BIODIVERSITY PATTERNS OF WETLAND MACROINVERTEBRATE ASSEMBLAGES IN THE SOUTH-WESTERN CAPE, SOUTH AFRICA

By

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ABSTRACT

Despite the recent surge in interest in wetland invertebrates, given their immediate importance in overall wetland functioning, these studies have largely been conducted in the northern hemisphere and very little is known in South Africa. In order to fill this knowledge vacuum, this study was conducted to investigate biodiversity patterns of wetland macroinvertebrates assemblages in the south-western Cape, South Africa. 140 wetlands were sampled in four geographic clusters, the Cape Flats, the West Coast, the Cederberg and the Agulhas Plain. Open-water, submerged vegetation and emergent vegetation habitats were sampled separately using a square-framed sweep net with a 23.5cm mouth and 80μm mesh and physico-chemical attributes measured at each site. A total of 126 taxa emanating from more than 26 000 individuals representing 73 genera and 51 families was recorded. Currently, five species new to science were also discovered, three from Hydraenidae (*Prosthetops* sp. nov, *Parhydraena* sp. nov and *Mesoceration repandum* Perkins, 2009), Hydryphantidae (*Hydryphantes* sp. nov) and Streptocephalidae (*Streptocephalus* sp. nov). However, all of these new species but one, were recorded from single location, suggesting that they might be rare or unique. Richness estimators predicted true taxon richness at about 20-47 taxon more than the observed taxon richness. The high number of uniques and singletons, as well as the Incidence-based Coverage Estimator, suggest that sampling was not adequate to capture the full biodiversity suite. However, I believe this is not necessarily true and this is discussed in detailed in the discussion. The sub-area Cederberg was found to be the biologically richest area, with the three of the new species recorded there. A significant difference was observed in relative abundance (RA) and frequency of occurrence between open-water habitat and vegetated habitats (submerged and emergent vegetation). On the other hand, a significant difference was not found between wetlands with different number of habitat types. No appreciable congruence was seen between different taxonomic groups (i.e. at order and family level) themselves', suggesting that neither can be used as a surrogate for the others. However, predators – which by the way had the highest frequency of occurrence and 2nd highest relative abundance after gatherers - were strongly correlated with overall assemblage and Hemiptera. In addition, together with Hemiptera they had ≥75% similarity with the overall assemblage, suggesting that they are fairly good surrogates for overall assemblage. These results are quite promising especially for biomonitoring programmes and warrant further research. Environmental variables contributed significantly higher in explaining assemblage composition, and the model containing pH, Phosphate, conductivity, turbidity and ammonium was found to explain significant variation in macroinvertebrate assemblage.

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CHAPTER 1

INTRODUCTION

This chapter gives an overview of the theoretical foundation of the whole thesis by discussing in details the reasons why understanding of wetlands and their invertebrates is important and how it contribute to practical application.

1.1 Why wetlands?

1.1.1 What is a wetland?

The term wetland is relatively new, encompassing many kinds of wet areas that are locally called marsh, swamp, fern, pond, bog, mire, vlei and pan (Allan *et al.* 1995; Davies and Day 1998; van der Valk 2006). Many different definitions of a wetland have been proposed in the literature but with little agreement on the universal definition; apparently it is much easier to recognize a wetland than to define it (Davies and Day 1998). Since wetlands occupy the intermediate position in the continuum between terrestrial and aquatic environments (Mitsch and Gosselink 2000), it is no wonder there is no universal definition for wetlands as this position varies with space and time. Consequently, there are dozens of wetland definitions currently in use. As a Contracting Party to the Ramsar Convention, South Africa adopts the Ramsar Convention's definition (Cowan and Riet 1998; DWAF 2004), which describe wetlands as "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres" (Cowan 1995). On the other hand, the National Water Act (NWA) (Act 36 of 1998) defines a wetland as a "land which is transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or the land is periodically covered with shallow water, and which in normal circumstances supports or would support vegetation typically adapted to life is saturated soil". These two definitions provide the necessary framework for wetland research and conservation in South Africa. However, the NWA definition effectively excludes rivers and estuaries, whereas the Ramsar Convention definition is accused of being too generic, and lacking the precision necessary for scientific inquiry (e.g. DWAF 2004). Consequently, there is general consensus that more specialised and specific definitions are needed.

It is, however, strange that a term which arose from the specific need to coordinate wise management of these endangered ecosystems is in fact difficult to define (Roggeri 1995). In an effort to provide a more specific definition Keddy (2000) called a wetland "an ecosystem that arises when inundation by water produces soils dominated by anaerobic processes and forces the biota, particularly rooted plants, to exhibit adaptations to tolerate flooding". Keddy (2000) further cautions not to get entangled in semantic arguments, since definitions are there to help us investigate nature, and investigations of nature should help clarify definitions. Consequently, as our knowledge of the wetland science grows we may expect definitions to accordingly change slightly. Therefore all the effort must be expended on understanding the dynamics of these enigmatic systems occupying an estimated 6% of the world's land surface (Maltby 1988). Irrespective of whatever definition one chooses to embrace, the distinguishing feature of all wetlands is the interplay between the land and water, and the resultant characteristics reflecting both (Cowan and Riet 1998). Generally, wetlands are recognized as land areas that show at least one of the three essential characteristics: specific hydrology, hydric soils and hydrophytic vegetation. However, field identification of these characteristics is often troublesome (Collins 2005). The difficulty with identifying wetlands by their hydrology is that the water it is not always present, this is especially true for south-western Cape dominated by seasonal wetlands (Dallas *et al.* 2006) which in somecase do not harbour hydrophytic plants. Presence of a wetland in the field is usually identified by the soil characteristics (e.g. Collins 2005; DWAF 2005). Nevertheless, hydrology is repeatedly mentioned as the most important feature of a wetland (Cowan and Riet 1998; Mitsch and Gosselink 2000; van der Valk 2006) given that it is the very reason for the wetland existence (Collins 2005). Furthermore, it affects other characteristics e.g. nutrient availability and soil anaerobiosis and in turn influencing the composition of wetland flora and fauna (Mitsch and Gosselink 2000).

1.1.2 Importance of wetlands

For many years wetlands have been considered "waste-lands", but because of their value they are increasingly being recognized as "wonder-lands". According to Maltby (1988) wetlands played a crucial role in sustainability and development of early prehistoric cultures. Christensen *et al.* (1996), introduces three important terms that are crucial when talking about the importance of wetlands. These are processes, goods and services. In addition, wetlands provide important functions, attributes and values which can be direct or indirect (Bowd 2005; Collins 2005; van de Valk 2006; see table 1.1). Wetlands are amongst the most productive ecosystems on earth, having socio-economic significance to many people, who in most cases are directly dependent upon them (Palmer *et al.* 2002; Schuyt 2005). Moreover, wetlands are increasingly being recognised for their crucial role in conservation of biological diversity (Gibbs 2000). Semlitsch and Bodie (1998) argued that small wetlands are not expendable, since the majority of natural wetlands are small but they are nonetheless, havens for biodiversity. As a result wetlands have a huge economic value, Costanza *et al.* (1997) estimated global economical value of wetlands to be US$ 4.9 trillion per year on average. However, a point must be made that not all values that wetlands provide can have monetary value attached to them, therefore the importance of wetlands should not be viewed in monetary terms only. Despite such knowledge about wetland values, Brown and Sullivan (1988) conceded that it is sometimes almost impossible to assess wetland values to society.

Table 1.1. The direct and indirect benefits of wetland processes, goods and services.

	Direct benefits	Indirect benefits
Processes	Water supply, sustained water flow	Water purification, flood attenuation, ground-water recharge, biogeochemical cycling.
Goods	Harvestable material, medicinal plants, fisheries	Grazing by wildlife, habitat for aquatic biota
Services	Socio-cultural significance, tourism and research, waste treatment	Biodiversity conservation, pollutants removal

1.1.3 Threats to wetlands

Despite being such vital systems, wetlands have been and continue to be under constant threat from human activities, degradation happening at an alarming rate. This is largely due to the fact that only until very recently, wetlands have been perceived as impediments to development and progress, and regarded as wasteland (Mitsch and Gosselink 2000; DWAF 2004). According to Bellamy (1993) the continued destruction of wetlands is the worst act of environmental vandalism being committed in contemporary history. To this end, according to the Ramsar Convention, it is estimated that 50% of all wetlands have been lost globally since the start of the industrial revolution (Dini 2004). On a continental scale, Finlayson and Davidson (1999) estimated that up to 56-65% of available wetlands have been drained for intensive agriculture in Europe and North America, 27% in Asia, 6% in South America and 2% in Africa. These figures might be slightly misleading since they are mainly considering larger wetlands. For small, isolated wetlands – which are dominant feature in the south-Western Cape, South Africa - the situation is different, given that in many places isolated wetlands i.e. not connected to rivers, are effectively not protected by law (Brown and Sullivan 1988). Although there has been no official national survey of wetland loss in South Africa, an estimated 35 – 50% of all wetlands are thought to have been destroyed (Breen and Begg 1989; Dini 2004; DWAF 2005). However, some parts of the world have recorded even higher destructions, i.e. approximately 70% of the Great Lakes coastal wetlands have been lost to anthropogenic disturbances, while the remaining ones are highly fragmented (Cardinale *et al.* 1998). In addition, urban spawl, deforestation and climate change just to name few, are other the often cited threats (Cowan and Van Riet 1998; Davis and Froend 1999; Dudgeon *et al.* 2006). Ignorant perception of wetlands as wasted lands, the fact that they harbour diseases vectors e.g. malaria mosquitoes, and lack of government interest, were considered by Maltby (1988) to be some of the reasons why wetlands have continued to be lost. Since the processes, goods and services of a wetland ecosystem are closely linked to its biological, chemical and physical characteristics and the interactions thereof (Roggeri 1995; US EPA 2002a), even without a net loss of wetland acreage, wetland functioning may be affected by changing these characteristics. For example, given the importance of hydrology in wetland formation and function, any undue changes on hydrology such as diversion of water courses and water abstraction, may yield deleterious consequences.

1.1.4 Conservation of Wetlands

Holdgate (1993) argues that, given that wetlands have been treated with such hostility by many human societies over so many years, their conservation seems almost counter-cultural. But human society can no longer afford to lose any more wetlands, given their recently realised economic and ecological importance. As an example, Schuyt (2005) reported 16 different goods and services on four large African wetlands. These goods and services are irreplaceable so if wetlands continue to be lost, the effect will be profound on the socio-economic stability of the dependent communities. The RAMSAR Convention is the first step in the right direction at international level to advocate wetland conservation. The RAMSAR Convention is an inter-governmental treaty promoting an integrated approach to managing wetland systems so that human use of these areas is undertaken in a way that retains the natural capital for future generations (Hails 1996). South Africa as a signatory to this treaty (Cowan 1995) is obliged to promote wise use and sustainable management of its wetlands. This is achievable through the implementation of the National Water Act (Act 36 of 1998), which requires that water resources (including wetlands) must be managed in an integrated or holistic manner. But to this end, focus has been on large permanent wetlands, with little focus on small temporary wetlands.

1.1.5 Wetland Research in South Africa

In a water-deficient country like South Africa, wetlands play a crucial role in managing our limited water resources, acting as vast sponges to hold run-off. Unfortunately, wetlands in the past have been neglected hence knowledge of their distribution, structure and function is scarce (Dallas *et al.* 2006). This is unfortunate considering that their distribution and characters reflect and modify their physical surrounding (Silberbauer and King 1991a). In order to understand wetlands, the first step is to actually recognize them as wetlands and for that a suitable classification system is required and there has an appreciable amount of work this topic. To this end, Cowan and Van Riet (1998) divided the country into various wetland regions according to climate, and these have been further sub-divided into four broad groups based on the geomorphology, namely plateau, mountains, coastal slopes and coastal plain. Detailed descriptions of the individual wetland regions are available in (Cowan 1995). Dini *et al.* (1998) provided the first attempt of classifying wetlands for the entire country, and Jones (2002) for Western Cape Province, while Ewart-Smith *et al.* (2006) provided the first national wetland inventory based on National land Cover 2000 advanced wetland layer. The Department of Water Affairs and Forestry mandated by the NWA have also been involved in a number of wetland research projects (see DWAF 2004 for details). Unsurprisingly, there are very few studies in that have looked at wetland macroinvertebrate assemblages (but Bowd 2005; Vlok *et al.* 2006; De Roeck 2007).

1.2 Why Invertebrates?

1.2.1 Invertebrates in wetlands

Recent advances in understanding of food webs, nutrient cycling and overall productivity of wetlands have turned increasing attention to the importance of invertebrates in the ecology and functioning of wetlands (Murkin and Wrubleski 1988; Batzer and Wissinger 1996). More importantly, the concerns about waterfowl and pest management have placed a high demand on information about wetland invertebrates (Batzer and Wissinger 1996). This is because among the wetlands-dwelling invertebrates, some are biting pests (e.g. Tabanidae and Culicidae) and potential vectors of disease. It is the same reason why in the past large areas of wetlands were been drained to control malaria (Murkin and Wrebleski 1988). However, there is a consensus among wetland scientists (Murkin and Wrubleski 1988; Krieger 1992; Batzer and Wissinger 1996) that wetland invertebrates are still poorly known and the very limited existing information is still scattered (but see Batzer, Rader and Wissinger 1999). However, Krieger (1992) attributed the general lack of research on wetland invertebrates to several possible reasons; pre-occupation with the control of insect pests; low economic value assigned to non-pests; small size; the difficulties encountered in sampling and identifying them. Studies on the ecology of wetland invertebrates are therefore of strategic importance in the quest to understand wetland ecology and biodiversity conservation. Although wetland macroinvertebrates are not as diverse as their river counterparts, they are different in having greater tolerance to low dissolved oxygen as anaerobic conditions prevail in wetlands. Furthermore, invertebrates overwhelmingly predominate wetland faunal communities and are taxonomically rich yet readily surveyed (Wissinger 1999). In addition to their use in water quality and ecosystem integrity assessment, wetland invertebrates have recently been used to delineate temporary wetlands (Euliss *et al.* 2002). Doupe and Horwitz (1995) in Australia used macroinvertebrate assemblages to evaluate success of wetland rehabilitations. Furthermore, invertebrate communities in temporary wetlands act as microcosms, providing useful systems for testing ecological theories (Batzer and Wissinger 1996; Blaustein and Schwartz 2001).

1.2.2 Invertebrates in the food chain

As invertebrates occur in virtually all wetlands they are an essential component of wetland food webs. One of the salient values of invertebrates in wetlands is the role they play in food chain support by linking primary production with higher levels (Murkin and Wrubleski 1988; Wissinger 1999). They consume algae, detritus, plants and microorganisms, and in the process provide an important food source for fish, amphibian and waterfowl (US EPA 2002a). Murkin and Wrubleski (1988) argued that because algal production in wetlands can be high with deleterious consequences, invertebrates feeding on algae are provide a big service to overall wetland functioning by controlling it. Because of invertebrates' high content of calcium (i.e. snails) and protein, they are the preferred food source during the high-energy demanding breeding and migration seasons for birds (Murkin and Wrubleski 1988). Euliss *et al.* (1999)

concedes that it was studies stressing the dietary value of invertebrates to waterfowl that provided the impetus for much of earlier research on wetland invertebrates, given that migratory waterfowl possesses such considerable economic value. Unfortunately, information on wetland invertebrates has been directed towards developing a better understanding of waterfowl ecology and management. Furthermore, invertebrates play a pivotal role in recycling of nutrients through their bioturbation activities (Krieger 1992, US EPA 2002a).

1.2.3 Invertebrates as Indicators

Since aquatic invertebrates are exposed directly to physical, chemical, and biological perturbations within the wetland, they might be useful tools for assessing wetland ecological integrity (Burton *et al.* 1999; Genes and Helgen 2002; US EPA 2002b; Uzarski *et al.* 2004; Bowd *et al.* 2006). According to Vlok *et al.* (2006), aquatic invertebrates are good indicators of overall ecological integrity because they integrate and reflect the effects of chemical and physical impacts occurring over extended periods. This is because wetland macroinvertebrates are differentially sensitive to human-induced perturbations (e.g. pollutants and nutrients) and are thus impacted differently. Different life history adaptations have been linked with different environmental conditions, suggesting that invertebrates will be good indicators thereof (e.g. Hall *et al.* 2004). Adamus *et al.* (2001) reported that the predominance of taxa with shorter generation times tends to indicate a recent perturbation (e.g. nutrient increase or disturbance), as they are at a competitive advantage in such situations relative to their longer-lived counterparts. It is widely accepted that the types and densities of invertebrates found at any point along the system, are a reflection of water quality, habitat availability, hydrological regime and general condition of the system. Therefore, invertebrate community composition is indicative of the condition prevailing in a wetland. As an example, Adamus *et al.* (2001) report that, at lower salinities, scrapers and epiphytic deposit-feeders predominate but that these are replaced by filter-feeders and benthic deposit-feeders at higher salinity. Chironominae containing haemoglobin, therefore able to be more tolerant to reduced dissolved oxygen levels, appear to replace Orthocladinae as eutrophic conditions prevail (Adamus et al 2001).

1.3 Rationale

First of all, I believe that the above deliberations make it clear why it is vital to have a good understanding of wetland macroinvertebrate assemblages, given their importance to overall wetland ecology. Although South Africa is the signatory of RAMSAR convention (Cowan 1995), wetlands have until very recently been neglected, consequently our knowledge of their distribution, abundance and associated assemblage structure is scarce (Malan and Day 2005a; Dallas *et al.* 2006). The situation is even worse for small temporary wetlands, although they are a dominant feature in the landscape in south-western Cape. In order to protect our wetlands and their accompanying resources as required by the National Water Act (Act 36 of 1998), we need to first know where and what biological assemblages are present. Understanding the patterns and processes that influence diversity and distribution of biota and ecosystem functioning, is the prime goal for biodiversity conservation. Furthermore, Malan and Day (2005b) argued that to develop biomonitoring protocols and to link the presence of macroinvertebrate assemblages with certain conditions, requires a detailed knowledge of what species may be found where and their habitat requirement. Unfortunately such information is still lacking in South Africa. This study therefore, aims to contribute to the body of knowledge about the wetland ecology by studying biodiversity patterns of wetland invertebrate assemblages. In addition, it will contribute to our understanding of freshwater biodiversity, which is woefully incomplete especially with regard to invertebrate distribution.

1.3 Questions the thesis is investigating

1) Description of biodiversity patterns of macroinvertebrate assemblages in temporary wetlands in the south-western Cape, South Africa: **Chapter 2**
2) Assessment of congruence of wetland macroinvertebrate assemblages at different taxonomic levels: **Chapter 3**
3) Assessment of the effect of physico-chemical parameters on wetland macroinvertebrate assemblages in the south- western Cape- **Chapter 4**
4) Conclusion –**Chapter 5**

1.4 MATERIALS AND METHODS

1.4.1 Study Area

This study focused on the south-western Cape (see Figure 1.1) defined by Silberbauer and King (1991a) as the part of South Africa, south of 31^0 and west of 22^0 and as the south-western corner of the Cape Floristic Region (CFR) by Linder (1991). The CFR is a unique terrestrial phytogeographic region different from the rest of Southern Africa (Werger 1978), with some 9000 plant species represented by 68% and 19% endemism for species and genera respectively (Goldblatt and Manning 2000). Based on the composition of Southern African fauna Balinsky 1962 (cited by Harrison 1965) posited that during the Mesozoic most of the sub-continent must have been in a southern temperate-zone and occupied by temperate-zone fauna. As the continent moved northwards and temperatures increased, much of the fauna was driven into montane regions, which acted as refugia (Harrison 1978; Picker and Samways 1996), except in the south-western Cape, where temperatures are somewhat more moderate. Furthermore, the region has been shown to support high levels of freshwater fauna endemism (Wishart and Day 2002), and it is of significant international importance (Myers *et al.* 2000; Olson and Dinerstein 2002; Thieme *et al.* 2005) as a global biodiversity hotspot. However, the region is under severe threat from land transformations for agriculture and urban development and alien invasion (Rouget *et al.* 2003). In addition, the region has a unique Mediterranean-type climate that is not found anywhere else in sub-Saharan Africa, containing cool wet winters and relatively dry warm summers. Unfortunately, predictions suggest that south-western Cape will be hardest hit by climate change (Midgley *et al.* 2002; 2005) creating new management challenges.

1.4.2. Types of wetlands sampled

As noted by Dallas (*et al.* 2006) in their extensive compilation of wetland studies in the Western Cape Province, temporary wetlands predominate in the south-western Cape, giving a strong impetus for making them the focus of the current study. This observation follows (Williams 1997) assertion that temporary wetlands are traditionally most abundant in drier parts of the globe, as is the study area of this study. Williams (1997; 2006) describes temporary wetlands as water bodies that experience recurrent dry phase of varying lengths. In this part of the world, temporary wetlands usually get inundated during winter and dry-out in summer. It is important that we understand the ecology of this systems, given their contribution to development of ecological and evolutionary theories and testing thereof (Blaustein and

Schwartz 2001). In addition, because of their small size in comparison to their permanent counterparts, temporary wetlands are highly threatened (Semlitsch and Bodie 1998).

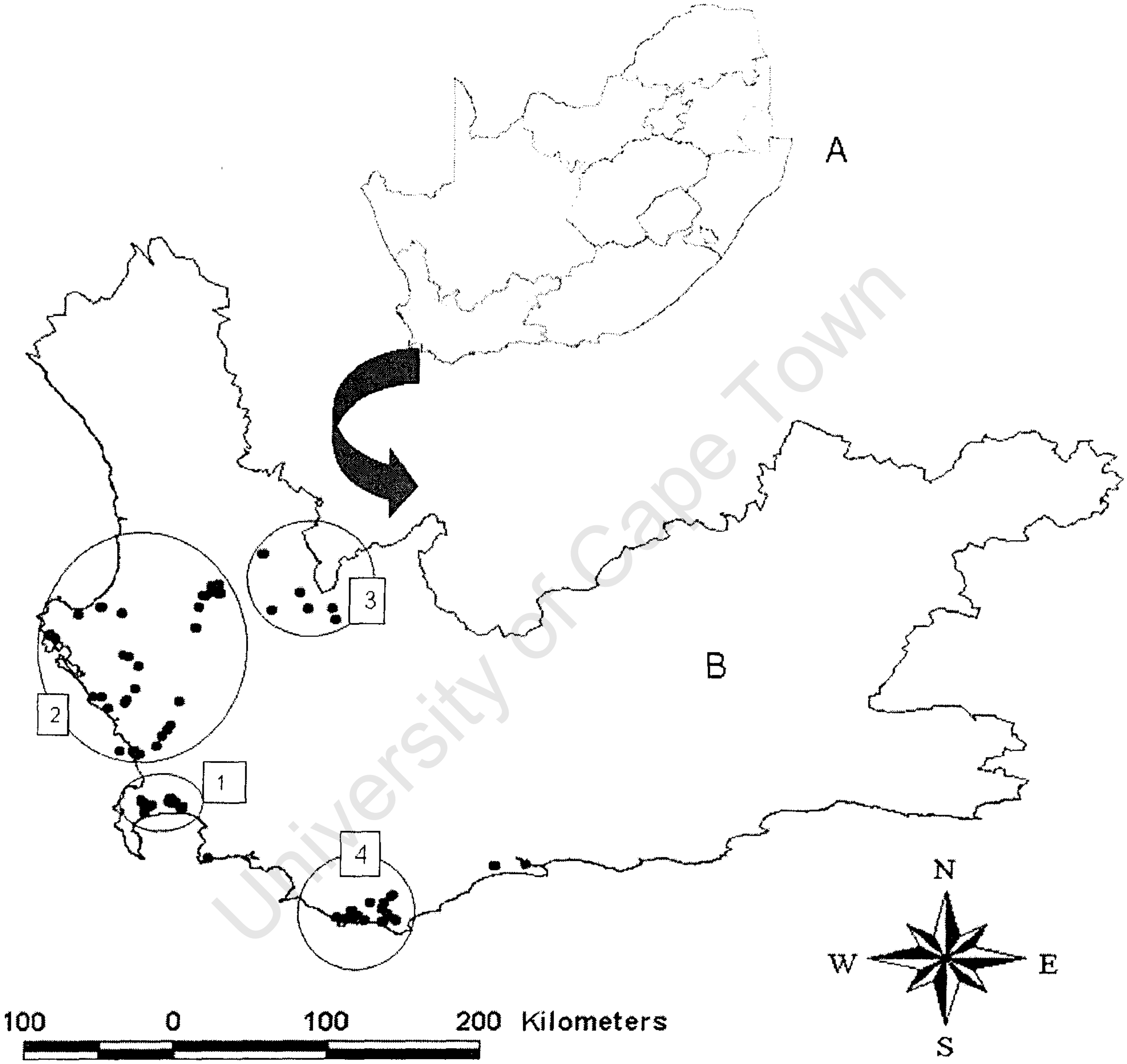

Figure 1.1 A- shows a map of South Africa with the outline of all the provinces and the study area (Western Cape) highlighted and B- shows the distribution of individual wetlands and the wetland-clusters (or sub-areas) sampled in the present study; 1: Cape Flats, 2: West Coast, 3: Cederburg and 4: AgulhasPlain.

1.4.3 Macroinvertebrate Collection

Each sample was made of a composite of nine sweeps taken from three different areas (3 sweeps in each), with each sweep one metre long (*sensu* Dietz-Brantley *et al.* 2002; Stenert and Maltchik 2007). Macroinvertebrate assemblages were sampled semi-quantitatively using a square-framed sweep net with a 23.5cm mouth and 80μm mesh, since such nets are known to be effective (Cheal *et al.* 1993; Turner and Trexler 1997; Batzer *et al.* 2004) and to facilitate movement through dense vegetation (Davis *et al.* 1999). Although it is beyond the scope of this thesis, a number of studies have done a sterling job of assessing the effectiveness of different sampling gears (Cheal *et al.* 1993; Turner and Trexler 1997; Batzer *et al.* 2001; Bowd 2005) and sweep-net has been hailed as a sampling gear of choice. However, this method effectively excluded benthic dwellers, but this component of the assemblage is thought to be relatively insignificant given its harsh anaerobic environment. Relative abundance was expressed as numbers of macroinvertebrate individuals per wetland sample (i.e. per nine sweeps), because according to Batzer *et al.* (2001) sweep-net data should not be expressed in terms of area or volume, but rather, in terms of sampling effort (i.e., numbers of organisms/standardised sweep). Collection was done between July and early September 2007.

1.4.4 Macroinvertebrate Processing

All samples were fixed in 5% formalin in the field and transferred to 70% ethanol back in the lab. After carefully removing most of the vegetation, twigs and other unwanted materials, macroinvertebrates were picked for a total of 20mins. Based on the preliminary trials, this time was found to be optimal for expending equal efforts in processing in each sample and qualitatively picking-up all taxa. The last 5 minutes was dedicated to picking rare, animals not picked before. Picking of the invertebrates alone took three hours per wetland (excluding counting and identifying - nine samples in total per wetland, 20 minutes per sample). Macroinvertebrates were identified to lowest possible taxonomic level using the series of the Guides of the Freshwater Invertebrates of Southern Africa (Day *et al.*. 1999, 2001, 2003, 2008, de Moor and Day 2002 and de Moor *et al.*. 2003a, 2003b) and the help of specialists (see Acknowledgements). Most taxa were identified to genus or species, but chironomids were identified only to subfamily. It is important to mention at this point that only macroinvertebrates (i.e. those animals identifiable with the naked eyes, excluding cladocerans, copepods, ostracods) were considered in this study. Benthic dwellers such as nematodes, oligochaetes etc. were however, omitted in this study, as were semi-aquatic and terrestrial species.

1.4.5 Taxonomic identification

All specimens were identified at least to family level but efforts were made to identify them to as low a taxonomic level as possible, using the series of the Guides to the Freshwater Invertebrates of Southern Africa (Day *et al.* 1999; 2001; 2003; de Moor and Day 2002; de Moor *et al.* 2003a; 2003b; Stals 2008). Representatives of all identifications except Diptera (because of lack of specialist) were sent to specialists (the list of which is given in the Acknowledgements) for verification. Coleoptera, Hemiptera, Mollusca, Amphipoda and Anostraca, were identified mainly to species level. Dipterans (i.e. chironomids and culicids) were identified to subfamily and generic level respectively. Ephemeroptera, which are represented by only one genus (*Cloeon*) in standing waters in this part of the world, could only be identified to generic level Although there are nine species of this genus (*Cloeon*: Baetidae) in South Africa, it is almost impossible to tell them apart at nymphal stage without the adults (Baber-James and Lugo-Ortiz 2003).

CHAPTER 2:

DESCRIPTION OF BIODIVERSITY PATTERNS OF WETLAND MACROINVERTEBRATE ASSEMBLAGE

This chapter provides a basic description of the macroinvertebrate assemblages, focussing on aspects of biodiversity, estimation of the true biodiversity using a range of richness estimators and comparisons of different habitats.

2.1 INTRODUCTION

2.1.1 Wetland invertebrate communities

Over and above its exceptional botanical diversity, the south-western Cape is also known for its diverse and highly endemic stream communities (Picker and Samways 1996; Wishart and Day 2002). Unfortunately, the same cannot be said about its wetland communities due to the limited research and our little understanding of these systems. Of all wetland communities, invertebrates tend to overwhelmingly dominate in abundance and diversity (Gaston 2000a), and yet they remain largely under-studied (Krieger 1992; Batzer and Wissinger 1996). Although there has been a surge of interest in research on wetland invertebrates during the last decade culminating in a voluminous book by Batzer, Rader and Wissinger (1999), most of the work has been done in North America, while very little is known about wetland invertebrate assemblages in South Africa (Malan and Day 2005a). In an attempt to address the knowledge short fall, this study therefore aims to assess the biodiversity patterns of wetland macroinvertebrate assemblages in the south-western Cape. Such understanding of wetland invertebrate biodiversity is crucial for wetland management and restoration as well as in implementing aquatic biomonitoring programmes. Temporary wetland systems – the focus of this study - are of even greater significant importance, since they support unique biota that is not found in either aquatic or terrestrial ecosystems (Wiggins *et al.* 1980; Wissinger 1999), albeit with less biodiversity than its permanent counterparts (Collinson *et al.* 1995; Williams 1996; 2006). It is the peculiar and dynamic nature of temporary wetlands (e.g. Ebert and Balko 1987) that allow them to support species that are not found in any other habitats as well as others that attain their greatest populations in temporary systems (Williams 1997).

In addition to the large branchiopod orders commonly known to be uniquely temporary wetlands inhabitants, namely, the Anostraca (fairy shrimps), Conchostraca (clam shrimps) and Notostraca (tadpole shrimps) (Seaman *et al.* 1995; Hamer and Brendonck 1997; De Roeck *et al.* 2007), Wissinger (1999) indicates that other entire families like the marsh beetles (Helodidae), marsh-loving beetles (Noteridae), marsh flies (Sciomyzidae), phantom crane flies (Ptychopteridae), velvet water bugs (Hebridae) and water measurers (Hydrometridae) are also exclusively found in temporary wetlands. Moreover, Wissinger (1999) argues that in nearly all aquatic families of invertebrates, specialization to wetlands has occurred at the lower taxonomic levels, for instance the genus *Cloeon* in the baetid family of mayflies in Southern Africa (Baber-James and Lugo-Ortiz 2003).

2.1.2 Adaptations to temporary wetlands

Invertebrates adapted to the dynamic and demanding environments of temporary wetlands have developed various adaptations that allow them to survive and successfully exploit these highly productive habitats (Brendonck and Williams 2000; Williams 2006). Williams (1996) listed two such "strategies", namely physicochemical and biological adaptations. To date much is known about the physiological adaptations of temporary wetland fauna, but the opposite is true for biological adaptations. Williams (1997) groups the main adaptations evolved by temporary water invertebrates into three categories, 1) physiological tolerance, 2) life-history modification and 3) migration. Wissinger (1999) further divides these evolutionary adaptations into five "strategies", 1) desiccation tolerance, 2) timed emergence with adult survival in adjacent terrestrial habitat, 3) aerial dispersal from other wetland or aquatic waters, 4) immigration and emigration in flood waters and 5) passive dispersal on other animals. Perhaps, the most fundamental adaptation of temporary wetland invertebrates is their ability to withstand desiccation (Schneider and Frost 1996).

2.1.3 Habitat structure

The diversity and density of invertebrates in wetlands, as in other aquatic habitats, is largely dictated by habitat structure. In order to completely understand invertebrate communities and the role they play in wetland ecology, it is important to understand the effect of habitat heterogeneity (Krieger 1992; Benke *et al.* 1999). In addition to being a critical source of carbon, aquatic vegetation provides physical habitat for organisms and is a good substrate for depositing eggs, for shelter and for refuge against predation. Consequently, a positive correlation between vegetation cover and invertebrate taxa has been recorded (e.g. Voigts 1976). Furthermore, vegetation modifies the environment, by affecting light penetration, temperature and dissolved oxygen in the water column (Tessier *et al.* 2004). Wetlands containing a high density and diversity of aquatic plants have been reported to support a more diverse fauna than their counterparts because they provide more niches for species to coexist (Findlay *et al.* 1989; Krieger 1992; Hann 1995; Euliss *et al.* 1999; Wissinger *et al.* 1999). In addition, different invertebrate assemblages are often associated with different plant species or plant communities (Euliss *et al.* 1999). Tessier et al (2004) studying invertebrates associated with emergent (*Schoenoplectus lacustris*), submerged (*Myriophyllum spicatum*), and floating-leaved (*Trapa natans*) vegetation reported that submerged vegetation supported higher invertebrate biomass per weight than emergent vegetation, while floating vegetation was somehow intermediate. The same observation was made by Cattaneo *et al.* (1998), reporting that beds of submerged vegetation hosted significantly higher macroinvertebrate and algae densities. Moreover, areas with aquatic vegetation have been reported to support higher numbers of invertebrates than bare areas (Cardinale *et al.* 1998; Sternert *et al.* 2008). However, Voigts (1976) found that the largest number and greatest diversity of aquatic invertebrates appear to be produced when open habitats are interspersed with the vegetated habitats. Following on these studies, the present study will investigate differences in macroinvertebrate assemblages among different habitats (i.e. open-water, emergent vegetation and submerged vegetation habitats) and in wetlands with different numbers of habitats.

2.1.4 Aims and objectives

The overarching aim of this chapter is to assess and describe biodiversity patterns of macroinvertebrates inhabiting temporary wetlands in the south-western Cape. The following specific objectives will be pursued:

1. Estimation of taxon richness using a range of richness estimators
2. Assessment of the relative abundance and frequency of occurrence of different taxa, at varying taxonomic levels i.e. generic, familial and order/class level.
3. Assessment of the relative abundance and frequency of occurrence of invertebrates belonging to different functional feeding groups and with different life-history attributes.
4. Assess variation in relative abundance and frequency of occurrence of macroinvertebrates from different habitats (i.e. open-water habitat, submerged vegetation and emergent vegetation habitats.
5. Assessment of the variation between wetlands with a different number of habitat types.

2.2 MATERIAL AND METHODS

2.2.1 Habitat Types

Wetlands sampled in this study were divided into three broad habitat types, namely: open-water, emergent vegetation (plate 1.1) and submerged vegetation (plate 1.2) and these habitats types were sampled separately and processed separately. An effort was made to sample as much representative patches of each habitat type as possible. However, in cases where there was no apparent distinction between habitats or were habitat(s) missing, three separate samples were still taken. Care was taken not to disturb the other habitat(s) while sampling the other. The open-water samples were taken at least five metres into the wetland depending on its size, and characterised by being totally devoid of any vegetation or structure i.e. in the water column. Submerged vegetation habitat type was characterised by the presence of highly structured and complex architecture of either floating or submerged vegetation including species such as *Isolepis rubicunda*, *Potamogeton petinatus*, *Chara glomerate* and *Paspalum vaginatum*. On the other hand, emergent vegetation habitat type was less structurally complex having simple, dominated by species such as *Typha capensis*, *Phragmites australis*, *Bulboschoenus maritimus* and *Juncus kraussii*.

2.2.2 Physico-chemical Factors

Measurements for water depth, wetland size, and the following water chemistry (pH, conductivity, dissolved oxygen & temperature using YSI meters provided by the Department of Zoology, University of Cape Town) as well turbidity, were taken *in situ*. While all the other water chemistry measurements were done back in the laboratory by the Department of Oceanography, University of Cape Town.

2.2.3 Functional Feeding Groups (FFGs)

Macroinvertebrates were assigned to one of the five functional feeding groups (*sensu* Whiles and Golowitz 2005), using best available literature (Merritt and Cummins 1996, Day *et al.* 1999; 2001; 2003; 2008; de Moor and Day 2002; de Moor *et al.* 2003a; 2003b; Stenert and Maltchik 2007) and professional judgement. These FFGs were predators, gatherers, filterers, scrapers and shredders. Although FFG analysis has rarely been studied in lentic waters, Merritt *et al.* (2002) recently used FFG in the bioassessment of river oxbows in southwest Florida.

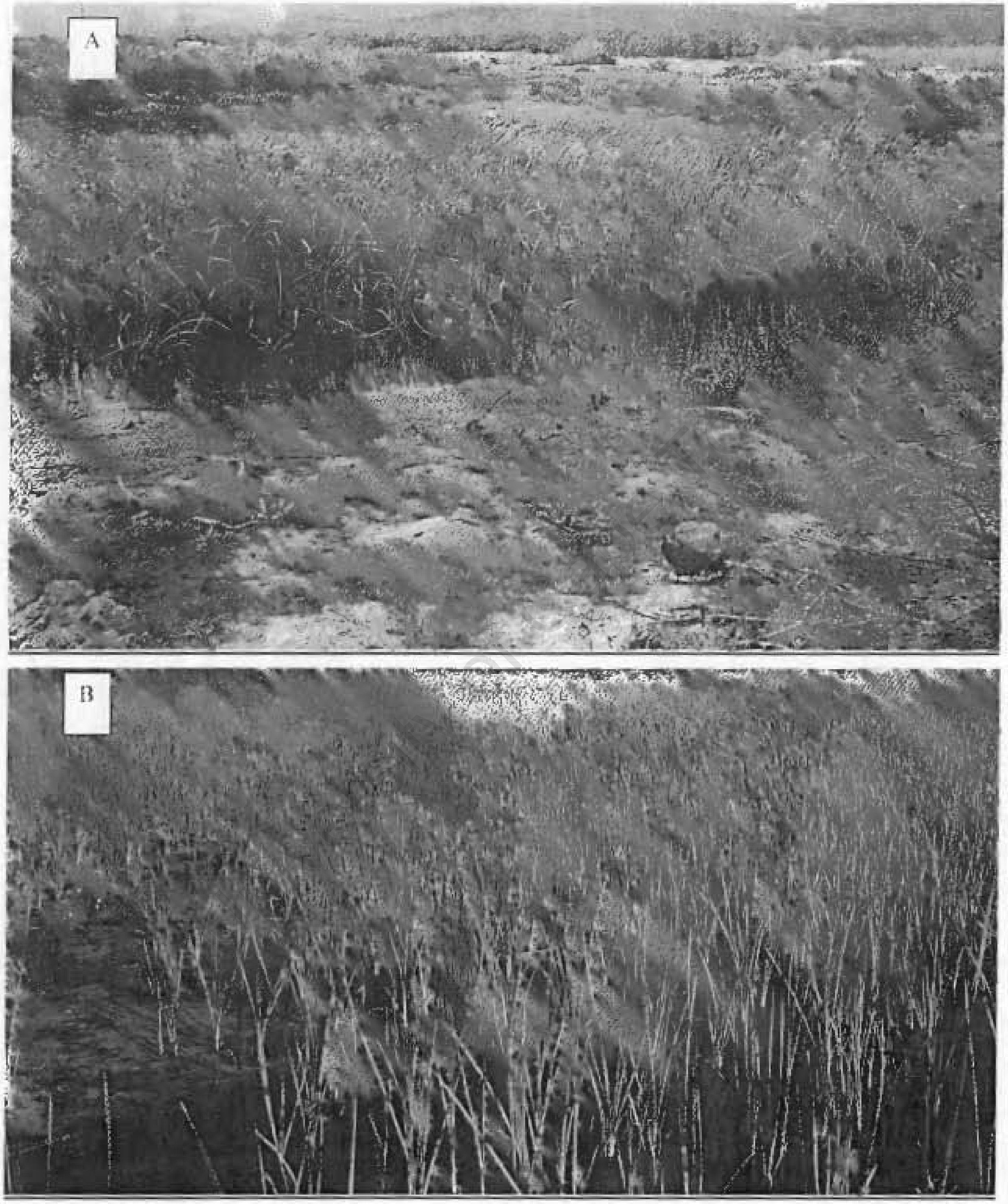

Plate 2.1. Showing examples of emergent vegetation (e.g. Typha capensis), a) wetland in Kuils River area, b) wetland in Koeberg area.

Plate 2.2. Showing an example of submerged vegetation habitat (i.e. *Isolepis rubicunda*).

only two genera (*Cloen* and *Sigara*) were found to occur in more than half the sites, while no genus contributed <20% in terms of the relative abundance, the closest was *Tomichia* with 19%.

Gatherers and predators were the most prevalent FFGs, occurring in more than 120 wetlands, whereas in terms of abundance, predators and scrapers dominated. Predators were the only FFG to be found in 130 wetlands, and represented an abundance of more than 20% to overall assemblage. Such dominance of predators has important ecological functions, in terms of controlling nuisance wetland taxa like mosquitoes. Predominance of predators was reported to be coupled with many rapid-turnover (i.e. short life-cycle) prey taxa (Merritt *et al.* 2002). Furthermore, proliferation of predators is usually correlated with the increased length of hydroperiod (Schneider and Frost 1996), these results are in agreement with Whiles and Golowitz (*et al.* 2005) who reported that collector-gatherers, scrapers, and predators were the dominant functional groups in their study. Gatherers were also found to dominate invertebrate biomass in the Carolina Bays (Taylor *et al.* 1999), contributing 65–92% of total abundance in Platte River basin (Whiles and Golowitz 2005). In my study, as in Taylor *et al.* (1999), shredders were under represented contributing only 5% to overall assemblage abundance and occurring in fewer than half of the wetlands. More than two-thirds of the wetland macroinvertebrates was represented by transient taxa. Although transient taxa are generally active flyers (i.e. insects) they going to be heavily impacted by increasing habitat transformation causing more and more isolation of individual wetlands, as they have been shown to be influenced more by insular characteristics than by landscape features (Hall *et al.* 2004). The overwhelming abundance of transient taxa over resident taxa, is believed to be the function of sampling time rather than sampling size, since wetlands communities change temporarily.

Although this study did not find differences between vegetated habitat types (i.e. submerged and emergent) themselves, but they supported significantly higher abundances and had more frequency of occurrence taxa than their open-water counterpart. Many other researchers have echoed this observation (Voigts 1976; Benke *et al.* 1999; Wissinger 1999; De Szalay and Resh 2000). However, Suren *et al.* 2008 found little effect of vegetation on invertebrate community. Beckett *et al.* (1992) in a Wisconsin lake in the USA reported that mean benthic invertebrate densities in the sediments of habitat with vegetated; *Ceratophyllum demersum* and *Potamogeton nodusus* were 13 and seven times those of nearby non-vegetated areas. One of the plausible explanations for the observed difference between vegetated and non-vegetated habitats is that vegetation increases structural complexity and surface area, thereby providing additional living space for taxa to co-exist. In addition, vegetation modifies both physical and chemical environment. The work of Beckett, Aartila and Miller (1992) did not find support for the conjecture that differences between habitats are a result of lack of a detrital food base, but instead they proposed that differences might be due to disturbance effects in areas lacking vegetated habitats, and increased predator efficiencies in open areas.

2.2.4 Life-history Adaptations

Taxa were classified into two life-history adaptations (*sensu* Taylor *et al.* 1999; Hall *et al.* 2004), namely resident and transient, based on the organism's ability to disperse, given that this adaptation plays a crucial role in organism's existence (Bilton *et al.* 2001). Resident taxa were defined as organisms that are incapable of active flight but rely on passive dispersal through wind or other animals (Bohonak and Whiteman 1999). These taxa constituted mainly non-insects e.g. molluscs and crustaceans which, because of their inability to actively avoid unfavourable conditions such as drying out have developed drought resistant life stages (e.g. eggs or cysts) (Wiggins *et al.* 1980; Schneider and Frost 1996; Williams 1996). On the other hand, transient taxa have the capacity of actively avoiding unfavourable conditions simple through flying; therefore this category was made of winged insects capable of active dispersal. Because of the difference in dispersal capacities that affect survival and existence (e.g. Brose 2003), organisms displaying these different life-histories respond differently to local environmental conditions (Swartz and Jenkins 2000; Anderson and Smith 2004; Hall *et al.* 2004).

2.2.5 Taxon Richness

It has long been recognized that it is virtually impossible to detect all species and their relative abundances due to sampling limitations (Magurran 2004; Sutherland 2006). As one of the ways of addressing this problem ecologists use a range of richness estimators and rarefaction curves. These techniques generate the expected number of species in a small collection of individuals drawn randomly from a large sample, based on all species actually discovered (Gotelli and Colwell 2001). Sample-based rarefaction curves were compiled to determine the degree of sampling representivity (Gotelli and Colwell 2001). Sampling may be considered adequate or representative when the species-accumulation curve and the richness estimators converge closely at the highest observed values (e.g. Longino *et al.* 2002).This was done for the whole data set (i.e. whole study area, n=140), and for the sub-areas, the West coast (n=51), the Cape flats (n=51), the Cederberg (n=8) and the Agulhas plain (n=23). Mean values of the abundance-based estimator Chao 1, the incidence-based Chao 2, and the first- & second-order Jack Knife estimators (Jack 1 & 2) were plotted together with the (Mao Tau) observed taxon richness (S_{obs}). All these richness estimators were used together because they yield different results under different conditions (i.e. none is perfect for all conditions). Estimates using non-parametric techniques based on species incidence have been reported as providing the most accurate and precise estimates (Foggo *et al.* 2002; Ulrich *et al.* 2003; Walter and Moore 2005). For example, the non-parametric Jackknife-1 estimator is calculated to overcome sample-size inadequacies and to estimate how many species are actually present in sampled habitats (e.g. Oertli *et al.* 2008). Non-parametric asymptotic functions; the Incidence Coverage Estimator (ICE) and Michaelis–Menten richness estimators were used to evaluate sample-size adequacy (Colwell and Coddington 1994), as was the parametric Abundance-based coverage estimator (ACE). Calculations were made with EstimateS software, version 8.0 (Colwell 2006).

2.2.6 Statistical Analyses

Statistical differences between the three habitat types described above were assessed using ANOVA in SPSS (Version 16.0 for Windows, SPSS Inc., 2007). Furthermore, an analysis at wetland level was conducted based on how many discernable habitat types the wetland has. Wetlands were divided into three categories, wetlands with, 1) all three habitat types, 2) two habitat types and 3) only one habitat type (which was usually just open water with no vegetation) and subjected to the same analysis as above. Given the contentious issue of taxonomic resolution (e.g. Bailey *et al.* 2001; Lenat and Resh 2001; King and Richardson 2002) the analyses were performed at different taxonomic levels, i.e. genus, family and order/class. Analyses of these different taxonomic levels were conducted using two datasets, namely relative abundance and frequency of occurrence. Abundance (which is effectively the number of individuals) was recorded as relative because the sample used was semi-quantitative (Batzer *et al.* 2001). Frequency of occurrence is defined as the number of times a taxa is recorded in the wetland. To assess the differences based on macroinvertebrate assemblages between the sub-areas (e.g. Cape flats, West Coast, Cederberg and Agulhas Plain), a multidimensional scaling plot was drawn using Primer software (Clarke and Warwick 2001).

2.3 Results

More than 26 000 individuals representing 126 taxa were founding this study. Currently a total of five species confirmed to be new to science, three in the Hydraenidae (P. D. Perkins *pers. comm*), one in the Streptocephalidae (M. Hamer *pers. comm*) and one in the Hydryphantidae (R. Gerecke *pers. comm*) were discovered. Three of these new species were recorded from the high mountainous Cederberg area (Streptocephalidae: *Streptocephalus* sp. nov, Hydraenidae: *Prosthetops* sp. nov and Hydraenidae: *Mesoceration repandum* Perkins, 2009), and one (Hydryphantidae: *Hydryphantes* sp. Nov) from Mfuleni area in the Cape flats cluster, while (Hydraenidae: *Parhydraena sp. nov*) appeared to be widespread as it was found in both Agulhas plain area and Piketberg area in the West Coast cluster.
The observed number of taxa (S_{obs}) is, a little short from the estimated "true" number of taxa, as the taxon accumulation curve has not quite reached the asymptote (figure 2.1) and the richness estimators (i.e. Jack and Chao) are still nowhere near to converging with the observed number of taxa (S_{obs}) (see Gotelli and Colwell 2001 for details). Different richness estimators yielded slightly different estimates of predicted actual richness, but they were all higher than the observed taxon richness. Chao 1 richness estimator predicts "true" taxon richness to be 135 taxa, while Chao 2 predicts true taxon richness to be 153. On the other hand 1st order Jacknife (Jack 1) predicts true taxon richness to be 156 and 170 for the 2nd order Jacknife (Jack 2). The same trend - as in the whole data set - appears also in the sub-areas (i.e. Cape flat, Agulhas Plain, Cederberg and West Coast) (see figures 2.2-2.4 and table 2.1). Second order Jacknife and Chao 2 richness estimators consistently yielded the highest and lowest taxon estimates, respectively, in all instances (see figures 2.1-2.4). The results from table 2.1, further reiterate the fact that sample size in this study was inadequate to capture the full potential richness, given the high number of singletons (taxa with only one individual) and uniques (taxa that occur in a only one sample): 11 and 30, respectively. There was a relatively good graphic separation of the different sub-areas based on their macroinvertebrate assemblages (see figure 2.5). In addition, Incidence-based Coverage Estimator (ICE) showed S_{obs} to be at least 28 taxa short of the estimated "true" taxon richness in the area that might have not been sampled due to sampling or analytical biases (Gotelli and Cowell 2001; Magurran 2003), thus indicating the incompleteness of the sampling. In contrast, the Abundance-base Coverage Estimator (ACE) and the Michaelis-Mentis richness estimator yielded taxon estimates fairly similar estimated true taxon richness compared to the observed.

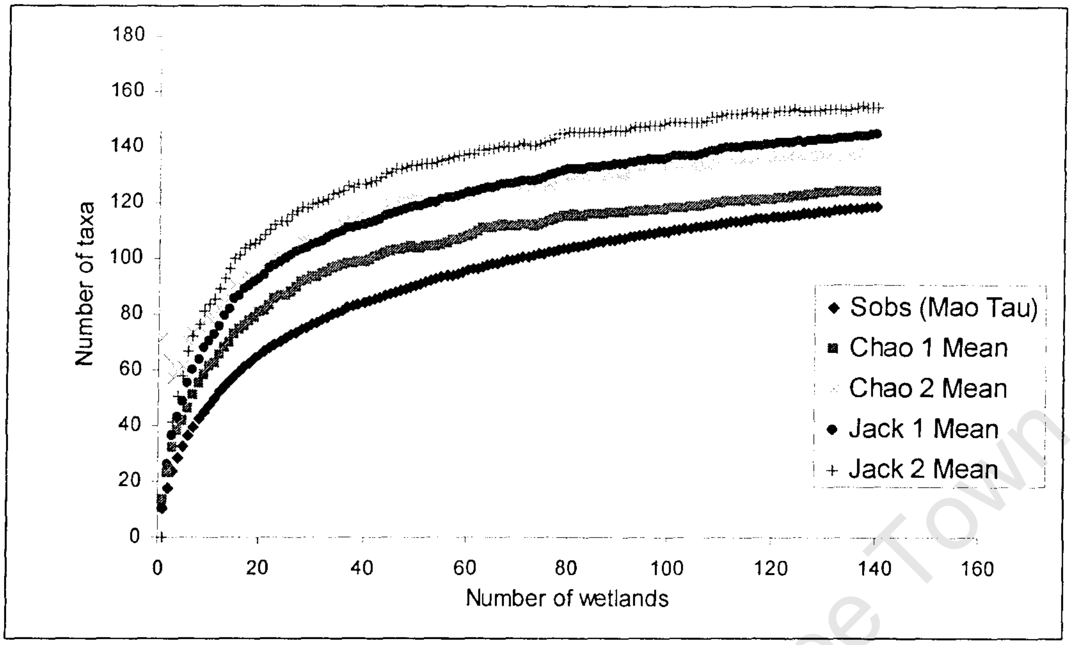

Figure 2.1 Sample-based taxon accumulation curves of wetland macroinvertebrate assemblages for the whole data set.

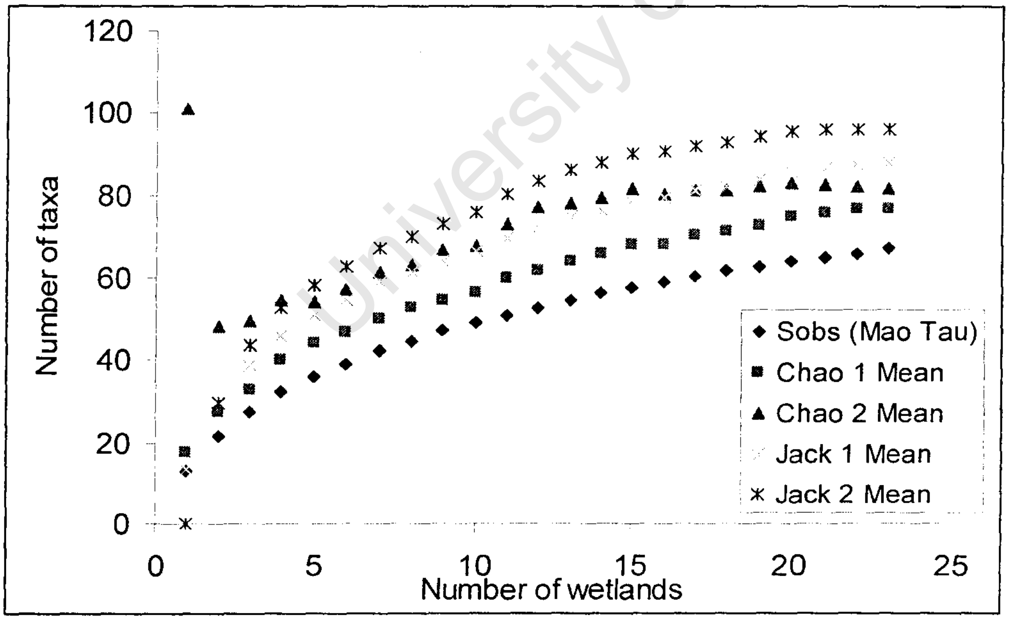

Figure 2.2 Sample-based taxon accumulation curves of wetland macroinvertebrate assemblages for Agulhas Plain cluster.

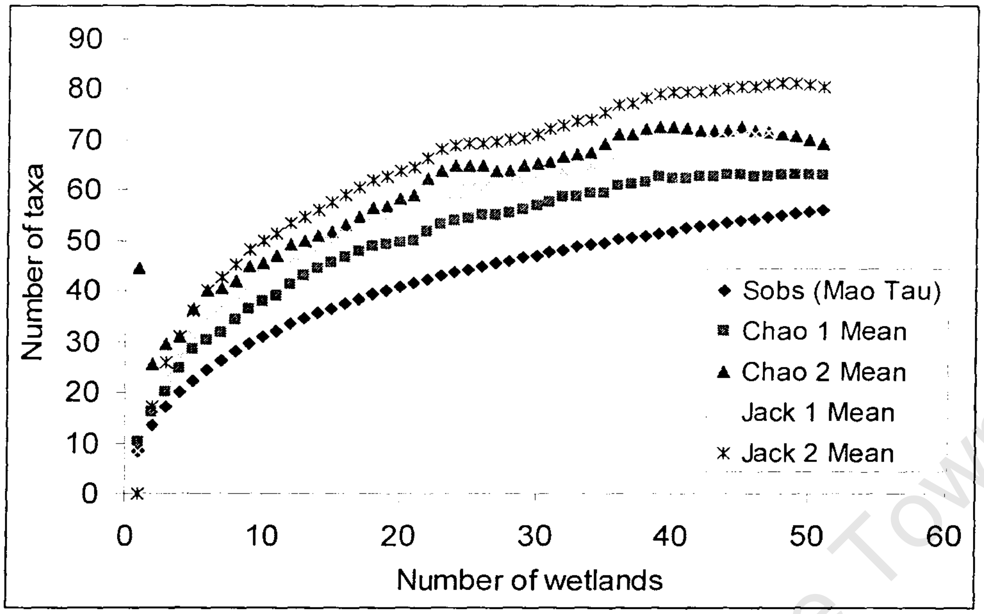

Figure 2.3 Sample-based taxon accumulation curves of wetland macroinvertebrate assemblages for West Coast cluster.

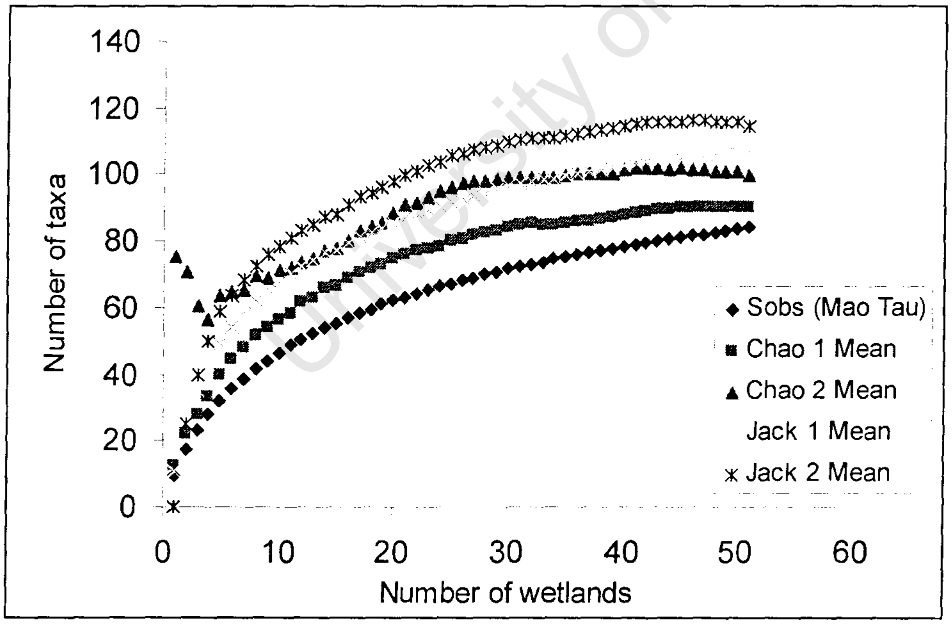

Figure 2.4 Sample-based taxon accumulation curves of wetland macroinvertebrate assemblages for Cape Flat cluster.

Table 2.1 The number of sites, observed taxa (T_{obs}), and the mean values for the: singletons, uniques, Abundance-base Coverage Estimator (ACE), Incidence-based Coverage Estimator (ICE) and the Michaelis-Mentis richness estimator (MM_{mean}) of the sample-based rarefaction curves.

	Sites	**T_{obs}**	**Singletons**	**Uniques**	**ACE**	**ICE**	**MM**
Whole data	140	126	11	30	133	154	129
Agulhas	23	67	13	22	78	90	79
West Coast	51	56	11	17	67	74	60
Flats							
berg							

*Taxa with only one individual. ^{a}Taxa that occur in a only one sample.

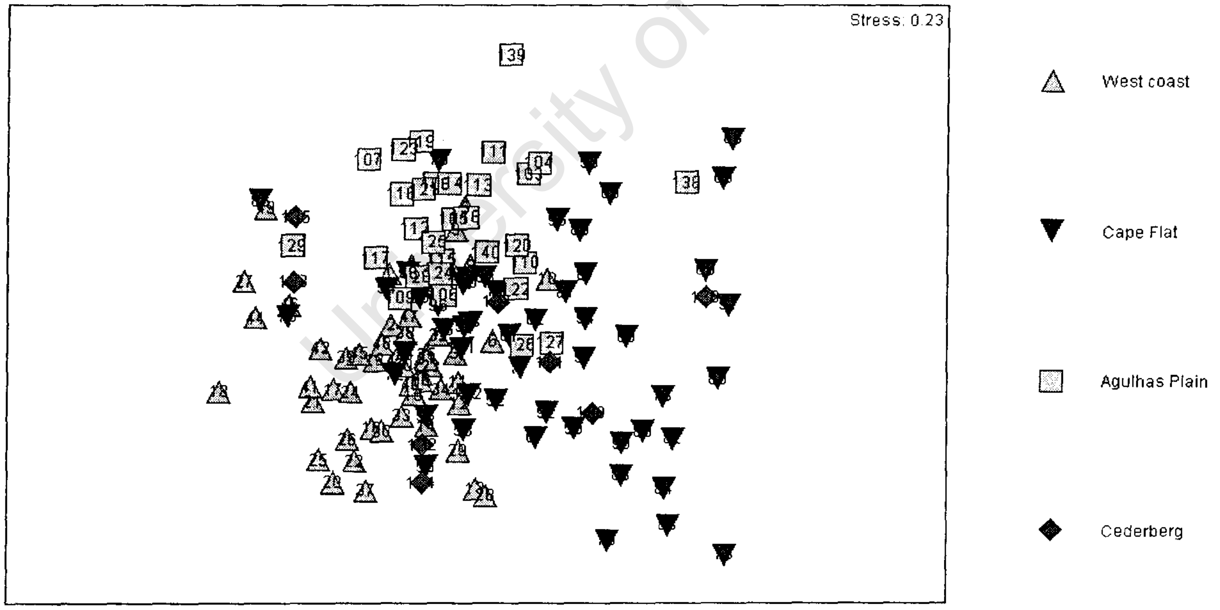

Figure 2.5. Multidimensional Scaling plot showing the association of wetlands based on the relative abundance of assemblages from different areas

2.3.1 Order/Class level resolution

Diptera exhibited the highest relative abundance contributing nearly a third of the total number of individuals for the entire assemblage. Coleoptera had the second highest relative abundance followed by Gastropoda, Hemiptera and Ephemeroptera (in their order of dominance), all contributing ≥10% to the overall assemblage (see figure 2.6). Acarina and Odonata had the least relative abundance, contributing only 2% and 1% respectively to overall assemblage. The Acarina contributed the greatest number of families a total of nine, followed by Coleoptera and Hemiptera with six families each, Gastropoda (five), Crustacea (four), Odonata and Diptera (three each).

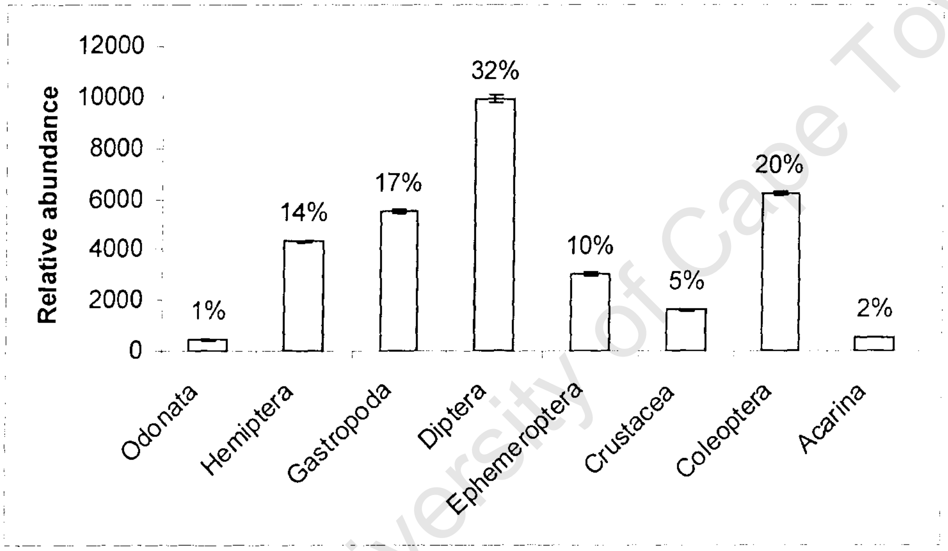

Figure 2.6 The relative abundance of wetland macroinvertebrate orders. The percentage above each bar, indicates the overall contribution of that order to overall relative abundance.

2.3.2 Family-level resolution

A total of 51 families were recorded in this study, but, only twenty had a relative abundance of more than 100 individuals and were therefore included in the graph (see figure 2.7). Chironomidae overwhelming dominated the overall assemblage abundance contributing 20%, followed by Dytiscidae, Pomatiopsidae, Culicidae and Baetidae (in their order of dominance) all contributing more than 10%. The top five most dominant families together contributed more than two-thirds of the overall assemblage abundance. Chironomidae was made up of the three subfamilies Tanyponinae, Chironominae and

Orthocladinae, contributing approximately 1%, 76% and 23% respectively of the total chironomid assemblage. Although the families Stratiomyidae, Gerridae and Scirtidae had a relative abundance of more than 100 individuals as the cut-off point to be included in the graph, they each contributed less than one percent to the total assemblage. Moreover, a substantial number of the other families only contributed just a percent to overall assemblage (figure 2.8). A slightly different pattern appears with the frequency of occurrence analysis, where the Dytiscidae topped the list, occurring in more than 130 wetlands out of the 140 sampled. Although frequency of occurrence does not necessarily imply richness, dytscids were also the most speciose family. The Chironomidae was the only other family that occurred in more than 100 wetlands out a 140 sampled, occurring in 108 sites. Culicids, notonectids, corixids and baetids were the only other families in addition to chironomid and dytiscid to be found in more than half of the sampled wetlands. In total, only 18 families occurred in more than 20 out of the 140 sampled wetlands. Interestingly, the Pomatiopsidae, which is the third most abundant family was found at only 45 sites.

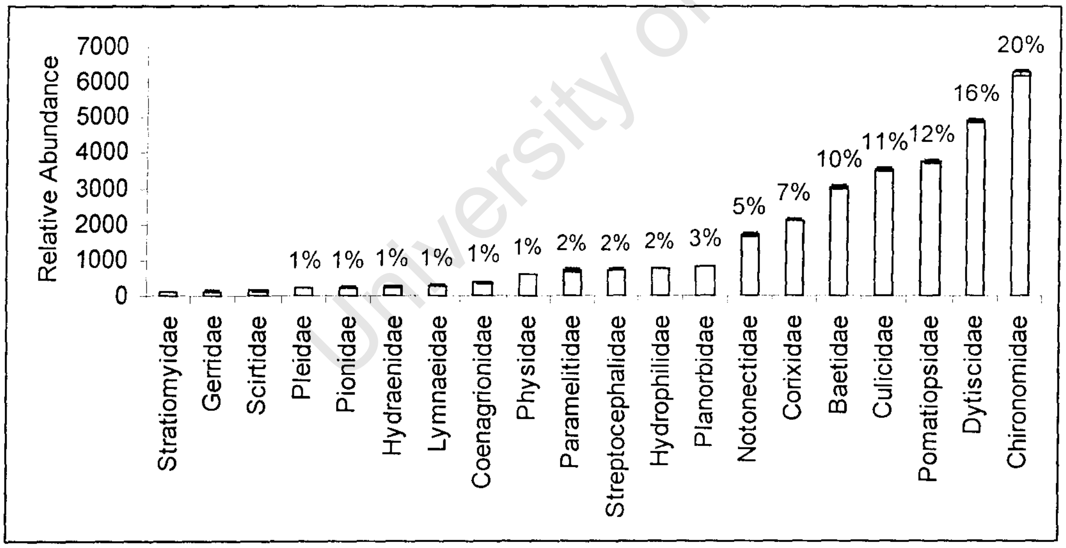

Figure 2.7. Relative abundance of wetland macroinvertebrate families with their standard deviations. Only those taxa with more than 100 individuals were included. The percentage above each taxa, indicates the overall contribution of that taxa to overall relative abundance.

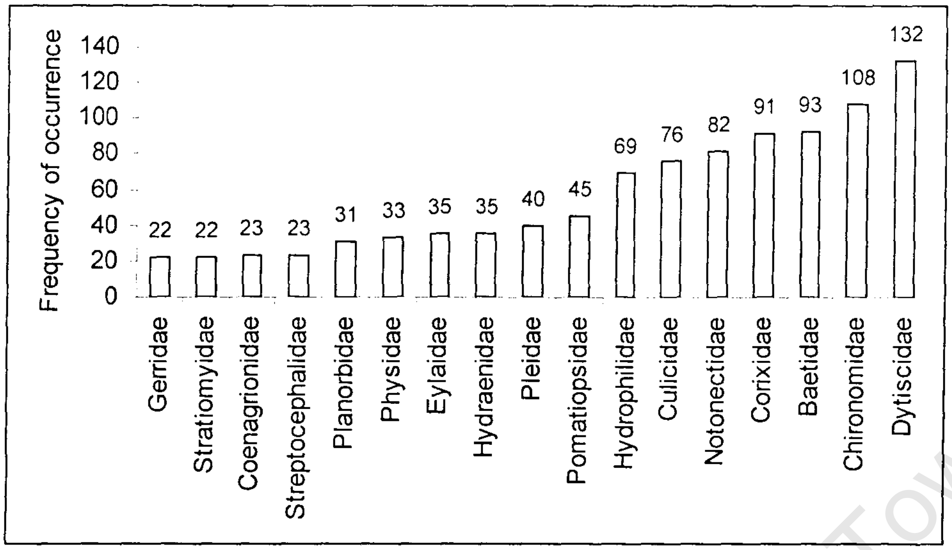

Figure 2.8. Frequency of occurrence of wetland macroinvertebrate families. Only those families that occurred in more than 20 wetlands are included. Above each bar graph is the absolute value of the frequency of occurrence of that family.

2.3.3 Genus level resolution

A total of 73 genera was identified in this study, although, the actual number of genera collected might by more than this, considering that for some taxa, such as Chironomidae and Hydracarina, it was not possible with our limited current taxonomic understanding to identify to genus level. On other hand, some specimens of taxa like Odonates, were too small to be correctly identified to lower taxonomic levels (P. Simaika *pers. comm*). The Hydrophilidae and Dytiscidae contributed the highest number of genera (ten each), followed by the Hydraenidae with nine, Culicidae (four), Coenagrionidae and Hydryphantidae (three each), and Corixidae, Eylaidae, Gerridae, Haliplidae, Notonectidae, Physidae and Planorbidae each contributing two genera. The ephemeropteran genus *Cloeon*, being almost exclusively lentic, exhibited the highest frequency of occurrence, occurring in 93 wetlands out of 140 (figure 2.9). Although it is next to impossible to tell *Cloeon* species apart at the nymphal stage (which is the stage recorded in this study), nine species of this genus have been recorded in South Africa (Barber-James and Lugo-Ortiz 2003). Together with the Hemipteran genus *Sigara,* which had the second highest occurrence being recorded in more than 90 wetlands, they were the only genera found in more than half the wetlands. The coleopteran genus *Canthyporus,* the hemipteran *Anisops and Notonecta* and the dipteran *Culex* all were found in more than 50 wetlands. In total, only 22 genera were found in more than 15 wetlands, which was the cut-off point for inclusion in the graph, with water mite *Neumania* and the conchostracan *Leptestheria*, just missing the cut-off occurring in 15 wetlands. Pomatiopsid genus: *Tomichia* was found to have the highest relative abundance, contributing 19% to the total assemblage abundance. The significance of *Tomichia* is that all eight recorded species in Southern Africa are actually endemic, found mainly on the coastal lowlands (Appleton 2002). *Cloeon*, *Culex* and *Sigara,* respectively all contributed ≥10% to overall assemblage abundance. Most other genera represented by greater 100 individuals, contributed very little (1% or 2%) to overall abundance (figure 2.10).

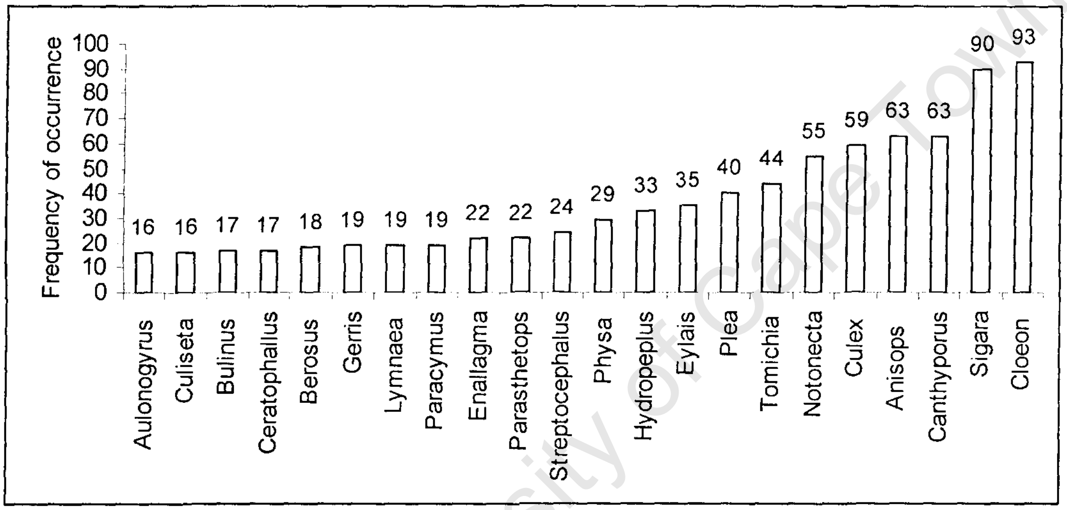

Figure 2.9. Frequency of occurrence of wetland macroinvertebrate genera. Only those genera that occurred in more than 15 wetlands were included. Above each bar graph is the absolute value of the frequency of occurrence of that genus.

2.3.4 Functional feeding groups

Predators and gatherers were found in most wetlands, 130 and 124 respectively, followed by scrapers which occurred in 95 wetlands, while filterers and shredders only occurred in fewer than half of the sampled wetlands (figure 2.11). However, gatherers generally made of small invertebrates including oligochaete worms, cladocera, chironomid larvae, isopods etc, feeding on small particles, dominated in terms of relative abundance contributing more than a third to the total abundance. Predators and scrapers had pretty similar abundances, differing by just one percent in their overall contribution to relative abundance (see figure 2.12). Filterers and shredders contributed the least to overall assemblage abundance at 14% and 5% respectively.

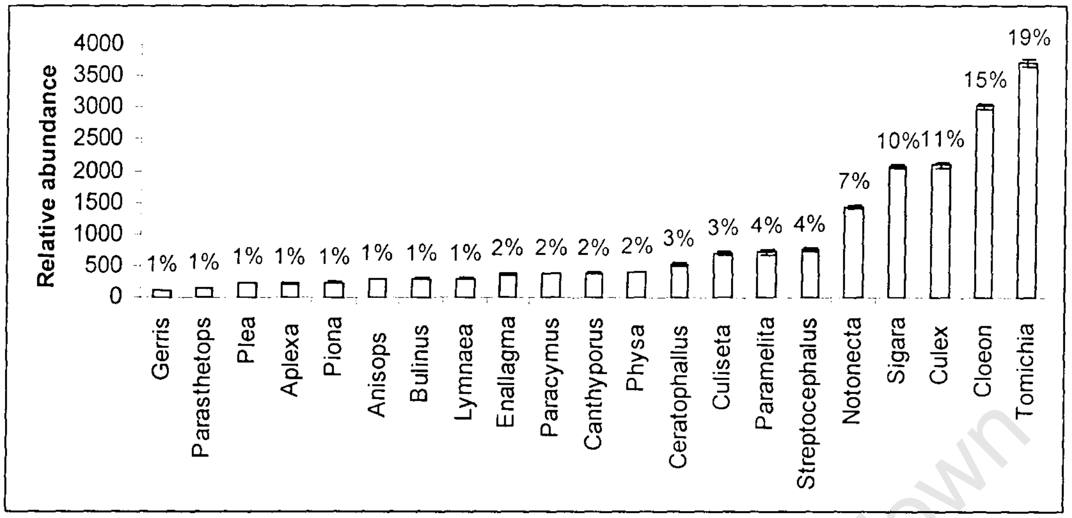

Figure 2.10 Relative abundance of wetland macroinvertebrate genera with their standard deviations. Only those genera with more than 100 individuals were included. The percentage above each bar, indicates the overall contribution of that genus to overall relative abundance.

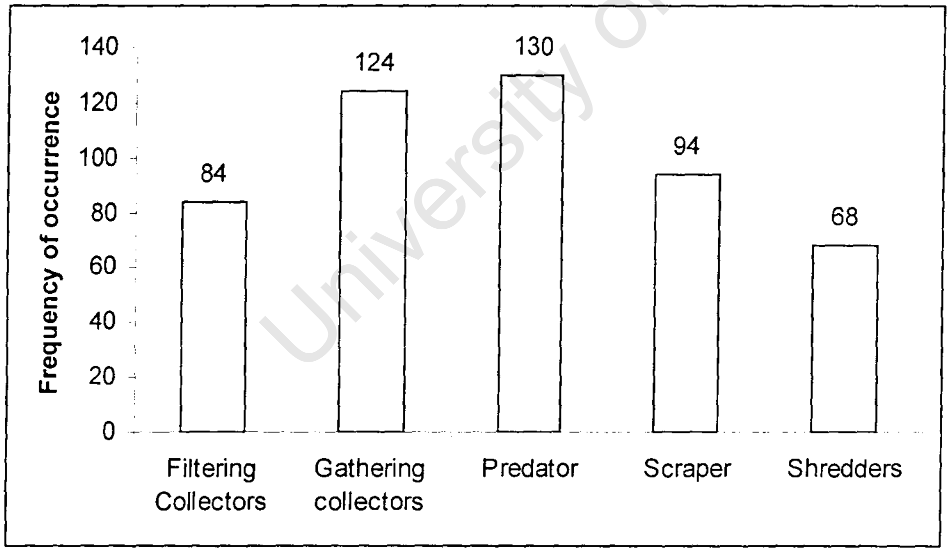

Figure 2.11. Frequency of occurrence of wetland macroinvertebrate functional feeding groups (FFG). Above each bar graph is the absolute value of the frequency of occurrence of that FFG.

2.3.5 Life history strategy

Transient taxa overwhelmingly dominated macroinvertebrate assemblages as evident from both data sets. In terms of relative abundance (figure 2.13), they accounted for more than two-third of the total relative abundance. While resident taxa with fewer than a thousand individuals, in comparison with over 15 000 for transient taxa, contributed just 29% to overall relative abundance. Resident taxa occurred in just over 100 sites out of the 140 sampled, compared with 139 for the transient taxa (figure 2.14).

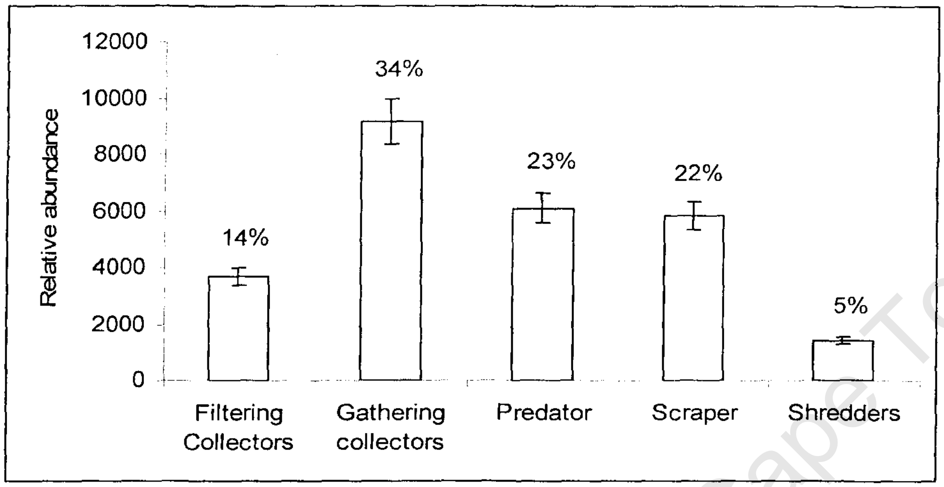

Figure 2.12. Relative abundance of wetland macroinvertebrate FFG with their standard deviations. The percentage above each bar, indicates the overall contribution of that FFG to overall relative abundance.

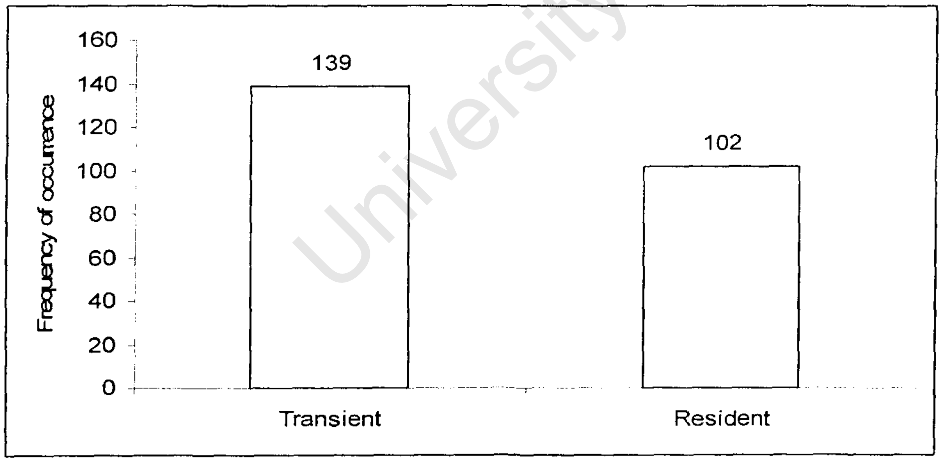

Figure 2.14 Frequency of occurrence of wetland macroinvertebrate LHA. Above each bar graph is the absolute value of the frequency of occurrence of that LHA.

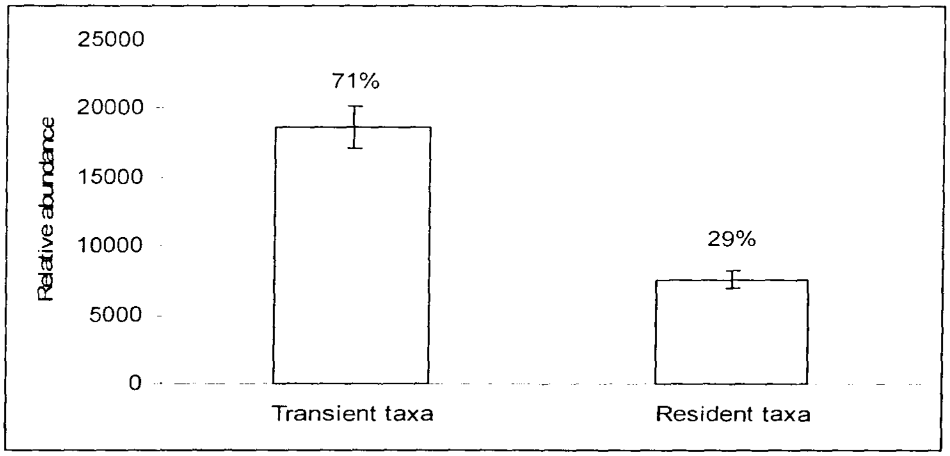

Figure 2.13 Relative abundance of wetland macroinvertebrate Life History Adaptation (LHA) with their standard deviations. The percentage above each bar, indicates the overall contribution of that LHA to overall relative abundance.

2.3.6 Habitat types

A statistically significant difference in the relative abundance of the total macroinvertebrate assemblage was found between open-water and submerged vegetation habitats, but not emergent vegetation habitat (figure 2.15). Submerged vegetation habitat had a mean of 13 individuals per wetland, while emergent vegetation and open-water habitats had 12 and 7, respectively. However, frequency of occurrence of invertebrates was significantly greater in both vegetated habitats (submerged and emergent) than open-water habitat (figure 2.16). On average per habitat, open-water harboured just fewer than 4 taxa, while both vegetated habitats hosted roughly 8 taxa. No statistically significant differences were observed between wetlands with different numbers of habitat types using both datasets. However, wetlands with a single habitat type tended to have a lower but not statistically significant taxon richness (figure 2.17), averaging about 9 taxa per wetland, whereas, wetlands with two and three habitat types averaged around 11 taxa. The same pattern was seen with the relative abundance analysis, although the differences between the means were not large (see figure 2.18).

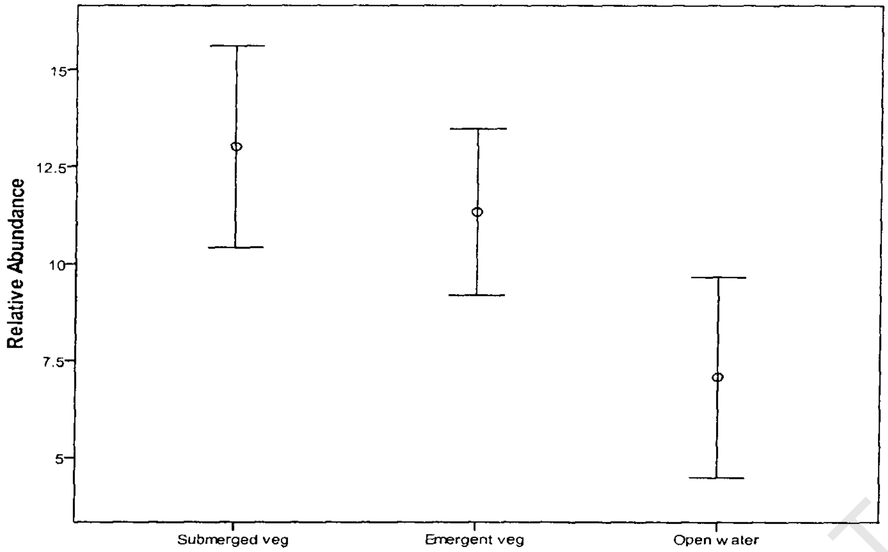

Figure 2.15. The relative abundance of wetland macroinvertebrates in different biotypes. Error bars show 95.0% CI of mean; centre of the bar (o) represent the mean. Anova F=3.742, p=0.024, df=2.

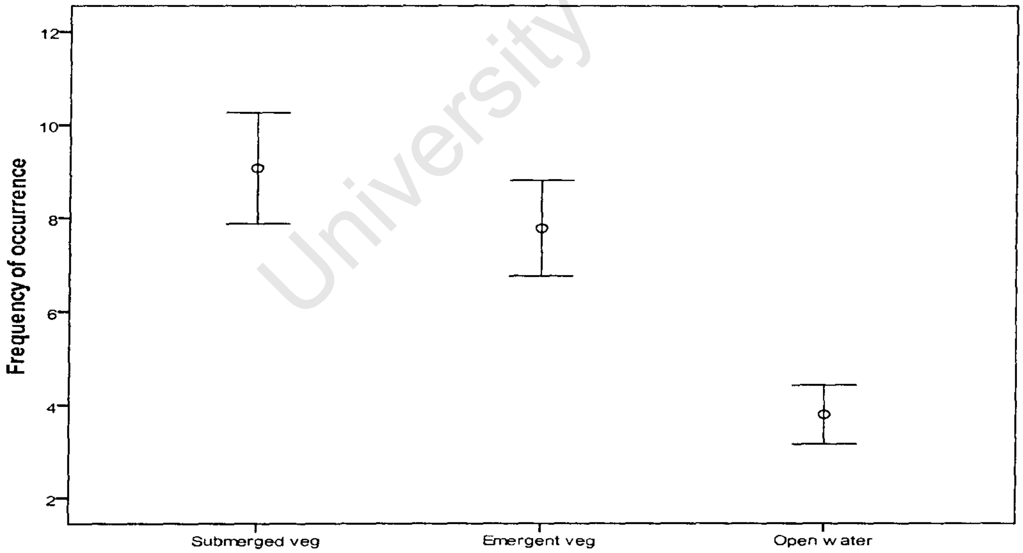

Figure 2.16 The frequency of occurrence of wetland macroinvertebrates in different biotypes. Error bars show 95.0% CI of mean; centre of the bar (o) shows mean. Anova F=31.794, p=0.000, df=2.

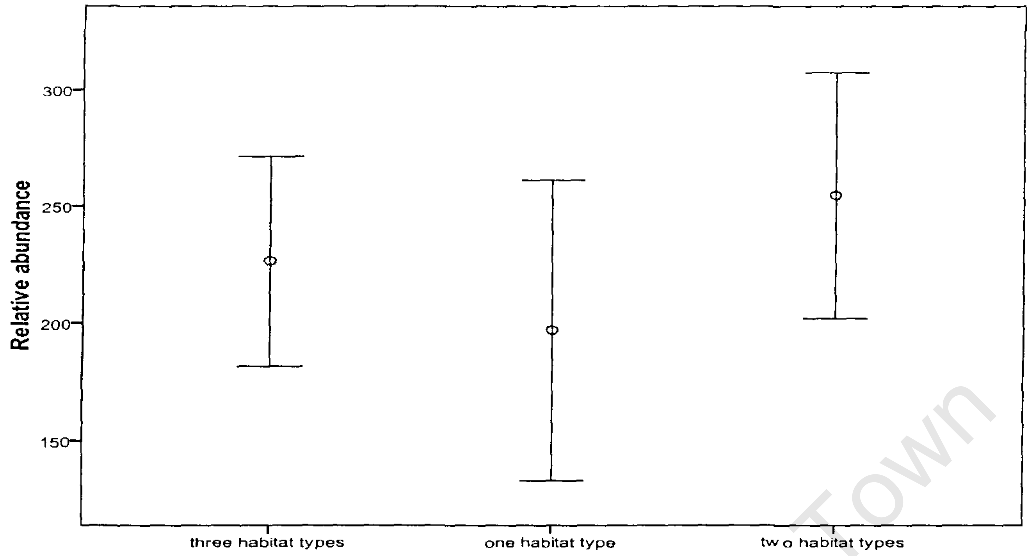

Figure 17 Relative of wetlands with different number of identifiable habitats. Showing the mean and the error bar denotes the 95% confidence interval of the mean. Anova F=1.530, p=0.151, df=2.

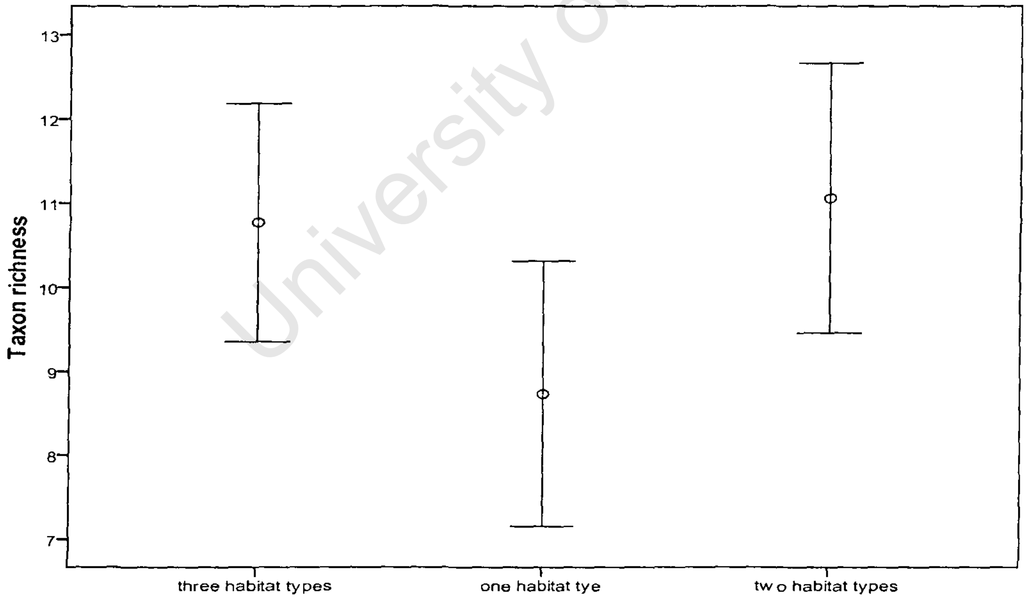

Figure 2.18. Taxon richness of wetlands with different number of identifiable habitats. Showing the mean and the error bar denotes the 95% confidence interval of the mean. Anova F=2.434, p=0.092, df=2.

2.4 DISCUSSION

In nature, the observed (or sampled) taxon diversity (S_{obs}) is not always a true representation of the actual diversity present in that area. This may be for a number of reasons, including, for instance, sampling bias (Magurran 2003; Southwood 2006) and behavioural or physiological adaptation by some taxa, e.g. those that undertake diel migration (e.g. Marklund *et al.* 2001). In this study S_{obs} was found to be an under-representation of the estimated actual or true taxon diversity for the south-western Cape. The extent of the difference between the S_{obs} and estimated "true" richness varied depends on which richness estimator is used (Figure 2.1). The strengths and weaknesses of such richness estimators are beyond the scope of this chapter but are discussed somewhere else (Walter and Moore 2005, Hortal, Borges and Gaspar 2006). The idea that the "true" potential taxon richness was not observed in this study because wetlands exhibited a gradient of disturbance. And that this idea of "true" species richness only holding true in pristine environments is not supported, because the true richness estimates were derived from the empirical data. In fact, the work of Brose *et al.* (2003) has shown that sometimes some other estimators (e.g. the 2nd order Jacknife richness estimator or Jack 2) perform significantly better than S_{obs} in estimating the true richness. If this assertion holds true in this study, Jack 2 suggested that the S_{obs} was 44 taxa short of the estimated "true" richness. In this study, Jack 2 constantly yielded higher estimates of "true" taxon richness through all the data sets (whole data set and sub areas), with Chao 2 and Jack 1 richness estimators having pretty similar middle estimates and Chao 1 having the lowest estimates (Figures 2.1 – 2.4). Foggo *et al.* (2003) in their evaluation of techniques used for extrapolating species richness techniques using British littoral pond invertebrate data, concluded that the Chao 2 richness estimator was the best performer. In my study Chao 2 estimated the true taxon richness to be 158, 27 taxa more than the observed taxon richness (S_{obs}).

The high number of uniques and singletons can be explained as either; the sample size (n= 140 sites) was insufficient in capturing the potential full regional (south-Western Cape) diversity, or as a reflection of the uniqueness of macroinvertebrate harboured by the individual wetlands. I strongly suspect that the latter explanation is more plausible. Nevertheless, the different richness estimators for the sub areas (i.e. Cape flats, Agulhas plain and West coast) were far from converging with the S_{obs} curve some how supporting the other explanation. The Cederberg area was exceptionally diverse and the observed taxon richness was a far cry from the true potential taxon richness of the area, as it is had the highest number of singletons and uniques probably indicating that the number of samples is inadequate for estimating the true richness of the area. Taking into account the fact that only 8 wetlands were sampled in this sub-area, this is not surprising. Cederberg is incredibly diversed as evident from the discovery of three out of the five new species discovered in this area. Walter and Moore (2005) argued that persistence or increase of singletons results in the rising of the species-accumulation curve indicating that the total potential true species richness in the area has not been reached. Moreover, the incidence-based coverage estimator (ICE), abundance-based coverage estimator (ACE) and the Michaelis-Menten richness estimator (MM) despite small discrepancies (see table 2.1), all showed that sample size did not adequately represent the estimated "true" potential richness. Although, this study found little agreement on the results of MM model and the ICE, other studies have found them to perform similarly (Longino *et al.* 2002; Brose *et al.* 2004). ICE in particular - which is a robust measure indicating sampling completeness (e.g. Longino *et al.* 2002) - revealed that the observed taxon richness in this study was at least 20 taxa short of the actual richness. Foggo *et al.* (2003) found ICE - which is independent of sample size - to be reliable but consistently a slight over-estimator. However, these authors (Foggo *et al.* 2002) cautioned that counting individuals beyond an abundance of two yields little additional information if the aim is simply to quantify maximum species richness in a pond. This is crucial since abundance based estimator (ACE) relies heavily upon accurate sampling of abundance profiles, something rarely achieved in real life given the sampling constraints (Gotelli and Colwell 2001).

The fact that despite some discrepancies all the different richness estimators, predicted slightly higher "true" richness than that observed, convincingly tells us that this is a real phenomenon, not just a statistical artifact. This may suggest that our understanding of biodiversity and distribution of wetland macroinvertebrates is still grossly inadequate. This may not be a surprise, given that the Western Cape is recognized as an exceptional biodiversity hotspot harbouring unique and endemic biota (Werger 1978; Picker and Samways 1996; Goldblatt and Manning 2000; Myers et al 2000; Olson and Dinerstein 2002; Wishart and Day 2002). This study was quite comprehensive in its sampling (in terms of geographic coverage), and perusal of the literature yields no other comparable study. In addition, the fact that observed taxon accumulation curves did not reached asymptotes reiterates the fact that we are dealing with a sheer diverse study area, supporting high number of rare taxa. To adequate sample rare taxa, sampling needs to be carried repeatedly on the same area. A weak point about this study, though, is that wetlands were only sampled once. However, this must be taken in context, given that the objective of this study was to investigate overall large-scale (regional) biodiversity patterns. Therefore, these results show a snap-shot of the assemblage at that particular time, which might not be a true representation of the entire assemblage given the dynamic nature of temporary wetland macroinvertebrates (Rader, Rader and Wissinger 1999). Perhaps that is why the observed taxon richness is shown to be 20 - 47 shorter of the estimated richness, because species richness is known to increase with increasing hydroperiod (Scheider and Frost 1996).

Considering the technical challenges of obtaining taxon diversity, this study recorded 126 taxa with five confirmed new species from a once-of sampling coupled with extreme taxonomic burden. The Cape Flats yielded the highest number of taxa, followed by the Agulhas plain then the West Coast and the Cederberg. However, despite the Cederberg registering the lowest cumulative observed taxon richness, it was by far the richest per wetland since only 8 wetlands supported almost half the taxon richness of the whole study, and harboured the three new species. The results of this study are comparable with other studies undertaken in the Mediterranean-type regions, although conducted over extended periods of time. For example, Boix *et al.* (2001) found 113 taxa in a large (3.1ha) temporary pond in the NE Iberian Peninsula, whereas Halse *et al.* (2002) working in south-Western Australia collected 150 aquatic invertebrates from five large wetlands although some were permanent. Hall *et al.* (2004) studying Playas of the Southern High Plains of Texas, USA, found 107 taxa. The discovery of five species new to science from the samples of this study goes to show how little we know about wetland invertebrates in this part of the world. This is extremely important considering that beetles and anostracans (the flagship taxa of temporary wetlands) are one of the relatively well studied groups. At the moment it is still difficult to say much about rare, endemic and conservation-important taxa, since the adequate understanding of how many species actually occur in these systems, let alone their definitive distributions, is still not well understood. The same sentiment is also shared in south-western Victoria, Australia (Robson and Clay 2005).

The order Diptera was found to exhibit the highest abundance, followed by the Coleoptera. This observation is in line with a study by Oertli *et al.* (2008), conducted in a Swiss National Park reporting Chironomidae (Diptera) and Coleoptera to be the most dominant taxa. Furthermore, Whiles and Golowitz (2005) working on the central Platte River Wetlands in Nebraska, United States, reported that insect communities were dominated by dipterans and coleopterans. The same observation was made on the west coast of the South Island of New Zealand, where the invertebrate fauna was reportedly dominated by insects such as Chironomidae (in particular Tanypodinae and Orthocladiinae) and

Ceratopogonidae (Suren *et al.* 2008). These authors (Suren *et al.* 2008) noted that the dominance by chironomids might have management implications as chironomids are important food for fish and waterfowl (Batzer and Wissinger 1996). From these cited studies and the current one, it appears that chironomid midges have a lot to do with dipteran dominance of assemblage biomass. In agreement with Panatta *et al.* (2006), who reported that the Chironominae exhibit the greatest richness, followed by Tanypodinae and Orthocladiinae, the result of the present study followed the same trend with Chironominae accounting for more than two-thirds of the chironomids abundance. Representatives of other taxonomic groups like oligochaetes, nematodes, water mites, crustaceans and gastropods, have also been reported to be dominant component of the macroinvertebrate communities elsewhere (Batzer and Wissnger 1996; Hall *et al.* 1999; Wissinger 1999; Whiles and Golowitz 2005) indicating that they are tolerant to environmental conditions prevailing in wetlands (Brönmark and Hansson 1998). Oertli *et al.* 2008 noticed the conspicuously poor representation of odonates in low land ponds in Switzerland, the same observation seen in this study and shared by Taylor *et al.* (1999), who suggested that perhaps this was because the ponds had dried the previous years.

Family-level analysis of relative abundance showed that Chironomidae contributed 20% of the assemblage abundance. Together with Dytiscidae, Pomatiopsidae, Culicidae and Baetidae (in their order of dominance) these families contributed more two-third of the total assemblage. However, a slightly different view appears when considering the frequency of occurrence, where Dytiscidae topped the list, occurring in more than 130 sites. Only other five families - in addition to the Dytiscidae - occurred in more than half of the sites; these include Chironomidae, Baetidae, Corixidae, Notonectidae and Culicidae. Interestingly this list excludes the Pomatiopsidae which is one of the top five most abundant families. The large number of genera (10 each), in the Dytiscidae and Hydrophilidae are in agreement with the results of Robson and Clay (2005), closely followed by yet another beetle family, the Hydraenidae with 9 genera. From the fact that only 18 families out of the 51 found in this study occurred in more than 20 out of the 140 sampled wetlands and that only 20 families were represented by more than 100 individuals, goes to show that temporary wetland communities are dominated by relative few taxa. The fact that only a handful of families contributed more two-thirds to the overall assemblage, might be the reason why temporary wetland invertebrates are less biodiverse compared to their permanent counterparts (Collinson *et al.* 1995). On the other hand, it can be equally argued that this also goes to show that temporary wetland invertebrates are unique (sensu Wissinger 1999). Furthermore,

CHAPTER 3

ASSESSMENT OF CONGRUENCE OF WETLAND MACROINVERTEBRATE ASSEMBLAGES AT DIFFERENT TAXONOMIC LEVELS

This chapter addresses the issue of assemblage congruence as it has important implications for biodiversity assessment. It starts of by reviewing the different surrogate methods currently used to estimate biodiversity and then attempt to apply some of these to the current study.

3.1 INTRODUCTION

3.1.1 Biodiversity and Biomonitoring

Biologists have always been fascinated by the sheer biological diversity exhibited by planet Earth. However, it has proven to be quite a daunting undertaking to understand and document, since it varies both in space and time (Gaston 2000a; Myers *et al.* 2000). Species richness – which, simply put, is the number of species at a site - has become the standard biological measure for assessing biodiversity (Gaston and Spicer 1998). But Harper and Hawksworth (1994) argue that the biological diversity of an area is more than just the numbers of species present. The lack of information about the diversity and distribution of many species poses a major impediment to identifying areas of high biodiversity conservation priority (Breid *et al.* 2007; Hirst 2008). Complete species inventories for many areas currently do not exist and performing such surveys is often prohibitively expensive and laborious (Balmford *et al.* 1996b; Lawton *et al.* 1998; Báldi 2003; Lovell *et al.* 2007). It is even a greater task for small taxa such as the invertebrates given their large numbers (Myers *et al.* 2000) coupled with problems of taxonomic identification and need for a wide range of sampling strategies to cover the full spectrum of biodiversity (Southwood 2006).

Although fresh water occupies only 0.8 % of the Earth's surface, it supports almost 6% of all described species (Dudgeon *et al.* 2006), emphasising the need for rigorous biodiversity research in freshwater ecosystems. The fact that freshwater ecosystems are more highly threatened than their terrestrial counterparts (Dudgeon *et al.* 2006), makes freshwater biodiversity conservation an urgent matter. In addition, contrary to the conventional use of biodiversity information to make inferences about species, Jones *et al.* (2008) posit that freshwater biodiversity is used to make inferences about the status of the ecosystem. For example, in the use of biomonitoring techniques, the emphasis is not merely on the occurrence of the taxon *per se* but more on the ecological condition signified by its occurrence. This is because freshwater organisms, invertebrates in particular, have high fidelity to their environments. Therefore, a lack of proper understanding of natural spatio-temporal variation of invertebrate biodiversity, because of difficulty in assessing it, prevents conjectures to be made about ecosystem status. Simply put, lack of biodiversity understanding is an impediment to development and implementation of biomonitoring techniques.

3.1.2 Surrogacy/indicators

Owing to the difficulties - alluded to above - in investigating biodiversity, researchers have come up with a number of shortcuts for monitoring, documenting and studying biodiversity. Shortcuts to measuring biodiversity enable prioritization of efforts in the face of limited time, personnel and funding (Andelman and Fagan 2000; Bried *et al.* 2007). This is especially important in the light of looming global climate change, which is expected to alter many organisms' biogeographic patterns and cause the extinction of some taxa (Midgley *et al.* 2002; 2005). The concept of using surrogates has been hailed as a promising shortcut to measuring biodiversity (Caro and O'Doherty 1999; Andelman and Fagan 2000). It relies on the principle of determining only a representative subset of the assemblage, thereby significantly cutting costs (Balmford *et al.* 1996b; Briers and Biggs 2003). Cardaso *et al.* (2004) asserted that surrogacy can be seen either as a preliminary approach if it is not possible to have all taxa identified, or as an end in itself in regions where most species are unknown, or when no resources are available for further identification (e.g. Balmford *et al.* 1996b). However, the extent to which surrogates can successfully be applied hinges on the level of concordance of chosen surrogates with the entire assemblage (Bini *et al.* 2008; Hirst 2008; Mazaris *et al.* 2008).

3.1.3 Concordance

Jackson and Harvey (1993) define assemblage concordance as the degree to which patterns in assemblage structure across a set of sites are similar among different taxonomic groups. Such concordant patterns can arise from several mechanisms, i.e. biotic and abiotic interactions acting across time and space (Gaston and Williams 1996, Heino 2002; Heino *et al.* 2005; Grenouillet *et al.* 2007; Bini *et al.* 2008). In the literature, variable degrees of congruence at different scales have been recorded, causing discrepancies about the scale at which congruence is pertinent to biodiversity assessment. The highest degree of congruence has generally been reported at continental (Pearson and Carroll 1999; La Ferla *et al.* 2002; but see Anderson 1995), and regional scales (Gaston and Williams 1996), while studies at local scale have typically reported low concordance (Gaston 1996; Lawton *et al.* 1998). Moreover, concordance among freshwater organisms (e.g. Grenouillet *et al.* 2007) has rarely been studied compared to other ecosystems. Consequently, the utility of surrogates for biodiversity conservation and bioassessment is rather poorly developed for freshwater ecosystems (Heino *et al.* 2005; Heino and Soininen 2007). This is particularly troublesome given the urgent need to identify and conserve the last havens of biodiversity in the light of absent species-level information for many taxonomic groups. Throughout this chapter concordance is used synonymously with congruence.

In the literature, three types of surrogates are generally promoted (*e.g.* Monero *et al.* 2007): 1) indicator groups or taxa, 2) richness among higher taxa, and 3) environmental surrogates. Below, these surrogate methods are reviewed, but the first two will be the focal subject of this chapter.

3.1.4 Indicator groups or taxa

Indicator taxa should possess a set of properties like being cost-efficienct and easy to sample, being applicable at different spatio-temporal scales and, more importantly, strongly correlating with the represented assemblage (McGeoch 1998). In addition, they should be sensitive and their responses easily measured (Clark and Samways 1996). Caro and O'Doherty (1999) provide an eloquent review of the different indicator groups, which they grouped as ecosystem health indicators, population indicators, umbrella species, flagship species and biodiversity indicators. In the literature, a number of wetland macroinvertebrates have been recorded as indicators belonging to some of these different categories. Examples are, branchiopods as flagship species (De Roeck *et al.* 2007), odonates as umbrella species (Breid *et al.* 2007), and beetles and bugs as biodiversity indicators (Sánchez-Fernández *et al.* 2006; Apinda-Legnouo 2007). Furthermore, Clark and Samways (1996) used odonates as indicators of biotype quality in Kruger National Park rivers, while Foote and Hornung (2005) used them as biological indicators of the impact of grazing. Moreover, several freshwater taxa (e.g. fish, birds, plants and macroinvertebrates) have been used extensively as indicators in monitoring the status of freshwater habitats with respect to potential pollutants and/or nutrient enrichment (Davies and Day 1998; Wissinger

1999; Dickens and Graham 2002). Barlow *et al.* (2007), caution, however, that although the indicator taxon concept may be valid for some taxa, it fails for those exhibiting highly idiosyncratic responses to land-use change, to which freshwater biodiversity is highly susceptible.

Indicator taxa are usually assumed to be congruent with the represented assemblage, although this assumption is rarely been tested. Bini *et al.* (2008), for example, argue that biomonitoring programme in freshwater ecosystems have used indicator groups and assumed that the results can be extrapolated to other unstudied groups. Despite the wide usage of indicator taxa, a number of authors (e.g. van Jaarsveld *et al.* 1998; Kotze and Samways 1999; Lovett *et al.* 2000; Lovell *et al.* 2007) have shown empirical evidence against the use of single indicator taxa. Briers and Biggs (2003) argue for instance, that taxa that are good pond biodiversity indicators are not necessarily good indicators for lakes or other freshwater habitats. Moreover, taxa that appear to be good indicators in one geographical area, may not necessarily be representative of richness patterns elsewhere, given co-variation of richness being highly spatially structured (Briers and Biggs 2003). Although biodiversity indicators (Caro and O'Doherty 1999) have been extensively used in terrestrial biodiversity conservation, Briers and Biggs (2003) argue that little has been done to develop indicator taxa for assessment of freshwater invertebrate biodiversity. That is why the present study explores this notion further.

3.1.5 Use of Higher taxa (Taxonomic surrogacy)

The taxonomic surrogacy concept is based on the idea that it is possible to use higher taxonomic level data (i.e. genera, families, orders) to predict patterns of species richness. Taxonomic surrogacy has been used in a number of fields, e.g. paleontology, community perturbation studies and conservation biology (Bertrand *et al.* 2006). Mandelik *et al.* (2007) list three underlying assumptions to this approach, 1) that there are fewer genera, families, orders, etc (hereafter referred to as higher taxonomic levels) than species; 2) that the sampling effort required to achieve a representative sample is lower for higher taxonomic levels than for species and 3) the distribution of species within higher taxonomic levels is relatively homogeneous (i.e., there is little variation in the number of nested species within each higher taxon). This cheap and quick shortcut approach has proved to be quite useful, since there correlations between higher-taxon richness and species richness have been reported (Gaston and Williams 1993; Williams and Gaston 1994; Gaston 2000b). Balmford *et al.* (1996a) have shown that species richness at a local level may be better predicted by higher taxonomic levels than by the species richness of other putative indicator groups. Many studies (Gaston and Williams 1993; Williams and Gaston 1994; Villasenor *et al.* 2005; Li *et al.* 2006; Heino and Soininen 2007) but with the exception of Andersen (1995) and Fjeldså (2000), have generally concluded that the number of higher taxa is highly significantly and often strongly correlated with species richness i.e. number of species.

Balmford *et al.* 1996(b), working in the tropical forests of Sri Lanka, demonstrated that targeting woody plant genera and families rather than species reduces survey costs by a minimum of 60% and 85% respectively. The effectiveness of taxonomic surrogacy also depends on strong correlations existing between higher-taxon richness and species richness. Using three taxonomic groups, the Coleoptera, Acari and Diptera, Báldi (2003) tested this concept in central Hungary and concluded that there is strong congruency and therefore higher taxon (family) diversity is in deed a good surrogate of species diversity. On the other hand, Cardaso *et al.* (2004), studying spiders, suggested that only generic richness is a good surrogate of species richness (Grelle 2002; Mazaris *et al.* 2008). Andersen (1995) cautions, however, that mere correlation between higher taxa and species richness is not sufficient, since they are statistically dependent, so it is the accuracy of prediction that counts. According to Lovell *et al.* (2007) the use of taxonomic surrogacy shows good potential in species-poor higher taxa and/or in regions where biodiversity is well documented. If this holds true, though, it defeats the whole purpose of using taxonomic surrogacy in the first place. Considering that the approach is subject to a series of limitations such as sampling effort, data quality and spatial autocorrelation (Balmford *et al.* 1996a; Grelle, 2002; Cardoso *et al.*, 2004), cautious application must be exercised. Furthermore, Bertrand *et al.* (2006) argue against the use of taxonomic surrogacy on the basis that it is founded on misunderstandings of the relationship between different phylogenetic components of diversity. Nevertheless, despite such challenges taxonomic surrogacy is still widely employed in conservation science and will be tested further in this chapter.

3.1.6 Environment surrogates

Practically, it is not possible to be able to identify, or just to be able to make a list of all the species present in any given place, given that they are dynamic, changing in both space and time. The idea of using the characteristics of the physical environment, which are usually readily available, as predictors of overall biodiversity is quite attractive. Environmental data are relatively inexpensive to acquire, as compared to taking biological inventories and in many cases they are the only option for conservation planning in bio-data-poor areas (Faith and Walker 1996; Ferrier 2002; Monero *et al.* 2007). Faith (2003) argues that environmental data should not replace species data though, but should be used in tandem to make assertions about biodiversity. One of the advantages of using environmental data is the extrapolation of biodiversity information from data-rich areas to data-poor areas within the same environment (Faith 2003; Kleynhans *et al.* 2005). Biodiversity is known to display patterns that are reflected in spatially variable combinations of environmental factors such as climate, soils and geology. In addition, environmental diversity is assumed to reflect the turnover among species, as different species prefer different environmental conditions (Faith and Walker 1996). Moreover, the recent advances in geostatistics, geographic information systems, remote sensing and computational hardware and software make the use of environment surrogates even more appealing (Monero *et al.* 2007). Ferrier (2002) concedes that although this alternative approach confers obvious benefits, problems may arise if congruence is poor between environment and actual biological distributions. According to Araújo *et al.* (2003), the mis-match between environment and biota is because species tend to have smaller range sizes and their distributions are usual a consequence of historical rather than environmental factors. However, Lombard *et al.* (2003) reported that broad habitat units would be good surrogates for Proteas in the Cape Floristic Region, because they represent 56–79% of the species from there. Wessels *et al.* (1999) and Sarkar *et al.* (2005) have also reported positive results about the use of environment surrogate, but the surrogate method will not be tested further in this study.

3.2 Aim and Objectives

The aim of this chapter is to test the congruence between macroinvertebrate assemblages at different taxonomic levels. Specific objectives are to:

1. Examine congruence between macroinvertebrate taxonomic orders, functional feeding groups and life-history attributes;
2. Examine congruence between macroinvertebrate families;
3. Assess the congruence between species, genus and family, in order to see if higher taxonomic levels (e.g. genus and family) can reliably be used instead of species-level information.
4. Test if the three data sets (species richness, assemblage composition and assemblage structure) yield similar or different results.

3.3 MATERIAL AND METHODS

3.3.1 Data manipulation

In avoidance of the apparent bias shown by other studies that examine species richness alone as pointed out by (Barlow *et al.* 2007), two additional biodiversity measures were examined. These were assemblage composition (based on presence-absence data) and assemblage structure (based on relative abundance data). Since not all specimens were identified to species level, perhaps it is more fitting to use the word "taxon" instead of "species" when referring to the lowest level of identification achieved, therefore hereafter, "species" is used synonymously with "taxon". When assessing congruency between a taxon and the cumulative total of all taxa, the data for that taxon were removed from the total to prevent a Type 1 error. Eight taxonomic higher-level (e.g. order) groups were found in the study, namely Acarina, Coleoptera, Ephemeroptera, Hemiptera, Gastropoda, Odonata, Diptera and Crustacea. Classification and identification of functional feeding groups (FFG) and life history attributes are given in chapter 2.

3.3.2 Congruency pattern analyses based on species richness

Species richness, which is defined as the number of species per specified area or unit (Magurran 2004), was employed in this study as the count of taxon in a wetland and care was taken to apply equal sampling effort in every wetland. Spearman's rank correlations were used to test correlations in SPSS version 16.0. Since Ephemeroptera are represented by only one taxon, this order was omitted from this analysis, therefore seven taxonomic groups (Acarina, Coleoptera, Hemiptera, Gastropoda, Odonata, Diptera and Crustacea) were analysed. For congruence between taxonomic levels (namely species, genus and family), only Coleoptera and Hemiptera were used because these groups are best known and were identified mostly to species level.

3.3.3 Congruency pattern analyses based on assemblage structure and composition

Analysing patterns in species assemblage, both the relative abundances (assemblage structure) estimates and presence-absence (assemblage composition) datasets were used (e.g. Heino *et al.* 2003; Barlow *et al.* 2007; Lovell *et al.* 2007; Heino et al 2008). A Bray-Curtis Similarity matrix was constructed for each taxon using Palaeontological Statistics (PAST) version 1.81 (Hammer, Harper & Ryan 2008). As is common practice for analysis of assemblage data, the contribution of abundant taxa was adjusted relative to less abundant taxa (Clarke and Warwick 2001) using square-root data transformations. This transformation was done according to Zar (1999) to prevent Type 1 error that occurs when sites without representatives are excluded from the analysis. Correlation between every pair of similarity matrices was computed using Mantel Analysis in PAST. The Mantel test computes the correlation coefficient ρ between the corresponding sample elements of each pair of similarity matrices. The ρ-value indicates the strength of the observed relation with 0 denoting no relation, and 1 denoting a perfect correlation between two matrices. The significance of the coefficient is then tested using a permutation test ($n = 999$ permutations), in which ρ is recalculated following repeated randomisation of the original sample matrices (Clarke and Gorley, 2001).

3.3.4 Familial taxonomic level

Although there has been substantial debate regarding optimal design, sampling, sample processing and analytical approaches for ecological studies, one of the most contentious issues is taxonomic sufficiency. Jones (2008) describes taxonomic sufficiency as a "pragmatic concept in which the level of identification is balanced against the need for information", and this is determined primarily by the study objective. Marshall *et al.* (2006) concede, however, that choice of appropriate taxonomic resolution is a compromise between the cost of obtaining data at high taxonomic resolutions and the loss of information at lower resolutions. Hewlett (2000) examined the influence of taxonomic resolution on 165 streams and found that generic-level identifications offered no substantial advantage over family level identifications. Bowman and Bailey (1997) reported similar results in their review of ten data sets from published studies of freshwater benthic macroinvertebrate communities. Moreover, Marshall *et al.* (2006) reported that very little information (<6%) was lost by identifying taxa to family (or genus), as opposed to species. In freshwater systems, family-level identification is often preferred for biodiversity and biomonitoring programmes (Marshall *et al.* 2006; Li *et al.* 2006; Heino and Soininen 2007; Jones 2008), because lower taxonomic resolution (species or genus) sometimes requires collection of flying adults and/or precise life stages (e.g. Baber-James and Lugo-Ortiz 2003; Grenouillet *et al.* 2007). Now given the importance of family-level data in bioassessement in particular, this chapter seeks to test the congruency between taxa at this taxonomic level, in order to evaluate the value of using one or a combination of taxa as surrogates for biodiversity assessment. Only the families that occurred at least more than 30 times and contained more than two taxa (genera or species) were included in the taxon richness congruency analysis and for abundance analysis, only families with more than 500 individuals were included.

3.3.5 Comparison of the three datasets

To compare the variation of the three datasets in capturing congruence between different taxa and, within the overall assemblage, second-stage non metric multi-dimensional scaling (MDS) (e.g. Bilton et al 2006) and cluster analyses were performed within Primer (Clarke and Warwick 2001). Second-stage MDS is effectively an MDS of MDSs' correlation coefficients (the merits of which are explained elsewhere Chapman *et al.* 2006 cited in Clarke and Gorley 2006).

3.4 RESULTS

Table 3.1 Matrix showing the strength of the cross-taxon congruency between higher taxa, functional feeding group and life history attributes. Above the diagonal are, Spearman rank correlations (r) determined using species richness; values in brackets are significant *P* values. Below the diagonal are Mantel tests (r) determined using assemblage structure (value above) and assemblage composition data (value below).

Coleo		**0.231** **(0.006)**	0.108 (0.206)	**0.177** **(0.036)**	0.030 (0.723)	**0.273** **(0.001)**	**0.321** **(0.000)**	**0.213** **(0.012)**	0.089 (0.296)	**0.568** **(0.000)**	**0.293** **(0.000)**	**0.602** **(0.000)**	**0.661** **(0.000)**	**0.190** **(0.024)**	**0.350** **(0.000)**
Acari	-0.084 -0.028		0.029 (0.738)	0.043 (0.616)	**0.406** **(0.000)**	**0.302** **(0.000)**	**0.307** **(0.000)**	-0.007 (0.935)	0.137 (0.935)	**0.516** **(0.000)**	**0.380** **(0.000)**	**0.334** **(0.000)**	**0.329** **(0.000)**	**0.693** **(0.000)**	**0.401** **(0.000)**
Crust	-0.005 -0.040	0.004 0.001		-0.090 (0.290)	0.114 (0.181)	-0.115 (0.175)	-0.037 (0.664)	**0.368** **(0.000)**	**-0.195** **(0.021)**	-0.046 (0.589)	0.090 (0.289)	**0.204** **(0.015)**	-0.066 (0.439)	**0.415** **(0.000)**	-0.023 (0.783)
Dipte	0.045 -0.004	**0.066** 0.016	-0.023 -0.014		-0.018 (0.834)	**0.281** **(0.001)**	0.137 (0.107)	**0.501** **(0.000)**	**0.647** **(0.000)**	**0.333** **(0.000)**	**0.175** **(0.038)**	0.023 (0.791)	**0.545** **(0.000)**	0.005 (0.956)	**0.243** **(0.004)**
Gastr	0.016 0.001	**0.175** **0.132**	-0.002 0.001	**0.093** 0.008		**0.205** **(0.015)**	**0.215** **(0.011)**	-0.148 (0.082)	0.100 (0.242)	**0.283** **(0.001)**	**0.820** **(0.000)**	**0.170** **(0.044)**	**0.177** **(0.037)**	**0.813** **(0.000)**	**0.213** **(0.006)**
Hemip	0.051 0.043	-0.039 -0.028	0.019 0.007	-0.060 -0.004	0.002 0.023		**0.405** **(0.000)**	0.045 (0.601)	**0.356** **(0.000)**	**0.864** **(0.000)**	**0.323** **(0.000)**	0.036 (0.673)	**0.765** **(0.000)**	**0.221** **(0.009)**	**0.419** **(0.000)**
Odona	-0.116	**0.185**	-0.023	0.013	**0.054**	-0.024		**-0.198** **(0.019)**	**0.249** **(0.003)**	**0.578** **(0.000)**	**0.323** **(0.000)**	0.141 (0.096)	**0.483** **(0.000)**	**0.294** **(0.000)**	**0.478** **(0.000)**

	-0.076	**0.083**	-0.010	0.001	**0.008**	-0.104									
	0.048	-0.031	**0.119**	**0.107**	**0.032**	0.015	-0.022								
Filter	**0.059**	-0.005	**0.056**	**0.151**	**0.033**	-0.017	**0.052**		0.045 (0.598)	0.063 (0.456)	-0.022 (0.793)	0.131 (0.124)	**0.247** **(0.003)**	0.059 (0.489)	**0.221** **(0.009)**
	-0.054	-0.003	0.021	**0.414**	-0.004	**0.133**	-0.073	0.0173							
Gathe	0.003	-0.017	0.011	0.351	0.006	**0.227**	0.078	0.003		**0.364** **(0.000)**	**0.174** **(0.040)**	-0.044 (0.608	**0.571** **(0.000)**	0.058 (0.498)	**0.491** **(0.000)**
	0.112	-0.063	-0.056	-0.009	-0.009	**0.663**	-0.045	0.001	**0.094**						
Preda	0.118	-0.049	-0.053	0.052	0.002	**0.507**	-0.089	-0.016	0.133		**0.445** **(0.000)**	**0.198** **(0.019)**	**0.875** **(0.000)**	**0.393** **(0.000)**	**0.889** **(0.000)**
	0.099	**0.097**	-0.009	**0.050**	**0.628**	**0.085**	0.022	0.012	0.028	**0.068**					
Scrap	**0.133**	**0.041**	-0.020	-0.044	**0.431**	**0.133**	-0.041	-0.011	0.057	**0.107**		**0.212** **(0.012)**	**0.405** **(0.000)**	**0.704** **(0.000)**	**0.578** **(0.000)**
	0.145	**-0.097**	**0.103**	0.005	**0.042**	**0.072**	0.006	0.009	**0.143**	**0.068**	**0.072**				
Shred	**0.114**	**0.093**	0.001	0.002	**0.033**	-0.005	0.008	0.000	0.005	-0.003	0.014		**0.315** **(0.000)**	**0.349** **(0.000)**	**0.396** **(0.000)**
	0.054	**-0.080**	-0.023	**0.088**	**0.433**	**0.041**	-0.026	0.023	**0.045**	**0.116**	**0.446**	**0.046**			
Resid	0.092	**0.085**	**0.011**	-0.018	**0.297**	**0.067**	-0.056	0.016	0.043	**0.165**	**0.416**	**0.024**		**0.255** **(0.002)**	**0.937** **(0.000)**
	0.122	-0.019	0.027	**0.373**	0.010	**0.195**	-0.068	**0.049**	**0.403**	**0.221**	0.009	0.050	0.007		
Trans	0.140	-0.021	-0.027	0.196	0.000	0.140	-0.031	0.029	0.206	0.284	-0.027	-0.003	-0.031		**0.526** **(0.000)**
	0.058	0.027	**0.048**	0.006	**0.051**	**0.153**	0.001	0.005	**0.242**	**0.098**	**0.026**	**0.029**	0.004	**0.099**	
Ephem	**0.056**	0.016	**0.073**	0.042	**0.068**	**0.240**	-0.036	-0.009	**0.306**	**0.069**	**0.073**	**0.040**	0.019	0.053	
Total*	0.025 (0.262)	0.015 (0.319)	0.025 (0.256)	-0.007 (0.945)	**0.056** **(0.000)**	-0.081 (0.988)	-0.063 (0.934)	0.002 (0.392)	**0.212** **(0.000)**	**0.219** **(0.001)**	**0.059** **(0.002)**	0.034 (0.838)	**0.126** **(0.000)**	**0.487** **(0.000)**	

Key: Coleo = Coleoptera, Acari = Acarina, Dipte = Diptera, Gastr = Gastropoda, Hemi = Hemiptera, Odona = Odonata, Filte = Filtering Collectors, Gathe = Gathering Collectors, Preda = Predators, Scrap = Scrapers, Shred = Shredders, Resid = Resident and Trans = Transient.

Correlation coefficient (r) shows the strength of the relationship, 0 denotes no relationship and 1 denotes a very strong relationship. Bold values represent a significance of $P<0.05$. $n = 140$ for each taxon. *Assemblage structure analysis only.

Table 3.2. Matrix showing the strength of the cross-family congruency. Above the diagonal, Spearman rank correlations (r) determined using species richness, the values in the bracket are significant (*P*) value, and below diagonal Mantel tests (r) determined using assemblage structure (value above) and assemblage composition data (value below).

	Total	Corix	Dytis	Hydro	Noton	Physi	Plano	Pleid[a]	Eylai[a]	Hydra[a]	Chiro[b]	Baetid[b]	Strep[b]	Ortho[b]	Culicid
Total		**0.321** **(0.000)**	**0.390** **(0.000)**	0.141 (0.096)	**0.293** **(0.000)**	0.097 (0.255)	**0.178** **(0.036)**	**0.452** **(0.000)**	**0.227** **(0.007)**	0.121 (0.154)					
Corix	**0.057** **(0.006)**		0.127 (0.134)	-0.088 (0.303)	**0.398** **(0.000)**	-0.065 (0.446)	0.009 (0.912)	0.105 (0.217)	0.163 (0.055)	0.125 (0.140)					
Dytis	0.042 (0.200)	-0.017 -0.021		**0.184** **(0.030)**	0.112 (0.186)	-0.106 (0.214)	0.062 (0.468)	**0.328** **(0.000)**	-0.020 (0.819)	**0.369** **(0.000)**					
Hydro	-0.011 (0.596)	-0.020 -0.001	-0.028 0.002		0.114 (0.180)	-0.055 (0.520)	-0.129 (0.128)	**-0.264** **(0.002)**	0.052 (0.539)	-0.024 (0.778)					
Noton	-0.019 (0.698)	**0.132** **0.152**	-0.057 0.009	-0.057 0.003		**-0.203** **(0.016)**	-0.078 (0.358)	**-0.228** **(0.007)**	0.132 (0.120)	-0.002 (0.977)					
Physi	-0.009 (0.551)	-0.018 0.018	-0.030 0.001	-0.018 -0.002	-0.057 **0.046**		**0.449** **(0.000)**	0.047 (0.585)	0.164 (0.053)	-0.083 (0.329)					
Plano	0.022 (0.295)	-0.003	-0.004	-0.004	0.028	-0.004		**0.279** **(0.001)**	0.136 (0.109)	-0.048 (0.578)					

		0.000	-0.036	-0.005	0.009	**0.336**						
Strep[b]	0.089 (0.063)	0.032 0.029	-0.030 -0.077	-0.018 -0.001	-0.057 -0.013	-0.018 0.001	-0.004 -0.011	-0.003 0.011	***0.069*** ***0.133***			
Chiro[b]	-0.007 (0.604)	**0.163** **0.198**	-0.003 0.003	**0.099** **0.068**	0.007 **0.057**	-0.003 0.032	-0.006 0.043		0.006 0.025			
Ortho[b]	-0.032 (0.869)	-0.005 0.010	-0.030 0.008	-0.020 0.000	-0.011 -0.007	-0.018 0.007	-0.003 0.002	-0.003 0.032	**0.028** 0.024	-0.027 -0.004		
Baeti[b]	**0.099** **(0.000)**	0.101 0.147	**0.043** 0.036	0.017 **0.028**	**0.122** 0.152	0.010 0.001	-0.027 -0.016					
Culic[b]	-0.027 (0.837)	-0.009 -0.005	-0.018 0.009	**0.037** 0.013	-0.018 -0.005	-0.018 0.000	-0.057 0.006	**0.028** -0.005	0.025 **0.027**	-0.018 **0.026**	-0.009 0.014	
Pomat[b]	-0.009 (0.564)	-0.009 -0.001	-0.018 -0.018	-0.020 0.014	-0.011 0.006	-0.018 0.026	0.058 **0.053**	-0.010 0.006	0.009 0.024	-0.065 -0.039	-0.034 -0.006	-0.033 -0.006

Key: Baeti = Baetidae, Chiro = Chironominae, Corix = Corixidae, Culic = Culicidae, Dytis = Dytiscidae, Hydro = Hydrophilidae, Noton = Notonectidae, Ortho = Orthocladinae, Physi = Physidae, Plano = Planobirdae, Pomat = Pomatiopsidae, Pleid = Pleidae, Eyla = Eylaidae, Hydra = Hydraenidae, Strep = Streptocephalidae.

[a]Not included in the Mantel analysis because it was represented by fewer than 500 individuals [b] Not included in the Spearman analysis because it was species-depauperate.

Correlation coefficient (r) shows the strength of the relationship, 0 denotes no relationship and 1 denotes a very strong relationship. Value in parentheses is the *P*-value. Bold values represent a significance of <0.05. *n*= 140 for each taxon. *Relative abundance data analysis only.

3.4.1 Congruency patterns based on species richness across higher-taxonomic groups, functional feeding groups (FFG) and life-history attributes

Most of the cross-taxon correlations (i.e. between higher taxa themselves) were rather weak, none greater than 50%, albeit most being statistically significant (see Table 3.1). Acarina correlated significantly with most other taxa, attaining the highest correlation (r=0.406) with the Gastropoda. Figures 3.1 & 3.2 show the strong correlations between the Acarina *vs* Gastropoda, and the Odonata *vs* Hemiptera, respectively. In contrast, weakest correlations were found between the Gastropoda *vs* Diptera, and the Odonata *vs* Crustacea. All taxa but the Crustacea had a highly significant, positive correlation with total invertebrates (r <0.50). Figure 3.3 shows the relationship between Acarina (which showed relatively strong congruency (r >0.40) as did the Odonata and Hemiptera) with total invertebrates. Generally, correlations between FFGs and taxonomic groups were relatively stronger. Scrapers *vs* Gastropoda and predators *vs* Hemiptera were most strongly correlations (r >0.800) (see figure. 3.4 & 3.5). On the other hand, the relationships between shredders *vs* Hemiptera and Diptera were weakest (r <0.05). Gastropoda had the strongest, and highly significant, congruent with transient taxa (Figure 3.6), while Hemiptera were more strongly congruency with resident taxa (r >0.70). Congruencies between FFG themselves were rather weak (Table 3.1), with only scrapers and predators attaining congruency of greater than 0.40. Relationships between FFGs and life history strategies were generally significant and relatively strong, with predators and residents, and scrapers and transient yielding the highest correlations. Predators were the only FFG with very strong congruence with the total invertebrate assemblage (r ~0.90) (figure. 3.7). Resident taxa had a very interesting relationship with the total invertebrates (see figure. 3.8), having more than 90% congruency.

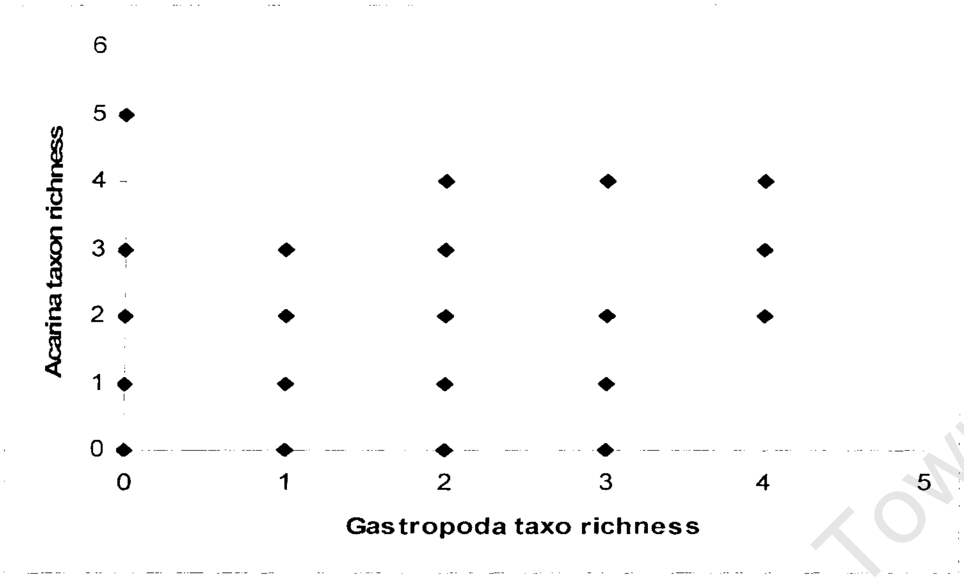

Figure 3.1 Congruency between Gastropoda and Acarina taxon richness, r=0.406, *P* <0.001.

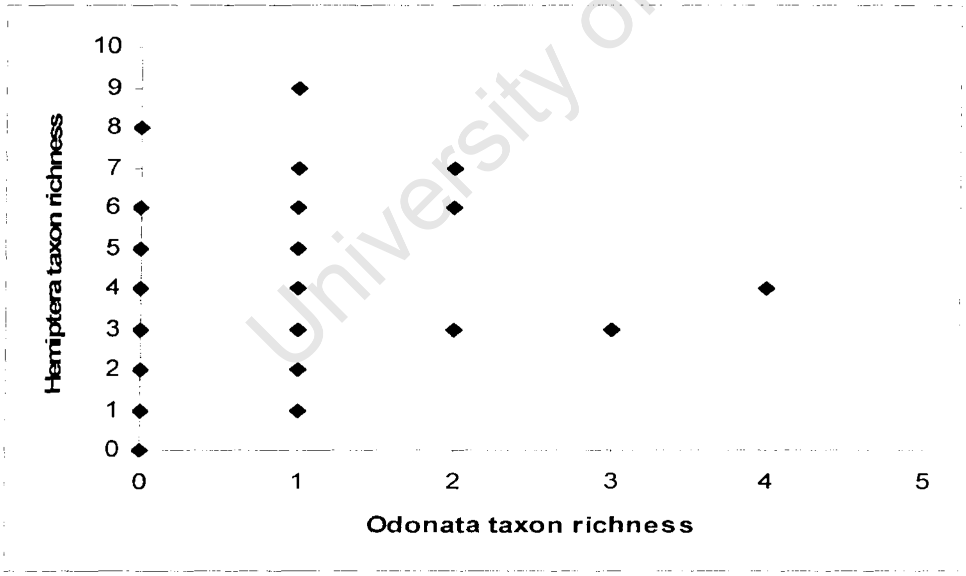

Figure 3.2 Congruency between Odonata and Hemiptera taxon richness, r =0.405, *P* <0.001.

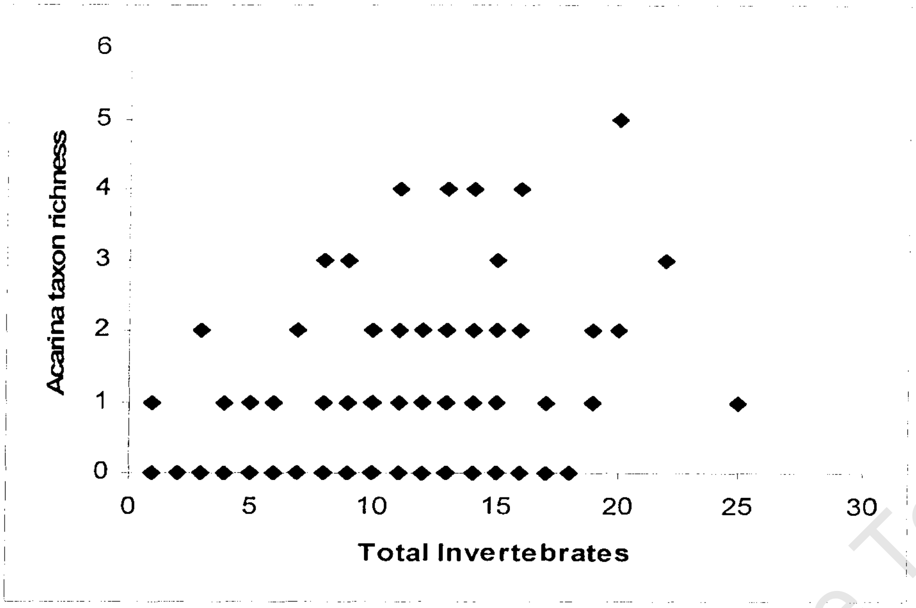

Figure 3.3 Congruency between Acarina and total invertebrates, r =0.401, $P < 0.001$.

Figure 3.4 Congruency between scrapers and Gastropoda taxon richness, r = 0.820, $P < 0.001$.

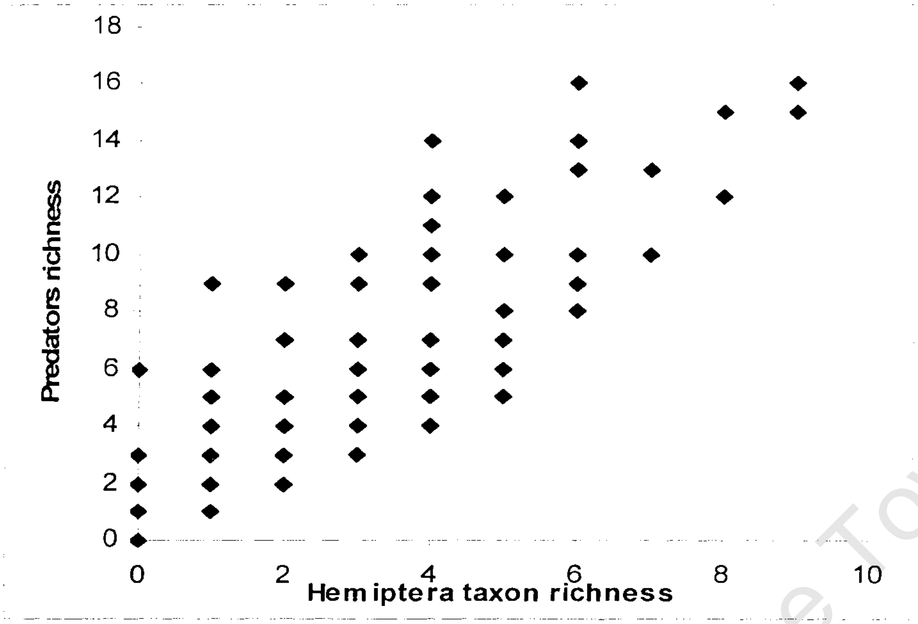

Figure 3.5 Congruency between predators and Hemiptera taxon richness, r = 0.864, *P* <0.001

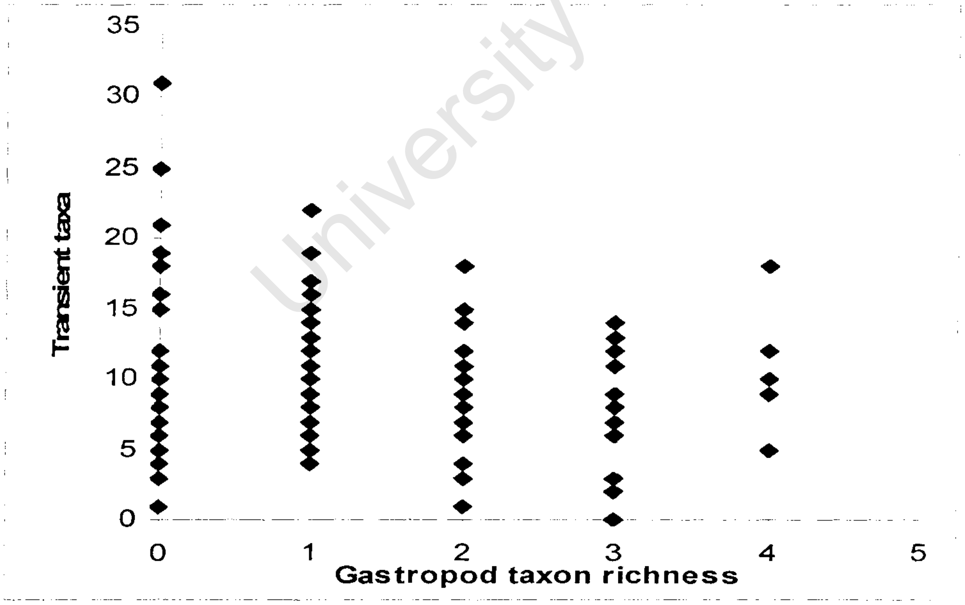

Figure 3.6 Congruency between Gastropod and transient taxa, r = 0.813, *P* <0.001

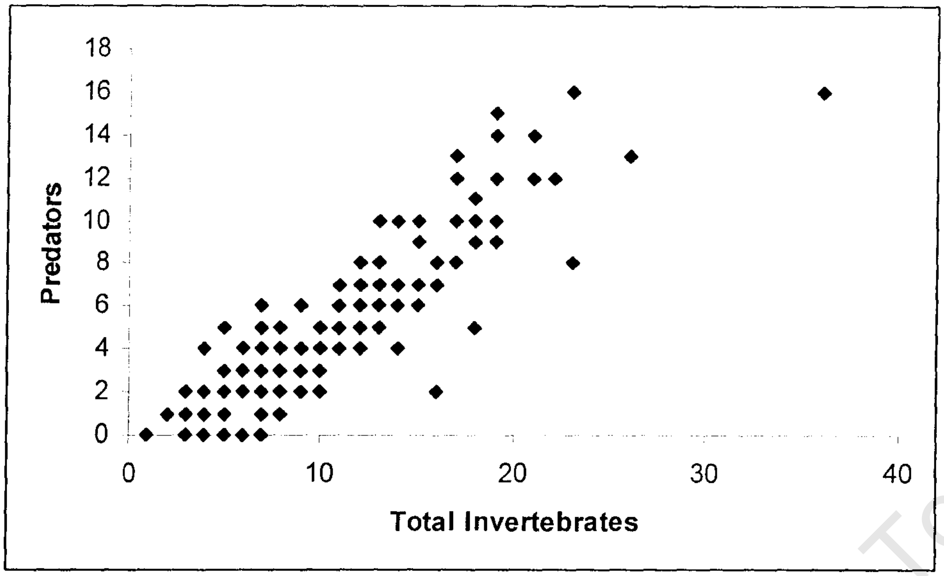

Figure 3.7 Congruency between predators and total invertebrates, r =0.889, $P < 0.001$

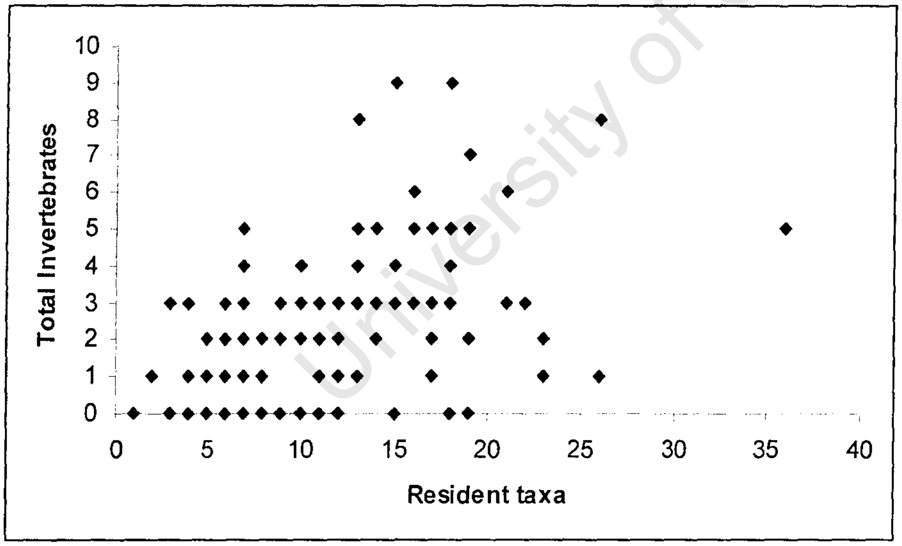

Figure 3.8 Congruency between resident taxa and total invertebrates, r =0.937, $P < 0.001$

3.4.2 Congruency based on assemblage structure across higher taxonomic groups, functional feeding groups and life history attributes

Congruencies between taxonomic groups themselves using relative abundance data were rather weak, characterized by few significant relationships (see Table 3.1). Hemiptera *vs* Ephemeroptera (r =0.15), Acarina *vs* Gastropoda (r =0.18) and Acarina *vs* Odonata (r =0.19) were the only cross-taxon correlations with more than 10% congruence. Gastropoda were most weakly congruent ($\rho<0.001$) with both the Hemiptera and the Crustacea. All taxa showed very weak relationship with the otal invertebrates, all but the Gastropoda having non-significant relationships ($P>0.05$). Although the relationships between taxa and FFG were weak, most of them were significant, partly because Hemiptera and Gastropoda had significant relationships with most of the FFGs. The strongest congruency between FFG and individual taxa was shown by Hemiptera *vs* predators and Gastropoda *vs* scrapers. On the other hand, Acarina *vs* gatherers, Diptera *vs* shredders and Gastropoda *vs* gatherers had the weakest correlations (r $\leq$0.005). Transient taxa showed good congruence with total invertebrates (r =0.49). Both gatherers and predators had similar congruence with the total invertebrates (r >0.20). Filterers and shredders were the only FFGs with a non-significant relationship with total invertebrates.

3.4.3 Congruency based on assemblage composition across higher taxonomic groups, functional feeding groups and life history attributes

In general all congruencies were weaker even than those calculated for relative abundance (see Table 3.1). The strongest congruency was seen between Acarina and Gastropoda (r =0.13); this relationship is weak but significant. Odonata *vs* Diptera, Gastropoda *vs* Crustacean, Coleoptera and Gastropoda, and Crustacea *vs* Acarina yielded the weakest congruencies (r =0.001). Although congruencies between higher taxa and FFGs were weak, they were stronger than those between the higher taxa themselves. As in the analysis using relative abundance data, the strongest correlations were observed between predators *vs* Hemiptera (r =0.51) and Gastropoda *vs* scrapers (r =0.43), respectively. The weakest congruency occurred between Crustacea and Shredders. Scrapers *vs* Predators yielded the strongest congruence, when comparing FFGs to themselves. Resident taxa *vs* Gastropoda (r =0.29) and Diptera *vs* Transient taxa (r =0.19) yielded the highest congruencies between higher taxa and life histories, while Predators *vs* Transient taxa (r =0.28) and Scrapers and Resident taxa (r =0.42) had the highest congruencies between FFGs and life histories.

3.4.4 Congruency across families based on species richness

Cross-family congruencies were generally weaker than expected, given that this taxonomic level is normally used in biomonitoring programs. No cross-family congruence yielded a correlation of even 50% (see Table 3.2). A good number of correlations were non-significant, in particular those involving the Eylaidae and Hydraenidae. In contrast, the Pleidae had predominantly significant relationships with other families. The strongest and most significant correlations (r <0.001), were seen between Planorbidae *vs* Physidae (r =0.45), Notonectidae *vs* Corixidae (r =0.39), and Hydraenidae *vs* Dytiscidae (r =0.37), whereas the weakest correlation was observed between Hydraenidae and Notonectidae. Six out of nine families (see Table 3.2) had a significant relationship with the total invertebrates. The Pleidae, Dytiscidae and Corixidae had good relationships with total invertebrates; 45%, 39% & 32% respectively.

3.4.5 Congruency across families based on assemblage structure

Overall, the congruencies based on relative abundance data were very weak, explaining less than 10% of the variance, and were to a large extent not significant. Only four cross-family relationships yielded more than 10% similarity, namely, Corixidae *vs* Baetidae (r =0.10), Notonectidae *vs* Baetidae (r =0.12), Corixidae *vs* Notonectidae (r =0.13), and Corixidae *vs* Chironominae (ρ=0.16), whereas Planorbidae *vs* Orthocladinae, Physidae *vs* Chironominae, Chironominae *vs* Dytiscidae and Corixidae and Planorbidae showed the weakest relationships. Individual families also failed dismally to explain any significant variation in the total invertebrates (r<10%). The Corixidae and Baetidae were the only families that showed significant correlation with total invertebrates albeit very weak.

3.4.6 Congruency across families based on assemblage composition

Cross-family congruencies were very weak, and three correlations (Planorbidae *vs* Corixidae, Orthocladinae *vs* Hydrophilidae and Culicidae *vs* Physidae) yielded no relationship at all (r =0.00). The strongest congruencies were observed between the Planorbidae *vs* Physidae (r =0.34) and the Chironomidae *vs* Corixidae (r =0.19).

3.4.7 Relationship between lower and higher taxonomic levels

In the cases of both the Coleoptera and Hemiptera, a very strong correlation (r >0.90) was observed between the different taxonomic levels, species-genus-family (see figures. 3.9-3.14). The strongest correlation for Hemiptera was observed between genus *vs* family (r =0.97), and between species *vs* genus (r =0.99) for Coleoptera. Rather weak correlations were, however, observed between coleopteran taxa and total invertebrates (see figures 3.15-3.1).

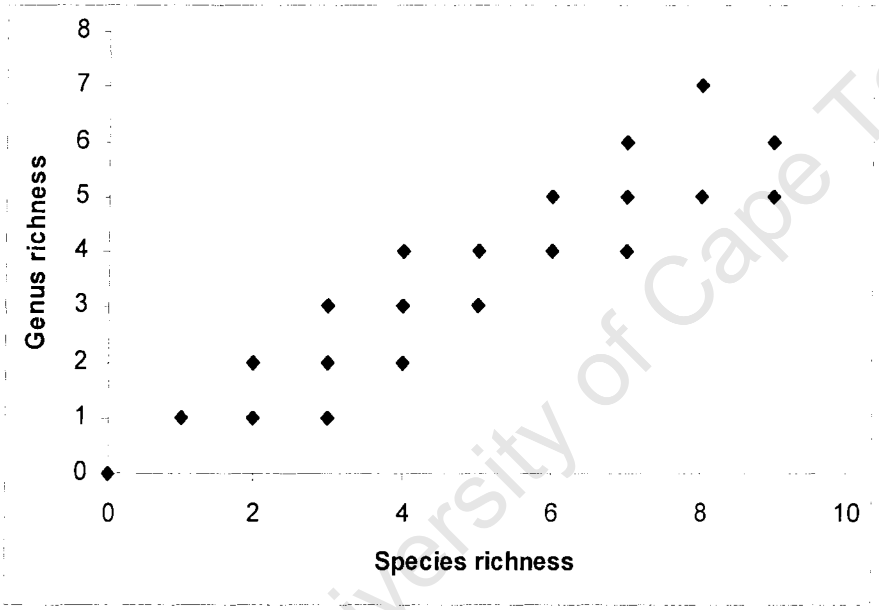

Figure 3.9 Coleopteran species richness plotted against generic richness, r =0985, P <0.01

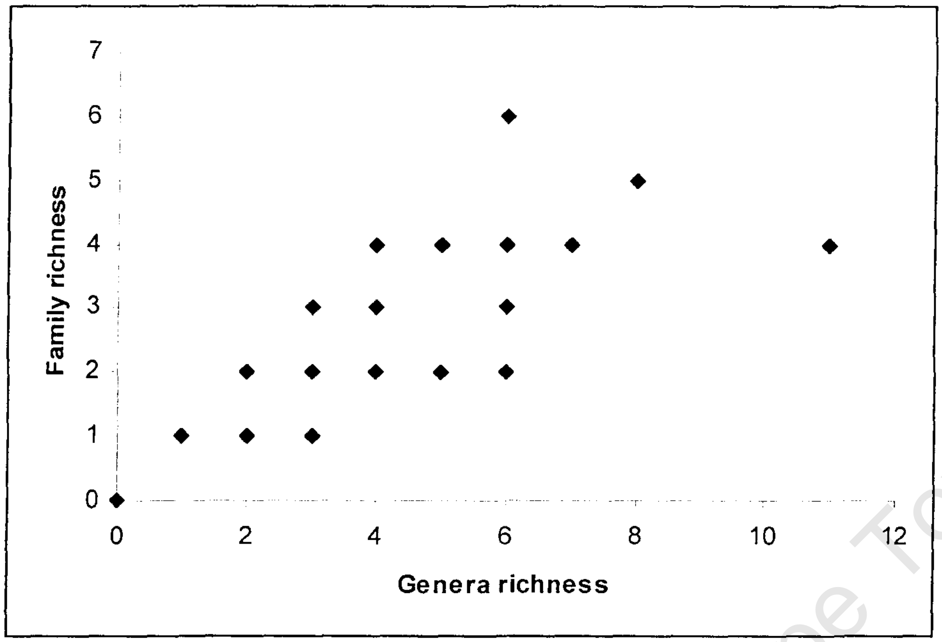

Figure 3.10 Coleoptera generic richness plotted against family richness, r =0.917, *P*<0.001

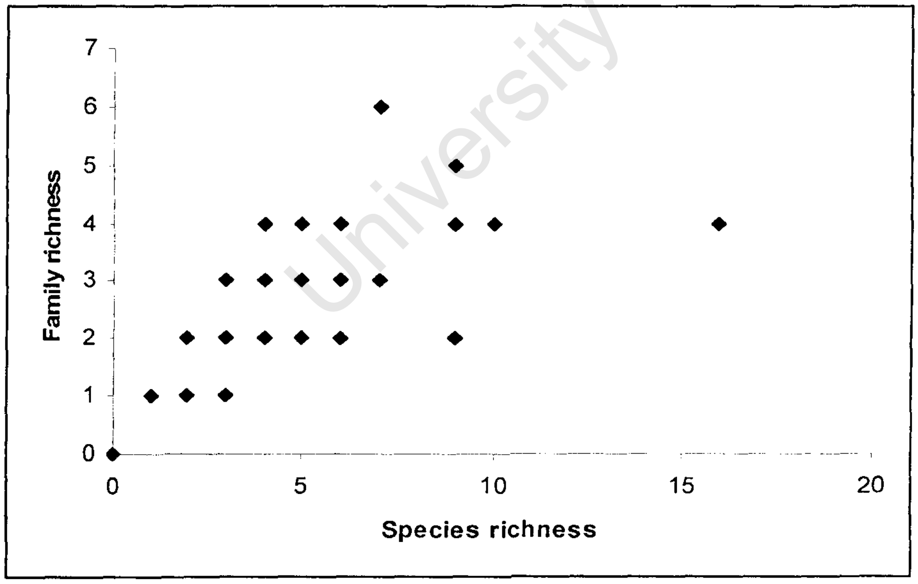

Figure 3.11 Coleoptera species richness plotted against family richness, r =0.904, *P* <0.01

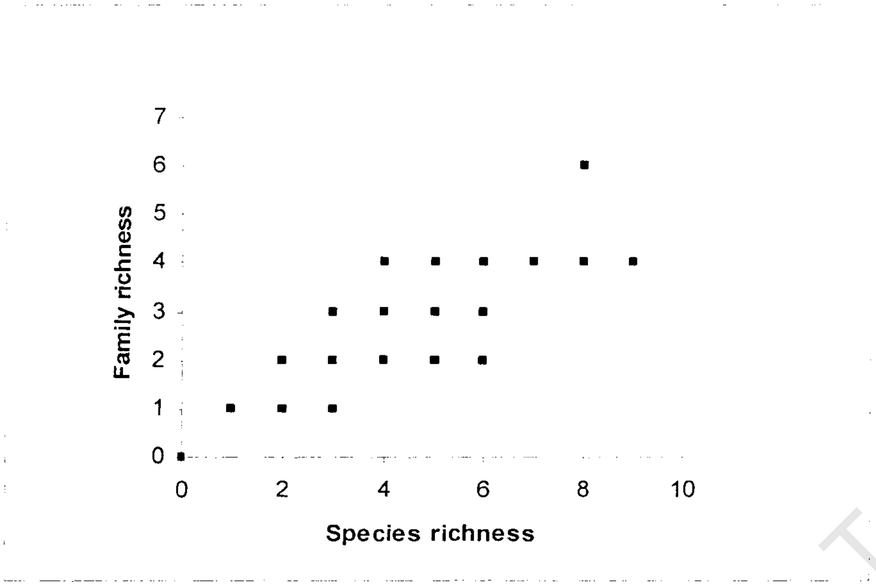

Figure 3.12. Hemipteran species richness plotted against family richness, r =0.913, $P < 0.01$

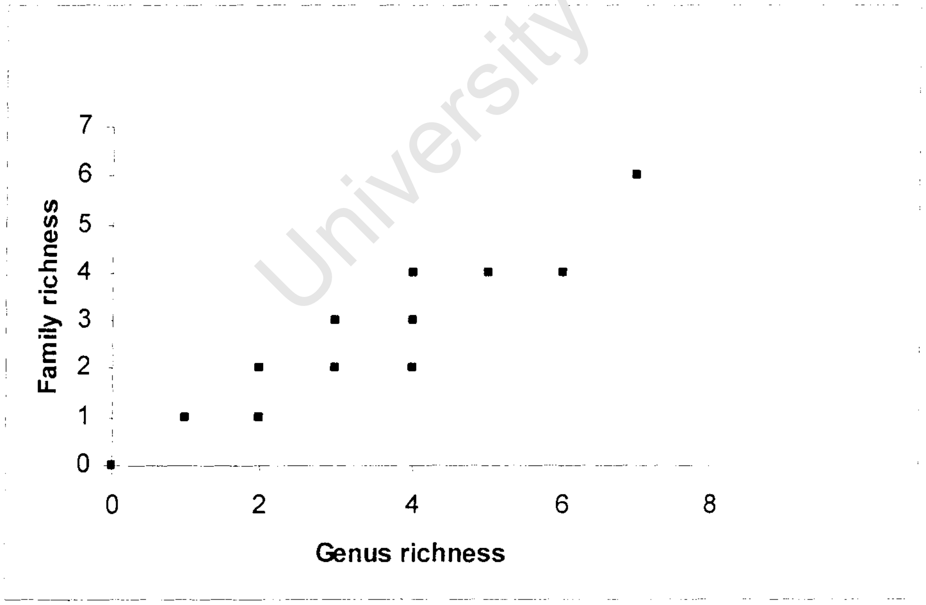

Figure 3.13. Hemipteran generic richness plotted against family richness, r =0.965, $P<0.01$

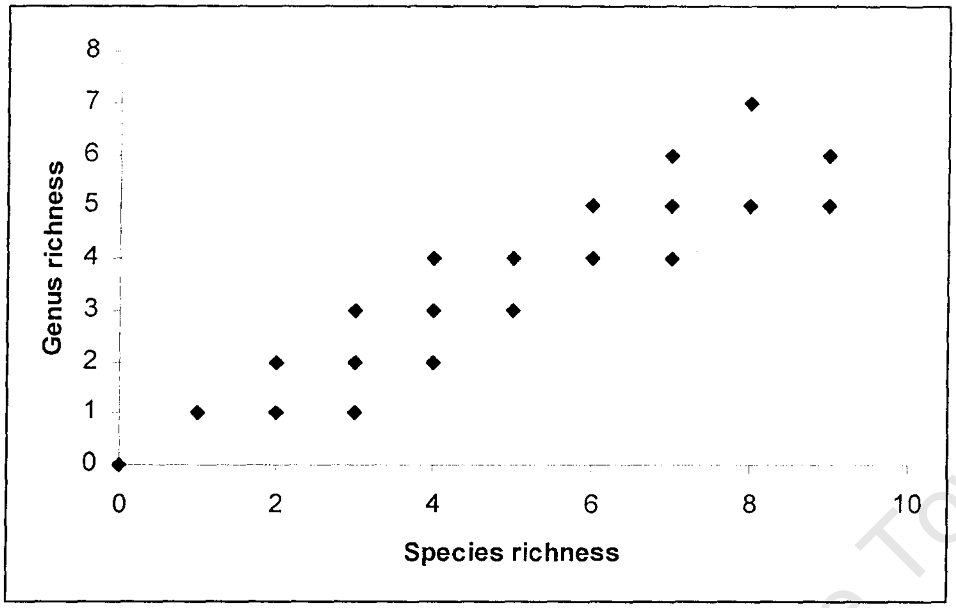

Figure 3.14 Hemipteran species richness plotted against genus richness, r =0.948, *P* <0.01

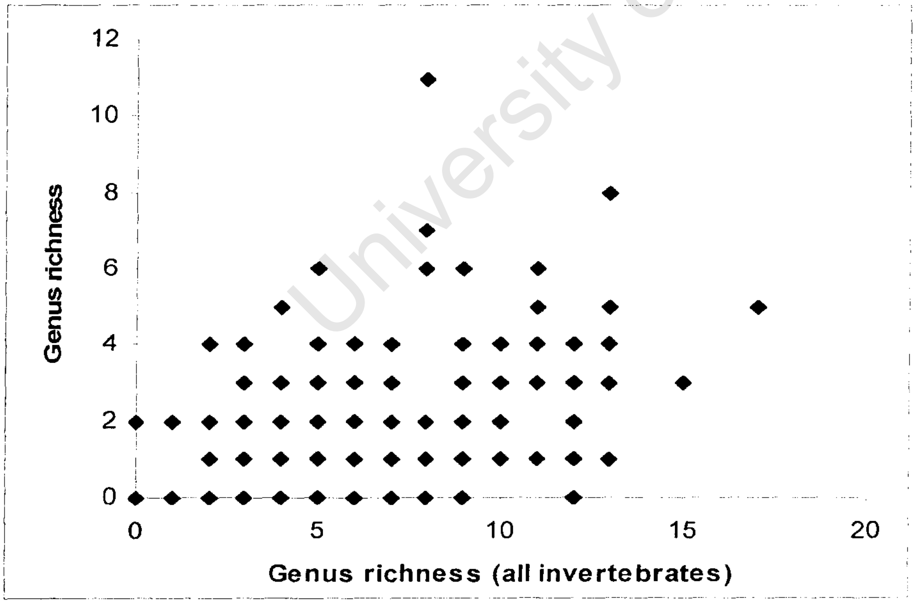

Figure 3.15 Coleopteran generic richness plotted against generic richness for total invertebrate assemblage, r =0.339, *P* <0.001

Figure 3.16 Coleopteran species richness plotted against familial richness for all invertebrates, r =0.365, *P* <0.001

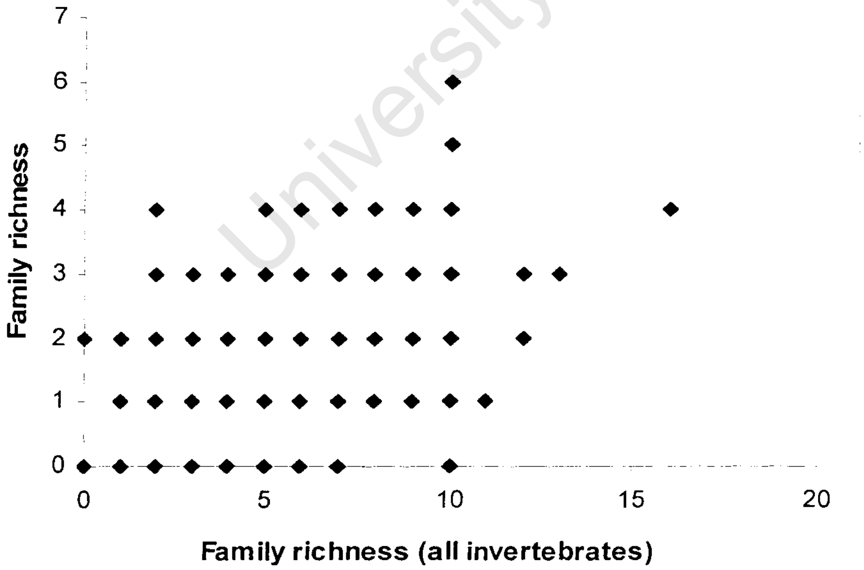

Figure 3.17 Coleopteran familial richness plotted against total invertebrates' familial richness, r =0.374, *P* <0.001

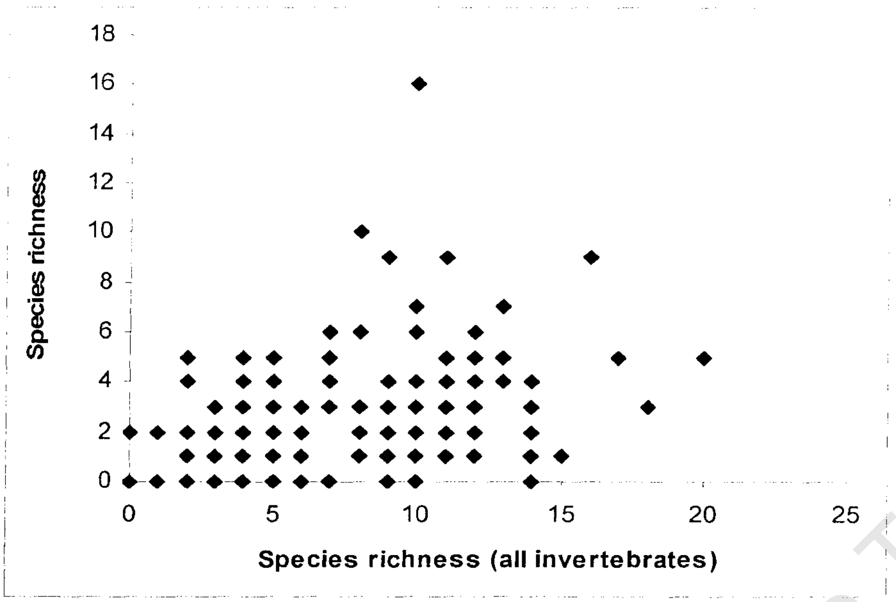

Figure 3.18 Coleopteran species richness plotted against species richness for all invertebrates, $r = 0.365$, $P < 0.001$

3.4.8 Comparison of results obtained from the three data sets

Analysis of the species richness dataset at higher taxonomic levels (Table 3.1) yielded a much higher number of significant cross-taxon correlations (78%) than for assemblage structure (48%) and assemblage composition (31%). Species richness datasets yielded consistently slightly higher similarities between taxa and overall assemblage (Table 3.3). The Hemiptera and Gastropoda were as similar to total assemblage as to each other (≥75%), this observation being observed with all data sets (see Table 3.3). All the three datasets using second stage MDS, showed predators and Hemiptera being more closely related to each other and total assemblage and clustered with transient taxa. This observation was further corroborated by the cluster dendrogram (Figures 3.17- 3.19).Gastropoda, resident taxa and shredders were also more closely related to each other and usually formed the second most similar cluster to overall assemblage.

Table 3.3 Percentage similarity of individual taxa with the overall assemblage, calculated by second-stage analysis of similarity matrices for the different datasets.

	Species richness	Assemblage structure	Assemblage composition
Acarina	60	58	
Coleoptera	58	56	56
Crustacea	55	53	53
Diptera	68	68	68
Filterers	55	53	53
Gastropoda	77	72	72
Gatherers	68	68	68
Hemiptera	81	75	75
Odonata	60	58	51
Predators	81	75	75
Resident	71	68	68
Scrapers	77	72	72
Shredders	58	56	56
Transient	75	61	61
Ephemeroptera		59	59

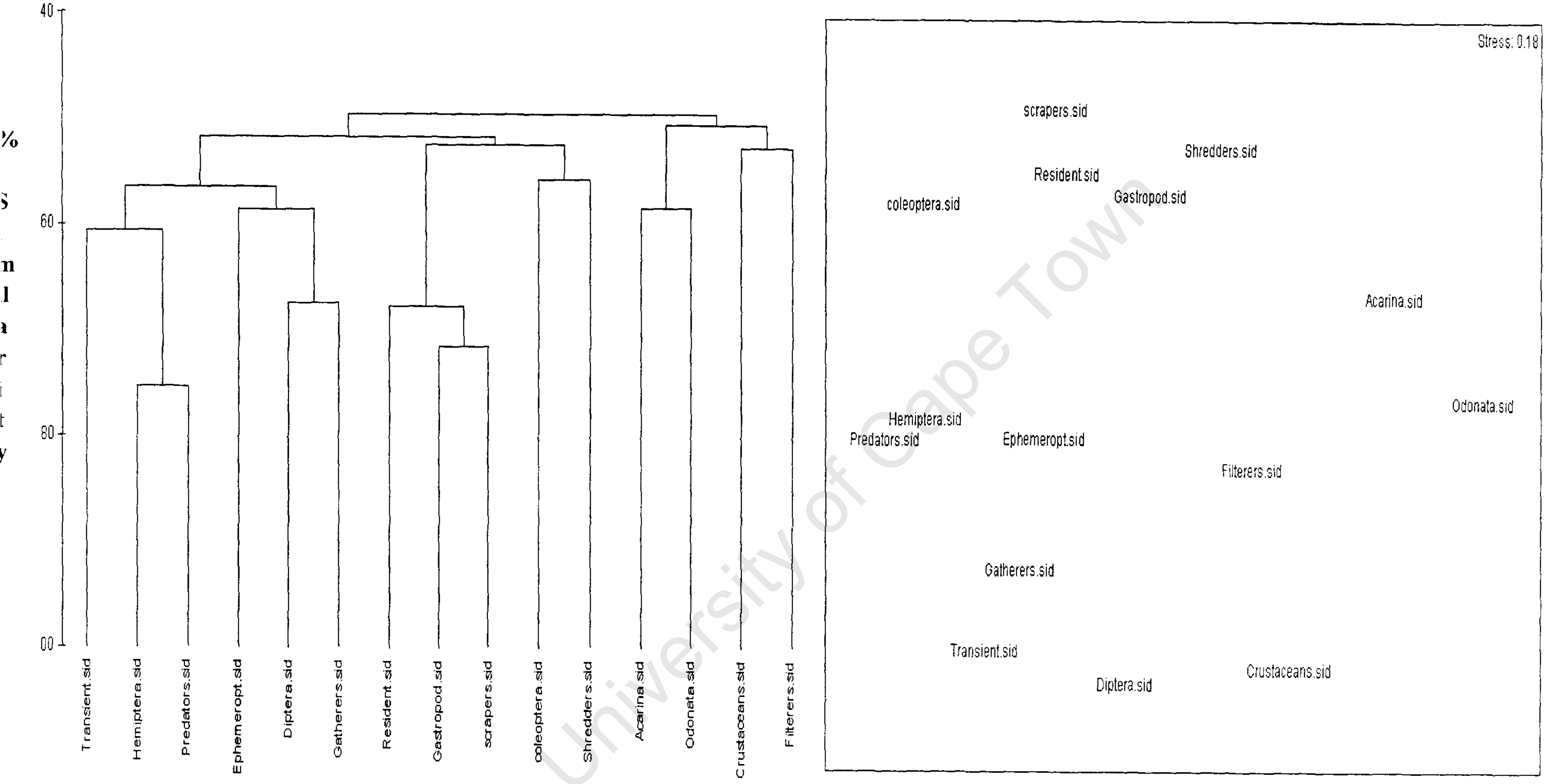

Figure 3.19. Cluster dendrogram and non-metric multidimensional scaling (MDS) ordination showing the assemblage similarity based on relative abundance data.

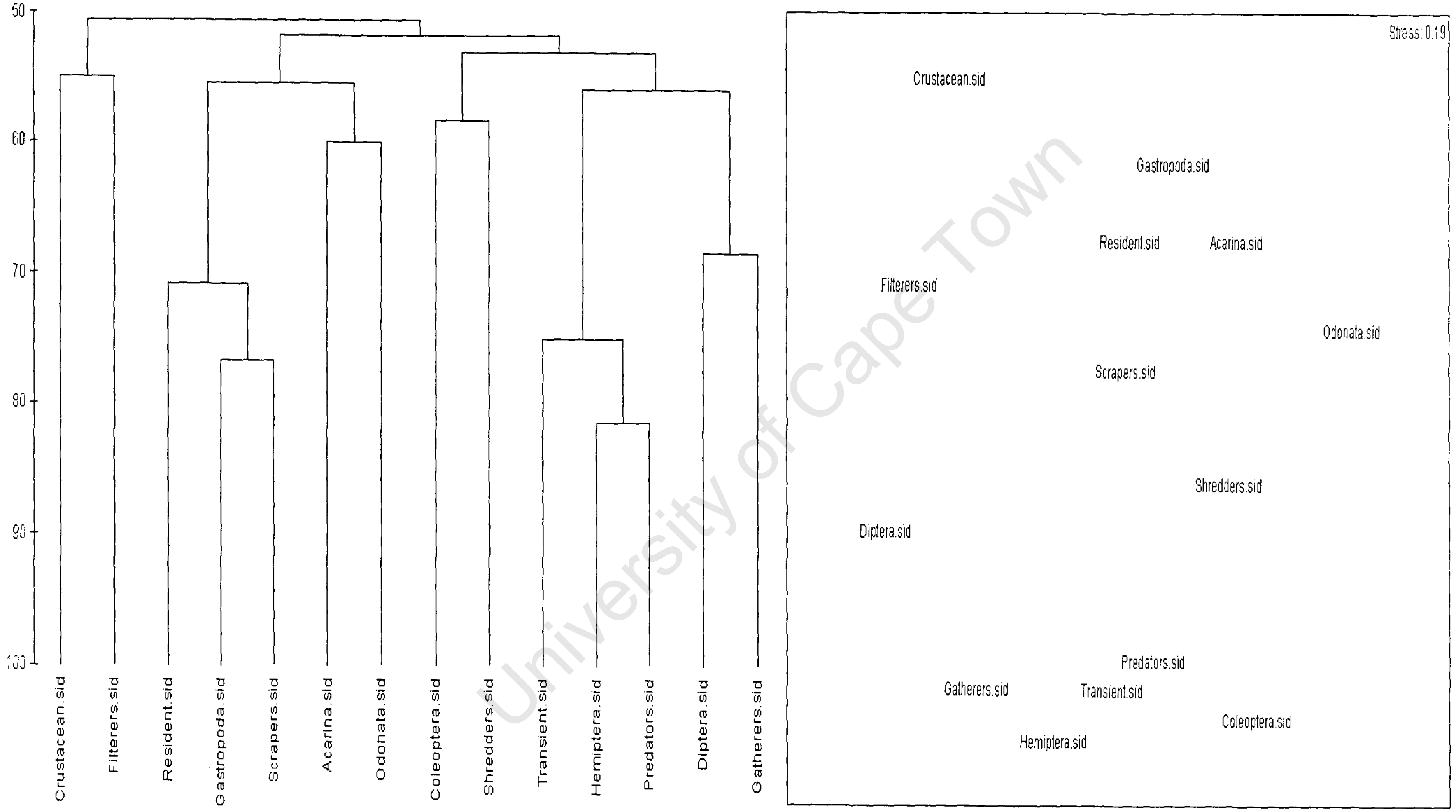

Figure 3.20. Cluster dendrogram and multidimensional scaling (MDS) ordination showing the assemblage similarity based on species richness.

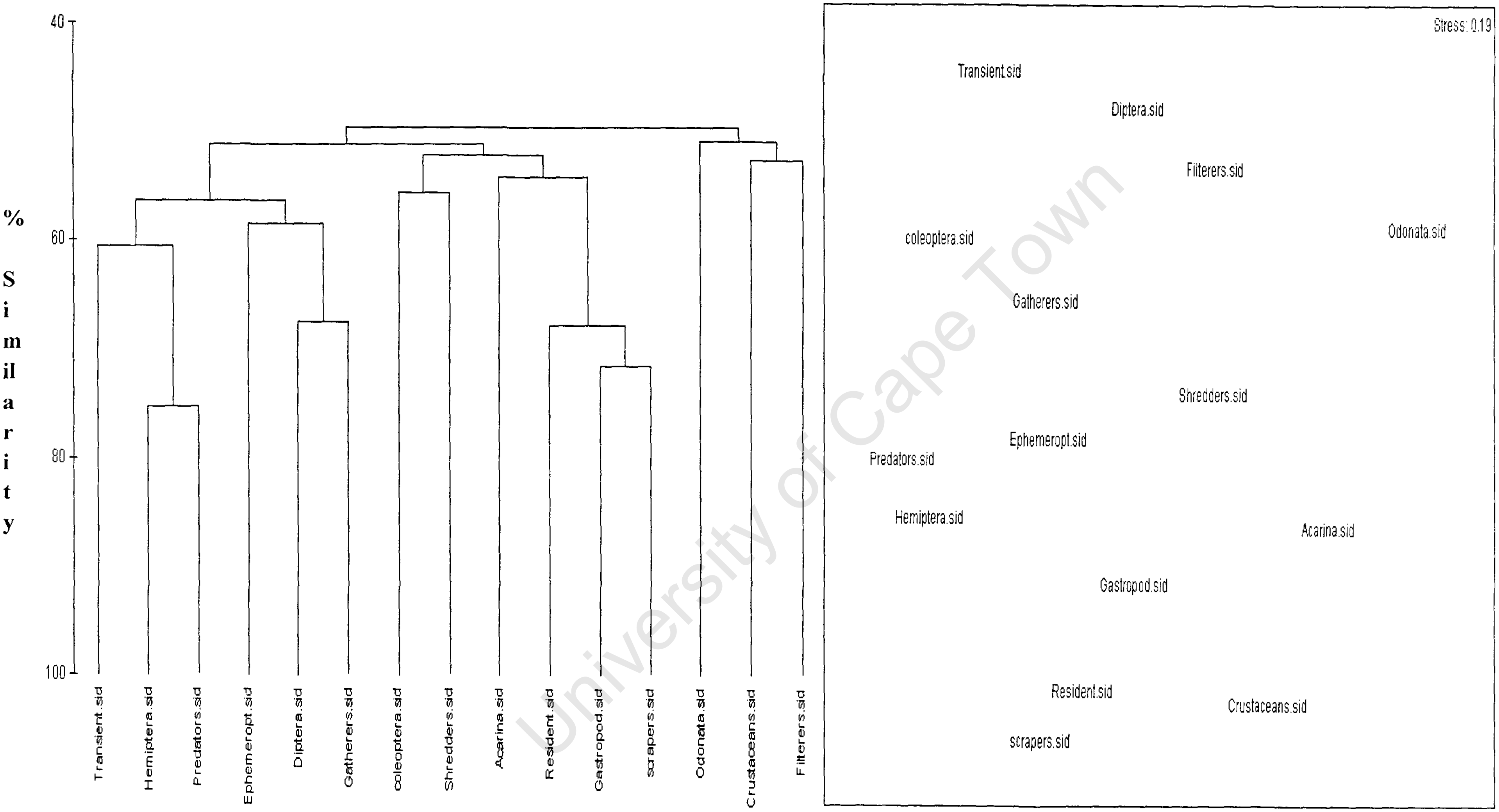

Figure 3.21. Cluster dendrogram & multidimensional scaling (MDS) ordination showing the assemblage similarity based on presence-absence.

3.5 DISCUSSION

In aquatic habitats, congruence of assemblages is important to facilitate biomonitoring of the ecological integrity of these delicate ecosystems, by doing rigorous bioassessment of a representative sample (or surrogates) instead of dealing with the entire aquatic assemblage. However, this study found congruencies between higher taxa themselves to be dismally weak, with no one taxon even having a 50% correlation with one another. The highest congruence observed was 40%, found between the Odonata *vs* Hemiptera and between the Acarina *vs* Coleoptera using the species richness data set. When using relative abundance data 19% correlation was the highest cross-taxon congruence found between the Acarina *vs* Odonata and 13% between the Acarina *vs* Gastropoda using presence-absence data. It was even worse for cross-family comparisons, results from all the three data sets revealed the same pattern of discouragingly weak congruencies. Such lack of cross-taxon congruence suggests that no individual taxon is a good representative or surrogate for other taxa. Moreover, for both order and family level, individual taxa failed to account for a significant variation in the total invertebrate assemblage, further suggesting that none can be used as a surrogate for the overall assemblage. These results are in keeping with other freshwater studies (Allen *et al.* 1999a; b; Heino *et al.* 2005; Bilton *et al.* 2006; Bini *et al.* 2007), all of which reported low cross-taxon congruencies, rendering the use of a single taxon as a predictor of overall macroinvertebrate species richness problematic (but see Heino 2002; Briers and Biggs 2003).

The lack of congruence between wetland macroinvertebrate families in this study, is particularly unfortunate since this is the taxonomic level used in biomonitoring programmes (Marshall *et al.* 2006; Jones 2008). Allen *et al.* (1999 b) attributed low concordance among taxonomic groups to the fact that different-sized organisms may perceive the environment in profoundly different ways and therefore respond at different scales. However, Bini *et al.* (2008), working with Rotifera, Cladocera and Copepoda in 30 Brazilian reservoirs, and Grenouillet *et al.* (2007) studying fish, diatoms and benthic macroinvertebrates in a south-western French stream, reported strong congruencies between their study taxa. Sánchez-Fernández *et al.* (2006), working in the Segura river basin (SE Spain) reported that Coleoptera, Ephemeroptera, Plecoptera and Tricoptera were significantly correlated with total invertebrate assemblage.

An encouragingly strong congruence, however, was observed from all three data sets between the scrapers *vs* Gastropoda and between the predators *vs* Hemiptera, suggesting that Hemiptera and Gastropoda can act as surrogates for their respective FFGs. This, however, should be treated with caution since there is the possibility of a Type 1 error due to possible dominance of these taxa in their FFGs. Predators also had a very strong congruence with the total invertebrate assemblage, suggesting that predators can be used as a surrogates for overall invertebrate assemblage. This is strengthened by the fact that both data sets (species richness and assemblage structure) showed the same pattern. These results suggest, therefore, that the overall invertebrate assemblage can be adequately assessed by concentrating the often-limited resources (time and expertise) on predators. It is important to bear in mind, though, that although this study was conducted over a large geographic area, it was conducted over a single growing season, therefore temporal effects still need to be taken into consideration. But the current results are promising and warrant further investigation.

Predators were also found to be well correlated with the Hemiptera, but the Hemiptera *per se* did not have the greatest congruence with the overall assemblage as did predators, making the default conclusion about its value as a surrogate for the overall macroinvertebrate assemblage troublesome. However, both Hemiptera and predators exhibited a consistently high similarity (see table 3.3) with the overall percentage similarity, this being observed with all data sets, and suggesting that both Hemiptera and predators can reliably be used as surrogates for overall assemblage. The Hemiptera possess many of the characteristics discussed by Sánchez-Fernández *et al.* (2006) that make good surrogates (e.g. taxonomic and faunistic relatively well understood). According to Lovell *et al.* (2007), when selecting surrogates, a correlation coefficient of greater than 75% should be used as an optimal level of congruence, since below this value the relation is likely to be weak, and if used as a surrogate, misinterpretation may occur. The fact the Hemiptera and predators had ≥75% similarity, further strengthens the argument of using these taxa as surrogates. The results of the current study have promising practical implications for biodiversity assessment, but must be taken cautiously and perhaps more research is still needed to refine them. Briers and Biggs (2003) caution against generalising of congruent relationships observed in one area and extrapolated to unstudied taxa and/or ecosystems. This further emphasise the need for further research in order fully to understand the dynamics of these systems.

Ironically, when using species richness data, Gastropoda (which are exclusively sessile i.e. flight-less) had the strongest congruence with transient taxa (which are capable of flight). And the Hemiptera (which are flight capable) had the highest congruence with resident taxa (which are flightless). These observations are rather baffling, given the polarized life histories of these taxa (Hall *et al.* 2004). However, this irony falls away when assemblage structure and composition datasets are used, in fact the opposite is seen. Gastropoda had the highest correlation of all taxa with resident taxa, while Hemiptera exhibited the second highest correlation after Diptera with transient taxa (Table 3.1). Although these observations are somehow closer to reality, still the correlations were rather weak, making it tricky to come to concrete conclusions from such results albeit promising. The fact that resident taxa explained more than 90% of the variance in the total invertebrate assemblage using species richness data, further gives impetus to undertaking additional research to verify and improve on the results of the current study. The same significant pattern, albeit weaker, was observed with assemblage composition data. Moreover, resident taxa had the strongest congruency with predators, which also explained a significant variance in total invertebrate assemblage. This further corroborates the conjecture made above that predators can act as a surrogate for overall invertebrate assemblage.

For both case taxa i.e. beetles and bugs examined in the study, all taxonomic levels (e.g. species, genus & family) were strongly congruent (ρ=0.900), suggesting that higher taxonomic levels (genus and family) could well be used as surrogates for species richness. Several studies have reported that species-level identification is not necessary for broad-scale aquatic monitoring (e.g. Hewlett 2000) as it yields similar results to family-level identification (Marshall *et al.* 2006). Heino and Soininen (2007) reported similar results, as they found that species richness was strongly correlated with genus and family richness for both macroinvertebrates and diatoms. Cardaso *et al.* (2004) and Lovell *et al.* (2007) have argued that such strongly congruent patterns usually occur in species-poor taxa, but these two taxa (beetles and bugs) were the most speciose taxa in the study area. However, a different view emerges as comparisons are made with the whole assemblage. Using beetles - given their high diversity in this study (see chapter 2) and our fairly good taxonomic understanding – very weak correlations were found when comparing different taxonomic level (see figure 3.15- 3.18). The same pattern was also seen even when correlating coleopteran species richness against total assemblage family richness. It can therefore be concluded from these results that for individual taxa, different taxonomic levels can used with equal confidence, but for comparisons between taxonomic groups and overall assemblage care must be taken since were low correlations.

Owing to the sampling, taxonomic and resource constraints involved with biodiversity research, the use of higher taxonomic levels provides an appealing alternative. As enables rapid generation of results because of reduced identification times required (e.g. Balmford *et al.* 1996a). Báldi (2003) showed that only 208 (families) instead of 3707 (species) needed to be identified in his study of terrestrial Coleoptera, Diptera and Acari in central Hungary. Andersen (1995) in his quest for correlation between ant species and genera, reported that the relationship was confounded by biogeographic factors, and strongly influenced by sampling intensity and sampling area. The present study avoided these pitfalls by sampling one biogeographic area, the south-west of the Cape Floristic Region and standardizing sampling intensity and area throughout the study. I would, however, like to see if the same pattern would hold for the other taxa and also for different areas within the CFR (e.g. Paavola *et al.* 2006; Grenouillet *et al.* 2007).

Although species richness has been the prime index used to assess biodiversity, studies have suggested that species richness alone maybe insufficient as a measure of biodiversity (e.g. Su *et al.* 2004), partly because species richness is highly sensitive to sampling effort (Gotelli and Colwell 2001) while retaining little biological information (Barlow *et al.* 2007) and not necessarily correlated with other biodiversity measures (Heino *et al.* 2008). Moreover, Bilton *et al.* (2006) argued that since some communities are species-poor, an approach which relies entirely on species richness may fail to achieve key conservation goals. Therefore, the current study added two more biodiversity measures based on assemblage composition (presence-absence) and structure (relative abundance), since these have been found to add more additional ecological information (Bilton *et al.* 2006). Species richness analysis, yielded a higher number of correlations, however, and these correlations tended to be stronger than those attained with assemblage structure and composition analyses. Lovell *et al.* (2004), working on savanna terrestrial invertebrates, observed similar findings. Su *et al.* (2004), however found strongest cross-taxon congruence when using community structure between plants, birds and butterflies, and poor congruence when assessing species richness. Variation in results depending on which data set is in use indicates that different data sets assess different aspect of biodiversity. As a result, the current study suggests that all data sets should be used together, as they seemed to be complementary, rather than the conventional way of using species richness as the only measure of biodiversity.

CHAPTER 4

ASSESSMENT OF THE SPATIAL AUTOCORRELATION AND PHYSICO-CHEMICAL FEATURES ON WETLAND MACROINVERTEBRATE ASSEMBLAGES IN THE SOUTH-WESTERN CAPE, SOUTH AFRICA

This chapter starts off by explaining spatial autocorrelation and its importance in analysis of the effect of physico-chemical features, and later assesses the effect of the physico-chemical variables measured in this study on the structure and composition of wetland macroinvertebrate assemblages.

4.1 INTRODUCTION

4.1.1 Spatial autocorrelation

In ecological data, spatial autocorrelation – technically defined as the lack of independence between pairs of observations at given distances in space (Cliff and Ord 1981; Legendre 1993) – is a relatively common phenomenon (Koening 1999). Simply put, spatial autocorrelation is the similarity of variables based on the proximity of collecting sites, as a factor explaining the observed pattern. Spatial autocorrelation arises because the variable of interest itself is spatially autocorrelated (i.e. it changes as a function of space) or the variable of interest is related to another variable that is spatially structured (Legendre and Legendre 1998). It provides information critical to interpreting population dynamics, predicting population status at unsampled locations and facilitates monitoring programs (see Koening 1998; 2001; Lloyd *et al.* 2006).The presence of spatial autocorrelation, however, results in overestimation of the number of degrees of freedom in an analysis (Legendre and Legendre 1998). Such overestimation of degrees of freedom artificially narrows confidence intervals and lead to Type-I errors, i.e. the false rejection of null hypotheses. Therefore, spatial autocorrelation should be checked before analyses of biotic distribution are performed (Wilkinson and Edds 2001).

Spatial autocorrelation of assemblages implies that the systems (i.e. wetlands) are open and that there is movement of organism through space (Lloyd *et al.* 2006). Because wetlands are discrete habitats embedded in terrestrial landscapes, effective management and conservation of their inhabitants depend on the understanding of how populations in one habitat depend on the proximity with other wetlands (Wissinger 1999). Temporary wetland assemblages behave metapopulations (e.g. Hanski and Gilpin 1998). Persistence of metapopulations, however, requires low spatial autocorrelation over large geographic areas (Koenig 2001). Because otherwise if there is high spatial autocorrelation, catastrophic events will result in extirpation of all metapopulations, and ultimately leading to permanent extinction. Consequently, Koenig (1998; 2001) posits that declines in species exhibiting extensive spatial autocorrelation should be examined more seriously, since they may reflect large-scale population declines covering much or all of the species' range. This is particularly important for temporary wetland assemblages given the dynamic nature of their habitat. Moreover, populations demographically autocorrelated over large geographic areas may be particularly vulnerable to the detrimental effects of habitat fragmentation (Koening 1998), because such assemblage similarity is probably maintained largely by dispersal (Bilton *et al.* 2001; Bohanak and Jenkins 2003; Vanschoenwinkel *et al.* 2007).

Although correlational studies do not conclusively identify causal effects underlying observed ecological patterns, describing and quantifying spatial patterns in nature can lead to a better understanding of the relative importance of the processes that create them. Analysis of spatial autocorrelation provides a step closer in understanding the relative importance of the variables that structure the observed biodiversity patterns (Legendre 1993). A key issue in understanding biodiversity distribution, is knowing to what extent is it constrained by local environmental variables versus spatial factors (Grenouillet *et al.* 2007) and this was performed using Mantel test (Manly 1986). It is never easy to separate the effect of environment and space, because much of the variance attributed to environmental variation can be alternatively explained by the spatial pattern underlying it (Legendre 1993). Therefore, the Partial Mantel test (Smouse *et al.* 1986), which allows assessment of the relative importance of different hypotheses seeking to explain the observed pattern; by shielding the effect of the other, will be used.

4.1.2 The Effect of physico-chemical features

Knowledge of the relationship between biological communities and the environment is crucial for the understanding of overall wetland structure and function. Environmental extreme variability of temporary wetlands poses constraints to physicochemical and biological processes (see review by Williams 1996) of its inhabitants. Consequently, biological communities have evolved adaptations to deal with such variations (Wiggins, Mackay and Smith 1980; Wellborn, Skelly and Werner 1996). Macroinvertebrate assemblage in wetlands has been reported to be affected by a number of environmental factors in the literature, for example area (size), habitat heterogeneity, hydrology, hydroperiod, altitude, water chemistry (e.g. salinity & pH), nutrient enrichment, isolation, land management practices, biological interactions (predation in particular), water depth and temperature

(Collinson *et al.* 1995; Hanson and Riggs 1995; Batzer and Wissinger 1996; Williams 1996; Brönmark and Hansson 1998; Batzer *et al.* 1999; Euliss and Mushet 1999; Rader *et al.* 2001; Heino 2000; Zimmer *et al.* 2000; Oertli *et al.* 2002; Batzer *et al.* 2004; Hall *et al.* 2004; Tarr *et al.* 2005; Whiles and Goldowitz 2005; Woodcock *et al.* 2005; Batzer *et al.* 2006; Williams 2006; Waterkeyn *et al.* 2008). The effect of water chemistry may also indirectly affect invertebrate assemblages by affecting the abundance and diversity of macrophytes, which in turn control the type and physical substrate and food resources available. In contrast, freshwater animals themselves also play a significant role in modifying the environment, through direct or indirectly nutrient cycling (e.g. bioturbation processes) (see Nanni 2002).

Because of the complexity of natural phenomena, biological communities are borne of many influences, and identifying discrete variables is usually difficult and rare in nature. However, Weigel *et al.* (2003) assert that discerning the relative influence of environmental variables is a prerequisite to prudent management of aquatic resources. Nicolet *et al.* (2004), studying temporary ponds of England and Wales, found water chemistry, particularly pH and alkalinity, to be the main environmental factor influencing the composition of communities. On the other hand, Zimmer *et al.* (2000), working on semi-permanent prairie wetlands of Minnesota, concluded that fish abundance was the most influential variable than environmental factors influencing invertebrates. In northeastern Finland lentic water bodies, surface area, moss cover, total nitrogen and water hardness were reported to be the most influential environmental factors (Heino 2000). Some studies (Tangen *et al.* 2003; Batzer *et al.* 2004), however, have found invertebrate assemblages to be unresponsive to environmental gradients. This could be true for temporary wetland inhabitants given they are routinely exposed to pronounced and unpredicted environmental changes Batzer *et al.* (2004). Furthermore, Oerti *et al.* (2008), studying high alpine ponds in Switzerland, reported that invertebrate assemblages were only weakly influenced by local environmental variables, however, the opposite was found by Mykrä *et al.* (2007) in Northern Finland.

There is almost a consensus (e.g. Leeper and Taylor 1998; Whiles and Goldowitz 2005; Waterkeyn *et al.* 2008) that hydroperiod (i.e. the length of inundation) is the most influential factor determining invertebrate assembly in temporary waters. Early research showed that as hydroperiod lengthens, general diversity increased (Schneider 1999) so as predator abundance (Wiggins *et al.* 1980). This lead Schneider and Frost (1996), studying temporary pond communities in Wisconsin to conclude that the processes structuring them were hierarchically organised by hydroperiod. The main problem with interpreting the effect of hydroperiod is that it is confounded by or covaries with a number of other factors. For example, hydroperiod has been recorded to be highly correlated with wetland size

(March and Bass 1995; Studinski and Grubbs 2007), water depth & volume (De Roeck 2007), water temperature & dissolved oxygen (Schneider and Frost 1996; Tarr *et al.* 2005), predators (Schneider and Frost 1996; Spencer *et al.* 1999) and conductivity & pH (Schneider and Frost 1996). On the other hand, Wissinger *et al.* (1999) found little evidence that hydroperiod directly affected community structure beyond the fact that only a few invertebrates exploited extremely short-duration ponds. Furthermore, Batzer *et al.* (2004) argue that in most studies, the effects of hydroperiod on temporary wetland communities are found only in extreme environmental gradients.

4.1.3 Aims and Objectives

The over-arching aim of this chapter is to assess the effect of spatial autocorrelation and physico-chemical variables on the wetland macroinvertebrates. With the following specific objectives:

1. Assess the correlation between spatial (i.e. geographic distances between wetlands), macroinvertebrate assemblage and environmental data were tested.
2. Assess individual effect of geographic distance while controlling for environment and *vice versa* to macroinvertebrate assemblages.
3. Assess the relative importance of different physico-chemical variables on structuring macroinvertebrate assemblages.

4.2 MATERIALS AND METHODS

4.2.1 Spatial Autocorrelation

The relationships between macroinvertebrate assemblages, environment and geographic distances between wetlands were assessed by the Mantel test (e.g. Legendre and Fortin 1989; Legendre and Legendre 1998). In addition, the effect of environmental variables on macroinvertebrate assemblage patterns was assessed after removing the effects of geographical distance between sites and *vice-versa* by performing partial Mantel tests (Smouse, Long and Sokal 1986). The Mantel statistic (r_M) was calculated for each matrix pair comparison and tested to see if it differed from those expected under the null hypothesis (i.e. no correlation) using Monte Carlo permutation tests (999 iterations). All statistics were performed using Pattern Analysis, Spatial Statistics and Geographic Exegesis (PASSAGE) - a free software program courtesy of Rosenberg (2001).

4.2.2 The effect of physico-chemical parameters

Maximum, minimum, average and standard deviation values for all the physico-chemical parameters measured in this study are given in Table 4.2. To assess the spatial configuration of wetlands based on their physico-chemicals, non metric multidimensional scaling plot was produced using Primer software (Clarke and Warwick 2001).The relationship between individual macroinvertebrate families and physico-chemical variables was tested using univariate multiple linear regression (stepwise forward selection) in SPPS (version 16 for Windows, SPSS Inc., 2006). The forward stepwise selection procedure was employed to create explanatory models, and an individual variable was added to the model only if its inclusion yielded a statistical significance ($p \leq 0.05$).The relationship between individual physico-chemical parameters was tested using nonparametric Spearman's correlation analysis, also in SPPS. Only those relationships that yielded significant results are presented.

Detrended correspondence analysis (DCA) was first used to decide on the multivariate ordination method, and redundancy analysis (RDA) was found to be most appropriate (see Lepš and Šmilauer 2003 for procedure). To identify the relationship between environmental variables and macroinvertebrate assemblages, RDA was performed in CANOCO software (version 4.5 (ter Braak and Šmilauer 2002). This analysis was conducted separately for the whole data set and for individual sub-areas (i.e. Cape Flats, Cederberg, West Coast and Agulhas Plain). RDA explains variation in a set of response variables as a function of multiple axes that are combinations of explanatory variables (Lepš and Šmilauer 2003). Stepwise RDA was used to build models to explain variance in individual family, by forward selecting variables that explained significant variation ($p \leq 0.05$). For this analysis only families with more than 500 individuals were included. Stepwise RDA is a multivariate technique in the correspondence analysis family, that is similar to stepwise multiple regression in univariate statistics, but RDA incorporates several dependent variables at once (ter Braak and Šmilauer 2002). Significant explanatory variables were selected with forward selection using 100 Monte Carlo permutation tests (Lepš and Šmilauer 2003).

4.3 RESULTS

4.3.1 Spatial Autocorrelation

Mantel analyses showed that macroinvertebrate assemblages were significantly correlated with geographic distance and environment (see Table 4.1a & b), for both presence/absence and relative abundance data. However, environmental factors were responsible for double the amount of variation in macroinvertebrate assemblage than geographic distance. Environmental factors explained 36% of the variation in macroinvertebrate assemblage, while the spatial variables were responsible for only 15% (Table 4.1). Interestingly, this observation did not change even after controlling for the effect of the other variables using partial Mantel test (Smouse, Long and Sokal 1986). The relationship between geographic distance and environment was negative and not significant. The fact that presence/absence and relative abundance data yielded very similar results suggests that they both have similar merits.

Table 4.1(a). Mantel tests ($r_{M)}$ between geographic distance, assemblage (based on relative abundance) and environment. Above the diagonal: Mantel tests results, below the diagonal: partial Mantel tests results. Probability based on 999 permutations.

	mblage	aphic ce	nment
blage			
aphic distance			(ns)
nment			

* denotes significance after Bonferroni correction (P>0.001); ns (non significant)

Table 4.1(b). Mantel tests (r_M) between geographic distance, assemblage (based on presence / absence) and environment. Above the diagonal: Mantel tests results, below the diagonal: partial Mantel tests results. Probability based on 999 permutations.

	Assemblage	Geographic distance	Environment
Assemblage		0.144*	0.367*
Geographic distance	0.162*		-0.017(ns)
Environment	0.373*		

* denotes significance after Bonferroni correction (*P*>0.001); ns (non significant).

4.3.2 The effects of Physico-chemical features

Wetlands sampled in this study were very variable in their measured physico-chemical variables (see Table 4.2). For example, pH ranged from 4.1 – 10.1, whereas water depth ranged from 2.50 – 0.10m. Most environmental variables (e.g. conductivity, turbidity, wetland area etc) were extremely variable, evident from the fact that standard deviations were much larger than the means.

The four sub-areas (clusters) sampled in this study separated relatively well in space as seen in the MDS plot (Figure 4.1). West Coast sites grouped fairly together, although widely spread. On the contrary, Agulhas Plain and Cape Flats were clustered fairly together.

Using univariate multiple regression analyses pH, turbidity and conductivity were included in many models that explained significant variations in numbers of individuals in several macroinvertebrate families (see Table 4.4). Temperature and NO_2 significantly contributed only to the model that explained variance in Potamiopsidae together with area and dissolved oxygen. In addition to contributing significantly to models explaining variance in Chironominae, Culicidae and Paramelitidae, pH was also found to be the sole variable significantly explaining variation in Corixidae and Notonectidae. Turbidity was found to be the only physico-chemical variable significantly important for Baetidae and Hydraenidae, while also contributing immensely to models explaining variance in Dytiscidae and Streptocephalidae. Variation in abundances of the Pionidae, Coenagrionidae, Physidae and Planorbidae were significantly explained only by conductivity.

Table 4.2 Variation of the measured physico-chemical variables.

	Mean	Standard deviation	Maximum	Minimum
Depth (m)	0.55	0.47	2.50	0.10
Temperature (^{0}C)	18.93	4.18	28.60	10.80
pH	7.68	1.12	10.10	4.10
Conductivity (mS/m)	36.72	46.58	186.70	0.10
Turbidity (NTU)	53.73	160.28	1000.00	0.40
Dissolved Oxygen (mg/l)	6.61	3.65	24.20	1.20
NH_4 (ug/l)	304.33	837.11	5146.28	0.23
PO_4 (uM)	4.28	10.64	91.21	0.02
PO_4 (ug/l)	132.59	329.92	2827.36	1.15
$NO_3 + NO_2$	184.30	1105.33	9196.39	0.01
NO_2 (ug/l)	13.92	127.19	1493.27	0.01
NO_3 (ug/l)	170.38	1010.50	7703.11	0.04
Altitude (m)	81.68	213.83	1191.00	0.50
Area (m^2)	4211.37	6486.13	41448.00	502.40

The Pomatiopsidae, Notonectidae, Corixidae and Chironominae were highly correlated with the first axis of the RDA (Figure 4.2a) as shown by the length of the arrow. Out of the five significantly important physico-chemical parameters, only conductivity was correlated with the second axis, while the rest were correlated with first axis. Conductivity was also highly correlated with Hydrophilidae and Scirtidae, while the family Corixidae was correlated with turbidity and the Chironominae with phosphate and ammonium (Figure 4.2c). Although the second axis of RDA yielded slightly higher species-environment correlations (see Table 4.5), the first axis explained the largest variance and together they accounted for more than 60% of the total variance observed and had the largest eigenvalues. The First axis explained 33.5% of assemblage-environment variation, while the second axis accounted for 28%.

Table 4.4 Multiple linear regression models explaining variance in macroinvertebrate families.

	Multiple R	Multiple R^2	Adjusted R^2	Choosen factors	F	*P*
Chironominae	0.512	0.262	0.251	NH4	46.004	0.000
				pH	4.569	0.034
Dytiscidae	0.294	0.087	0.073	Turbidity	7.107	0.009
				pH	6.033	0.015
Potamiopsidae	0.533	0.284	0.263	DO	26.201	0.000
				Temperature	7.748	0.006
				NO_2	7.173	0.008
				Area	4.979	0.027
Culicidae	0.391	0.153	0.128	Conductivity	9.794	0.002
				pH	9.743	0.002
				Turbidity	4.897	0.029
				PO_4	4.405	0.038
Baetidae	0.210	0.044	0.037	Turbidity	6.363	0.013
Corixidae	0.319	0.102	0.095	pH	15.634	0.000
Notonectidae	0.353	0.124	0.118	pH	19.590	0.000
Orthocladinae	0.197	0.039	0.032	Altitude	5.552	0.020
Planorbidae	0.415	0.172	0.166	Conductivity	28.739	0.000
Hydrophilidae	0.365	0.133	0.120	pH	16.977	0.000
				NH_4	5.434	0.021
Streptocephalidae	0.357	0.128	0.115	turbidity	12.357	0.001
				Altitude	4.062	0.046
Paramelitidae	0.415	0.172	0.160	pH	28.300	0.000
				DO	4.209	0.042
Physidae	0.408	0.167	0.161	Conductivity	27.632	0.000
Coenagrionidae	0.340	0.115	0.102	Conductivity	12.072	0.001
				area	6.076	0.015
Lymnaeidae	0.478	0.228	0.217	Altitude	39.763	0.000
				turbidity	4.416	0.037
Hydraenidae	0.267	0.071	0.065	turbidity	10.594	0.001
Pionidae	0.281	0.079	0.072	Conductivity	11.788	0.001
Pleidae	0.169	0.029	0.022	PO_4	4.054	0.046

Table 4.5_Variance explained by the first four axes of the RDA.

	Axes				
	1	2	3	4	
Eigenvalues	0.085	0.070	0.048	0.020	
Species-environment correlations	0.624	0.713	0.632	0.506	
% Variance of assemblage data	8.5	7.0	4.8	2.0	
% Cum. variance of species data	8.5	15.5	20.3	22.3	
% Cum. variance of species-environment	33.5	61.1	80	87.7	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.254

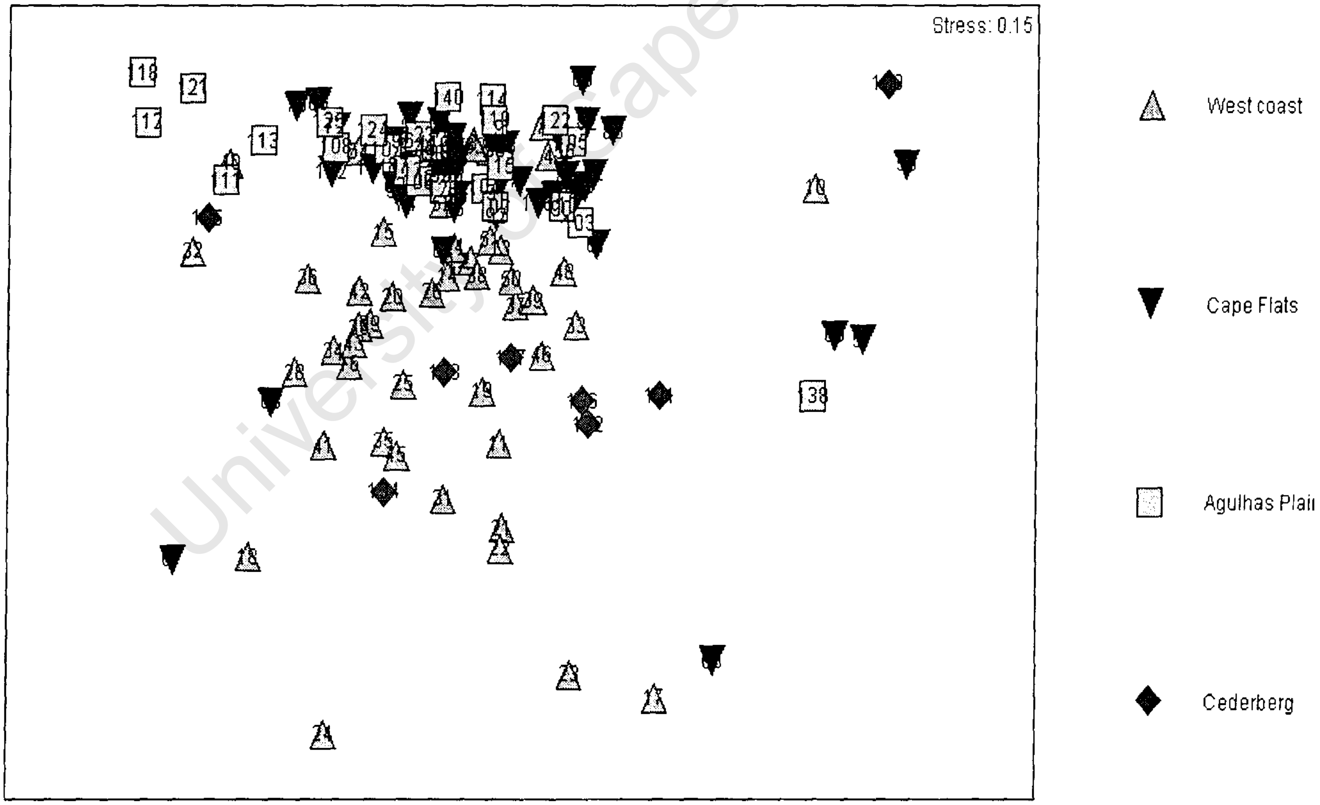

Figure 4.1 Non metric multidimensional scaling plot showing arrangement of wetlands from the four sub-areas based on their physico-chemical variables

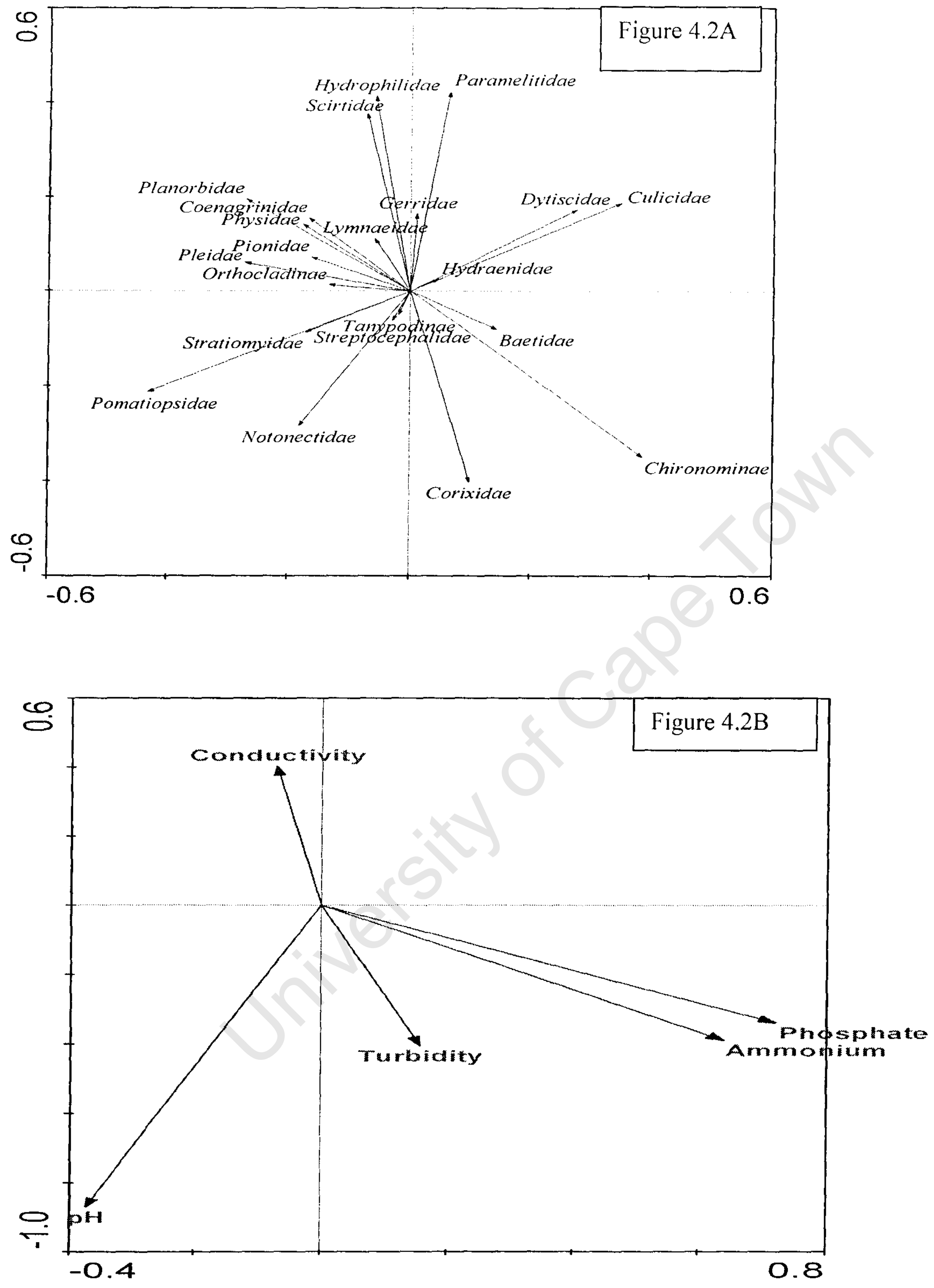

Figure 4.2 Ordination diagram (RDA) of the first two axes illustrating the relationship a) macroinvertebrate families alone, and b) physico-chemical parameters (only those that yielded significant contribution).

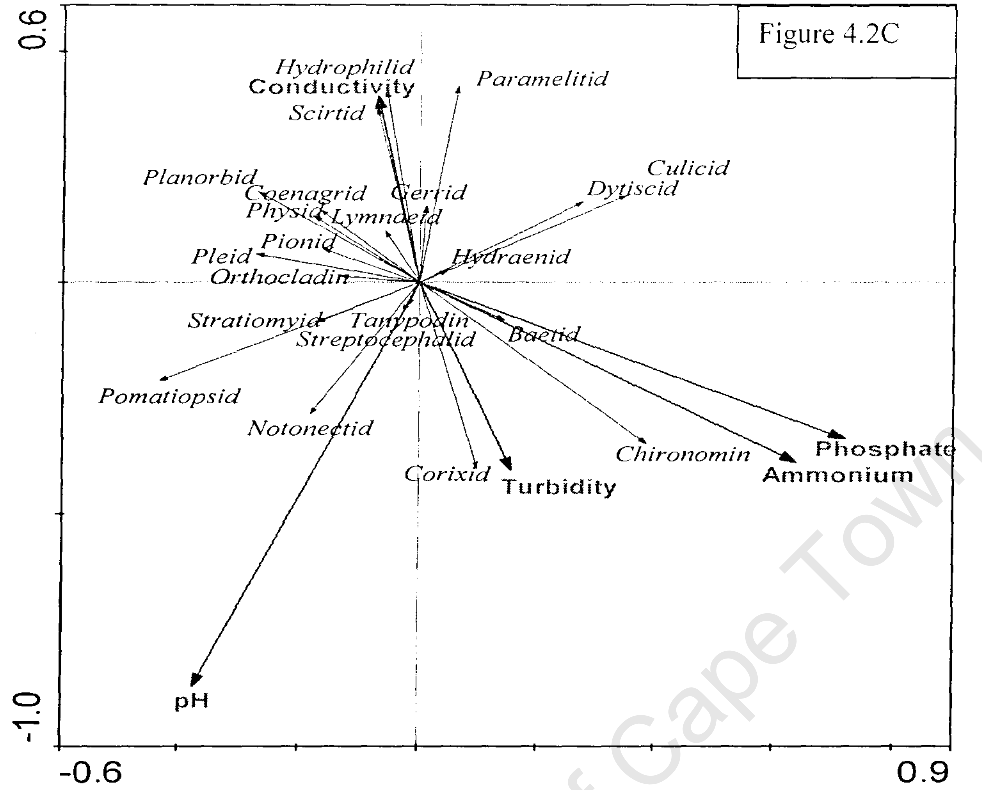

Figure 4.2c Ordination diagram (RDA) of the first two axes illustrating the relationship showing both macroinvertebrate and physico-chemical variables.

Stepwise RDA results of the whole dataset (see table 4.6) revealed that out of the 14 measured physico-chemical variables in this study, only five (i.e. pH, phosphate, conductivity, turbidity and ammonium, respectively) were included in the model that significantly explained the variation in assemblage data. These variables explained a significant share of 80% of the total variance. pH and phosphate, by far, contributed more to explaining overall macroinvertebrate assemblage, with each accounting for more than a 20% of the total variance explained by the model. For sub-areas, the Cape Flats cluster had altitude, conductivity, pH and temperature being the variables that constituted the model that explained the significant variation in macroinvertebrates, while in the West Coast cluster it was altitude, dissolved oxygen, tubidity, ammonium and conductivity. For Cederberg and Agulhas Plain clusters, models constituted by only one variable were found, it was phosphate for Cederberg and water temperature for Agulhas Plain (Table 4.7).

Table 4.6 Physico-chemical variables that significantly contributed to explaining the variance in assemblage data.

	Variance explained	%variance explained	F	*P*	Cumulative variance	% Cumulative variance
pH	0.060	23.622	8.795	0.005	0.060	23.622
Phosphate	0.058	22.835	9.057	0.005	0.118	46.457
Conductivity	0.036	14.173	5.838	0.005	0.155	61.024
Turbidity	0.023	9.055	3.755	0.005	0.177	69.685
Ammonium	0.019	7.559	2.067	0.025	0.204	80.315

Table 4.7 Physico-chemical variables that significantly contributed to explaining the variance in assemblage data in the different sub-areas as detected through RDA.

	F	P	Variance explained (VE)	Cumulative VE
		West Coast		
Altitude	4.701	0.005	0.081	0.081
DO	3.511	0.020	0.059	0.140
Turbidity	2.925	0.010	0.046	0.222
Conductivity	2.684	0.025	0.040	0.262
Ammonium	2.261	0.025	0.036	0.289
		Agulhas		
Temperature	4.428	0.015	0.156	0.156
		Cederberg		
Phosphate	2.731	0.030	0.281	0.281
Cape Flats				
Altitude	4.347	0.005	0.085	0.085
Conductivity	4.660	0.005	0.077	0.169
pH	1.995	0.015	0.067	0.204
Temperature	2.199	0.005	0.054	0.242

4.4 DISCUSSION

4.4.1 Spatial autocorrelation

Although biotic interactions undoubtedly play a critical role in shaping ecological communities (Williams 1996) in temporary waters, they are not as highly regarded as environmental and spatial variables in explaining patterns of biotic communities. However, Wilkinson and Edds (2001) argue that biotic processes provide circumstantial evidence in explaining biodiversity patterns that may not be necessarily explained by environmental differences. Environmental variables in this study accounted for more than a third of the variation in macroinvertebrate assemblages, and together with spatial variables they accounted for just over half, leaving the other half unaccounted for. Biotic interactions may well be important in explaining the remaining variation. To the best of my knowledge all the wetlands studied here were fishless given that fish presence is cited as a major influential biotic variable (e.g. Hanson and Riggs 1995 and Zimmer et al 2000). Moreover, spatial autocorrelation itself may result from biotic interactions. For example, mutually beneficial aggregation may lead to positive autocorrelation or competition and predation leading to negative autocorrelation (Legendre 1993). In temporary wetland systems, positive autocorrelation is likely to happen at the beginning of rainy season as wetlands fill with water, providing bountiful food (Batzer *et al.* 2006) for early colonizers. On the other hand as hydroperiod lengthens, it inevitably leads to aggregation of predators and competitors (Wellborn, Skelly and Werner 1996) that can ultimately cause negative autocorrelation.

Both the environmental and spatial data exhibited significant correlations with macroinvertebrate assemblage data, as seen with both relative abundance and presence/absence data (Table 4.1a & b). This trend was repeated even after removing the effect of th other variable (*sensu* Smouse *et al.* 1986). Grenouillet *et al.* (2007) reported that although significant correlations existed between stream assemblages and both environmental and spatial matrices, partial Mantel tests revealed that correlations between stream assemblages and environmental distances were non-significant. Environment and spatial data were found not to be significantly correlated, indicating that local habitat conditions were not spatially autocorrelated. Furthermore, the environment appeared to play a far more important role in affecting macroinvertebrate assemblages than spatial data, with pretty much double the correlation coefficient. However, Grenouillet *et al.* 2007 found that environment and geographic distances exhibited similar correlations. Although, Lloyd, MacNally and Lake (2006) did not find appreciable temporal differences (i.e. between years), they found significant differences in spatial autocorrelation between two geographically adjacent rivers of the south-eastern Australia. They noted that this kind of idiosyncratic spatial pattern of stream invertebrate assemblages makes it difficult to use for ecological assessment and restoration. Analysis of spatial autocorrelation in the current study revealed the relative importance of environment over spatial factors in structuring macroinvertebrate assemblages, as a result the effect of environmental variables was further investigated.

4.4.2 The Effects of physico-chemical variables

A combination of five physico-chemical parameters (i.e. pH, phosphate, conductivity, turbidity and ammonium) contributed to a statistically viable model that explained 80% of the variance in the macroinvertebrate assemblage (see Table 4.6). It can be safely said that pH and phosphate are the two most important environmental parameters in structuring wetland macroinvertebrate assemblages in the Western Cape since they individually contributed more than 25% to the overall model. Phosphate has also been reported (Jeppesen *et al.* 2000) to influence biodiversity patterns. Silberbauer and King (1991a), interested in the water chemistry of wetlands in the south-western Cape) reported that sodium and chloride ions were dominant in wetlands near the coast, while bicarbonate anion dominates inland. They argue that, where ionic ratio is controlled by evaporation or rainfall sodium and chloride will predominate, whereas if geology of the area is more important bicarbonate anions will prevail. The current study also found wetland macroinvertebrate assemblages from different sub-areas to be differential responsive to environmental variables, as evident from different explanatory models (see Table 4.7). Although (Silberbauer and King 1991) did not associate environmental variability with biota, this work provided some crucial insights in understanding which environmental variables are important for wetland invertebrates in the south-western Cape.

(Jones 2002), found models incorporating; soluble reactive phosphate (SRP), total nitrogen, divalent cations and sulphate in winter and turbidity, SRP, divalent cations and sulphate in summer were to best explain the variance in wetland animal data in Western Cape. However, both these studies (i.e. Silberbauer and King 1991a; Jones 2002) were conducted in both temporary and permanent wetlands, which are known to exhibit different properties. De Roeck (2007) working on temporary wetlands in the same area, reported that conductivity, nutrient concentrations and water clarity had a direct and significant influence on macroinvertebrate community composition. Jones (2002), pointed out that animals in these wetlands (i.e. south-western Cape) may be affected more by ionic concentrations than other water chemistry characteristics. However, Apinda-Legnouo (2007) working on artificial lentic water bodies of the Western Cape, reported that aquatic plants, naturalness, conductivity, elevation and temperature were significantly associated with beetle and bug assemblages

Interestingly, the results of the current study did not show wetland area and water depth to have major influences on macroinvertebrate assemblages. This is important given that they are use as a proxy for hydroperiod (*sensu* De Roeck 2007), the effect of which, is well known in wetland biotas (Schneider 1999; Brooks 2000; Baber *et al.* 2003; Tarr *et al.* 2005). The results of the current study, however, are in agreement with Eitam *et al.* (2004) who reported that surface area was not a statistically significant factor in their study of temporary pools' zooplankton richness. On the other hand, Tavernini *et al.* (2008), also studying zooplankton assemblage reported the opposite, with surface area and maximum depth significantly influencing species richness (Stenert *et al.* 2008).

De Roeck (2007) reported that the family Culicidae was negatively associated with water depth, hydroperiod and surface area while the opposite was true for the Hemiptera. Wetland surface area is quite important because it covaries with and affects other variables such as habitat heterogeneity, water permanence, niche availability and colonization rate, just to name but a few (Ebert and Balko 1984; March and Bass 1995; Della Bella *et al.* 2005). Although the literature records conflicting results with regards the effect of wetland size on the structure of invertebrate assemblages, the work of Stenert and Maltchik (2007) revealed that this relationship is significant only for permanent wetlands. This view is shared by several other studies (Lake *et al.* 1989; Schneider and Frost 1996; Batzer *et al.* 2004; Hall *et al.* 2004) that did not find evidence for a relationship between assemblage richness and area in temporary wetlands. Consequently, the result of the current study and several others (Gibbs 1993; Semlitsch and Bodie 1998; Snodgrass *et al.* 2000; Oertli *et al.* 2002) do not support the practical use of wetland size as a basis for wetland prioritization for conservation. Given that some small wetlands harbour special and unique populations (Semlitsch and Bodie 1998).

Studinski and Grubbs (2007) reported that water depth was the best predictor of invertebrate richness and abundance, with most taxa preferring shallow habitats. The work of Magnusson and Williams (2006), revealed that water depth is closely associated with the patterns of dissolved oxygen, conductivity and pH. Fairchild *et al.* (2000), interested in the effect of microhabitats on beetle assemblages found higher abundances near shore, and suggested possible responses to increased temperature and dissolved oxygen. Furthermore, the current study found temperature and dissolved oxygen to be positively correlated with a number of other physico-chemical factors (see table 4.3), showing the intricate complicated nature of physico-chemical interaction. Typically, increase in temperature results in decreased dissolved oxygen concentrations in the water (Williams 1996), but this study found a positive correlation, but the note the current study variables were spot-measurements. In fact, Kagalou *et al.* 2006 reported that dissolved oxygen and temperature seemed to be the main environmental factors affecting community diversity.

Considering that South African waters are characteristically turbid (Meintjes *et al.* 1994), it came as a no surprise for turbidity to be one of the main influential physico-chemical parameters. Over and above to contributing 9% to the model that significantly explained the overall assemblage composition, turbidity was found to be significantly positively related to a number of individual taxa including Branchiopoda: Streptocephalidae. This observation is in agreement with De Roeck *et al.* (2007) who reported a close correlation between turbid water and branchiopods. There is some evidence to suggest that the close correlation between branchiopods and turbidity may be partly due to the fact that branchiopods disturb sediment while feeding (Barclay and Knight 1984). Turbidity can be advantageous by decreasing risk of predation by visual predators (Woodward and Kiesecker 1994), whereas elevated turbidity can reduce light penetration for autotrophic communities leading to reduced primary production (Maitland 1990). Furthermore, turbidity was significantly correlated with altitude, ammonium and total nitrogen in the current study.

Macroinvertebrate assemblages have been reported to be correlated with altitude (Oertli *et al.* 2002; Jacobsen 2004), but this study found no such evidence. Stenert and Maltchik (2007) also found no significant effect of altitude on macroinvertebrate richness, but they conceded that this maybe because the altitudinal gradient (~1000m) they studied was insufficient to recognize the limiting effects of altitude. All the different test performed in this study revealed that in deed pH was quite influential in structuring macroinvertebrate assemblage. The same observation has been recorded elsewhere (Nicolet *et al.* 2004). The effect of pH on biota is generally well appreciated (e.g. Woodcock *et al.* 2005) since it is known that some invertebrates select habitats with specific pH (Batzer and Wissinger 1996). Corixidae and Notonectidae were found to be only significantly correlated to pH.

In agreement with other studies (Boix *et al.* 2008; Stenert *et al.* 2008), conductivity was found to be the third (see table 4.6) most influential physico-chemical variable and significantly correlated with RDA axis 2 which explained 38% of the assemblage-environment variation. In addition, it was significantly correlated with Hydrophilidae and Scirtidae. The dynamic nature of wetlands and interconnected-ness of the physico-chemical parameters requires an integrated and systemic approach. The results of the study contribute significantly to our understanding of the relative importance of large scale physico-chemical parameters. Such understanding is vital for managing and long-term monitoring of these systems.

CHAPTER 5: CONCLUSION

The impetus for this study comes from the demand for information about temporary wetland macroinvertebrate assemblages from both theoretical and applied perspectives. The dynamic nature of temporary wetlands' assemblages provides an invaluable platform to develop and test ecological and evolutionary theories. On the other hand, with the increasing degradation of wetland ecosystems, wetland managers are looking into developing biomonitoring programmes (as in rivers and streams e.g. SASS) to assess long-term ecological changes. Because of their differential response to disturbance, invertebrates are a logical choice to be used for biomonitoring programmes. However, knowledge of what assemblages are found where and what conditions are they most likely to be found at, is a prerequisite to achieve these above mentioned crucial tasks. In addition from a biodiversity conservation perspective, we know very little about wetland assemblage in the south-western Cape, which is unfortunate given the region, is a biodiversity hotspot with high levels of endemism but threatened. Therefore the over-arching aim of this thesis was to assess biodiversity patterns of temporary wetland macroinvertebrate assemblages in the south-western Cape. This was achieved by pursing specific objectives set out in individual chapters, all aimed at unravelling something about the nature of wetland macroinvertebrate biodiversity.

Chapter 2 was concerned with actual macroinvertebrates and describing their diversity in the whole study area. A total of 119 taxa emanating from 51 families representing 73 genera was recorded, which was comparable with other Mediterranean-type climate regions. This study was the first of its kind, and contributes immensely to our understanding of wetland macroinvertebrate biodiversity in this area. Currently, five species new to science were discovered in this study, these were coming from Hydraenidae, Streptocephalidae and Hydryphantidae. The fact that new species were recorded in the first two families, which are the relatively well studied taxa in temporary waters, goes to show how woefully incomplete our knowledge of these system is. Considering that four of these new species were recorded from single locality highlights how rare and hence threatened these species are. Using a range of richness estimators (the abundance-based estimator Chao 1, the incidence-based Chao 2, and the first- & second-order Jack Knife) observed species richness was found to between 6 to 36 lesser than the predicted "true" richness. Chao 2 and Jack 2 which have been reported to be good richness estimators elsewhere, predicted true richness in this study to be 138 and 155, respectively. However, it was not the aim of this study to identify the best richness estimator, and I don't think with the current data I can conclusively answer that question. But the important point was that all the richness estimators showed that observed richness was lesser than the predicted "true" richness. Sample size appeared to be inadequate to capture the full suite of wetland macroinvertebrates in the study area, this is evident from the fact uniques and singletons were still high, while the incidence-based coverage estimator (ICE) was 20 taxa more to the observed richness. But, I believe that sample size per se was not inadequate but it was sampling intensity since this study was conducted on a single sampling season.

Assemblages were dominated by five families; Chironomidae, Dytiscidae, Pomatiopsidae, Culicidae and Baetidae, accounting for more than two-thirds of the overall relative abundance. With only five families; Dytiscidae, Culicidae, Notonectidae Corixidae and Baetidae, also present in more than half the sites. *Tomichia, Cloeon, Culex* and *Sigara* were the most dominant genera, each contributed more than 10% of total assemblage abundance and *Canthyporus, Anisops, Notonecta* and *Culex* were the only genera to occur in more than 50 wetlands. The fact that wetland assemblages were dominated by few taxa, may partly explain why temporary wetland invertebrates are considered unique and less biodiverse than their permanent waters' counterparts. Submerged vegetation habitat supported significantly higher macroinvertebrate abundances than open-water habitat, while both vegetated habitats (i.e. emergent and submerged) supported significantly higher occurrences of macroinvertebrate assemblages. This was in keeping with a large body of literature, therefore highlighting the need for vegetation management in wetland to promote invertebrate production.

There is still a need to improve our taxonomic understanding of many wetland macroinvertebrate taxa, given that a sizeable amount of them could not be identified to lower taxonomic levels. Nothing much could not be said about the conservation status of the taxa found in this study since we still don't know much about their ecology. Given the high number of singletons and rare taxa suggest that there is a high endemism, but more research is still needed to verify these observations.

The third chapter aimed at assessing the congruence between different taxonomic groups, this is fundamental for developing surrogates that can be used for biodiversity conservation and biomonitoring programmes. Specifically I intended to assess the use higher taxa to represent or as surrogate for lower taxa and compared with the overall assemblage, for this I used Coleopteran and Hemipteran different taxonomic levels i.e. species, genus and family. Strong correlations were observed between the different taxonomic levels of the same taxa, but comparing with the overall assemblage yielded weak congruencies. This suggests that higher taxa can be used as surrogate for lower taxonomic levels of the same taxa but does not appear to work well in representing the overall assemblage. Weak cross-taxon congruencies were observed between order and family taxonomic levels themselves as well as overall assemblage, this was seen using species richness, species present/absent and relative abundance data sets. The Hemiptera correlated very strongly with predators, which correlated well with overall assemblage, but because Hemiptera did not correlate well with overall assemblage, the logical conclusion of Hemiptera being surrogate of overall assemblage could not be inferred. However, assemblage similarity analyses revealed Hemiptera and predators achieving the commendable 75% similarity with overall assemblage, thereby implying these taxa can be used as surrogate for the overall assemblage. In fact Hemiptera has most of the characteristics needed for a good surrogate. Following this observation, the current study suggests that Hemiptera can be used instead of the whole assemblage, given the technical difficulty associated with such. This has appealing practical implication for biomonitoring programmes, but further research is still needed since sampling intensity was limited in this study.

The focus of the fourth chapter was assessing the relative effects of the spatial autocorrelation and physico-chemicals on the macroinvertebrate assemblages. Environmental variables were found to be more - almost as twice as – important in explaining variation in macroinvertebrate assemblages. A Model containing pH, phosphate, conductivity, turbidity and ammonium respectively, explained the significant variation in the assemblage structure, with pH and phosphate each contributing more than a quarter each to the model. The affect of these variables on macroinvertebrates is well demonstrated in the literature, but the extent to which they are important in the south-western Cape has never been shown. Although, hydroperiod was not measured, surface area and water depth were not found to be significantly important in explaining variation in macroinvertebrates assemblage, this has serious implication given that they are usually used as a proxy for hydroperiod.

In conclusion, this study contributed to our understanding of biodiversity patterns of macroinvertebrates inhabiting temporary wetlands in the south-western Cape and gave a glimpse into the effects of physico-chemicals. However, more research is still needed to test some of the theories that are starting to appear from this work and also given the practical implication this study possess.

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