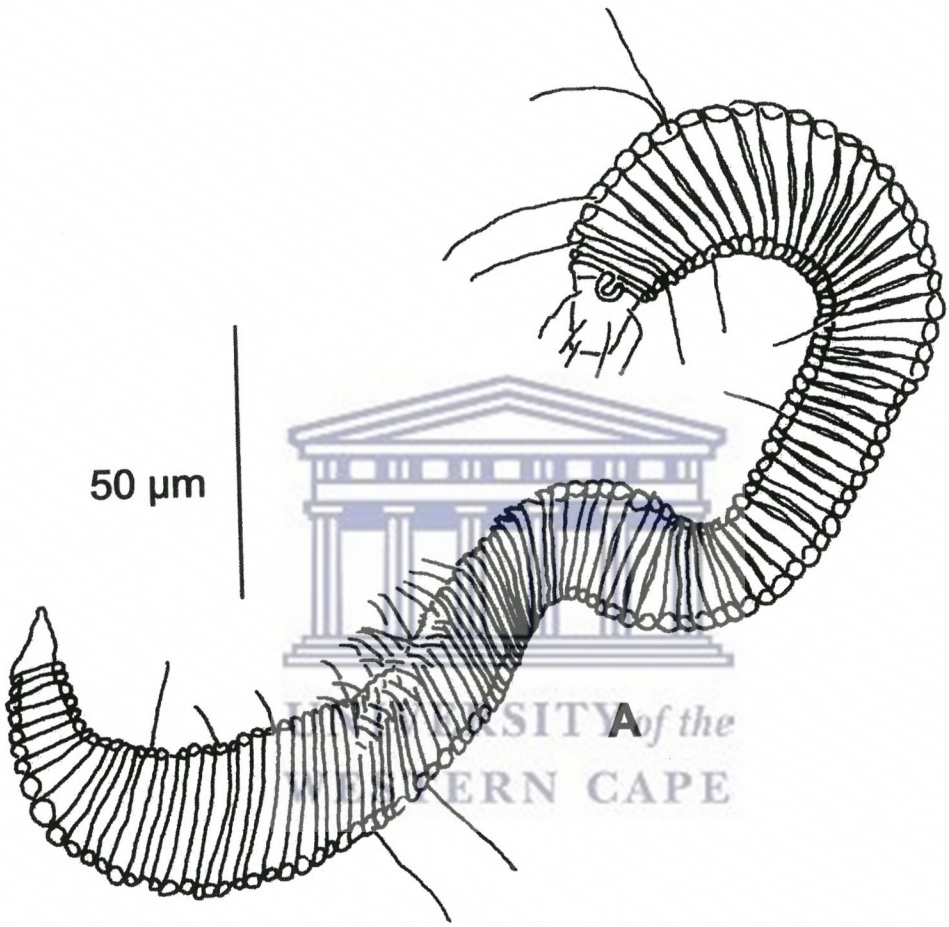

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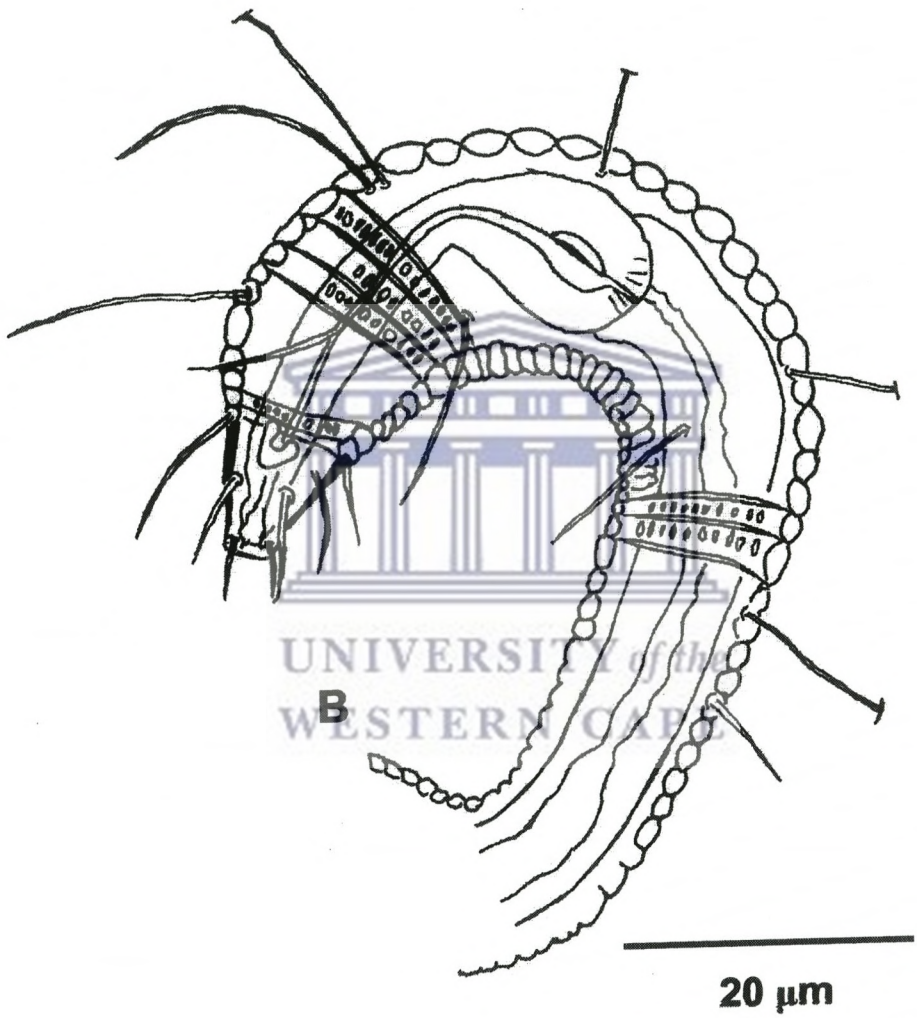


Figure 3. *Leptepsilonema saldanhae* sp.nov. C. Male. Posterior body region with reproductive system.

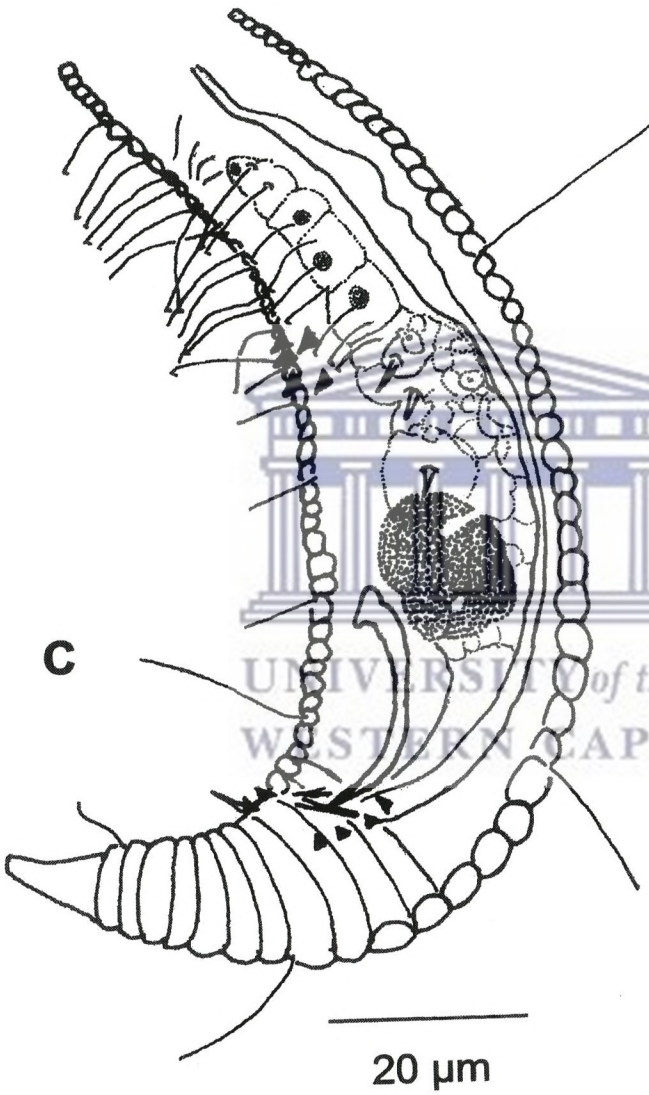
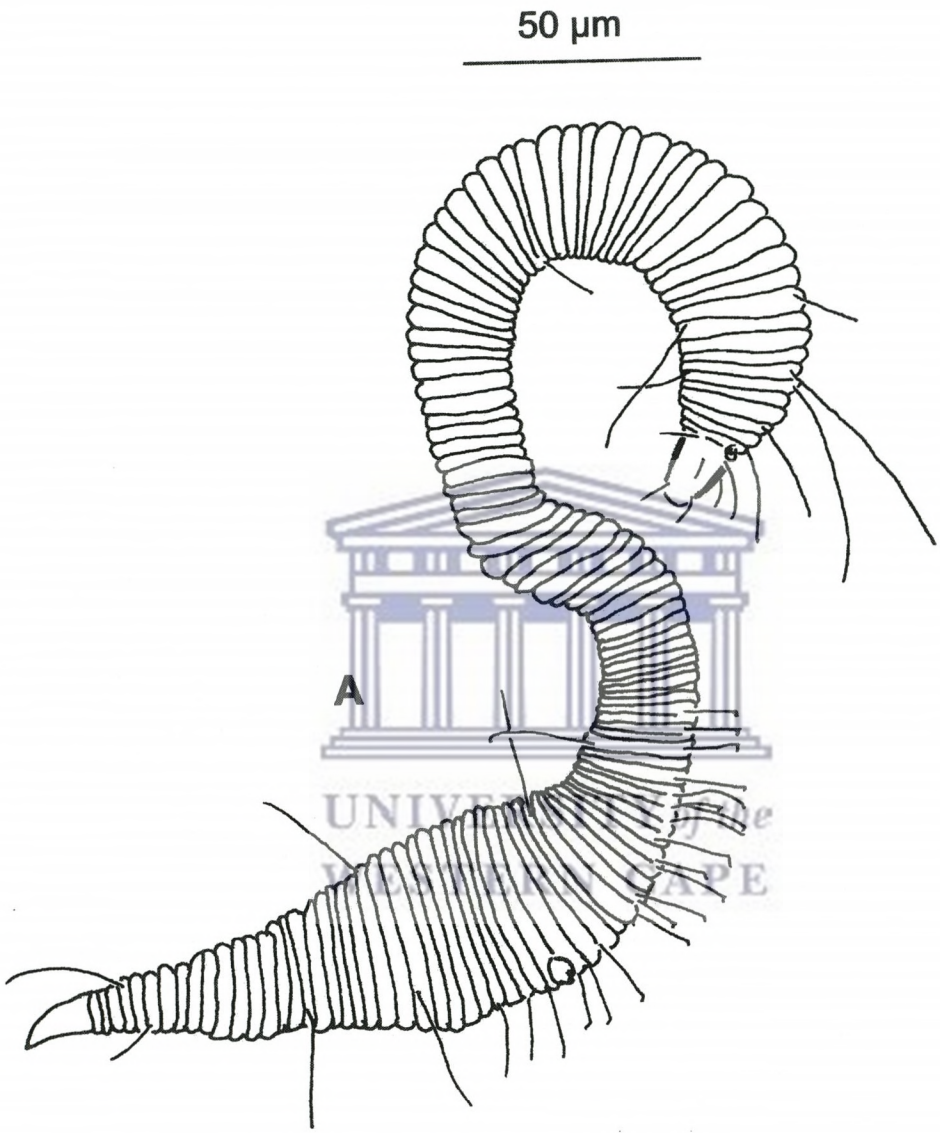


Figure 4. *Leptepsilonema saldanhae* sp.nov. A. Habitus of paratype female.



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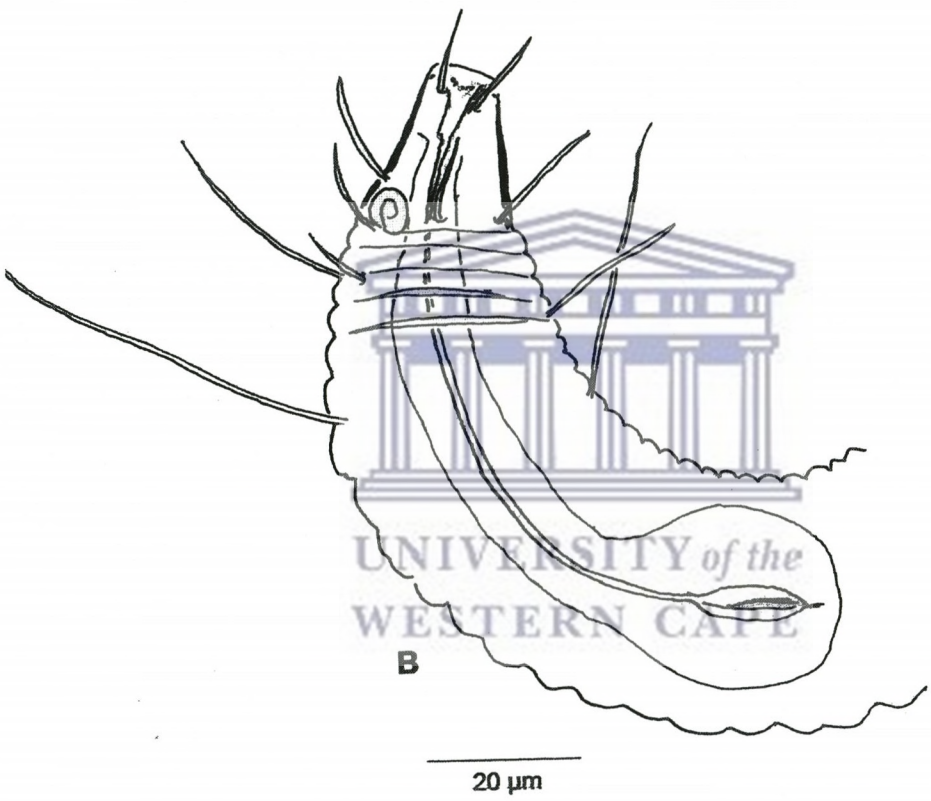
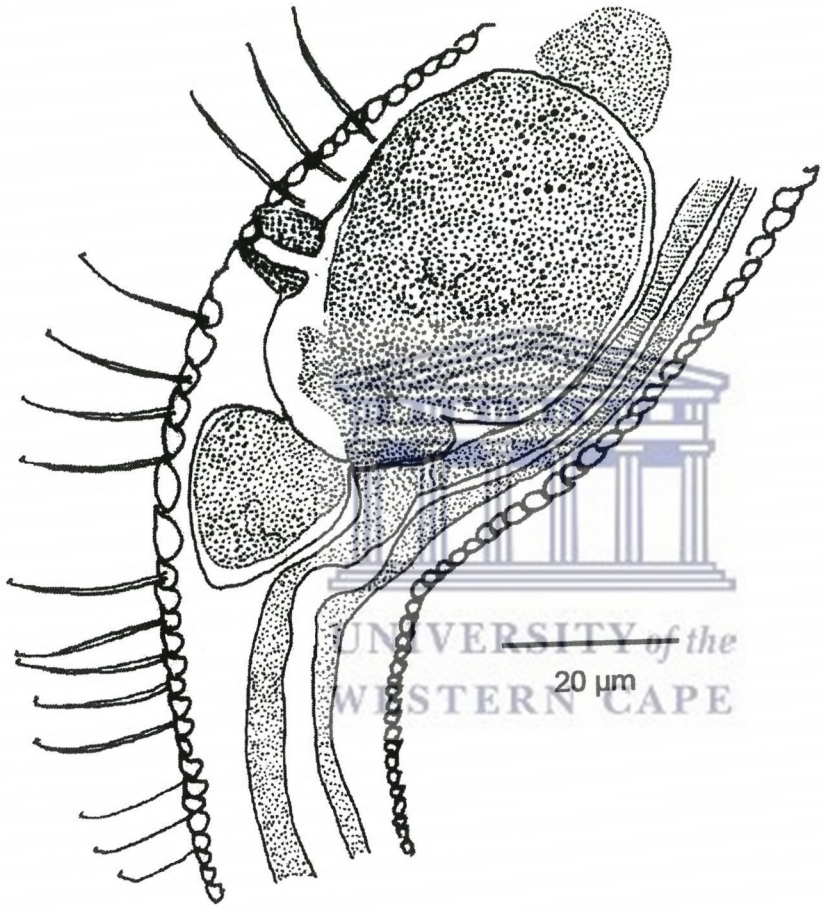


Figure 4. *Leptepsilonema saldanhae* sp.nov. C. Paratype female. Posterior body region with reproductive system.



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