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A STUDY ON THE WATER CHEMISTRY AND PLANKTON IN BLACKWATER LAKELETS OF THE SOUTH-WESTERN CAPE

BY

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Thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in the Department of Zoology, University of Cape Town, under the supervision of Dr J A Day.

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for my parents, Neville and Geraldine Gardiner,
for their support and trust in me.

DECLARATION

This thesis reports the results of original research which I have carried out in the Department of Zoology, University of Cape Town between 1981 and 1988. None of it has been submitted in whole or in part for any other degree and any technical assistance I have received is fully acknowledged

Signed by candidate

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ABSTRACT

Blackwater lakelets in the south-western Cape are amongst the most darkly coloured humic waters in the world. In addition the aquatic invertebrate fauna of this region represents a relict and highly endemic group of the South Temperate Gondwanian fauna.

The major environmental and biological variables were investigated over a period of fifteen months in six south-western Cape vleis (Suurdam, Gillidam, Sirkelsvlei, Grootrondevlei, Grootwitvlei and Rondevlei), which range in colour from a very dark brown to only slightly stained and vary in pH from 3.7 to 10.1.

Using absorbance and fluorescence measurements and the Folin-Ciocallteu reagent, relative measures of the quantity and quality of humic compounds were obtained. Suurdam, Gillidam and Sirkelsvlei contained waters of greatest humic content (Suurdam mean A_{290} = 6.561), with a common mid-winter to spring minimum; levels were lower in Grootrondevlei and Grootwitvlei (Grootrondevlei mean A_{290} = 0.996), with a common mid-winter to spring maximum; and lowest in Rondevlei (mean A_{290} = 0.284), with a slight peak in winter. Maxima were related to increased inflow of water with winter rain. Humic compounds in Suurdam, Gillidam and Grootrondevlei were of relatively high molecular weight and phenolic content, indicating an allochthonous origin. In Sirkelsvlei humic compounds were of lower molecular weight and phenolic content, possibly as a result of precipitation of the higher molecular weight fraction due to the high total salinity. Grootwitvlei and Rondevlei had lower molecular weight fractions probably as a result of autochthonous humic production, precipitation with calcium and greater rates of humic degradation; a higher molecular weight allochthonous fraction was present in winter in these two vleis. Buffering at low pH and the complexation of both iron and soluble reactive phosphorous were evident in Suurdam and Gillidam.

Catchment geology, atmospheric precipitation, evaporation and the input of vertebrate excreta explain the inorganic chemical environments of the vleis. Acid, well-leached soils and calcareous sands resulted in mean pH values of 3.8 and 4.2 in Suurdam and Gillidam and 8.0 and 8.6 in Grootwitvlei and Rondevlei. The cation composition of the vleis on well-leached acid soils was primarily determined by the atmospheric precipitation of marine salt; evaporation and calcareous sands increased the salinity or relative calcium concentrations in some vleis. Animal excreta in Grootwitvlei and Rondevlei also alter the cation composition slightly, and increase the load of major nutrients. Nitrogen and phosphorous are largely of

biological origin. Nutrient levels in the vleis are variously affected by marginal macrophytes, the sediments, primary production and the levels of humics.

Chlorophyll *a* levels indicated low phytoplankton biomass in Suurdam, Gillidam and Grootrondevlei (Suurdam, mean chlorophyll *a* = 0.9 ug l^{-1}) and no distinct seasonality; intermediate levels in Sirkelsvlei (mean chlorophyll *a* = 11.6 ug l^{-1}) and high levels in Grootwitvlei and Rondevlei (Rondevlei, mean chlorophyll *a* = 60.4 ug l^{-1}) displayed a common mid- to late-summer peak. Summer stratification was present only in Suurdam and Gillidam. Maximum phytoplankton biomass of the different vleis related to pH, the quantity and quality of the humic substances, and the nutrient loading. Chlorophyll *b*: chlorophyll *a* ratios and chlorophyll *c*: chlorophyll *a* ratios indicated a dominance of *b*- and *c*-containing species in Suurdam, Gillidam and Grootrondevlei and a dominance of species containing only chlorophyll *a* in Grootwitvlei and Rondevlei.

Multi-dimensional scaling showed four distinct zooplankton community groupings. In Suurdam, the community was dominated by *Microcyclops crassipes* and was characterised by low zooplankton abundance (mean no.m^{-3} = 1783), a low species richness, an absence of limnetic cladocerans, and high species diversity (H') and evenness (J') indices. The community appeared to be limited by the low pH and the pH-dependent humic toxicity of the water.

The communities in Gillidam, Grootrondevlei and Grootwitvlei were dominated by *Metadiaptomus purcelli*; otherwise that of Gillidam showed similar characteristics to that of Suurdam and was probably limited by the same factors. Both communities contained individuals of small mean size, more likely a result of limitation by the chemical environment rather than of predation pressure. A number of large-bodied limnetic cladoceran species and *Lovenula simplex* were present in Grootrondevlei, but absent from Grootwitvlei, possibly as a result of a visual predation pressure.

In Sirkelsvlei the community was dominated by *Metadiaptomus capensis* and *Lovenula simplex* was present in lower numbers. Species richness, species diversity (H') and evenness (J') were low, with few limnetic cladoceran species present. High total salinity probably determines the community composition and seasonal variation.

The eutrophic Rondevlei contains a community dominated by cosmopolitan and common Pan-Ethiopian species, in contrast to the endemic south temperate Gondwanian species of the other vleis. The community was dominated by

Thermocyclops oblongatus, *Brachionus calyciflorus* and *Brachionus rubens,* and was characterized by greater species richness, and high species diversity (H') and evenness (J'). Total zooplankton abundances were much greater than in the other vleis (mean no.m^{-3} = 618944). Size-selective predation and the quantity and quality of the phytoplankton probably determine community composition.

It is concluded that zooplankton diversity and abundance are influenced, both directly and indirectly, by the concentration and character of the humic substances and the pH, particularly at high concentration and low pH.

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CHAPTER 1 : INTRODUCTION

Black waters, brown waters or humic waters are found in many parts of the world. In particular they are common in areas of acid, well-leached podsolic soils. They are a feature of the equatorial regions, where they have been investigated by, amongst others, Sioli (1944, 1968), Johnson (1967, 1968), Janzen (1974) and Rai and Hill (1980, 1981). Along the eastern and southern coasts of Australia black waters (referred to as coastal dune lakes) have been looked at by Timms (1982), Arthington *et al.* (1986) and others, and in the south-eastern United States studies by Nordlie (1976), Anderson *et al.* (1977) and Stoneburner and Smock (1980) have examined natural brownwater systems. In general, however, very little is known of the more southern and more tropical systems in comparison with the coloured waters of the north temperate regions. In northern America and Europe there is a lot more information available, from the early studies of Birge and Juday (1927, 1934) on the lakes of Wisconsin, to many more recent studies on the Scandinavian forest lakes (appendix 1.1).

In classical ecological terms these waters are classed as dystrophic and described as acid, brown in colour, low in available nutrient levels, low in planktonic productivity (although littoral plant production may be high), low in bacterial numbers, and with depressed benthic and planktonic species richness and abundance. These features are obviously broad generalizations concerning water bodies stretched over a wide range of latitudes, with allochthonous inputs varying from deciduous forest to dune scrub. It is probably true to say, however, that dark waters are typically more oligotrophic than neighbouring clearwater or uncoloured systems.

In the south-western Cape there are several small coastal black- or brownwater lakelets (or vleis as they are referred to in the region). The waters that drain the fynbos vegetation (see chapter 2), which generally grows on acid well-leached soils, are normally stained to some extent; and cool, second-order, acid, brown-stained rivers are typical of the region. Water colour is however greater by orders of magnitude in some of the standing waters, where the intensity of the colour is high even by international standards. In fig. 1.1 colour values (measured against a platinum standard as Hazen units) are presented for over 130 lakes. The data were collected from the recent published literature and include a large number of Scandinavian lakes and some North American and mid-European lakes. Conspicuously absent are values from the equatorial regions and Australia, where no colour measurements were included in any of the studies examined. The high intensity of colour in the south-western Cape vleis is obvious when contrasted with the black and brown waters of other regions.

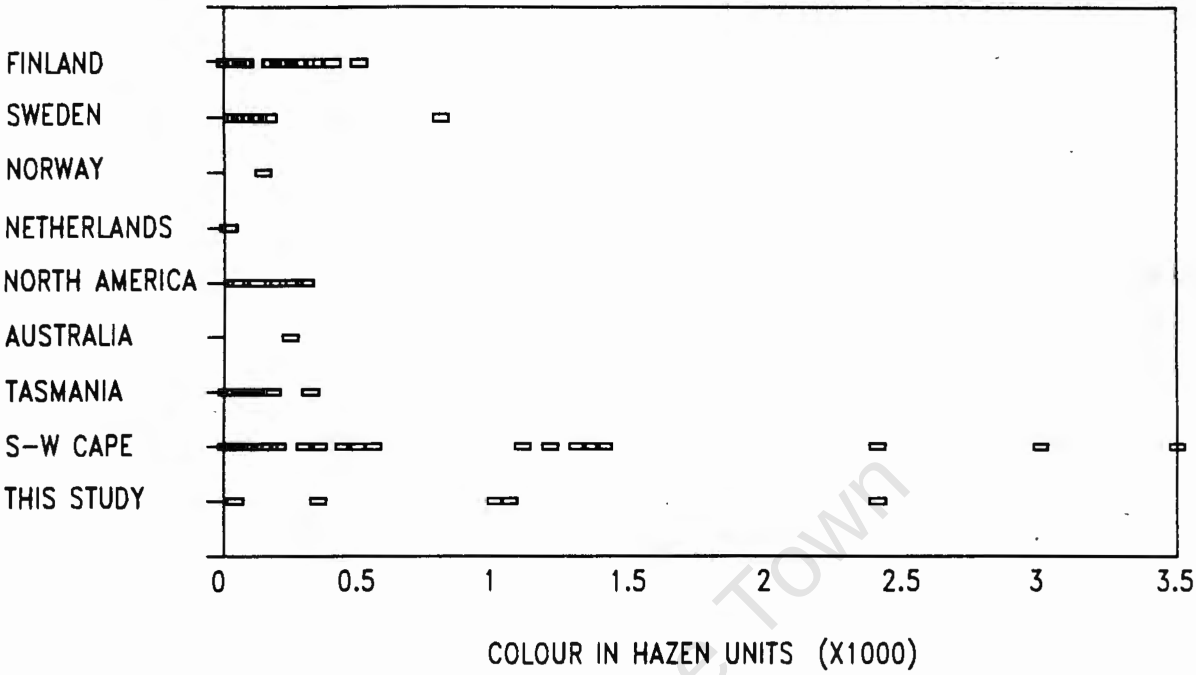

Figure 1.1 Colour measurements (in Hazen units) from over 130 brownwater or humic lakes in different parts of the world. The references from which these data were extracted are presented in Appendix 1.1.

Hutchinson (1957) comments that the colours of "the darkest bog waters" reach values of up to 340 units and Petersen and Persson (1987) state that a value of 600 units "is a high value for humic waters, but does occur in Sweden". Colour values comparable to those of the local vleis may well occur in some Australian dune lakes or in equatorial waters and it is unfortunate that so few studies throughout the world have included some measure of colour, absorbance or DOC in brownwater systems, let alone adhered to a standard measure.

The compounds that produce colour in these lakes are collectively termed humic substances (chapter 6) and a large amount of literature has centred on them in recent years. Much of the research has concentrated on the structural characteristics and chemical interactions of these compounds and very little has dealt with their specific or indirect effects on the biota of lake systems, whether as a result of concentration or of character.

Humic substances are either of autochthonous or of allochthonous origin. Much of the character of the mixture depends on the contribution and the character of the allochthonous fraction, which is the dominant component of darker brown waters. The allochthonous fraction is formed in the soils of the surrounding catchment and thus much of its final character is a consequence of the character of the vegetation, the soil type and composition of the underlying parent material, the climate and the drainage characteristics of the catchment.

The south-western Cape is characterised by a rich and diverse, sc~~l~~lerophyllous, heathland vegetation known as the Cape fynbos (or Cape macchia). The vegetation is stressed by a paucity of nutrients in the soils, nitrogen and phosphorus levels being extremely low (chapter 5). The tough and small-leafed plants are thus forced to retain their nutrients by relying on various adaptations (Di Castro and Mooney 1973, Specht 1979, 1981, Deacon 1981). These include the increased production of toxic 'defensive' secondary compounds to neutralize intruding organisms such as herbivores, bacteria and fungi by chemical means. The active toxic secondary compounds include alkaloids, stilbenes, tannins, coumarins, flavanoids, phenolic quinones and glycosides, and other phenolic compounds. The phenolic compounds exhibit a broad structural heterogeneity and form a diverse pool of aromatic compounds including mono- and dihydric phenols, phenolic quinones, coumarins, flavanoids, tannins, anthocyanins and phenolic glycosides. The inhibitory activity associated with phenolics can to a large extent be attributed to the quinones, which can react with proteins or intracellular amino acids, complex with metal ions, or interfere with enzyme synthesis, thereby inhibiting enzyme systems (Bate-Smith 1962, Levin 1971). Common fynbos plant families rich in these compounds are, amongst others, the Ericaceae, Rutaceae, Bruniaceae, Thymeleaceae and Leguminoseae. All contain complex mixtures of phenolics (Janzen 1974).

In the slowly-decomposing litter, the phenolic and other secondary compounds retard and even inhibit decomposition by the litter and soil microorganisms. They are leached as mobile organic compounds into the soil to collect and form the humic fraction in a characteristic ferrihumic soil horizon (Burges *et al.* 1964, Schnitzer and Kahn 1972, Janzen 1974). Further phenolic units are liberated during the decomposition of lignified tissues, celluloses and hemi-celluloses by soil bacteria and fungi and are incorporated into the humic compounds by the slow process of humification (chapter 6). The resultant humic substance is amorphous, brown or black, hydrophilic and acidic (Black and Christman 1963, Burges *et al.* 1964). The compounds can be considered as "polycondensates of random collections of those phenolic units immediately available in a particular micro-area of soil" (Burges *et al.* 1964). Their overall similarity is due to the fact that they are largely aromatic polymers with the chemical properties of the surface phenolic and carboxyl groups and physical properties associated with large polymeric systems. As a result of further leaching by surface or subsurface waters, the humic compounds are transported in a soluble or colloidal form to lentic systems or subsurface sand environments (Schnitzer and Kahn 1972). The noxious or toxic phenolic compounds are only superficially altered in the soil and might therefore be expected to have a negative effect (as polyphenolic humic substances) on the species diversity and abundance of the biota inhabiting the waters. Considering the large amounts of phenolics that should be available for humification as a result of the vegetation and soils of the south-western Cape, the compounds should be high in aromatic content. The intensity of colour in most waters is thus probably the net result of a high production of humics, low rates of degradation (as a result of the aromatic content) and a high solubility and availability as a result of base-cation-depleted, and in most cases skeletal, soils.

The importance of humic substances in aquatic systems has increasingly been realized in recent years. Apart from the obvious effects, such as limited light penetration and reduced visibility, the compounds are responsible for the depression of pH, low redox potential, and a variety of complexation and adsorption reactions with inorganic and organic chemical species. Complexation reactions fundamentally alter the availability and concentration of metals, major nutrients, and natural and synthetic organic compounds, including herbicides and pesticides, preventing breakdown and transport and causing their accumulation in the system (see chapter 6).

The effects on the biota are less well known. Low concentrations of humic compounds, regardless of the source, have been shown to exert a stimulatory effect on phytoplankton, resulting in increased yield, growth rate, radiocarbon uptake and chlorophyll concentration (Prakash and MacGregor 1983). These responses have tended to be both concentration-dependent and character-dependent, such that low molecular weight fractions have generated higher growth responses. High concentrations of humic compounds, however, tend to inhibit algal productivity (Prakash *et al.* 1975). This is not unexpected, as many phenolics cause a similar response: temporarily algistatic at low concentrations, but algicidal at high concentrations (Buikema *et al.* 1979). In a study on the sensitivity of different algal groups to phenol, Kostyaev (1973, in Buikema *et al.* 1979) concluded that chlorophytes were the most resistant, chrysophytes the least resistant and cyanophytes intermediate. Direct physiological effects of humic substances include interference with the process of oxidative phosphorylation (Visser 1987), stimulation at low concentrations and inhibition at high concentrations of cellular ion transport systems (Maggioni *et al.* 1987), interference with enzyme systems (Ruggiero and Radogna 1987, Sarkar and Bollag 1987) and increased protein, RNA and DNA metabolism (Prakash and MacGregor 1983). The physiological or metabolic effects should be highly dependent on the character of the humic compounds in terms of chemical composition, molecular size, surface activity and hydrophobicity.

The effects of humic compounds on aquatic animals are even less studied than those on the flora. Toxicity studies carried out with phenol showed that of the zooplankton, cladocerans are the least tolerant while copepods and ostracods are more tolerant (Buikema *et al.* 1979). They also showed that water mites were very resistant. Very few studies have however been conducted with natural mixtures of humic compounds. A study by Petersen and Persson (1987) showed that, up to a certain concentration, humic substances had beneficial effects on the survival and reproduction of acid-stressed *Daphnia magna*, but at higher concentrations and lower pH they became toxic. The biological activity of many organic compounds (including most phenolics) is pH-dependent and increases with decreasing pH (Petersen and Persson 1987). Decreased water hardness and increased temperature also increase the sensitivity of aquatic animals to phenolics (Buikema *et al.* 1977). The toxic effects probably result from increased lipid solubility and membrane permeability caused by the phenolic hydroxyl groups of the humic compounds. Amongst the vertebrates humic compounds in low pH waters have also been shown to contribute to the mortality of amphibians (Saber and Dunson 1978, Freda and Dunson 1986), but no studies are known of the effects on fish.

Virtually no studies exist on the seasonal variation in concentration and character of humic substances in aquatic ecosystems apart from those by Tipping and Woof (1983) and Visser (1984). Most studies concerning humic substances involve detailed investigations into the structure and the chemistry of preconcentrated humic extracts of soils and sometimes of waters, and very few, apart from studies such as De Haan (1983), have attempted to relate the documented effects to the physical, chemical and biological functioning of a particular aquatic system. The importance of characterizing and quantifying humic substances with as little modification as possible to the medium under study, using a number of sensitive techniques and involving relatively easily available equipment, has been pointed out by Buffle *et al.* (1982). However, apart from De Haan (1972, 1982), Stewart and Wetzel (1980, 1981) and Visser (1983, 1984), amongst others, few studies have attempted this. The six study vleis present a range of humic concentrations found in few other regions of the world, as well as humic polymers that should vary from high molecular weight and high aromatic content to low molecular weight and high aliphatic content. They thus present an excellent opportunity for a field study of the large-scale and seasonal effects of these substances. In addition the aquatic invertebrate fauna of the south-western Cape represents a relict and highly endemic group of the South Temperate Gondwanian fauna (Harrison 1978), yet little attempt has been made to catalogue or study the zooplankton fauna of the region (see chapter 9).

In this study the hypotheses I set out to test, were :

(i) Water colour reflects the quantity of humic substances in solution, and the concentration and character of each mixture of humic substances is determined by the extent of well-leached, acid podsols, and their associated fynbos vegetation, in the catchments.

(ii) the humic substances present in the water, as a result of their ability to participate in complexation and adsorption reactions with other chemicals, alter the inorganic chemical environment, in particular by maintaining low pH, high acidity and elevated levels of iron and soluble reactive phosphorus

(iii) the humic substances, when present in high concentrations, result in depressed levels of phytoplankton biomass

(iv) the humic substances, when present in high concentrations, result in depressed species richness of zooplankton and are associated with a characteristic blackwater zooplankton fauna.

To test the above, six south-western Cape vleis, ranging in colour from a very dark brown to only slightly stained (see fig. 1.1), and varying in pH from 3.7 to 10.1, were selected, and the major environmental and biological variables were investigated over a period of fifteen months. The aims were

(i) to examine the seasonal variations in the concentrations of humic substances and their character and to relate the changes to the catchment vegetation, geology, climate and topography

(ii) to examine the inorganic chemical environments of the vleis and to correlate the effects of the humic compounds on the inorganic character with the seasonal change in each vlei

(iii) to investigate the seasonal variation in phytoplankton standing crop as a function of the physical and inorganic and organic chemical environment

(iv) to describe the zooplankton communities present in each vlei, their diversity, structure and seasonality, and to attempt to establish the most important abiotic and biotic variables controlling these communities in the different systems.

The approach of this study has of necessity been broad. The lack of any baseline data, either physical, chemical or biological, for any of the six systems, as well as the scale of the project, dictated a broad sampling approach. The data collected and the discussions generated have however opened a variety of ideas for future research, some of which are proposed in the conclusion. It is a pity that these are beyond the scope of this project and I can only hope that someone following will make use of these fascinating natural laboratories of both endemism and extremity.

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CHAPTER 2 : DESCRIPTION OF THE VLEIS

The aim of this chapter is to describe the vleis and their catchments. Information on the geology and vegetation of the catchments is summarised for reference to discussion of the chemistry of each aquatic environment in later chapters. Observations and information on the marginal vegetation, ichthyofauna, avifauna and recent history of each vlei are also recorded because of the obvious impact each has on the chemistry and biota of the vleis.

LOCALITY

All six of the vleis lie within a distance of approximately seventy kilometres from the centre of Cape Town. The exact localities are noted in table 2.1 and in fig. 2.1. The vleis, which are separated by only 34 km of latitude and 44 km of longitude, are all coastal lakes in that they are all situated within four kilometres of the sea.

	Latitude(S)	Longitude(E)	Distance from the sea (km)
Suurdam	34° 18.78'	18° 25.40'	1.38
Gillidam	34° 18.17'	18° 26.45'	2.08
Sirkelsvlei	34° 16.12'	18° 24.87'	2.45
Grootrondevlei	34° 21.87'	18° 52.87'	0.55
Grootwitvlei	34° 21.70'	18° 53.42'	0.45
Rondevlei	34° 03.75'	18° 29.75'	3.50

Table 2.1 The localities of the six vleis and the shortest distance between each and the sea.

Three of the vleis, Sirkelsvlei, Suurdam and Gillidam, are located within the Cape of Good Hope Nature Reserve at the southern tip of the Cape Peninsula. The two Grootvleis (which for the purposes of this study will be referred to as Grootrondevlei and Grootwitvlei respectively) are located in Betty's Bay on the south coast to the east of False Bay. The sixth, Rondevlei, is protected as a bird sanctuary and lies on the western side of the Cape Flats, on the north coast of False Bay.

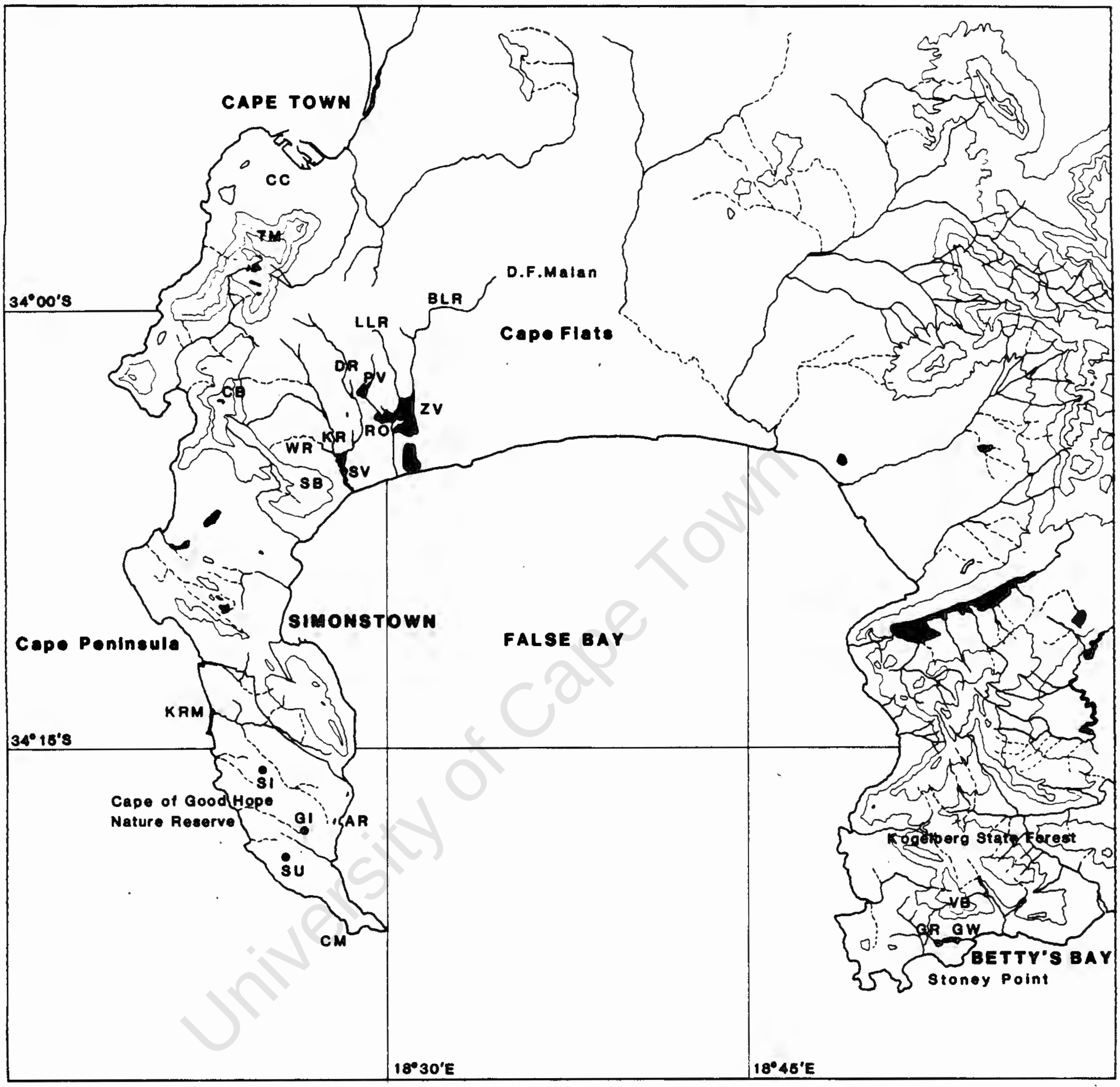


Figure 2.1 The localities of the six vleis Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO) Other localities indicated are the city centre (CC), Table Mountain (TM), Constantiaberg (CB), Steenberg (SB), Anvil Rock (AR), Cape Maclear (CM), Voorberg (VB), Big Lotus river (BLR), Little Lotus river (LLR), Diep river (DR), Keysers river (KR), Westlake river (WR), Krom river mouth (KRM), Princess vlei (PV), Zandvlei (SV) and Zeekoevlei (ZV).

CATCHMENT

GEOLOGY AND SOILS

All three of the Cape Point vleis lie on very shallow podsolic soils (well leached with a characteristic ferrihumic horizon and a pH of less than 4.0) which have been formed by the weathering of the underlying quartzitic sandstone of the Table Mountain series (TMS). Their catchments consist mostly of very shallow quartzitic podsols with some deposits of quaternary sandy soil.

The Betty's Bay vleis both lie on shallow tertiary to quaternary sandy soils which are generally podsolic in nature with a characteristic ferrihumic horizon. These sandy soils have been formed as a mixture of the weathered products of the underlying sandstones of the Table Mountain Series and recent finer sands of marine origin, and are well leached and acid. Occurring in places around the two vleis are lime rich deposits formed, according to Boucher (1978), by the removal of surface sands to expose a secondary enrichment zone of lime. The latter soils are thus alkaline in nature. The catchment or watershed stretches to the north of the vleis where the water drains rapidly off the steep slopes of largely exposed quartzitic sandstone (TMS) and very shallow weathered sandstone soil that make up the Voorberg mountain.

Rondevlei is one of a number of Cape Flats vleis. The catchments of Rondevlei and its two close neighbours Zeekoevlei and Princess vlei, are all situated on deep quaternary sandy soils, light grey and generally podsolic in nature. The vleis themselves are situated mainly on the white quaternary dune sands of the Cape Flats. However immediately to the west, adjacent to the Princess vlei and Rondevlei catchments, lies the Zandvlei catchment draining the quartzitic sandstone soils (TMS series) of the Steen and Constantiaberge through a large number of streams, joining to form the Diep, Keysers and Westlake rivers.

The Peninsula formation of the Table Mountain Group, which underlies the catchments of the Cape Point and Betty's bay vleis and lies adjacent and to the west of the Rondevlei catchment, consists of uniformly light grey, medium to coarse grained quartzitic sandstone. The formation is thought to have been deposited in a shallow marine high-energy environment (Rust 1967, Holiday and Tankard 1978, in Theron 1984). Weathering of the Table Mountain series results in a shallow, quartzitic, coarse sandy soil, normally acid and well leached and thus low in nutrient levels.

The grey-white quaternary dune sand on which the Cape Flats vleis are mostly situated is fine to coarse grained and contains a fairly high percentage of shell fragments. Lime deposits and calcareous sands are found amongst these aeolian dune sands. Inland of the dune sands, and occupying a large part of the catchments of the three Cape Flats vleis, is a light grey sandy soil, quartzitic in nature and containing some peat lenses. The sand is mostly a particularly pure silica sand with well rounded grains similar in size to the dune sand.

In summary, apart from the Cape Flats dune sands and the sands overlying lime deposits in Betty's Bay, the sandy soils in all three areas are podsolised to a large extent and thus are all well leached and acidic, with a diagnostic ferrihumic horizon.

Information on the geology and soils was extracted from Geological Survey Maps of the Cape (1984), a geological map of the fynbos region (Theron 1983), soil maps of the Dept. Agric. Tech. Services (1976) and Schloms *et al.* (1983), and from Dept. Agric. Tech. Services (1976), Boucher (1978), Lambrechts (1979) and Theron (1984).

DRAINAGE

Surface inflow into all three of the Cape Point vleis is indefinite and consists normally of surface trickle along the shoreline during the wet winter months. The vleis are filled mostly by seepage from the high water table of the marshy areas in which they are situated. The high water table results from the very shallow soils and the low gradient of the plains, causing areas to become waterlogged with temporary water bodies and marshes forming in winter (see also Dept. Agric. Tech. Services 1976). There is no surface outflow apart from seasonal flooding (or overflow) from any of the vleis. Sirkelsvlei is situated in an area of "indecisive catchment" (Harrison 1962) between two sandstone ridges with lower lying marshy ground at both the north-west and south-east ends. Seasonal overflow can occur at the north-west end (Taylor 1969)(see fig. 2.2c). Suurdam lies on particularly flat ground and receives a semi-permanent surface trickle into the eastern corner, while seasonal overflow occurs along the south-western shore (see fig. 2.2a). Gillidam lies closer to high ground and receives subsurface flow from the east, while seasonal overflow occurs along a small section of the western shoreline (see fig. 2.2b). The topography of the Cape Point area shows a gradual drop from east to west and thus most subsurface flow should be in this direction.

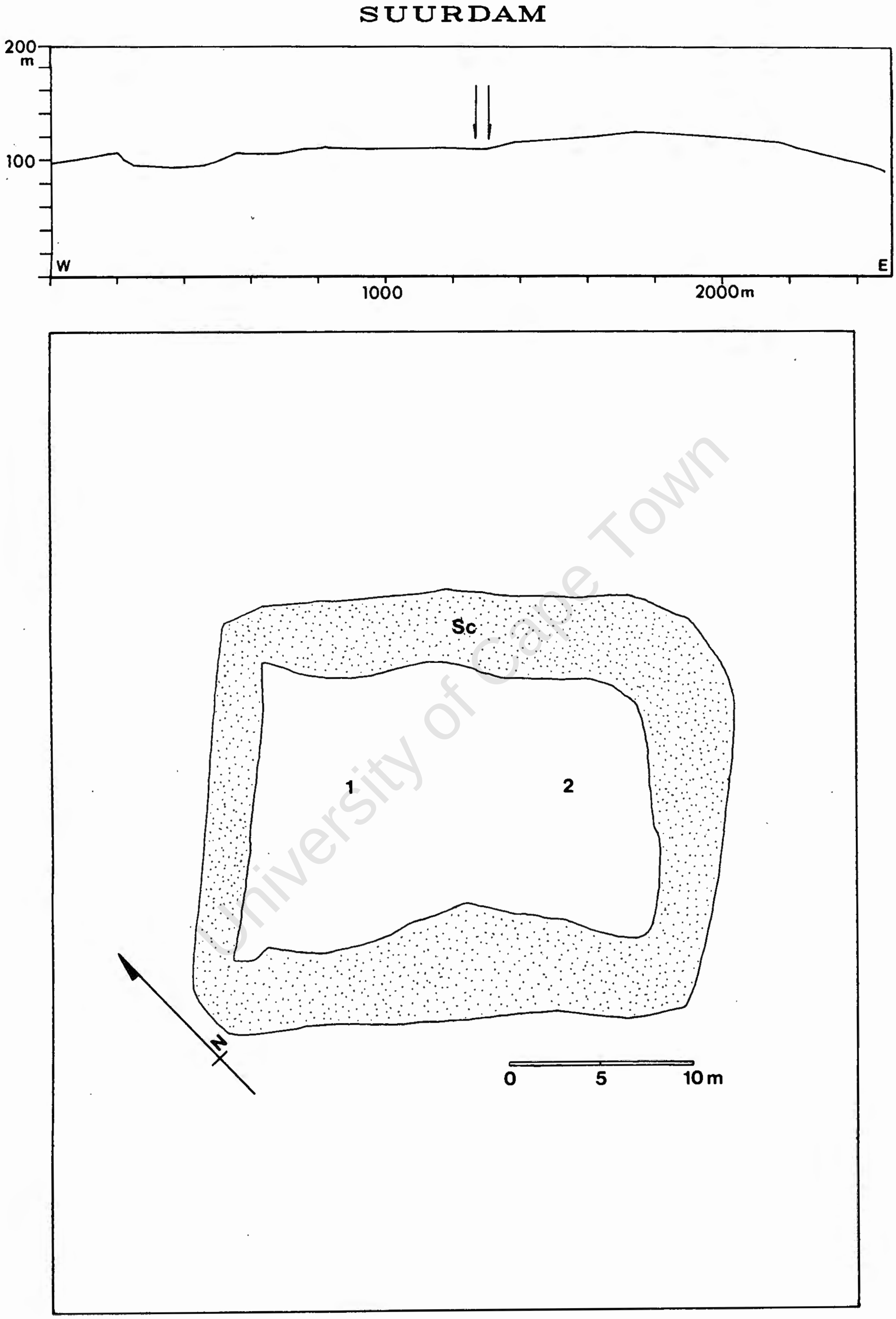


Figure 2.2a The vlei Suurdam (Cape Point) and a profile of the major catchment slope. Sc-*Scirpus prolifer* beds, 1 and 2 - sampling stations 1 and 2.

The two Betty's Bay vleis receive surface inflow through a number of small natural feeder streams entering on their northern shores (see figs. 2.2d and e). In addition a large inflow enters from the Disa stream, which has been diverted from its original course to flow into Grootrondevlei. The two vleis are connected by a short man-made stream, about 55 metres in length, which is piped beneath the road. Outflow from Grootrondevlei is thus *via* the short connecting stream on the eastern shore flowing into Grootwitvlei and outflow for Grootwitvlei is *via* a further stream draining from the eastern shore and flowing into the sea at Betty's Bay. Winter flooding occurs particularly along the south shore of Grootwitvlei and in the areas to the south of both vleis as a result of both precipitation and runoff from the Voorberg mountains, which rise steeply immediately to the north of the vleis. The soils of the coastal plain are also shallow (Dept. Agric. Tech. Services 1976, Boucher 1978) thus allowing a high watertable and the formation of small temporary waterbodies in the wet winter months.

The surface flow into Rondevlei enters through two culverted watercourses, both entering the vlei on the northern shore (see fig. 2.2f). The western watercourse (Italian Road canal) flows directly from Princess vlei through the high density-suburb of Grassy Park into Rondevlei and the eastern watercourse (Perth Road canal) originates and flows through the same suburb of Grassy Park. Zeekoevlei lies 150 metres to the east of Rondevlei, on slightly higher ground than the latter, which probably causes some subsurface interchange of water between the two. Zeekoevlei receives its inflow from the Big and Little Lotus rivers which flow mostly through lined canals in high density suburbs. The outflow of both vleis is artificially regulated by weirs flowing into lined canals, which join to form the Zeekoe river. The regulation of the water level by the weirs thus prevents the water exchange that must have occurred in the past during flooding.

VEGETATION

The south-western Cape is characterised by a rich and diverse, sclerophyllous, heathland flora known as the Cape fynbos. Evergreen, sclerophyllous shrubs and trees typically dominate the mediterranean regions of the world. The south-western Cape, with its hot, dry summers and cool, humid winters, forms one of the five mediterranean regions. Within the mediterranean regions Specht and Moll (1983) distinguish three major soil suites, each with its own type of vegetation structure. The three are strongly leached soils, moderately leached soils and calcium rich/high pH soils, all of which occur in the south-western Cape (Kruger 1979, Boucher and Moll 1981). As noted previously, the catchments of the

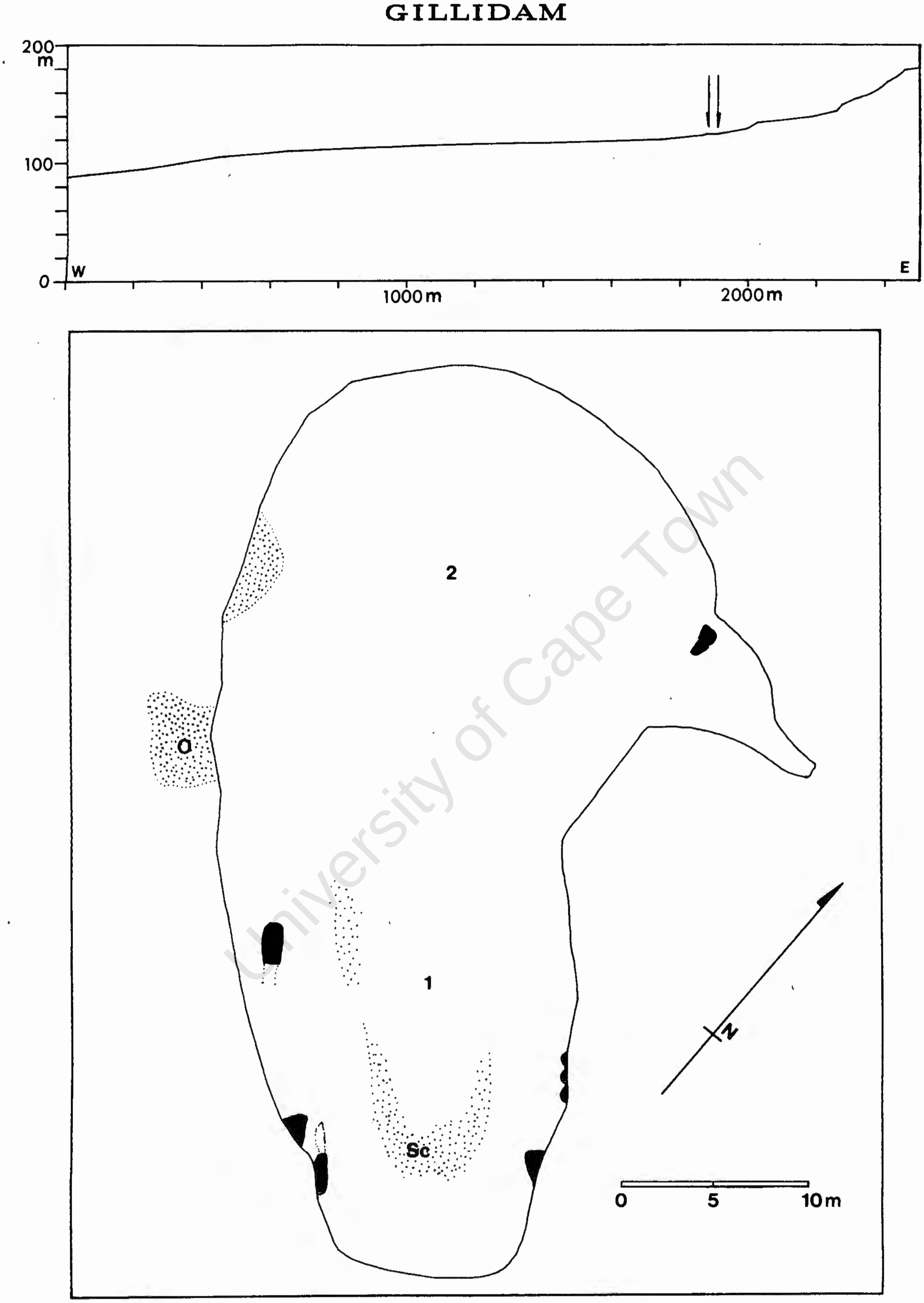


Figure 2.2b The vlei Gillidam (Cape Point) and a profile of the major catchment slope. Sc-*Scirpus prolifer* beds, O-overflow, 1 and 2 - sampling stations 1 and 2.

six vleis consist mostly of well-leached acid soils with some calcium-rich sands on the Cape Flats and less at Betty's Bay. The consequence of the acid, well leached sandy soils (with a paucity of most major nutrients) is the presence of a heath-type vegetation with sclerophyllous overstorey and understorey (Townsend 1982, Specht and Moll 1983) and a microbial population dominated by fungi rather than bacteria, resulting in less effective humification of the surface litter (Townsend 1982). The different microflora and slow decomposition lead to the development of a very acid, surface, mor humus horizon overlying a podsolic soil with a diagnostic ferrihumic horizon.

The Cape fynbos in the catchments of the Cape Point vleis is collectively referred to as mesic mountain fynbos (Moll *et al.* 1984). Taylor (1969), in his phytosociological analysis of the Cape Point vegetation, subdivided the fynbos into a number of associations or broad communities, which are defined by the habitats they occupy. The associations occupying the catchments of the three vleis are (i) upland mixed fynbos, (ii) restionaceous plateau fynbos and (iii) restionaceous tussock marsh.

Upland mixed fynbos occupies generally hilly or mountainous terrain (rarely level ground) and is thus a somewhat variable community. It is three-layered and consists of proteoid, ericoid and restioid elements lying on the very shallow, skeletal soils, generally well drained and composed of coarse white sand overlying TMS bedrock. Restionaceous plateau fynbos is generally found on the level ground of the central plateau where the soil is not seasonally inundated with water in winter. This community is two-layered with proteoid, ericoid, and restioid elements lying on deeper soils, also acid and podsolic, and composed of finer sand. It appears to be transitional between the upland mixed fynbos and the restionaceous tussock marsh, which occurs in abrupt transition in areas where the water table reaches the soil surface in winter, but where seepage is not strong enough to support *Berzelia-Osmitopsis* seepage scrub. It is generally a single-layered community consisting of restioid and ericoid elements.

Sirkelsvlei lies between two sandstone ridges, both vegetated with upland mixed fynbos. The marshy areas to the north-west and south-east consist largely of restionaceous tussock marsh. Suurdam is situated immediately below a terrace containing restionaceous plateau fynbos which drops gently to level ground containing restionacecus tussock marsh and the vlei itself. Upland mixed fynbos occupies the low sandstone ridges surrounding the flat ground. Gillidam lies on the western edge of a terrace sloping down from Anvil rock. It is thus situated on the

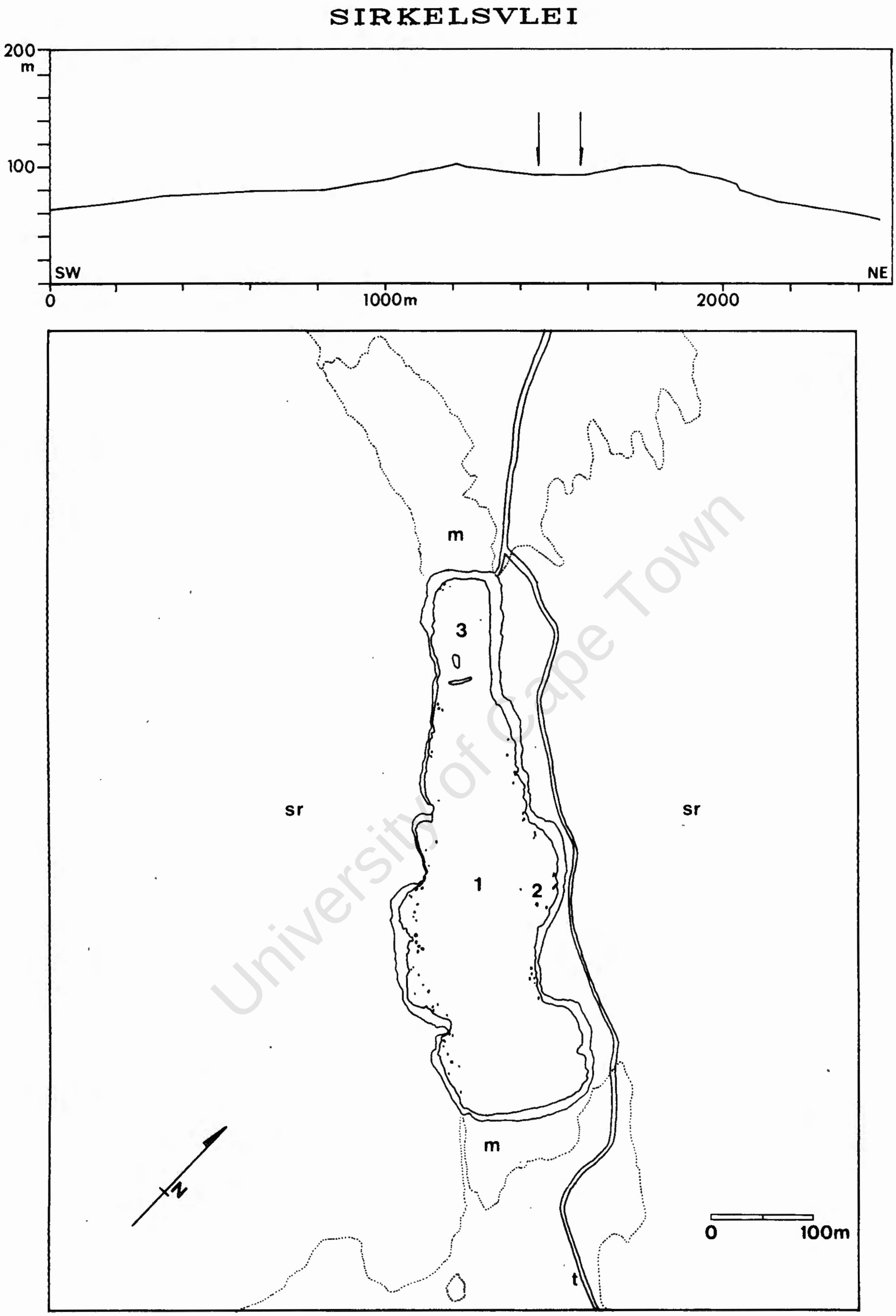


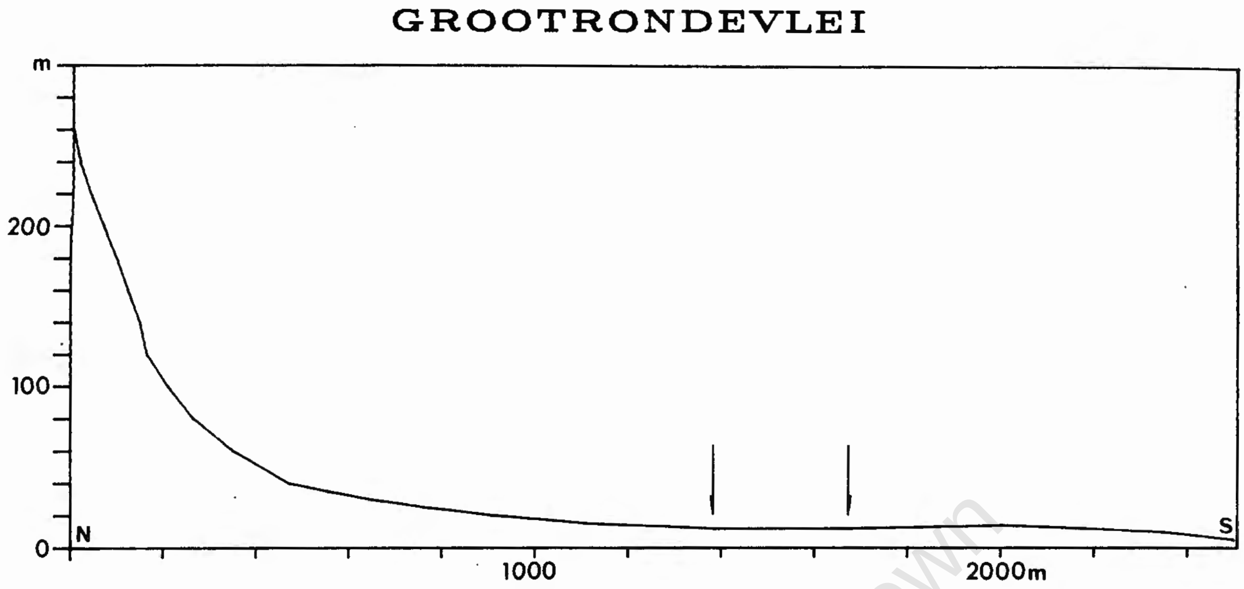
Figure 2.2c The vlei Sirkelsvlei (Cape Point) and a profile of the major catchment slope. sr-sandstone ridge, m-seasonally marshy ground, t-track, 1 to 3 - sampling stations 1 to 3.

edge of upland mixed fynbos just before the terrace steps gently down into restionaceous tussock marsh, into which the seepage drains.

Taylor (1969) also describes a seepage scrub association dominated by *Berzelia* and *Osmitopsis* and found in "permanently moist or wet seepage zones". The community commonly includes *Berzelia, Osmitopsis, Mimetes, Psoralea* and *Drosera* species as well as some Cyperaceae and occupies a fine, black, silty soil with a deep peaty layer. The banks of both Suurdam and Gillidam are lined with this community and to some extent so are the north-western and south-eastern ends of Sirkelsvlei.

The catchment of the Betty's Bay lakes also consists largely of mesic mountain fynbos. Boucher (1978) has described the plant communities or associations of this area in detail. The communities occupying the catchment are described as (i) mixed ericoid-restioid fynbos of the xeric and mesic seaward slopes, (ii) acid sand flats communities, (iii) *Erica-Osmitopsis* seepage scrub and (iv) limestone communities. The mountain slopes of the Voorberg support the mixed ericoid-restioid fynbos which is similar to the upland mixed community of Cape Point, and also lies on shallow, well drained white sandy soils. The acid sand flats communities appear on the landward side of the coastal plain on the mixed soils of sandstone and recent sands (generally two layered with restioid, ericoid and proteoid elements). Further seaward along the coastal plain, occupying a broad band in which the vleis are situated, is the seepage fynbos community, similar to the seepage scrub of Cape Point, but far more extensive in area around the vleis. A limestone community, alien to the catchments of the Cape Point vleis, occurs to the east of Grootrondevlei and to the south of both vleis on sands overlying limestone deposits. The community is generally tall, often with broader leafed plants.

Rondevlei lies on the edge of high-density suburbia and thus the natural vegetation of the catchment to the north has been replaced by housing and to some extent by disturbed and alien vegetation. No development has occurred as yet to the south, and the dunes are covered with both sandplain lowland fynbos and west coast strandveld on sand (from Jarman 1986). The small area within the sanctuary is relatively undisturbed, whereas the remaining area stretching south to the False Bay coast is under considerable environmental pressure from both trampling and the spread of alien plants such as *Acacia* spp.. The sandplain fynbos is confined to the deep acid sands and consists of low to mid-high graminoid shrubland whereas the west coast strandveld is restricted to the well drained sandy soils, often calcareous, with scattered shell fragments and consists of taller communities with a mixture of broad-leafed, evergreen, deciduous and succulent elements (Moll *et al.* 1984). The



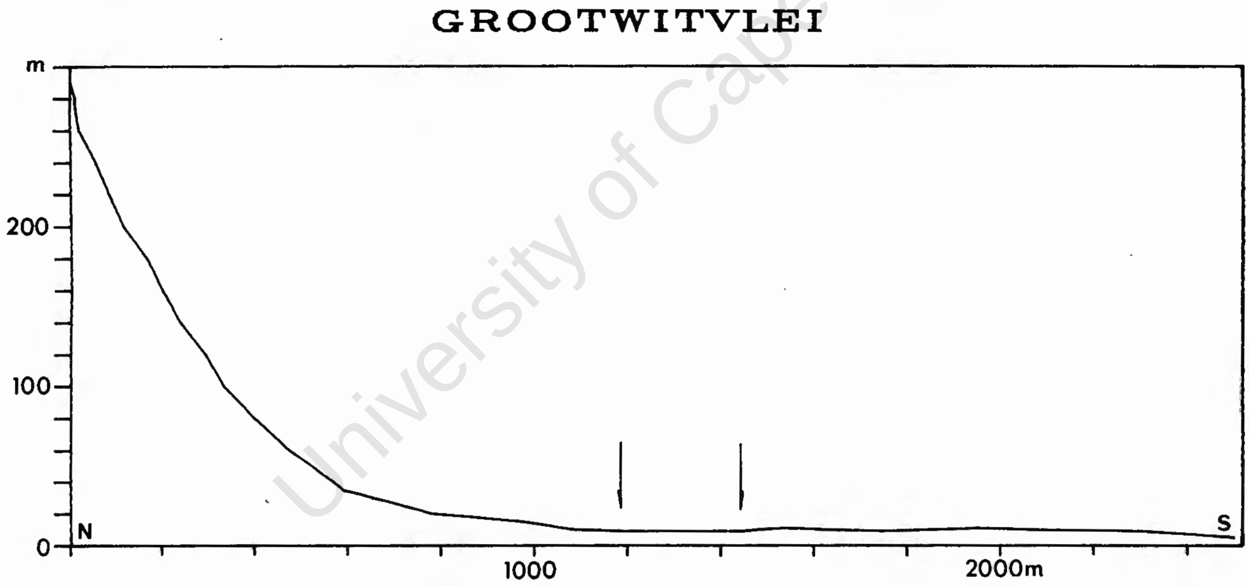


Figure 2.2d and e The Grootvleis (Betty's Bay) and a profile of the major catchment slopes of both. Ds-Disa stream, Fs-feeder stream, Os-outflow stream, P-*Phragmites australis* beds, M-other marginal vegetation, 1 to 4 - sampling stations 1 to 4.

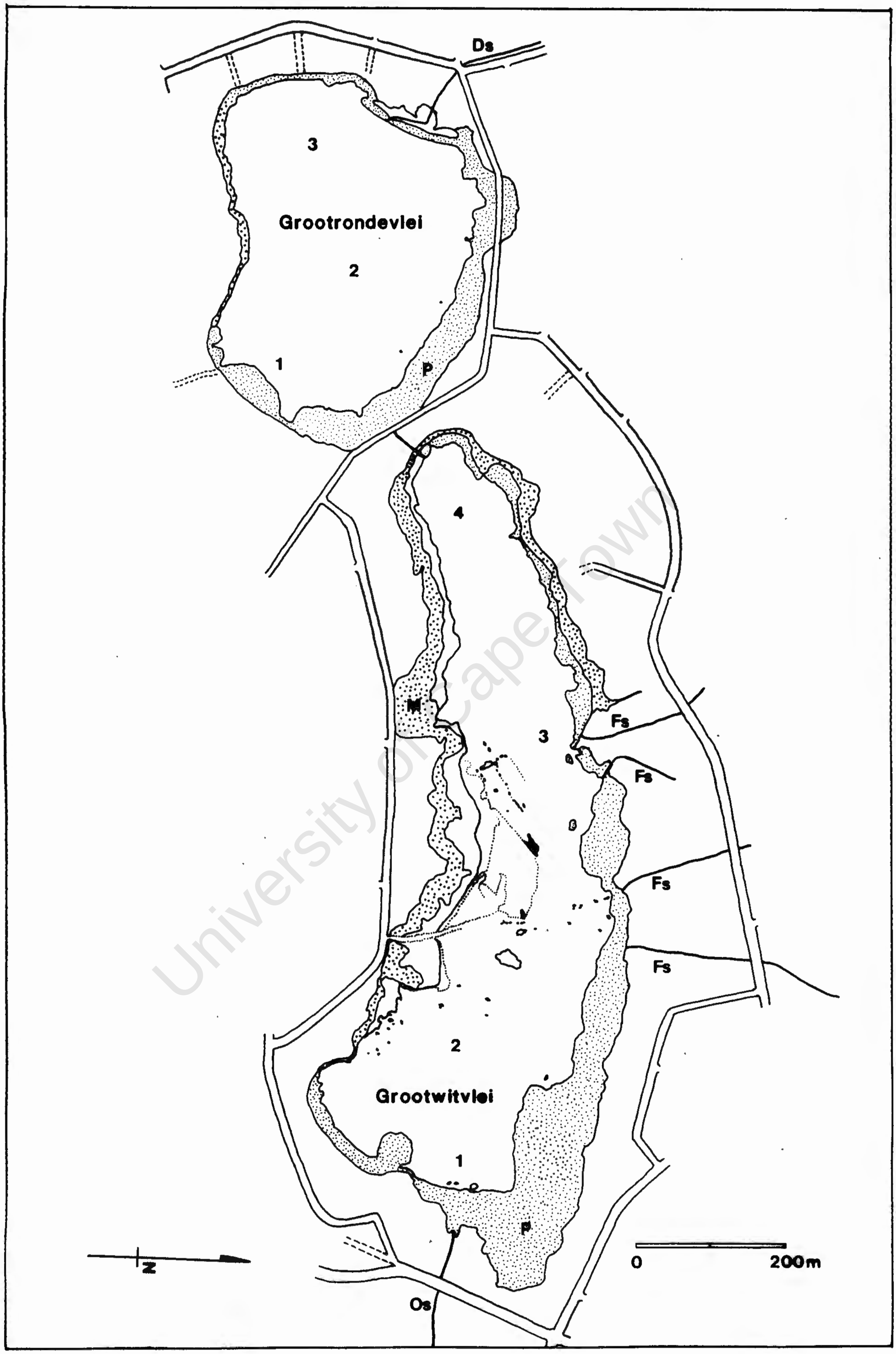


Figure 2.2d and e (cont.)

strandveld is classified as a broad-leafed shrubland transitional to Cape Fynbos communities.

In conclusion the major similarities of the catchment vegetations are as follows. For Cape Point and Betty's Bay

i) a relatively rapid drainage through a mixed upland fynbos or mixed ericoid-restioid fynbos on skeletal quartzitic sandstone soils and
ii) a slow drainage through fynbos seepage communities or restionaceous tussock marsh close to the vlei.

For Betty's Bay and Rondevlei

i) lowland fynbos communities occupying deeper acid mixed sands and
ii) communities favouring calcareous sands or sands overlying lime-rich deposits (of limited extent in Betty's Bay).
A summary of the vegetation and soil types is presented in Table 2.2 below.

community	UMF	RPF	RTM	MER	ASF	SF	LF	SLF	WCS
skeletal coarse white sand (TMS derived) low pH	*	*	*	*					
deep sands well-leached low pH		*	*		*	(*)		*	
deep sands lime deposits high pH							*		*
seasonal waterlogging			*			*			

Table 2.2 Summary of vegetation and soil types in the catchments of the six vleis. UMF-upland mixed fynbos, RPF-restionaceous plateau fynbos, RTM-restionaceous tussock marsh, MER-mixed ericoid-restioid fynbos, ASF-acid sand fynbos, SF-seepage fynbos, LF-limestone fynbos, SLF-sandplain lowland fynbos and WCS-west coast strandveld.

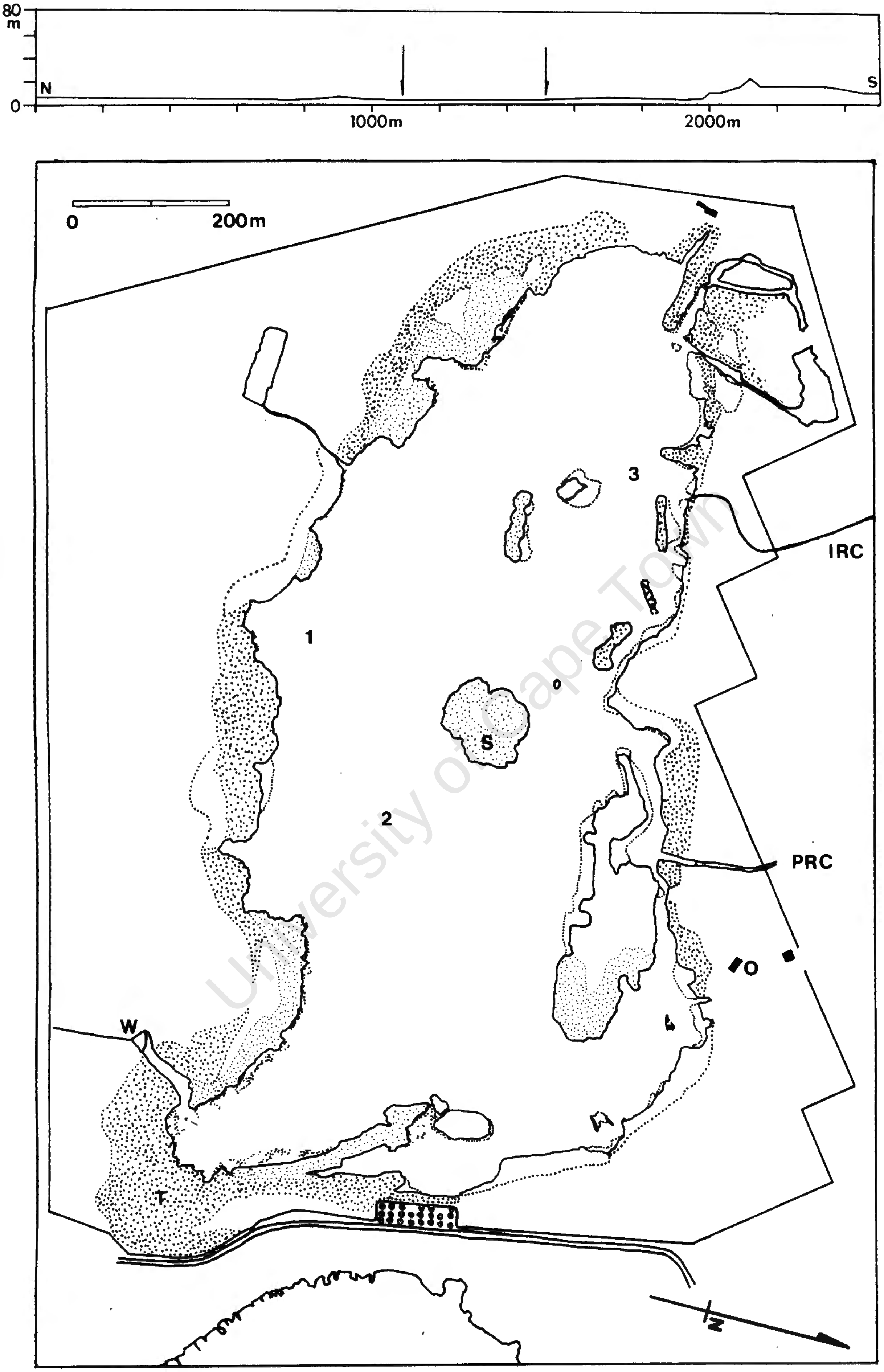


Figure 2.2f The vlei Rondevlei (Cape Flats) and a profile of the major catchment slope. T-*Typha capensis* beds, S-*Scirpus littoralis* beds, W-weir, O-office, IRC-Italian road canal, PRC-Perth road canal, GP-Grassy Park, 1 to 3 - sampling stations 1 to 3.

The consequences of having a catchment vegetated with an evergreen sclerophyllous heathland vegetation is a very slowly decomposing litter layer, poor in mineral nutrients and rich in condensed polyphenolic compounds and lignins (Read and Mitchell 1983). The most important Cape fynbos plant families contain high levels of toxic secondary compounds which affect both plant herbivory and microbial decomposition and thus affect the humic materials which leach into and stain the waters of the vleis.

LAKE MORPHOMETRY

Lake area (A_o) is measured as the surface area of open water (excluding areas of fixed or floating reeds, sedges or grasses) at maximum water level. Due to the shallow nature of the vleis, a drop in the water level of most can cause a large decrease in the surface area of the water. Suurdam and Grootrondevlei, however, differ from the other four vleis in that the surface area remains almost constant during the year. In Suurdam this is due to the negligible annual change in the water level, whereas in Grootrondevlei it is as a result of basin morphometry. Suurdam thus, for much of the year, has a very similar lake area to Gillidam (which has a larger maximum area). The lakes range in surface area from the very small Suurdam and Gillidam (both less than 1000 m^2) to the relatively large Rondevlei (almost 0.5 km^2)(see table 2.3 and figs 2.2a-f).

Lake length (L) is measured as the maximum distance between any two points on the shoreline without any land interruption. It is thus a measure of the maximum fetch or distance of open water that the wind from that direction can act on and is thus an important feature affecting the physical stability of the water mass. In the south-western Cape the prevailing wind direction is from the south-east in summer and from the north-west in winter (see chapter 4). During 1981 and 1982 wind of a strength greater than 2.5 $m.s^{-1}$ (often considerably so) blew from either direction for more than 440 days (60% of the period). Thus maximum lake length along a north-west/south-east line was measured as a more relevant measure of maximum lake fetch. Whereas Grootwitvlei and Rondevlei each have a maximum length double that of Grootrondevlei and Sirkelsvlei, along a north-west/south-east line the vleis are very similar in maximum fetch distance (in fact Sirkelsvlei exceeds Grootwitvlei). Suurdam and Gillidam are both an order of magnitude smaller in length and in fetch.

Maximum lake width (b) is measured as the maximum distance perpendicular to the maximum length (L) between two shoreline points and **mean**

lake width ($\bar{b}$), is the quotient of lake surface area (A_0) and maximum lake length (L). Both Sirkelsvlei and Grootwitvlei are long and narrow with a relatively short width in relation to length, in contrast to the remaining vleis, which are all more circular in shape.

Feature	Unit	SU	GI	SI	GR	GW	RO
Area(A_o)	m²	299	925	63000	114000	190000	475000
Length(L)	m	26.0	48.9	541	460	1018	1232
NW/SE Length ($L_{NW/SE}$)	m	22.6	48.9	536	428	484	617
Width(b)	m	17.3	30.3	157	360	345	517
Mean Width(b)	m	11.5	18.9	116	248	194	386
Shoreline (S_L)	m	74	141	1140	1520	3080	6232
Shoreline development (D_L)	-	1.21	1.31	1.62	1.27	1.95	2.55
Max Depth (Z_M)	m	1.5	1.4	1.4	1.7	1.7	1.6
Relative Depth (Z_r)	%	7.69	4.08	0.49	0.45	0.34	0.21

Table 2.3 Morphometric features of the six vleis. Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO).

Shoreline development (D_L) measures the 'irregularity' of the shoreline and is calculated as the ratio of the shoreline length to the circumference length of a circle with the same area as that of the lake. The minimum D_L value of one indicates a lake the shape of a true circle and increasing values indicate lakes with more irregular shorelines. The two largest vleis, Grootwitvlei and Rondevlei, have the greatest shoreline development, while Suurdam, Gillidam and Grootrondevlei show a low ratio of shoreline development. This may have some effect on lake productivity (see chapter 8).

The vleis are all very shallow and do not exceed two metres in depth at maximum water levels. Due to the extreme shallowness, the bathymetry was not plotted for any vlei. The volume (V) can thus not be calculated, but can be estimated due to its very close relationship to surface area (A_0).

Relative depth (Z_r) is given by maximum depth expressed as a percentage of the mean diameter. Most lakes have a percentage of less than two but deep lakes with relatively small surface areas can exceed a percentage of four (Wetzel and Likens 1979). Sirkelsvlei, Grootrondevlei, Grootwitvlei and Rondevlei all have small relative depths (less than 0.5) and thus a low water column stability. Suurdam and Gillidam are relatively very deep (due to their small size) and thus exhibit a high water column stability (see temperature in chapter 3) with resultant effects on the phytoplankton community (see chapter 8).

MARGINAL VEGETATION

The shore-line vegetation communities differ considerably between the Cape Point, Betty's Bay and Cape Flats vleis, apparently in relation to the drainage, the soils and the degree of disturbance at the margin of each vlei.

In Cape Point the three vleis are distinctive in their lack of associated reedbeds. Suurdam has a thick floating fringe of the short, fine, sedge *Scirpus prolifer*, extending approximately two metres out from the shore and, in the very shallow waters, a narrow fringe of the rooted macrophyte, *Laurenbergia repens*. Gillidam mostly lacks a fringe community, although *Scirpus prolifer* and some *Laurenbergia repens* are present in the south-eastern end. Sirkelsvlei has no fringe community distinct from the fynbos, which normally lies well above the water level. Seepage fynbos communities lie very close to the maximum water levels in all three of the vleis.

The two Betty's Bay vleis, in contrast, are flanked by extensive beds of *Phragmites australis*. Grootrondevlei has a bed 30 000 m^2 in area, and Grootwitvlei a bed of 54 500 m^2 along the northern and eastern shores. *Phragmites* is generally found in areas of flowing water (Boucher 1978) and the extent of the beds around the two Grootvleis appears to be limited by this factor. A strong seepage flow along the northern shores from the slopes of the Voorberg associated with the feeder streams should occur for most of the year and the flow through both vleis is in an easterly direction. The southern and western shores are lined mostly with a low tussock community of the restio *Chondropetalum tectorum* and the sedge *Juncus krausii*. *Juncus* prefers inundation for longer periods and thus fringes the water, while *Chondropetalum* lies closer to the edge (Boucher 1978). Some *Typha capensis* and *Scirpus littoralis* are also found along the edges of the vleis, but the beds are not extensive.

Rondevlei lacks these extensive beds of *Phragmites*, being fringed mostly by *Typha capensis* and the tall *Scirpus littoralis*. *Scirpus littoralis* is found in the water, generally with the lower half of the plant permanently underwater, whereas *Typha capensis* is restricted by depth and normally stands in shallow water, shorewards of the *Scirpus*. *Phragmites* is found in the other Cape Flats vleis, but is mostly in small patches. *Typha* evidently cannot tolerate either flow or increased salinities, whereas *Phragmites* is tolerant of both (Finlayson *et al.* 1983). Where the two co-occur *Typha* tends to spread at the expense of *Phragmites*, especially with increasing eutrophication of the water (from Boyd and Hess 1970, Dinka 1986). Rondevlei however lacked *Phragmites* before the spread of *Typha* within the vlei began to occur (possibly as a result of the widely fluctuating water levels in the past - see Recent History). *Paspalum vaginatum,* a grass, covers the remaining sandy and muddy beaches of the marginal areas.

Some note must be made of the phenology of the marginal vegetation as it determines the seasonality of any effects of marginal vegetation on water quality. In Cape Point *Scirpus prolifer* dies back noticeably in July and August, but in September begins to shoot and flower vigorously and by December has finished flowering. In Betty's Bay the emergent stems of *Phragmites* begin dying back in April , but by the beginning of August the new stems appear above the water and continue growing until flowering in December and January. *Typha* dies back later in winter than does *Phragmites*, and grows rapidly in early summer with flowering heads present for most of the summer months.

ICHTHYOFAUNA

Very little is known of the fish fauna in the vleis of the south-western Cape in general. Many of the vleis and rivers have suffered repeated introduction of exotic fish species during the last century, often with disastrous effects on the indigenous fish communities. In most cases the introduced species have flourished, but occasionally the vlei waters have dropped to very low levels, with the consequent death of the fish. Occasional netting is conducted in some of the vleis and the available information is summarised in table 2.4. The three vleis in the Cape of Good Hope Nature Reserve appear to support few fish. Suurdam has yielded no fish in repeated seine and hand netting while trapping frogs (*Xenopus* spp.) (M Picker pers. comm.). Gillidam has not been netted other than with zooplankton nets, in which tadpoles have been caught, but there has been no sign of any fish. Sirkelsvlei was stocked with *Oreochromis mossambicus* and *Tilapia sparrmani* around 1979/80. Both these species are indigenous to southern Africa, but not to the south-

Species	Status	Feeding class	SU	GI	SI	GR	GW	RO
Galaxius zebratus (Cape Galaxias)	e	(zp)				(*)	**	*
Cyprinus carpio (Common Carp)	a							**
Gambusia affinis (Mosquito fish)	a	(zp)						**
Micropterus salmoides (Large mouth bass)	a	(zp)			*			p
Oreochromis mossambicus (Mozambique tilapia)	w	zp			*			*
Tilapia sparrmanii (Banded tilapia)	w	zp			*			**
Sandelia capensis (Cape Kurper)	e					?	?	p

Table 2.4 The fish of the vleis - a summary of what is known of their presence, status and zooplankton feeding habits.

Information from Derek Clark (Cape of Good Hope Nature Reserve), Mike Picker (Zoology Dept, UCT) and Howard Langley (Rondevlei, Bird Sanctuary)

* present
e endemic
** - abundant
a - alien/introduced
p - no longer present
w - indigenous but locally introduced

zp - zooplankton a large proportion of diet
(zp) - zooplankton, probably a significant proportion of diet.

western Cape. In addition *Micropterus salmoides* was introduced prior to 1978 (D Clark pers.comm. (Cape of Good Hope Nature Reserve), H Langley pers.comm. (Rondevlei Bird Sanctuary) and Opie 1967). The relative abundances of these three species during 1981 and 1982 is not known, but numerous fish were found when the vlei dried briefly at the end of 1982. No records are available for netting in the Grootvleis. Grootrondevlei was stocked with fish prior to 1970 by the Cape Department of Nature Conservation, but no records of the species are available. When the Grootvleis were drained around 1970 a large number of fish were found in Grootrondevlei, but apparently few, if any, in the then separate Grootwitvlei (G Wilson pers. comm.(Betty's Bay Municipality)). There are no known records of any stocking since the vleis have been refilled (see Recent History). Grootwitvlei may contain mullet (*Mugil* or *Lisa* spp.; Mugilidae) which may enter through the outflow stream. In this study a number of *Galaxias zebratus* fry and juveniles were caught in Grootwitvlei in the zooplankton net, but no fish were caught in Grootrondevlei. Shoals of small fish were also noted in the shallows of Grootwitvlei, but not in Grootrondevlei.

Galaxias zebratus is a small (less than 7.5 cm), very hardy fish, endemic to the Cape coastal drainage basin and occurs in virtually all running waters and many standing waters. It is one of the few indigenous fish generally able to cope with predation by exotic species and endures a wide range of water conditions (Harrison 1952a, Jubb 1965, 1967). The species does occur within the Cape of Good Hope Nature reserve and is present in waters of similar quality to Suurdam and Gillidam (pers. obs.). It is doubtful whether it occurs in either of these vleis, however, not having been found in either this or a previous study (Gardiner 1980). It has not been found in Sirkelsvlei either (H Langley pers. comm.). It is likely to occur in Grootrondevlei, as well as Grootwitvlei, because of the close connection of the two vleis.

Sandelia capensis is another endemic species, confined to the South Coastal drainage basins, which can survive a wide range of water conditions, but which is eliminated by *Micropterus salmoides* in standing waters (Harrison 1952b, Jubb 1967). They have never occurred in the southern part of the Peninsula (Barnard 1943), but may well occur in the Grootvleis. The species occurred in Princess vlei and thus in Rondevlei, but was probably eliminated in the 1930s by the introduction of *M.salmoides* (Middlemiss 1975). The vlei has dried up on two occasions since then and neither species now occurs.

Rondevlei has a relatively rich fish fauna; *Cyprinus carpio* (introduced circa 1896), *Tilapia sparrmani* and *Gambusia affinis* (both introduced in 1960) are all abundant. *Galaxias zebratus* is present in small numbers, as is *Oreochromis mossambicus* (also introduced in 1960). *Galaxias* may compete with *Gambusia*, and *Oreochromis* appears to be limited by the relatively colder waters of the Cape (Crass 1964, Jubb 1965, 1967).

Effects of the fish on the aquatic environment may be numerous. Some of the most noticeable and relevant to this study may be i) an alteration in the structure of the zooplankton community by planktivorous fish, ii) an attraction of large numbers of birds and iii) large increases in the turbidity of water due to the feeding habits of *Cyprinus carpio* (Crass 1964, Jubb 1965, 1967). Fish species with the most pronounced zooplankton feeding habits appear to be the young of *Tilapia sparrmani* and *Oreochromis mossambicus* (Crass 1964, Jubb 1965, 1967). Although the bulk of their diet consists of diatoms, unicellular and filamentous algae, large quantities of zooplankton, especially *Daphnia* spp. are consumed. *Galaxias zebratus* is carnivorous, and consumes any small swimming creature, including the larger zooplankters (Harrison 1952a). *Gambusia affinis* and *Micropterus salmoides* both eat live food of all kinds and the young of both species probably mainly consume minute crustaceans and insects (Sterba 1962, Crass 1964, Jubb 1965, 1967). The possible effects of the planktivorous fishes will be discussed in chapter 9.

AVIFAUNA

The waterbird communities are also quite different in Cape Point, Betty's Bay and the Cape Flats. Many of the waterbirds depend on widely fluctuating and seasonally abundant resources and thus they are highly mobile and opportunistic (Guillet and Crowe 1985, 1986, 1987). The vleis under study are less widely fluctuating than many and the waterbird abundance reflects in many ways the overall productivity or trophy. A number of factors must be important in determining the abundance and diversity of waterbirds attracted to each vlei. Amongst these factors are the extent and type of reedbeds and floating and submerged vegetation, the presence of permanent islands and exposed rocks, the surface area, and the extent and nature of the littoral zone.

The three vleis at Cape Point attract few waterbirds (see table 2.5) even though a number of species present in other vleis are found close by. Yellowbilled duck are occasionally found sheltering on the vleis and, at Sirkelsvlei, Egyptian geese are more frequently seen and have nested at the vlei. Middlemiss and Langley (1975) recorded herons, little egrets and coot as well as waders and gulls along the coast and at the Krom river mouth, and breeding colonies of

Common name	Species	Feeding	SU		GI		SI		GR		GW		RO	
			%	No.	%	No.	%	No.	%	No.	%	No.	%	No.
Greatcrested Grebe	*Podiceps cristatus*	1									40	1.5± 0.6	100	7.2± 2.5
Dabchick	*Tachybaptus ruficollis*	2									40	no count	100	17.1± 9.1
Whitebreasted cormorant	*Phalacrocorax carbolucidus*	0							40	3.0±0.0	100	75±44.0	100	9.8± 5.6
Reed Cormorant	*Phalacrocorax africanus*	0							30	1.0±0.0	100	14± 8.0	100	32.7± 31.7
Herons	*Ardea* spp.	1									50	1.6± 0.5	100	23.6± 10.2
Little Egret	*Egretta garzetta*	1									30	5.3± 6.7	80	2.4± 2.0
Spurwing goose	*Plectropterus gambensis*	0									20	4.0± 2.8	100	2.2± 1.3
Egyptian goose	*Alopochen aegypticus*	0					30	2.3±0.6			70	2.7± 1.0	100	8.6± 3.5
Cape Shoveller	*Anas smithii*	2									10	4.0± 0.0	100	262± 186
Yellowbilled duck	*Anas undulata*	3	20	2.5±0.7	20	5.0±5.7	10	2.0	30	7.0±2.6	100	8.1± 7.8	100	149± 105
Cape Teal	*Anas capensis*	2									10	2.0± 0.0	100	3.9± 4.4
Redknobbed coot	*Fulcia cristata*	3									100	13.1± 6.4	100	36.4± 26.6
Blacksmith plover	*Hoplopterus armatus*	2					40	1.5±0.6			10	1.0± 0.0	100	12.0± 5.6
Small waders		2									30	15.3± 2.1	100	no count
Southern black-backed gull	*Larus dominicanus*	0							70	4.0±2.8	40	4.8± 4.9	100	7.3± 10.6
Hartlaubs gull	*Larus novaehollandiae hartlaubii*	0							10	1.0±0.0	20	3.0± 1.4	100	176± 223
Pied Kingfisher	*Ceryle rudis*	1									30	1.7± 1.2	60	1.5± 0.5
White pelicans	*Pelecanus onocrotalus*	1											100	50.9± 33.0
Spoonbills	*Platalea alba*	2											80	6.3± 4.2
Flamingos	*Phoenicopterus* spp	2+3											80	66.9±126.2
Redbilled teal	*Anas erythrorhyncha*	3											100	36.7± 28.9

Table 2.5 Waterbirds of the vleis - Percentage frequency of occurrence of species and the average number present (when occurring) from February 1981 - May 1982. Feeding categories - 0-not feeding, 1-mainly vertebrate, 2-mainly invertebrate, 3-mainly plant food. Counts for Rondevlei are from Howard Langley (unpubl.) and a supplementary count for the Grootvleis is from Ryan *et al.* (in press).

whitebreasted cormorants and yellowbilled duck on the cliffs at Cape Maclear and at the Krom river mouth respectively. The sites are all well within 12 kilometres from each other yet little use is made of the vleis, either as a refuge or as a feeding ground. Factors such as vlei size, and the lack of reedbeds and permanent islands, are probably the important limiting factors.

The two Betty's Bay vleis contrast sharply in their associated waterbird communities. Grootrondevlei fails to attract many waterbirds. Some yellowbilled duck, whitebreasted cormorants and Southern black-backed gulls are seen, as is an occasional Hartlaubs gull. In contrast Grootwitvlei has a diverse and abundant waterbird fauna (see table 2.5). The most obvious feature is the permanent breeding colony of whitebreasted cormorants on the small island, and most exposed rocks are occupied by roosting individuals. Redknobbed coot feed on the beds of *Potomogeton pectinatus.* The reason for such a difference must rest in a large part with the difference in basin morphology of the two vleis. The extensive rocky and sandy shallows and permanent island as opposed to a general lack of shallows in Grootrondevlei, appears to make Grootwitvlei a significantly more attractive waterbody.

Rondevlei is managed as a bird sanctuary and as such harbours a rich array of waterbirds. The vlei has islands, reedbeds and sandy shallows, and is large in size and highly productive. All the species found in the other five vleis occur in Rondevlei, as do many additional species not listed in table 2.5, and they normally occur in far larger numbers and most months of the year.

Having noted the large differences in the abundance of waterbirds in Rondevlei, Grootwitvlei and the remaining four vleis, it is important to assess the effects the waterbirds may be having on the waterbody. Since many of the species depend on "ephemerally superabundant resources" (Guillet and Crowe 1986, 1987) and are highly mobile, the effects of resource harvesting are unlikely to be great, with birds moving before any resource is exhausted. Far greater effects can be expected from the input of bird excreta, especially from those birds feeding at sea or on land and returning to roost on or above the vlei. Some studies have been done on the effects of bird excreta on the chemical regime of marine environments (for example Bosman and Hockey 1986, Bosman *et al.* 1986) and that of terrestrial environments (Weselow and Brown 1971, Allaway and Ashford 1984), but few exist on the effects on freshwater environments. Leentvaar (1967) and McColl and Burger (1976) have both examined the effects of gull excreta on the aquatic environment of small lake ecosystems and have noted changes in water chemistry. Leentvaar (1967) in particular noted increases in pH, conductivity, nitrogen, phosphorous, the plankton, coliform bacteria and organic matter in brown, acid, oligotrophic waters. He termed these influences of bird excreta on an environment 'guanotrophy'. McColl and Burger (1976), on the other hand, examined the effects on alkaline waters, reflecting the calcareous soils of a catchment similar to Rondevlei, and noted a decrease in pH, but increase in nitrogen and phosphorous, with a significant promotion of large algal blooms and highly productive stands of *Typha latifolia*. Both studies were conducted by comparison of lakes containing gull colonies with close-by lakes containing no gull colonies. The water chemistry of the two Betty's Bay lakes will similarly be compared in the following chapters; however in addition an attempt has been made to quantify some of the input into Grootwitvlei.

In Grootwitvlei a very large percentage of the input of excreta is from the white-breasted cormorants. This is due to the fact that they are large birds (ca. 3 kg), there are constantly high numbers (approx.75), and they have a permanent breeding colony on the vlei. In Appendix 2.1 I have attempted to calculate the quantity of excreta deposited into the vlei by the cormorants and arrive at a figure of between 1.2 and 1.5 tons of dry excreta per annum. The composition of dry excreta from mainly fisheating seabirds is shown in table 2.6, as well as the estimated input of each of the major nutrients and elements. In addition Grootwitvlei receives in the region of 54 700 regurgitated pellets and up to 111 young or eggs per annum (Appendix 2.1). Smaller numbers of waterbird from a number of other species obviously add to the effects of the breeding colony of cormorants.

Rondevlei has large numbers of many species of waterbirds, contributing a considerably greater total input of excreta than in Grootwitvlei. In addition there is a large input of excreta from two hippopotamuses that were reintroduced into the vlei in November 1981. The high nutrient levels of the water entering the vlei from the surrounding suburbs, combined with the high input from the hippopotamuses, makes it difficult to assess quantitatively the effects of the input from the waterbirds other than to add to the general eutrophy of the vlei.

RECENT HISTORY

CAPE POINT VLEIS

An account of the history of the area is given by Opie (1967). From about 1810 land was granted to farmers and vegetable growing and stock farming (with

% by mass of the dry excreta	Total N	NH_4-N	NO_3-N	Uric Acid N	Protein N	Total P	Ca	Mg	Na	K	C	H
White capped Noddies (*Anous minutus*) Allaway and Ashford 1984	14.4 (±1.0)					3.1 (±0.2)	3.2 (±0.3)	0.72 (±0.04)	1.8 (±0.1)	2.0 (±0.1)	26.2 (±0.6)	4.0 (±0.1)
White chinned Petrel (*Procellaria aequinoctialis*) Fugter 1985 Jackson 1986 fed on fish only	14.7 (±7.5) 18.0 (±3.0)	4.5 (±2.2)	0.5 (±1.0)			2.6 (±1.5)	4.1 (±4.2)	0.4 (±0.2)	2.1 (±1.5)	1.8 (±1.4)		
King Penguin (adults) (*Aptenodytes patagonicus*) Lindeboom 1984 Burger *et al.* 1978	20.0	1.4	0.1	16.3	2.2	0.4 1.8 (±0.9)	4.7 (±2.8)	0.7 (±0.2)	2.4 (±0.4)	3.1 (±0.7)		
Macaroni penguin (*Eudyptes chrysolophus*) Lindeboom 1984	22.0	1.4	0.1	18.2	1.9	0.4						
Gentoo penguin (*Pygoscelis papua*) Burger *et al.* 1978						3.4 (±2.4)	5.8 (±1.5)	0.8 (±0.3)	1.0 (±0.5)	3.6 (±0.7)		
Black-browed albatross Jackson (upubl.) fed on fish only	14.2											
Range in mg g^{-1} and in kg ton^{-1}	140 220	14 45	1 5	160 180	19 22	4 34	32 58	4 8	10 24	18 36	260	40

Table 2.6 The nutrient and elemental content of the dry excreta of certain, mainly piscivorous, sea birds.

consequent veld burning to provide grazing) developed on an extensive scale to supply the needs of Simonstown. In addition major salvage operations lasting many months were conducted on the many shipwrecks that occurred along the coast. In the early 1900s more productive farming on the Cape Flats and improved lines of transport outcompeted the farmers of Cape Point and many farms were abandoned. By the 1930s some subsistence farming remained and a few hundred cattle ranged over the area. *Acacia* spp. had invaded much of the area. In 1939 the Divisional Council of the Cape acquired the two southern-most properties and in the ensuing 26 years bought the remaining land of the reserve. Since then large game species have been introduced and alien plant species cleared. Although good records are kept of present-day activities in the reserve, a poor record exists of the activities in the earlier years and there is thus very little documented information on the recent history of the vleis. Much of the information noted below was supplied by Howard Langley who worked in the reserve from 1968 - 1975.

Sirkelsvlei is one of the few naturally formed waterbodies in the Reserve. The vlei has dried up on occasion, certainly in 1969, 1973 and 1982. Human disturbances include repeated stocking with bass (*Micropterus* sp.), use as a strafing range by aircraft during the Second World War, and the construction of rocky islands in 1969 and the late 1970s. As a result of strafing activities large numbers of empty cartridges accumulated in the vlei. Most of these were removed in 1969 when the vlei dried up and H Langley (pers. comm.) recalls removing truck loads of cartridges. The effects of the cartridges and their removal on the metal ion chemistry of the vlei are unknown. Island construction was initiated in an attempt to attract waterbirds to the vlei, but this proved unsuccessful and no use has been made of the islands.

Suurdam is an artificially created waterbody located in a naturally waterlogged area. It was excavated in 1969 and has suffered little if any disturbance since. It was created as a watering point for game species such as zebra, bontebok and springbok and it is unlikely that it has dried up since construction.

Gillidam, according to H Langley (pers. comm.), was also artificially created in an attempt to attract game species close to the road. It was excavated around 1973 and the only known disturbance it has suffered since has been the addition of quantities of $CuSO_4$ in the late 1970s because it was believed that the large game animals were suffering from a lack of copper in their diets. The immediate effects on the aquatic biota must have been interesting; there are not noticeably higher levels of copper in solution at present, however, most of the copper presumably having been complexed and precipitated out of solution by the humic compounds (see chapter 5).

THE GROOTVLEIS

The first written account of the Betty's Bay area was by a Lieutenant William Paterson journeying with Colonel Robert Gordon during October of 1877. He records seeing several wild buffalo and eland, as well as the larger lakes (Boucher 1978). In later years the area was used for stock farming and vegetable growing and the coast has served as a base for whaling activities. After the construction of good roads during the Second World War the area became increasingly popular as a seaside resort (Boucher 1978). Most of the development occurred immediately along the coastline, away from the vleis. The mountain catchment of the vleis falls within the Kogelberg State Forest and has for many years been protected by the Department of Forestry. In the late 1960s, however, development began of the area immediately surrounding the Grootvleis, seaward of the Kogelberg State Forest (Extension 227). Unfortunately the Betty's Bay Municipality appears to have no written records of the development and information recorded here was supplied verbally by Mr. G Wilson (of the Municipality) and Mr. D Waller (a local estate agent).

Judging from aerial photographs taken in 1938, the vleis showed similarities, now absent, to both the Cape Point vleis and Rondevlei. They appear to have been fed only by small seasonal feeder streams and subsurface flow. They were separated from each other by a narrow, thickly vegetated isthmus and subsurface seepage was evidently the only connection between the two. Since no outflow points were obvious for either vlei they must have experienced large seasonal fluctuations in water level, but appear to have remained permanent rather than temporary water bodies. There were no signs of *Phragmites* or other reeds fringing the vleis. Presumably the large changes in water level prevented the establishment of the marginal fringing communities of *Typha capensis, Phragmites australis* and *Juncus krausii* that are present in both the Grootvleis and Rondevlei today.

When development began, the vleis were drained by enlarging an original overflow point in Grootwitvlei and digging a connecting channel between the vleis. The dry bed of Grootwitvlei was then bulldozed to supply fill for a network of roads through the area designated Extension 227. The island was originally present, but may have been pushed up further during these activities. In the early 1970s (possibly 1971) the roadworks were completed and the vleis were refilled by diverting a more perennial stream, Disa stream (which also drains the Voorberg), into Grootrondevlei via an unlined canal. For the next few years Grootwitvlei emptied each summer until presumably the bottom resealed itself. Since then the vleis, although showing a significant seasonal change in water level, do not drop to the same low levels as occurred prior to draining. The alteration of the drainage pattern to a flow-through system and the establishment of an apparently higher mean water level with reduced seasonal fluctuations, are probably the major reasons for the establishment and expansion of the marginal reedbeds, in particular *Phragmites* and more recently *Typha* (at the outflow of Grootwitvlei). Since the completion of sampling, a number of houses have been erected on the edges of the vleis and a national road has been constructed between the vleis and the bottom slopes of the Voorberg. The reedbeds also continue to expand.

RONDEVLEI

The Cape Flats vleis are thought to have been formed as a result of the northward movement of the young dunes on that part of the False Bay coast (Stephens 1929, Mabbuth 1952). The rivers draining the mountains to the west and the flats to the north flow southwards until they meet the dunes, which are driven northwards by the summer south-easterly winds. Maps from the last century and earlier do not show Rondevlei separate from Zeekoevlei. Thus Rondevlei was probably formed as a result of wind-driven sand separating and cutting off a large bay of Great Zeekoevlei (Lewis 1928, Middlemiss 1975), presumably towards the end of the last century. In 1931 the neck between the two vleis was still a narrow sandy isthmus but by the early 1940's introduced *Acacia* spp. had stabilized the southern shores and sandy neck. The original outlet of Rondevlei was situated in the centre of the neck and the waters (over)flowed seasonally into Zeekoevlei before flowing to the sea. At that stage the vleis were more seasonal than at present and the greater part of the vlei bed was often exposed at the end of summer (recorded in 1928, 1930, 1931, 1932, and 1937 (Middlemiss 1975)). From the 1940s the levels of Zeekoevlei and thus Rondevlei were controlled by a series of weirs, until in 1958 a separate outlet to Rondevlei, controlled by a weir, was constructed in the south-eastern corner. This outlet joins the Zeekoevlei outflow stream (below the Zeekoevlei weir) and maintains the water level at a lower maximum level than before (Tschortner 1969, Middlemiss 1975). The consequences of the weirs were i) to separate the waters of Zeekoevlei and Rondevlei, ii) to reduce extreme seasonal drops in water level and iii) to prevent movement of sea water or marine fish into the vleis. The marine influence caused high salinities and alkalinities as well as a depauperate zooplankton fauna (Stephens 1929, Hutchinson *et al.* 1932). Since construction of the weir the mullet (*Mugilidae*) have disappeared (by 1960, according to Middlemiss 1975) and the waters have remained fresh with a rich zooplankton community. The vlei dried up in 1961 and in 1973, but increased stormwater inflow has supplemented the original Princess vlei inflow in recent years. The water has remained alkaline with a pH greater than 7 except during the rainy months (July and August) of the years 1953-1956. During these years rainfall was considerably higher than the average annual mean of 637 mm, calculated from 1952-1974 (Middlemiss 1975). The drop in pH in these months reflects the increased inflow of acid stream water via Princess vlei. The sanctuary was established in 1952 and consists of a fenced area of approximately 100 ha, including the vlei. Before the fence was erected the area was used for stock grazing, woodcutting and flower picking, while birds and fish were trapped, shot and speared in the vlei (Middlemiss 1975). Since the fence has been erected little disturbance has occurred other than the creation of several small islands by bulldozing in 1967 and 1970, the lowering of the water level in 1958 (Middlemis 1975) and the removal of the surrounding *Acacia* woodlands (Langley 1979). Since 1952 *Typha capensis* has spread from a small patch and now fringes most of the vlei. The *Scirpus littoralis* beds, on the other hand, have remained similar in distribution for the past 60 years (Middlemiss 1975). The spread of the vlei grass *Paspalum vaginatum* has been cause for concern for the wardens of the reserve as it colonises all available sand and mud flats which are important bird feeding areas. In 1979 water buffalo were introduced in the hope that they would control the *Paspalum* by grazing. This experiment was unsuccessful and in 1980 they were removed. In November 1981 two hippopotamus were introduced for the same reason. The *Paspalum* has since been eliminated, the hippopotamus have bred, been added to and some removed, and a considerable amount of stirring and trampling of bottom sediments and defaecation into the vlei, has taken place.

An interesting phenomenon that continues to occur within the vlei is the alternation between clear-water and turbid-water states, each lasting for a number of years. Accompanying the clear-water state is the appearance of *Pot~~o~~amogeton pectinatus* beds. The turbid state on the other hand results from dense blooms of phytoplankton, normally blue-greens. The reasons for the change in state are not known as very little attempt has been made to study the water chemistry and primary production of the vlei. Tschortner (1969) suggested that low water levels resulted in reduced mixing of the water and rapid growth of the *Pot~~o~~amogeton*, with concomitant uptake of most available nutrients. He suggested artificial fertilization in spring (during high water levels) as a means of eliminating the *Pot~~o~~amogeton*, after 50 tons of fowl manure added in late summer the previous year had served only to promote *Pot~~o~~amogeton* growth (Middlemiss 1975). Certainly the appearance of *Pot~~o~~amogeton* and its spread appears to be tied to a low-water event. Table 2.7 summarises what recorded information there is on the sequence of states. In each case after the vlei has dried (1928, 1932, 1959, 1961, 1973) the waters have remained clear for a number of years until the phytoplankton has regained its dominance. Common carp (*Cyprinus carpio*) may be important in this regard. Carp are well known for their ability to increase the turbidity of the water significantly as a result of their bottom feeding habits (Sterba 1962, Jubb 1965, 1967). Carp have been present since the beginning of the century, often "in numbers almost beyond belief" (Middlemiss 1975) and supporting a population of 100-300 white pelicans. Obviously mass mortalities would occur when the vlei dried, but recolonization would occur from Princess vlei. A gradual increase in carp numbers, to a point where turbidity levels detrimentally affect *Pot~~o~~amogeton* growth, and an increase in dissolved nutrients previously trapped in the sediments, might be important in causing the change from a clear to a turbid-water state.

1928 (Jan)	water present	turbid water, thick phytoplankton
1928	vlei dried	
1928	water present	clear water, *Pot~~o~~amogeton* present
1928	vlei dried	
1931	vlei dried	
1932	vlei dried	
1933	water present	clear water
1935	vlei dried	
1937	vlei dried	
1941	water present	clear water, thick *Pot~~o~~amogeton*
1944	water present	clear water, thick *Pot~~o~~amogeton*
1949	water present	turbid state, thick phytoplankton
1952-1958	water always present	turbid state, thick phytoplankton
1959	very low water levels	clear water
1961	vlei dried	
1962-1968	water always present	clear state, thick *Pot~~o~~amogeton*
1969-1972	water always present	turbid state, thick phytoplankton
1973	vlei dried	
1974-1976/77	water always present	clear state, thick *Pot~~o~~amogeton*
1977/78-1982	water always present	turbid state, thick phytoplankton

Table 2.7 A historical summary of drying events and alternate turbid and clearwater states in Rondevlei. Data from Tschortner (1969), Middlemiss (1975) and Langley (pers.comm.)

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Appendix 2.1 Description of the input and calculation of the quantity of excreta deposited into Grootwitvlei per annum by whitebreasted cormorants.

Input from the birds consists of excreta, regurgitated pellets, eggs, dead chicks, feathers and marine salts (from daily rinsing). The birds are piscivores, feeding in the sea and returning to roost and/or feed their chicks. Whitfield and Blaber (1979) recorded that cormorants spend less than 30% of daylight hours fishing and thus it is reasonable to assume that they are similar to their South American counterparts, the guanays, *Phalacrocorax bougainvillei,* in retaining their excreta until roosting (Vogt 1941 in Hutchinson 1950) (also for nest construction) and only producing pellets when roosting (Jordan 1959). On average two pellets, which consist mainly of fish bones, otoliths and eye lenses, are produced per adult bird per day are produced (Whitfield and Blaber 1979). The cormorants breed throughout the year in the south-western Cape (Brooke *et al.* 1982). On average 2-4 eggs are laid and 1-2 young fledged per nest (Olver and Kuyper 1978), so that 0-3 young or eggs enter the vlei per nest.

The average daily mass of excreta has not been measured for the cormorant, but can be estimated on the basis of the daily energy requirements of the birds. The daily energy expenditure (DEE) of seabirds of an average adult mass of 2986 g (averaged from Brooke *et al.* 1982), using the equation of Nagy (1987), is 2239 kJ.d^{-1}. Using an assimilation efficiency of 76.4%, averaged from that calculated for Jackass penguins (*Spheniscus demersus*) (Cooper 1977), and Cape gannets (*Sula capensis*) (Cooper 1978), both fish eaters, and whitechinned petrels (*Procellaria aequinoctialis)* fed on fish (Jackson 1986), daily energy ingested (DEI) is calculated at 2931 kJ.d^{-1}. The energy difference therefore equals that excreted, which is 692 kJ.d^{-1}. The average energy content of the dry excreta of Jackass penguins and Cape gannets (Cooper 1977, 1978) is 13.5 kJ.g^{-1}, thus the daily dry mass of excreta per bird is 42 g.d^{-1}. If the equation for the DEE of all birds is used (Nagy 1987) the daily dry mass of excreta equals 51 g.d^{-1}. Calculating from an average daily ingestion mass of 447 g of fish (from Du Plessis 1957, Junor 1972, Cramp and Simmons 1977), an energy content of whole fish of 22.8 kJ.g^{-1} dry mass and a dry mass/wet mass ratio 0.289 (from Cooper 1977), the average daily mass of dry excreta is 53 g.d^{-1}. The guanays of South America are slightly smaller and Vogt (1941, in Hutchinson 1950) has calculated their average daily dry mass of excreta to be 44 g.d^{-1}. Therefore an average daily dry mass of excreta of between 45 and 55 g per day per bird is estimated which, for an average of 75 cormorants, yields between 1.2 and 1.5 tons of dry excreta per annum. In addition Grootwitvlei receives in the region of 54 700 regurgitated pellets, and from 37 nest sites (counted in January 1981 by P. Ryan, in Brooke *et al.* 1982) up to 111 young or eggs per annum.

CHAPTER 3 : SAMPLING PROCEDURES

This chapter describes the collection and processing of samples before storage and final analysis. The methodologies of sample analysis are described in the respective chapters.

A total of seventeen sampling stations were selected in the six vleis - two each in Suurdam and Gillidam, three each in Sirkelsvlei, Grootrondevlei and Rondevlei, and four in Grootwitvlei. Each station was sampled monthly over a period of 15 months (February 1981 to April 1982) and samples were collected for water chemistry, phytoplankton and zooplankton analysis. In addition *in situ* measurements of temperature, dissolved oxygen, pH (details in chapter 5) and depth were taken. Observations were also made on the abundances of important waterbird species (except in Rondevlei, where regular monitoring is carried out), the phenology of the marginal vegetation and local weather conditions. Additional samples for water chemistry were collected from the inflow to Rondevlei (Italian Rd canal) in August 1981 and the inflow to Grootrondevlei (Disa stream) and outflow from Grootwitvlei in October 1981.

Samples of water for **chemical analysis** were collected within the surface 0.5 m using high density polypropylene containers, prewashed in Contrad, acid and double-distilled water (details in chapter 5). The samples were frozen on site using CO_2 ice and stored until analysis at -20°C. Care was taken that sample bottles were well sealed and that no airspace was present in any container. Before analysis samples were defrosted in circulating water baths at 25°C and conductivity was measured before filtering through 0.45 m Millipore cellulose acetate filters. Details of the different chemical analyses are described in chapters 5 and 6.

Phytoplankton samples were collected at the water surface (the top 0.2 m of the water column) using 1 *l* polyethylene bottles. Samples were stored immediately in a crushed ice - water mix (0°C) in darkness for not longer than six hours before filtering. For chlorophyll and phaeopigment analysis (chapter 8) a measured volume of the sample was filtered through 4.7 cm Whatman GF/C glass fibre filters onto which 2 ml of a 10% (w/v) $MgCO_3$ suspension had been pipetted. The amount of sample filtered depended on how much could pass easily through the filter before the filter clogged (due to the particulate load), and varied between 40 and 900 ml. The filter papers were immediately folded in half and wrapped in aluminium foil before being deep-frozen at -20°C. They were stored at this temperature for some months before analysis. For particulate carbon and nitrogen analysis (chapter 7) a measured volume of sample was filtered through a pre-ashed (@400°C for 6h), 4.7cm Whatman GF/C filter. Similar volumes were filtered; the filters were oven-dried at 45°C for 48 hours and stored in a glass desiccator until analysed.

Two **zooplankton samples** were collected at each station, one at the surface and one just above the bottom. The samples were collected as net hauls over a horizontal distance of 5 m. Because of the large seasonal fluctuation in water level, a smaller net was used when levels decreased to allow distinct top and bottom samples to be collected. This was only necessary in Gillidam, Sirkelsvlei and Rondevlei in the late summer months of the second year, however. The two nets filtered volumes of 332 and 173 litres respectively through nylon netting of 80μm mesh size. Once collected, samples were cooled to 0°C and frozen for immediate storage. These were later defrosted and fixed in 4% formalin (in water, buffered with hexamine), in a 75% (v/v) mixture with glycerol. Sample sorting and subsampling procedures are described in chapter 9. Bottom samples were used as a check on the homogeneity of the vertical distribution of the limnetic zooplankton species and horizontal patchiness effects were checked by comparison of stations within each vlei. Thus in each vlei a single sample was used for detailed analysis of the community each month and vertical and horizontal variation in distribution of the common limnetic species was checked with the remaining samples.

CHAPTER 4 : THE PHYSICAL ENVIRONMENT

INTRODUCTION

Meteorological forces exert a profound effect on waterbodies both directly through the input of radiant energy, the effects of air-mass movement, and the input of precipitation, and indirectly as a result of effects on the catchment, both the vegetation and the soil. They are of fundamental importance to the dynamics of freshwater systems and are responsible to a large degree for the physical processes occurring within any waterbody. The external variables driving these processes include solar radiation, air temperature, wind, precipitation and runoff, and the internal physical variables affected include water movement, light, temperature and suspended solids. The external variables further act in regulating the input of dissolved and suspended minerals, and fresh and refractory organic matter.

This chapter sets out to examine the external meteorological variables and to assess their variability both annually and between the vleis, as well as to examine the internal physical variables operating within each vlei.

CLIMATE

The climate which prevails over all three areas is Mediterranean and according to Koppens classification can be classified as Csb, Cfsa and Cfsb with a precipitation to evaporation ratio of more than 80 (Schulze 1947). The summers are usually hot and dry and the winters cool and wet.

The meteorological data discussed in the following sections were not collected at each vlei, but at weather stations close by, on similar terrain and at similar altitudes. The data for Rondevlei were collected at D F Malan weather station and for the Cape Point vleis at Cape Point weather station (see Fig. 2.1). There is no listed weather station in the close proximity of the Betty's Bay vleis and thus past representative data from Boucher 1978 were used. Rainfall data for Rondevlei and the Grootvleis were collected separately at Rondevlei and at the Harold Porter Gardens in Betty's Bay respectively.

SOLAR RADIATION

Solar radiation is quantified as the amount of energy received per unit area per unit time. The amount of solar radiation reaching the earth's surface at any instant depends on the quality of the atmosphere through which it passes as well as the length of path traversed (Straskraba 1980). The path length is largely latitude-dependent and the quality of the atmosphere is affected by the amount of gases, water vapour, aerosols and other pollutants, but mostly by the amount and type of cloud. The vleis all lie close together on a similar latitude so that the quality of the atmosphere, other than cloudiness, is similar. The amount of cloudiness (fig. 4.1a and b) does differ a little between the three areas with an average annual cloudiness in Cape Point of 4.3 ± 0.8 and at Rondevlei of 3.2 ± 0.8 (scale of 0-8). There is a similar seasonal variation in cloudiness between Cape Point and Rondevlei. The variation in daylength is also determined by latitude and together with cloud cover determines the average number of hours of direct sunlight (fig. 4.1~~c~~b). Screening effects by the surrounding terrestrial environment also reduce the ground-level incident solar radiation and the steep mountain immediately to the north of the Betty's Bay vleis must reduce the hours of sunlight in winter although no data are available.

AIR TEMPERATURE

Seasonal variation in the monthly average maximum and minimum air temperatures is shown in fig 4.2. The mean annual air temperatures for Cape Point, Betty's Bay and Rondevlei are 15.6, 16.5 and 16.7°C respectively. Cape Point thus has the narrowest mean annual temperature range, which was calculated as 4.2°C between 1927 and 1950 (Weather Bureau 1954), and is in fact the narrowest in the country. The mean annual air temperature range for Betty's Bay is similarly very narrow. The higher mean annual air temperature at Rondevlei reflects the increase in distance of the weather station from the sea. It must be noted that the weather stations at Cape Point and Betty's Bay are on the coast and thus the mean annual air temperature ranges will be slightly greater at each vlei than at the weather stations. However the weather station near Rondevlei (D F Malan) is further inland than the vlei (approx. 11 km from the sea, although only 40 m above sea level) so that Rondevlei itself will have a slightly narrower temperature range. The mean annual and mean maximal and minimal air temperatures are similar in range to those of the individual temperature ranges. The air temperature at all the vleis is thus well moderated by the close proximity of the sea, a small increase in range and mean temperature occurring with distance from the sea.

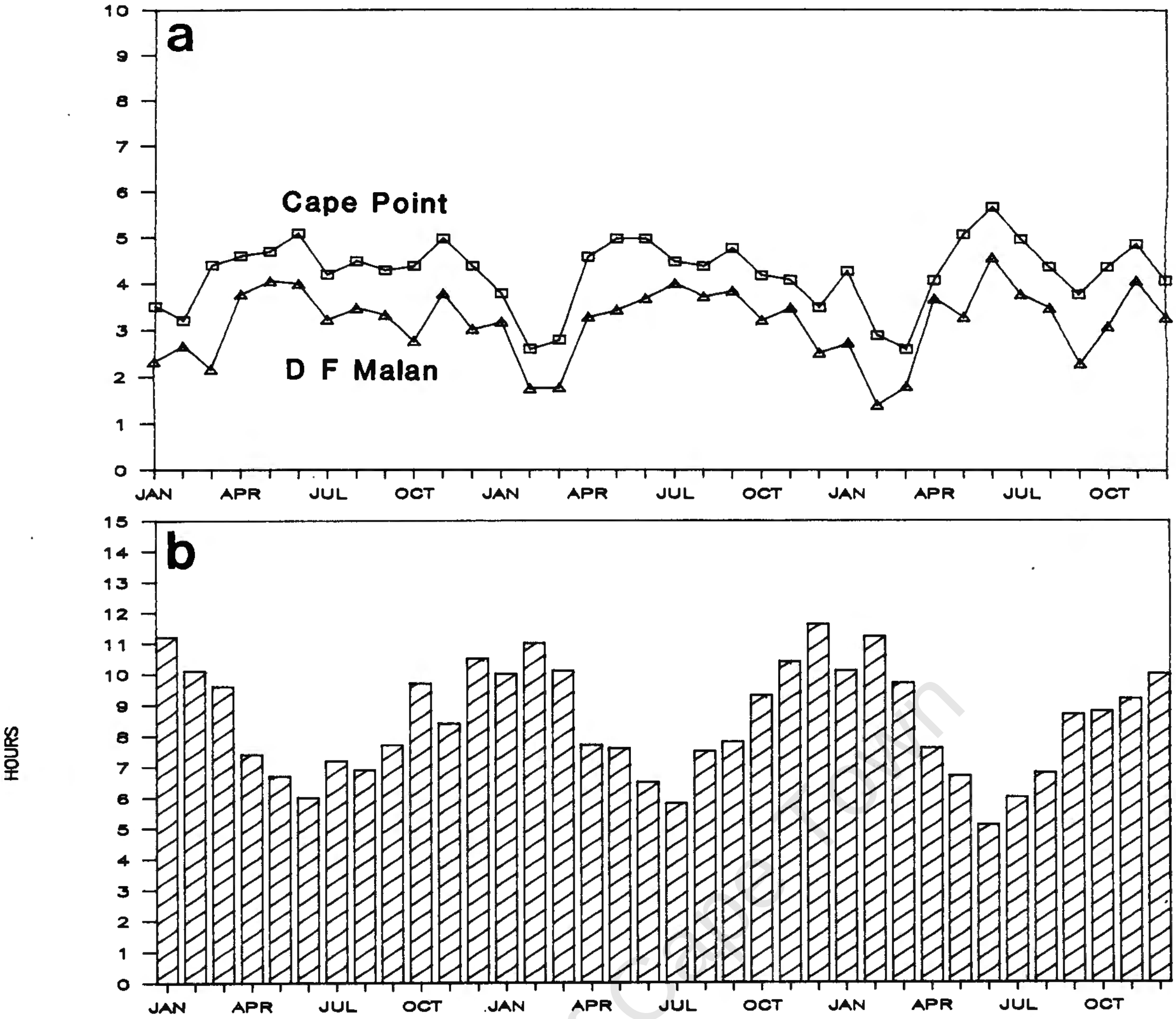


Figure 4.1 Cloud cover (a) and annual sunshine (b) in the south-western Cape calculated as monthly means between January 1980 and December 1982. Sunshine measured at D F Malan weather station as average hours of direct sunshine and cloud cover estimated on a scale of 1-8 at both D F Malan and Cape Point weather stations.

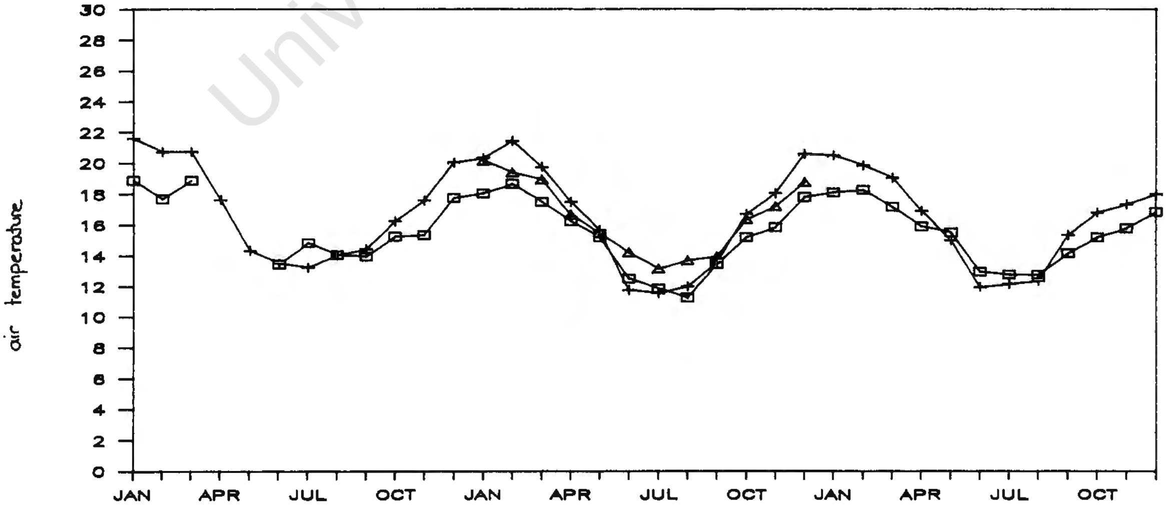


Figure 4.2 Air temperatures at Cape Point (□), Betty's Bay (△) and Rondevlei (+). Median monthly temperatures between January 1980 and December 1982.

Cape Point - mean annual temperature - **15.6°C**
mean monthly temperature range- 6.1°C (12.5-18.6)
Betty's Bay - mean annual temperature - **16.5°C**
mean monthly temperature range- 7.1°C (12.9-20.0)
Rondevlei - mean annual temperature - **16.7°C**
mean monthly temperature range-10.8°C (11.2-22.0)

RAINFALL

The south-western Cape is classified as a winter rainfall region, most rain falling in the autumn and winter months (from April to September) and the least in the summer months (from December to March). The winter rainfall is associated with cold frontal systems (cyclonic circulation) moving from the west, and orographic rains may last a number of days. Once the front has passed, the wind swings to the south-west and south and showers may continue to fall. Most rain falls over the mountains and in the higher peaks snowfalls may also occasionally occur, but are normally of short duration. In the summer months some rainfall can occur with the south-easterly and south-westerly winds that predominate at that time of the year. Monthly rainfall figures are displayed in fig. 4.3. The mean annual rainfall for the years 1980, 1981 and 1982 differs markedly between the three areas, with Cape Point receiving a relatively low 391 mm, Rondevlei an intermediate 603 mm, and Betty's Bay a relatively high 1084 mm. This may be related to the topography of the three areas as the Grootvleis lie immediately adjacent to, and in the rain shadow of, the Hangklip mountains and Rondevlei lies further from, but also to the south-east and east of, the Peninsula massif, whereas Cape Point lacks mountains to the west.

WIND

Wind is an important meteorological force in the south-western Cape, especially in localities close to the sea. The data for Cape Point and Betty's Bay were collected at the coast, but probably reflect conditions in the vleis. The data for Rondevlei are again from D F Malan airport, and thus the wind strengths may be slightly less than at the vlei, but the directions should be the same at the two sites. Wind-speed data are illustrated in fig. 4.4 for Cape Point and Rondevlei. Cape Point experiences on average high wind speeds (a mean annual wind speed of 8.3 $m.s^{-1}$) with little diurnal fluctuation. Rondevlei, on the other hand, experiences a lower mean annual wind speed of 4.9 $m.s.^{-1}$, with large diurnal fluctuations. Thus the mean annual wind speed measured at 08h00 is 3.3 $m.s^{-1}$ (s.d. between months ± 1.2) and at 14h00 is 6.5 $m.s.^{-1}$ (s.d. between months ± 1.9), a mean annual diurnal range of 3.2 $m.s^{-1}$. Detailed data for Betty's Bay are not available, but wind speeds on average seem to be close to those of Cape Point (pers. obs.) and Boucher (1978) presents data showing that on only 29% of the days of the year were wind speeds less than 5.3 $m.s^{-1}$ (Cape Point 42%, Rondevlei 37%). The summer wind pattern is dominated by south and south-east winds. These are caused by a ridging effect of the South Atlantic high pressure system which bends to the south of the country and

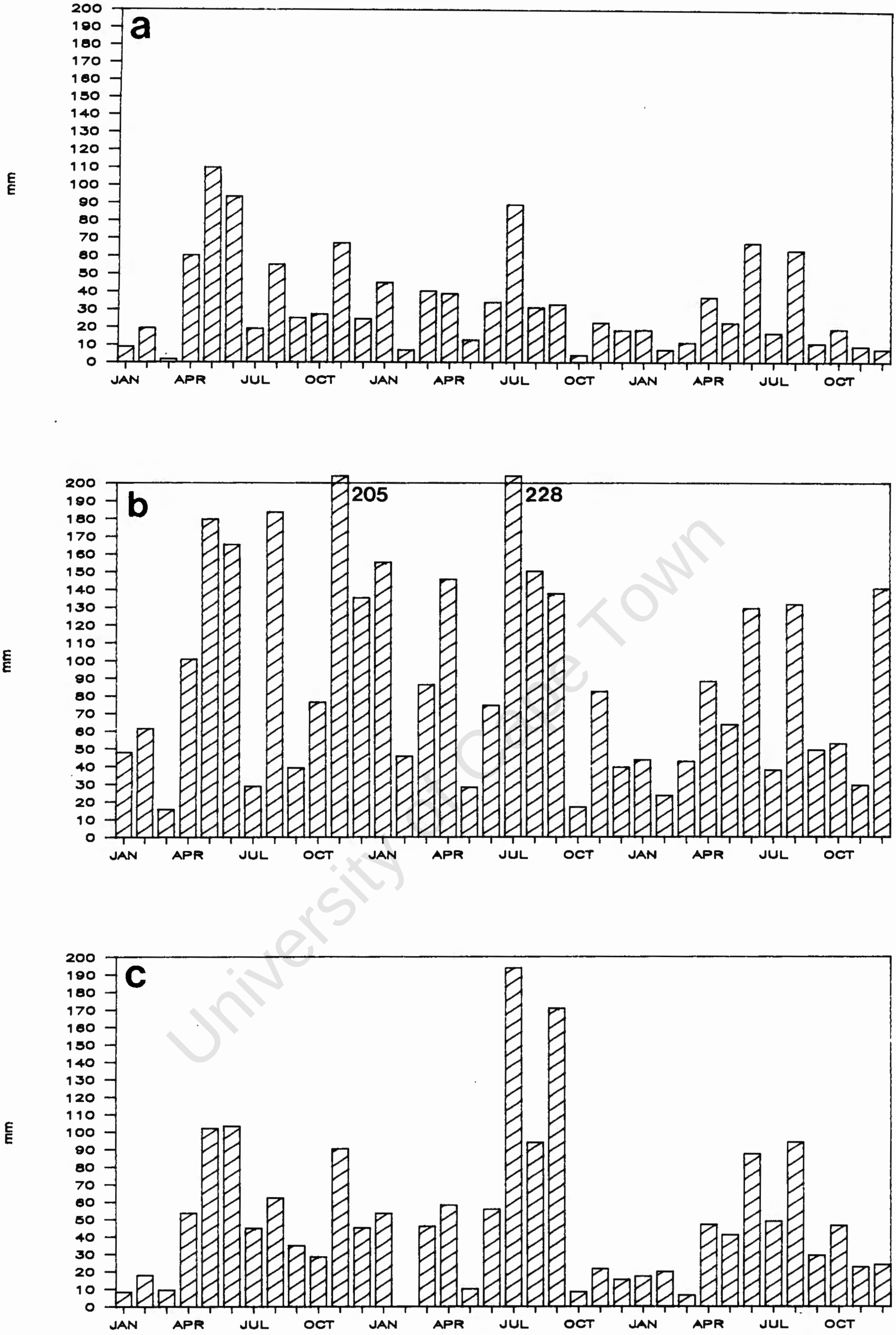


Figure 4.3 Rainfall at Cape Point (a), Betty's Bay (b) and Rondevlei (c). Monthly totals between January 1980 and December 1982.

annual rainfall - Cape Point - 390.7mm
- Betty's Bay - 1083.8mm
- Rondevlei - 602.6mm

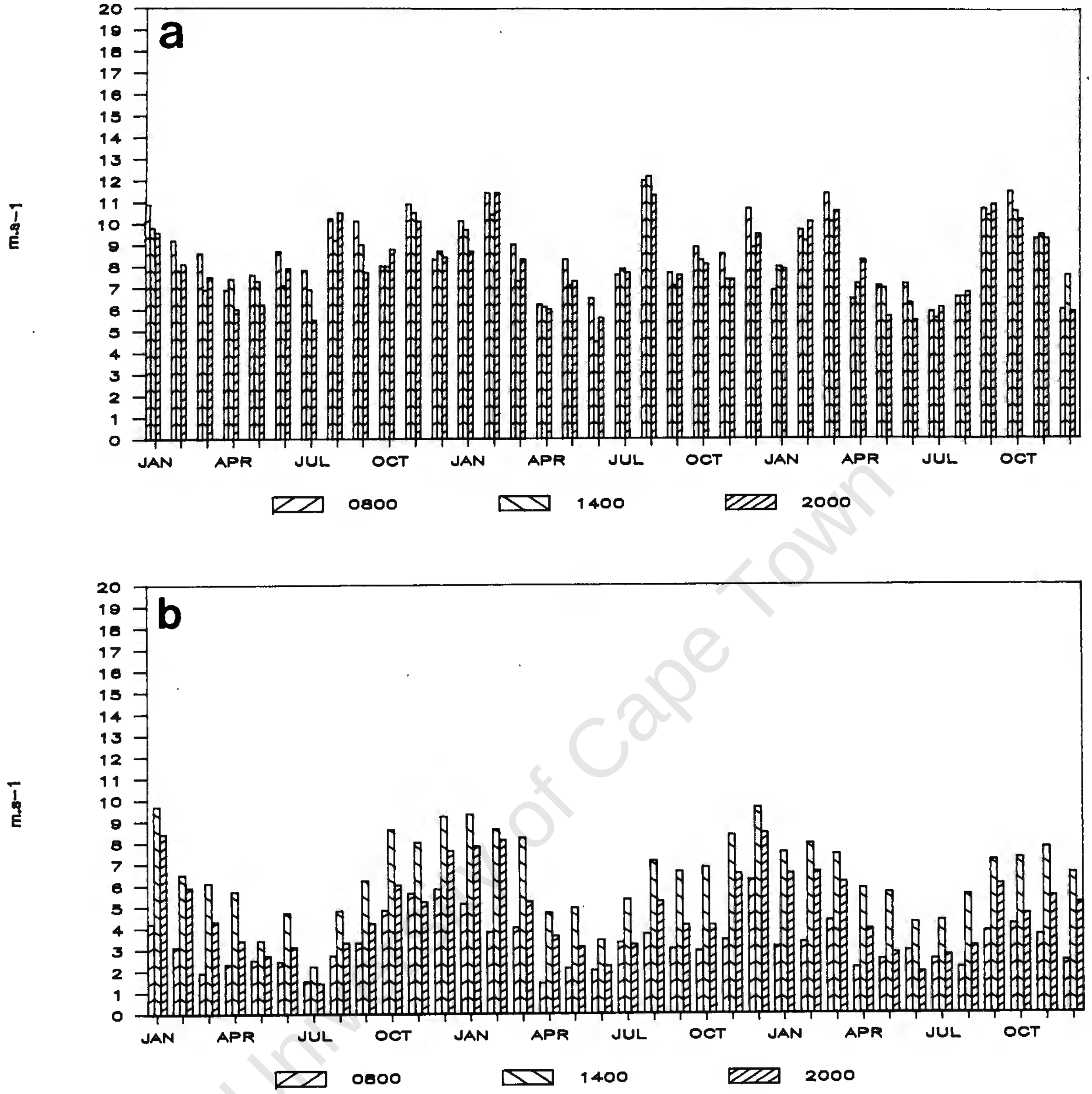


Figure 4.4 Wind speeds at Cape Point (a) and Rondevlei (b). Mean monthly wind speeds (m s^{-1}) at 08h00, 14h00 and 20h00. Mean annual wind speed - Cape Point - 8.3 m s^{-1}
- Betty's Bay - 4.9 m s^{-1}

4.1.a CAPE POINT WEATHER STATION

	N	NW	WSW	SSW	S	SE	E	NNE	Wind
	NNW	W	SW		SSE	ESE	NE		<1m.s^{-1}
	360-320	315-270	260-225	220-190	180-140	135-100	90-45	40-10	
JAN	-	5	12	-	4	9	-	-	-
FEB	1	4	6	-	2	15	-	-	-
MAR	2	2	6	-	3	15	-	-	3
APR	-	5	7	-	2	9	2	-	5
MAY	5	5	2	-	3	8	3	-	5
JUN	4	10	3	-	1	1	5	-	6
JUL	2	11	2	-	2	3	6	-	6
AUG	2	9	4	-	2	10	3	-	1
SEP	3	4	3	-	2	8	5	-	5
OCT	1	7	7	-	4	11	-	-	2
NOV	1	5	9	-	3	9	2	-	1
DEC	-	10	9	-	3	8	-	-	1
%	6	21	19	-	8	29	7		9

4.1.b BETTY'S BAY (FROM BOUCHER 1978)

	N	NW	W	SW	S	SE	E	NE	Wind
	NW	W	SW	S	SE	E	NE	N	<5m.s^{-1}
JAN	-	5	3	3	1	15	-	-	4
FEB	-	-	5	1	1	15	1	-	5
MAR	-	8	2	-	-	13	-	-	8
APR	1	5	1	-	-	10	-	-	13
MAY	-	6	1	1	3	7	1	-	12
JUN	-	11	3	-	-	4	-	-	12
JUL	-	6	2	2	1	5	-	-	15
AUG	-	12	3	-	-	7	-	-	9
SEP	1	7	3	2	-	7	-	-	10
OCT	1	6	4	1	-	16	-	-	3
NOV	-	1	3	1	2	17	-	-	6
DEC	-	6	1	-	-	16	-	-	8
%	1	20	8	3	2	36	1	-	29

4.1.c RONDEVLEI (D F MALAN WEATHER STATION)

	N	NW	WSW	SSW	S	SE	E	NNE	Wind
	NNW	W	SE		SSE	ESE	NE		<1m.s^{-1}
	360-320	315-270	260-225	220-190	180-140	135-100	90-45	40-10	
JAN	3	4	2	6	16	-	-	-	-
FEB	2	1	-	7	17	-	-	-	-
MAR	5	1	3	12	10	-	-	-	-
APR	7	1	3	8	8	1	-	-	3
MAY	13	1	1	4	8	-	-	1	3
JUN	14	1	1	1	4	-	-	2	6
JUL	13	2	1	2	7	-	1	-	5
AUG	9	3	1	1	14	-	-	1	2
SEP	7	4	1	3	14	-	-	-	-
OCT	7	1	2	2	17	1	-	-	1
NOV	6	3	3	5	14	1	-	-	-
DEC	8	3	1	6	14	-	-	-	-
%	26	7	5	16	39	1	-	1	5

Table 4.1 a, b and c. An analysis of wind direction in the three localities (in days) and the total percentage of the year in each respective direction (Cape Point and Rondevlei data from the Weather Bureau, Pretoria and Betty's Bay data from Boucher 1978)

often results in gale-force winds blowing for a number of days at a stretch. The south-easterly and southerly winds prevail for about 60% of summer and result in monthly average wind speeds greater than at other times of the year. The winter wind pattern is dominated by low-pressure, cold frontal systems moving over the Cape from the west and resulting in strong winds from the north-west backing to the west and south-west as the front passes. In between these systems a weak high pressure results in light southerly winds or calm conditions. An analysis of the wind direction is presented in table 4.1 and it clearly shows that all three localities conform to the above pattern of south to south-easterly winds in summer and north-westerly winter winds dominating for more than 60% of the year. For this reason lake fetch was measured as the maximum north-west/south-east distance in each vlei (chapter 2). The wind-speed at the water surface of the four largest vleis (Rondevlei, Grootwitvlei, Grootrondevlei and Sirkelsvlei) is unlikely to be affected to any extent by the surrounding vegetation or topography. The vegetation is low in relation to the large surface area of water, the surroundings are flat in most directions and high wind speeds are common. The two small vleis, Suurdam and Gillidam, however, have a relatively high marginal vegetation in relation to surface area, made higher by surrounding banks and a summer drop in water level. The wind speed at water level is thus normally significantly reduced, as is the effect of wind on the water mixing.

INTERNAL PHYSICAL ENVIRONMENT

THERMAL REGIME AND STABILITY

The morphometric feature common to all the vleis, and most important in determining the physical aquatic environment, is the extreme shallowness (chapter 2). Because they are shallow there is not enough water below the warmed surface layer to resist mixing by the frequent and strong winds. The depth is thus insufficient to maintain typical stratification and the entire water column frequently mixes. A lake that experiences frequent periods of water circulation, but has sufficient depth in relation to surface area, wind, etc., to form a hypolimnion, is termed polymictic (Wetzel 1983). The four larger vleis are unlikely ever to stratify over much of their full area as their relative depths are very small (chapter 2). The two smallest vleis, Suurdam and Gillidam, however, have far greater relative depths and do in fact experience stratification in summer. Sirkelsvlei, Grootrondevlei, Grootwitvlei and Rondevlei fall outside the strict category of polymictic lakes while, depending on diurnal stability, Suurdam and Gillidam may approach a diminutive form of monomixis.

The immediate and preceding weather conditions may have had a small deviating effect on the monthly measurements. However the data in figure 4.5 show a strong seasonal trend with few anomalies. The rapid heating and cooling of the surface in temporarily sheltered parts of the vleis during sampling in summer and autumn (very little wind) is noticeable between stations in the four larger vleis. The difference between the surface and bottom temperatures at most stations is minimal however, due to the lack of stability of the water column. A reduction of temperature with depth is thus lacking in these waters throughout the year. In contrast the summer stratification of Suurdam and Gillidam is obvious in the plot of surface and bottom temperature (fig 4.5). The maximum temperature difference recorded between epilimnion and hypolimnion was 9°C (Suurdam in September), but differences of between 2 and 5°C were more common. Both vleis are dark brown in colour (see chapter 6) and rapidly absorb solar radiation during the day. At night the surface waters lose heat to the surrounding air. The vlei volume in both cases is very small and thus the stratification is unlikely to be stable at night. In addition, during summer the depth of the thermocline varies considerably from 0.1 m below the surface to 0.05 m above the bottom of the vlei. Thus the stratification is both variable in strength and diminutive in structure, but is obviously present during summer.

The annual range of water temperature is similar in all of the vleis and varies from 11°C to approximately 26°C. The variability of the maximum temperature results from a few very shallow stations as well as temporarily stable water measured late in the afternoon with particularly high temperatures. A range of 16.5°C is computed by Straskraba (1980) for the surface waters of medium-sized lakes at the same latitude and at altitudes less than 2000 m. Extremely shallow lakes would be expected to show a greater surface temperature range. As a result of the maritime climate, however, the range (±15°C) in the vleis studied is less than the computed value. The sinusoidal pattern of seasonal variation closely follows that of the input of solar radiation (as reflected by air temperature in figs. 4.6 a,b,c and d). Short-term fluctuations in air temperature, because of the relatively shallow depths and small size of the vleis, can affect the water temperature significantly. Short periods of above-average air temperature in September and October caused higher-than-expected water temperatures in Rondevlei and the Cape Point vleis and similarly below-average air temperatures reduced the water temperatures in November. Mean annual surface temperature is computed by Straskraba (1980), for the same

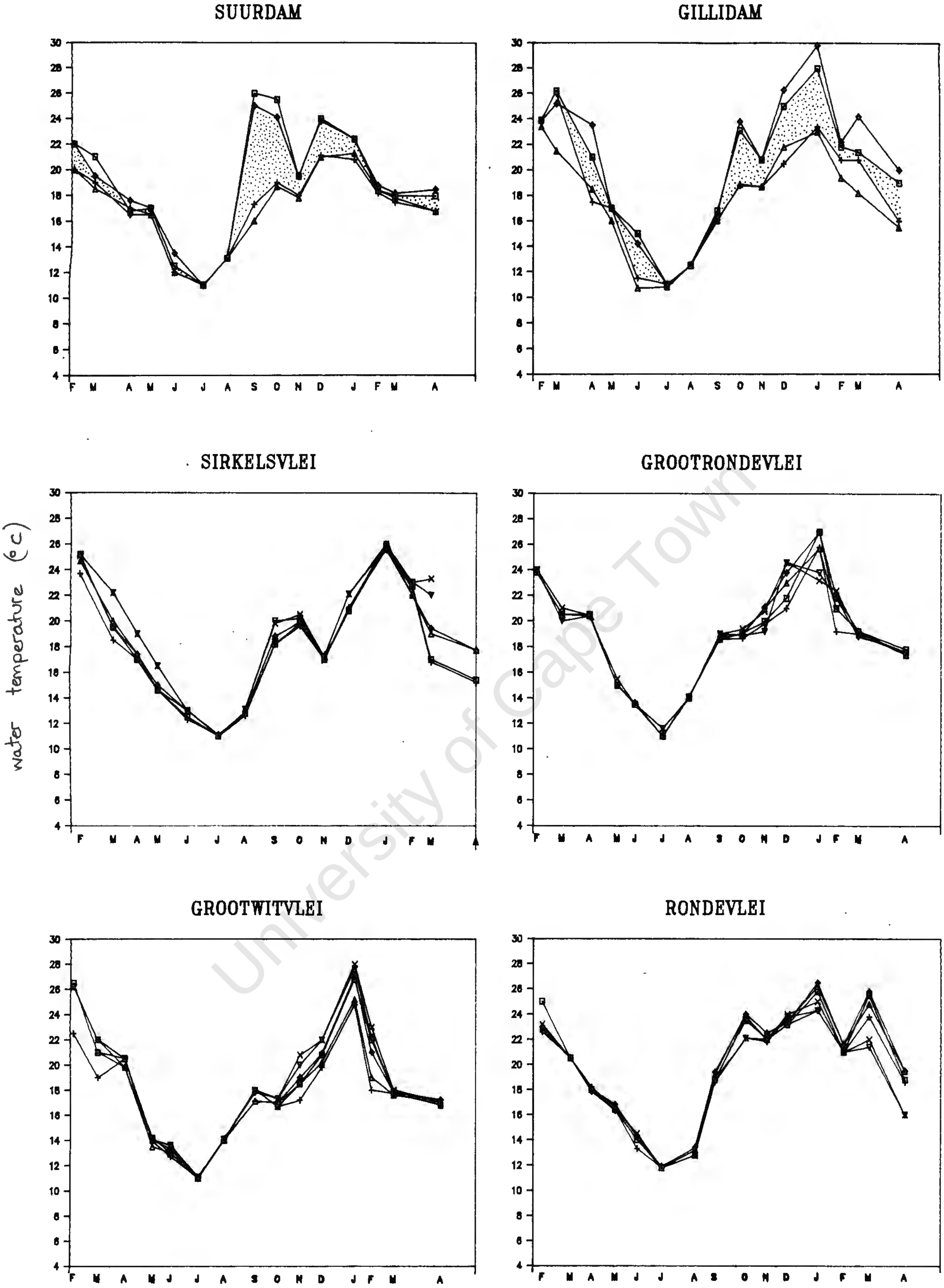


Figure 4.5 Surface and bottom water temperatures (°C)in the studied vleis. Surface temperatures at station 1 (□), station 2 (◇) and station 3 (×) and bottom temperatures at station 1 (+), station 2 (△) and station 3 (▽). The presence of a thermocline is indicated by [░].
Mean water temperature (°C) - Suurdam (18.0), Gillidam (19.2), Sirkelsvlei (18.5), Grootrondevlei (18.9), Grootwitvlei (18.7) and Rondevlei (19.5).

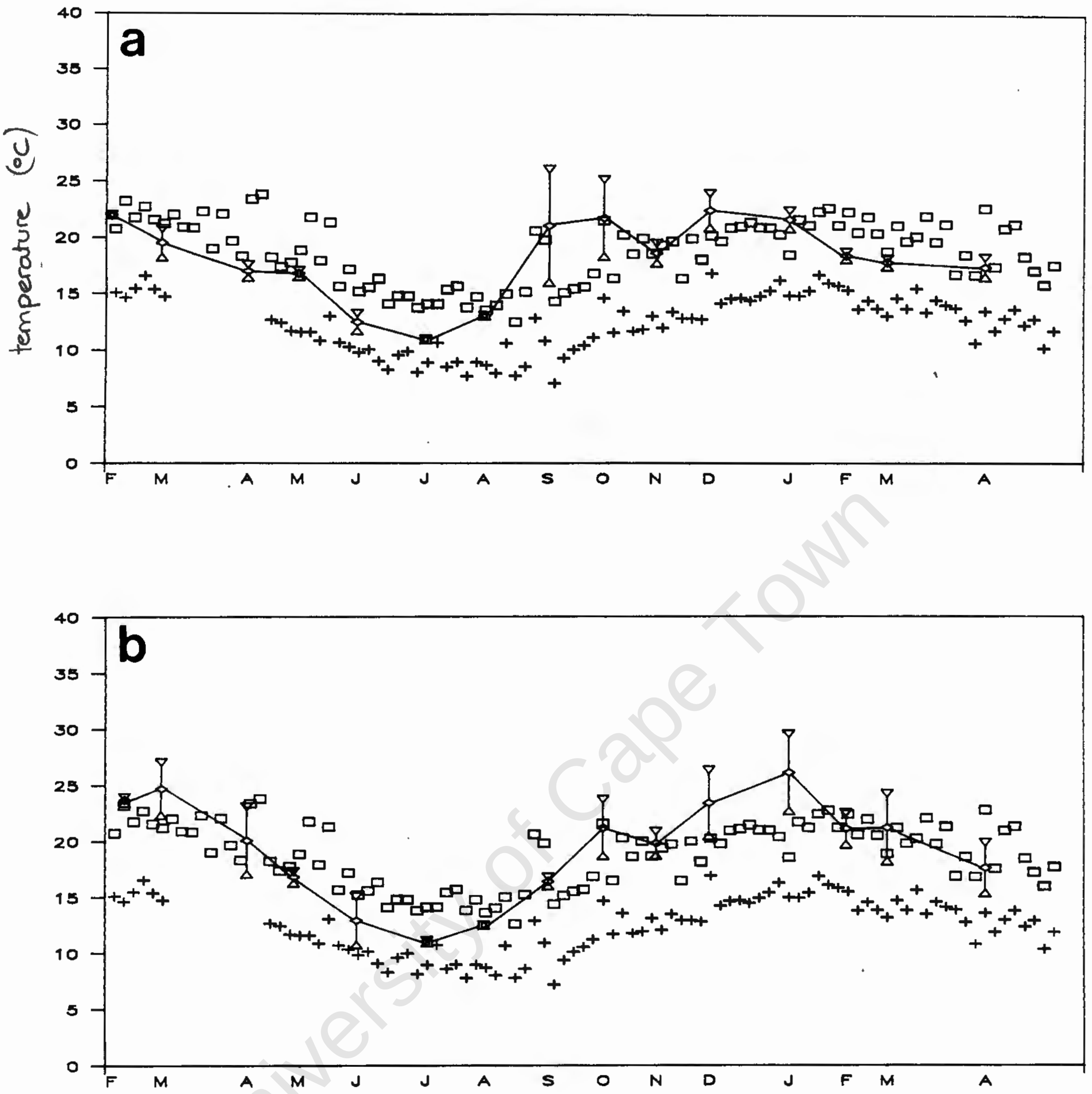


Figure 4.6 Water temperatures in relation to air temperatures (°C) in Suurdam (a), Gillidam (b), Sirkelsvlei (c) and Rondevlei (d). Maximum air temperature (□), minimum air temperature (+), mean water temperature (◇) and water temperature range (△).

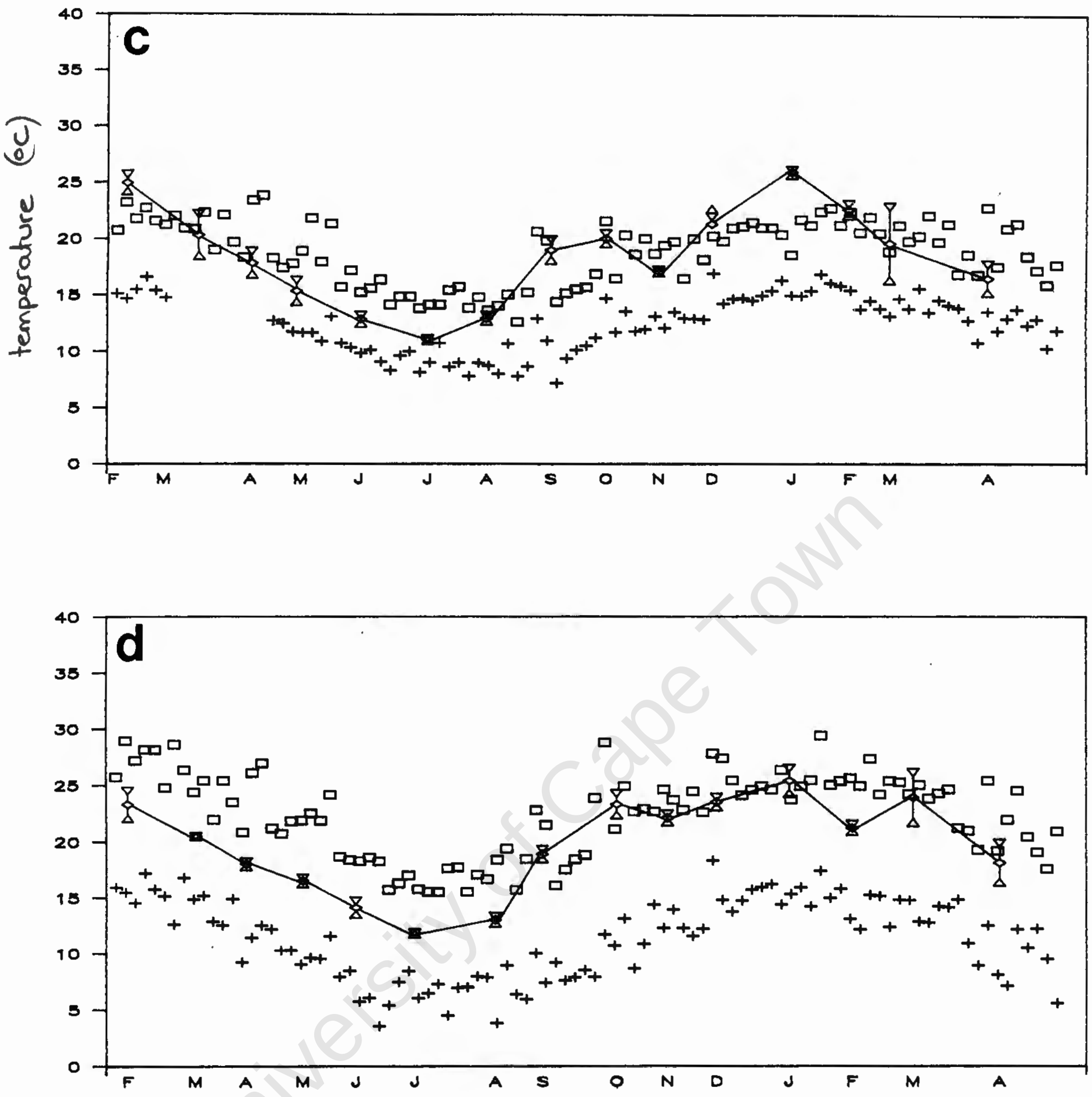


Figure 4.6 (cont.) Water temperatures in relation to air temperatures (°C) in Suurdam (a), Gillidam (b), Sirkelsvlei (c) and Rondevlei (d). Maximum air temperature (□), minimum air temperature (+), mean water temperature (◇) and water temperature range (△).

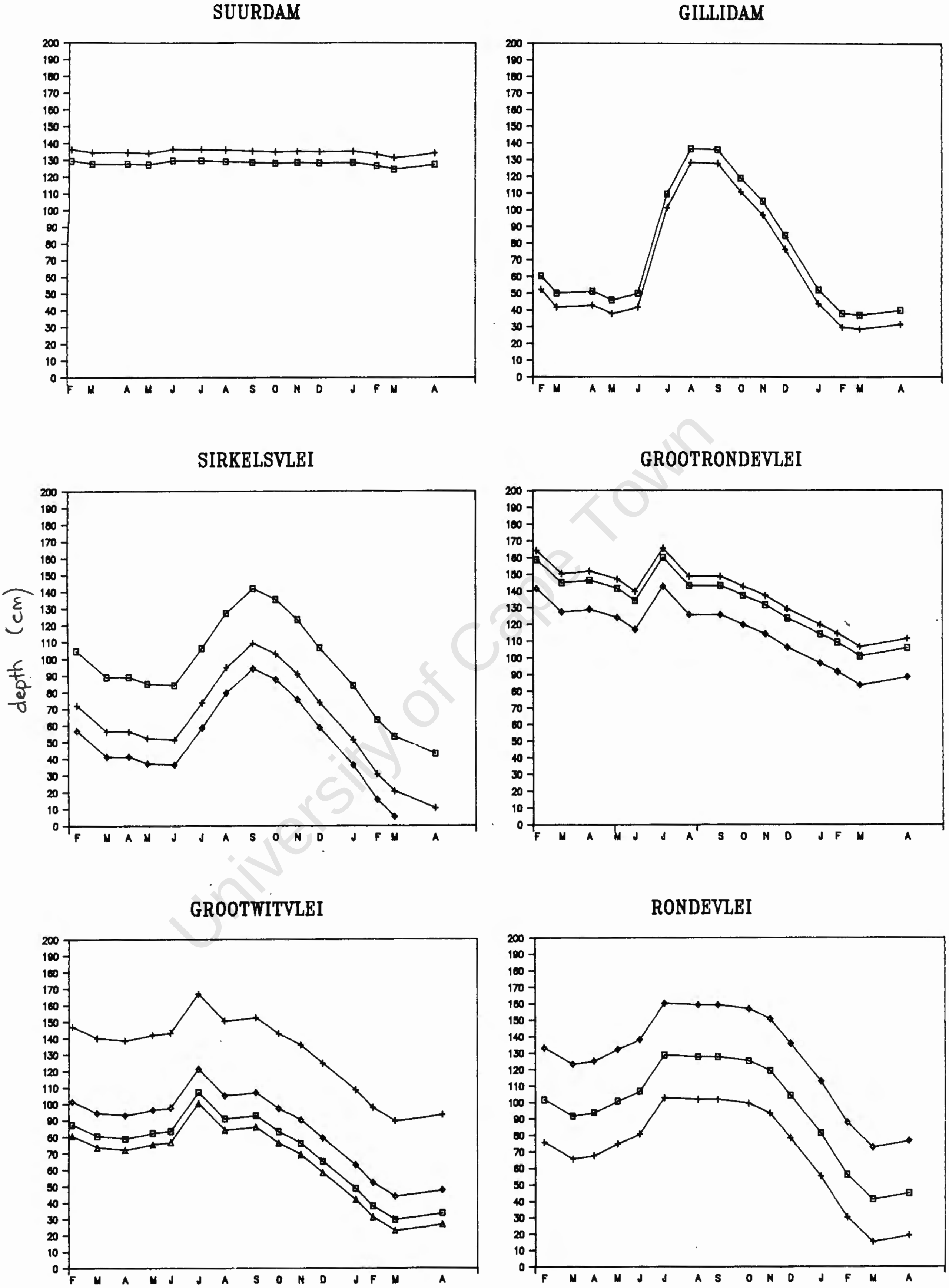
medium size lakes, to be 16.6 ± 2.4°C. The vleis display mean annual temperatures at the upper limit of this value, probably as a result of greater summer heating, for reasons mentioned above, as well as the low water-levels in summer and water colour, which allows a rapid heating of the water.

The heat budgets and the stability of the water columns of the vleis were not calculated. The very small size and generally large surface area in relation to depth result in a very limited heat storage and, as discussed earlier, little stability of the water column. Temperature, as a measure of the intensity of heat stored throughout the water column, is closely related to air temperature and thus was deemed a sufficient measure of the thermal regime.

WATER DEPTH

The annual fluctuation in water depth varies considerably both between the vleis and between years. All the vleis, except Suurdam, fluctuated by between 0.6 m and 1.0 m over the study period, whereas Suurdam showed a change in water level of only 0.05 m. This small annual fluctuation is due to the lack of outflow from the vlei (see chapter 2), the low wind speeds, and very short fetch at the surface of the vlei reducing the effect of evaporation. Both Sirkelsvlei and Gillidam are closed-basin lakes, but both presumably have a significant subsurface drainage and Sirkelsvlei, with its long NW/SE fetch, should suffer high rates of evaporation. As a result of the greater mean annual rainfall of that area, inflow from larger streams, and bigger immediate catchments, Grootrondevlei and Grootwitvlei both show smaller annual fluctuations (0.59 and 0.77 m) than the remaining vleis, other than Suurdam. With maximum water levels not exceeding a depth of 1.6 m, fluctuations as great as 1 m in Gillidam, Sirkelsvlei and Rondevlei might be expected to influence the biota and chemistry of the waters.

The seasonal pattern of fluctuation in water depth shows the summer water levels in 1981/1982 to be lower than those in summer in 1980/1981 in all three areas. This is a direct reflection of the rainfall received in each area. In the summer of 1981/1982, Cape Point, Betty's Bay and Rondevlei each received 2.7, 2.4 and 2.9 times less rainfall than in the same five summer months in 1980/1981. This resulted in water levels differences of 0.13 to 0.51 m between the two summer periods. The effect of winter rainfall is most marked in Sirkelsvlei and Gillidam, where seasonal waterlogging of the shallow soils provides much of the inflow. Open-basin vleis such as the Grootvleis, with a high annual rainfall, show a less pronounced winter maximum in water depth, except in July when exceptionally high



SUURDAM

GILLIDAM

SIRKELSVLEI

GROOTRONDEVLEI

GROOTWITVLEI

RONDEVLEI

Figure 4.7 Seasonal variation in water depth (cm) in the studied vleis at the different sampling stations. Station 1 (□), station 2 (+), station 3 (◇) and station 4 (△).

rainfall (228 mm) caused a sharp increase in water depth. Rondevlei falls somewhere between the Cape Point and Betty's Bay vleis, being an open basin, yet controlled by a weir and receiving an intermediate annual rainfall.

UNDERWATER LIGHT CLIMATE

Of the solar radiation that penetrates water, much is absorbed as heat by the water and by dissolved and particulate solids, while some other portions are utilized for photosynthesis. The radiation that enters is attenuated vertically by scattering and absorption. The character of the dissolved and suspended solids is important in determining the underwater light climate of any water. In particular the character and concentration of humic compounds, as noted earlier, is a particular feature of many of the vleis and is thus likely to be the primary determinant of the underwater light climate of these vleis. The absorbance and fluorescence characteristics of these compounds will be examined in chapter 6, and their effect on underwater light will be discussed. The effect of the suspended particle fraction can also be highly significant, but it is not discussed further other than the data presented in Chapter 7.

SUMMARY

The vleis follow the changes in meteorological forces closely as a result of their shallow nature and relatively small size. The climate is characterized by hot, dry summers and cool, wet winters and thus lowest water levels occur with highest water temperatures in the summer months and vice versa in the winter months. Wind is a particularly important meteorological force both as a result of the high mean wind speeds and the shallow water. Stable stratification seldom, if ever, occurs, except in Suurdam and Gillidam as a result of their large relative depths, and the few larger vleis are continually mixed throughout the year. Differences in temperature between the vleis are minimal. Air temperature ranges are narrow, moderated by a close proximity to the sea, and ranges of water temperature respond closely. Rainfall, however, differs markedly between the three localities, most likely as a result of the topography, and results in large differences in the winter flow, into and out of each system. Water level fluctuations are determined by the basin characteristics as well as the drainage into and out of the vleis and, except for Suurdam, are large relative to the water depth.

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CHAPTER 5 : INORGANIC CHEMICAL ENVIRONMENT

INTRODUCTION

The composition and abundance of elements in natural waters is widely variable, although lakes in close proximity to each other are likely to have similar chemical compositions. This is a result of the deciding influences exerted by the climate and catchment (geology and vegetation) on the overall chemical composition of the lake. The chemical environment is dynamic in lakes in contrast to the ocean, where steady-state distributions of many major elements exist (Sholkovitz 1985, Stumm and Morgan 1981). Movement of elements between different phases, as a result of biological and chemical reactions, controls the temporal and spatial distribution as well as influencing the final concentration in lake waters. Internal processes which affect this movement include mineral formation and precipitation, water column stratification and associated anoxia, sediment regeneration, complexation, sorption, and ion-exchange. Some of these more important elements in the biogeochemical cycle of lakes are oxygen, carbon, nitrogen, phosphorus and silica. The alkali and alkaline earth metals and chlorine, or carbon and oxygen (carbonic acid), are normally the most abundant.

Dissolved oxygen is essential for the existence of almost all forms of multicellular animal life as well as being a predominant participant in aquatic redox cycles. A constant supply is normally maintained in the surface waters as a result of wind-induced mixing and photosynthesis. Thermal stratification, however, can lead to seasonal anoxic conditions developing in the hypolimnia of deeper lakes as a result of respiration. The seasonal depletion of oxygen, either from the hypolimnia or from the bottom sediments of lakes, and the formation of C, N and S compounds by photosynthesis, tend to drive the redox processes in lakes (Stumm and Morgan 1981, Wetzel 1983). Although only a few elements, namely C, N, O, S, Fe and Mn, are predominantly involved in these processes, the concentrations of the alkali and alkaline earth elements can be linked, in particular, to the redox cycles of Fe and Mn (Sholkovitz 1985). An important facet of elemental cycling is thus closely coupled to the distribution of dissolved oxygen through the water column and the sediments.

pH refers to the concentration and therefore the activity of the hydrogen ion (H^+). It effectively forms the balance of the proton-yielding and proton-consuming processes occurring in the lake and its catchment. Aggrading biomass and humus, and oxidation reactions (nitrification, sulphur oxidation) all act to add H^+ to natural waters, while chemical weathering, ion exchange and reduction reactions (denitrification, H_2S production) all act to consume H^+, and therefore to increase the acid-neutralizing capacity of the water (Schnoor and Stumm 1985). The pH is thus determined by coupled redox and acid-base reactions.

Acidity differs from pH in that it is a measure of both the dissociated and undissociated protons in solution. Uncombined carbon dioxide, organic acids (humic, fulvic and tannic acids), mineral acids and salts of strong acids and weak bases are normally responsible for the acidity of water (Wetzel and Likens 1979). Together they represent the base-neutralizing capacity (BNC) of the water, forming the H^+ ion reservoir (Stumm and Morgan 1981, Schnoor and Stumm 1985).

Alkalinity on the other hand represents the acid-neutralizing capacity (ANC) of the water. Dissolved silicates, borates, ammonia, organic bases, sulphides and phosphates may contribute to alkalinity, but in general occur in very small concentrations in comparison to those of the carbonate species. Total alkalinity is therefore usually imparted by, and referred to as, the concentration of the bicarbonate, carbonate and hydroxyl ions. The phenolphthalein alkalinity is referred to as the concentrations of the carbonate and hydroxyl ions.

The most abundant inorganic chemical species in natural waters, other than dissolved oxygen and carbon dioxide, are the major ions. The four major cations (Ca^{2+}, Mg^{2+}, Na^+ and K^+) and the four major anions (HCO_3^-, CO_3^{2-}, Cl^- and SO_4^{2-}) normally dominate the ionic composition of fresh waters and effectively constitute the total salinity of the water. The major mechanisms that control the salinity of natural waters are atmospheric precipitation, the weathering of the catchment soil and rock, and the evaporation-precipitation process (Gibbs 1970, Feth 1971). Rainfall carries much of the atmospheric salt to lakes, and particularly in maritime regions accounts for a significant input of marine salts into fresh waters (Gorham 1961, Ogden 1982). The supply of ions to runoff and percolating water and the rate of weathering are both dependent on the composition of the soil and rock and its ion-exchange capacities. Climate further determines the temperature, wind, sunshine and rainfall inputs which in turn affect evaporation rates, turnover times and rates of reaction. Within the water body Na^+, K^+, Mg^{2+}, and Cl^- are highly soluble and show little fluctuation as a result of redox or coordinative reactions. The remaining major ions, namely Ca^{2+}, HCO_3^-, CO_3^{2-}, and SO_4^{2-}, display more dynamic levels due to their participation in cooordinative reactions. The last three also participate in redox reactions. The cycling of the inorganic carbon is in fact basic to the metabolism of lake waters and the cycling of sulphate is important in microbial metabolism.

Ionic ratios, in particular the ratio of monovalent to divalent cations, have been suggested as being important factors influencing the occurrence of distinct phytoplankton assemblages (Pearsall 1924, 1930, 1932, Droop 1958), but are probably of more use in the comparison of lake chemical enviroments (Talling and Talling 1965, Golterman and Kouwe 1980, Talling 1983). Certainly the monovalent/divalent ratio was found to exhibit a "spurious relationship" with the phytoplankton quotient in ninety-nine Scottish lakes (Shoesmith and Brook 1983).

The specific conductance of a water is a measure of, and is normally proportional to, the total ionic concentration or salinity, particularly in lakes dominated by the bicarbonate anion (Juday and Birge 1933, Rodhe 1949). Thus changes in the concentrations of the major ions will be reflected in conductivity changes. The positive correlation between pH and conductivity in bicarbonate lakes of intermediate pH does not apply to lakes with high levels dissolved organic matter or low salinity (Strom 1947).

Most transition metals are strongly complexed by humic compounds. In particular iron and copper both readily form complexes with humic compounds (see chapter 6) and their concentrations are thus strongly influenced by the levels and types of humic compounds present. They are however present in far lower concentrations than the major ions and thus do not normally contribute noticeably to the total salinity.

The term 'major nutrients' generally refers to the different forms of N, P and Si. Many other elements are also plant nutrients, but they are normally present in excess of growth-limiting concentrations. Nitrogen and phosphorus, in particular, are essential elements in primary production but often occur in highly irregular and growth limiting concentrations.

In terms of natural supply, phosphorus is normally the less abundant of the two in inland waters. Total phosphorus can be separated into two fractions: total particulate and total dissolved phosphorus. Total particulate phosphorus consists of phosphorus in organisms, and that adsorbed into inorganic complexes and onto dead particulate organic matter, while total dissolved phosphorus consists of orthophosphate, polyphosphate, organic colloids or phosphorus combined with adsorptive colloids, and low molecular-weight phosphate esters (Wetzel 1983). Soluble reactive phosphorus (SRP), which forms a large fraction of the total dissolved phosphorus and is defined purely on the basis of its reactivity with molybdate (Strickland and Parsons 1972, Wetzel 1983), constitutes a variable fraction of the total phosphorus. While Walmsley and Butty (1980) suggest that, on average, SRP constitutes about fifty percent of the total phosphorus concentration in a large number of South African impoundments, Talling and Talling (1965) and Thornton (1986) point out that the proportion can vary greatly (eg. from <10% to 70%) over a range of African lakes.

Total nitrogen is also separated into total particulate and total dissolved fractions. Total particulate nitrogen is dealt with separately in chapter 7. Total dissolved nitrogen is divided into a dissolved organic nitrogen fraction and a dissolved inorganic nitrogen fraction. Dissolved inorganic nitrogen consists of ammonia, hydroxylamine (very low levels), nitrate and nitrite, forming a dynamic fraction of 'available' nitrogen. Dissolved organic nitrogen, on the other hand, consists of amino nitrogen compounds and free amino nitrogen. It commonly makes up more than 50% of the total dissolved nitrogen, but, apart from the simple amino acids, much of the fraction is 'unavailable' and resistant to bacterial decomposition (Wetzel 1983).

The chemical attributes discussed above constitute most of those used to characterise the chemical environment of a fresh water body and include the most important inorganic chemical fractions in the water column. The aim of this chapter is to describe the chemical composition of the inorganic chemical environment and its seasonal changes rather than attempt to analyse or quantify the chemical interchanges in the system. Thus this study of the inorganic chemical composition is intended to establish and compare the mean and range of values of each variable and by following the seasonal variation to identify the factors most important in controlling the concentrations. The description and much of the explanation behind the seasonal variation is included in the results and discussion section, whereas the general discussion attempts to identify the most important factors, both internal and external, determining the chemical environment and the range of its variation. By characterising the inorganic chemical enviroment and its variability, a better understanding of the levels of humic substances (and their variation) and their effects on the limnetic biota should be possible.

METHODS

The analytical methods are summarised in table 5.1. In all analyses standards were made up using analytical grade reagents in double-distilled water (0.05 mS m^{-1}) prepared from tap water in a Fisons double distillation unit and stored in a 25l high-density polypropylene container. Sampling procedures and sample storage are discussed in chapter 3. Sample containers and all glassware were cleaned before use as follows - immersed in a 20% Contrad solution (prepared in double-distilled water) for 24 hours, rinsed twice in double-distilled water, immersed in a 10% HCl (Analar) solution for 12 hours, rinsed in double-distilled water, soaked in double-distilled water for 12 hours and oven-dried at 35 C.

Constituent	Method
Dissolved oxygen	Yellow Springs Oxygen meter YSI model 57, polarographic electrode
Temperature	Mercury thermometer (and the YSI model 57 thermistor)
Conductivity	Griffin conductivity bridge S75-90 IS 1335/7008
pH	(field) Hellige Lilliput pH meter model 750/750P (lab.) Beckman pH meter Φ70
Total alkalinity	HCl titration to indicator endpoint (Golterman *et al.* 1978)
Phenolphthalein alkalinity	HCl titration to indicator endpoint (Golterman *et al.* 1978)
Acidity	$Ba(OH)_2$ titration to indicator endpoint (Golterman *et al.* 1978)
Calcium Magnesium Iron Copper	Atomic absorption spectrophotometry Perkin Elmer 5000
Sodium Potassium	Flame emission spectrophotometry Instrumentation Laboratory Flame Photometer 243
Phosphorus (SRP) Nitrate (NO_3^-) Nitrite (NO_2^-) Ammonium (NH_4^+)	Technikon Auto Analyser (procedures described by Mostert 1983)

Table 5.1. Summary of the methods used for the analysis of the inorganic chemical constituents of the vlei waters.

Dissolved oxygen was measured *in situ*, in the top and bottom 0.20m of the water column, using a polarographic type membrane electrode. Interference resulting from the highly coloured humic waters was thus avoided. The electrode was air calibrated and results were expressed as percentage saturation of dissolved oxygen.

Conductivity was measured in the laboratory using a platinum electrode. The instrument was calibrated with a solution of 0.0100N KCl and results expressed as mS m^{-1} at 25 C.

pH was determined both in the field and in the laboratory using two separate meters. In the field a portable meter with a precison of 0.1pH unit was used and in the laboratory a meter with a precision of 0.001 pH unit, which in addition registered drift, was used to check the measurement. Both meters were calibrated with the two Beckman buffer solutions (pH 4.01, 6.86 and 9.18) closest in value to the observed sample pH. An accuracy of 0.05pH units was assumed (Standard Methods 1985). Temperature differences between the field and laboratory were thus in general not significant.

Total and phenolphthalein alkalinity were determined using the acidimetric technique described by Golterman *et al.* (1978) with end point indicators of methyl orange and phenolphthalein respectively.

Acidity was also determined using the method described by Golterman *et al.* (1978) with an endpoint mixed indicator of thymol blue and phenolphthalein. Levels were expressed as mmol l^{-1} of strong base added to reach a pH endpoint of 8.6.

Levels of calcium, magnesium, iron and copper, were determined using atomic absorption spectrophotometry. In all cases the samples and standards were spiked with NaCl to a final concentration of 1000 mg l^{-1} to correct for interference. Standards were made up from 1000 mg l^{-1} Analar standard solutions (BDH). Calcium and magnesium levels were both determined using a nitrous oxide-acetylene flame at wavelengths of 422.7 and 285.2nm respectively (lamp current 7mAmps and slit width 0.7nm). Iron and copper levels were determined using the cooler air-acetylene flame. Iron was measured at a wavelength of 248.3nm (lamp current 30mAmps and slit width 0.2nm) and copper at a wavelength of 324.8nm (lamp current 15mAmps and slit width 0.7nm). Copper levels were only measured for September as they were close to the detection limit (not greater than 0.03 mg l^{-1}), without employing preconcentration methods. The results for all the metals are presented as mmol l^{-1} and umol l^{-1} quantities. Humic substances are well known to form complexes with various metals, in particular iron, which may interfere with the determination of the soluble fraction of each metal. Leyden *et al.* (1982) however have shown that little or no serious interference effect results from determination by atomic absorption spectrophotometry.

Levels of sodium and potassium were determined by flame emission spectrophotometry, a method accepted as being more sensitive than atomic absorption spectrophotometry for these two elements. The method involves a 1:200 dilution of each sample with lithium diluent (15 mmol l^{-1}) which acts as an internal standard. A further series of standards was made up from an IL standard of sodium and potassium in the ratio of 140:5.

Correspondence analysis was performed on the monthly sets of cation molar percentages of all the vleis in order to identify differences between vleis in terms of their cation composition. Correspondence analysis is a data analysis technique which displays rows and columns of a data matrix in low-dimensional space, usually as a two-dimensional plot, with similar elements of the matrix lying close together. Because both rows (vlei samples) and columns (cations) are projected on to the plot, it is possible to identify which samples are similar and the cations responsible for the similarity. It was performed using a package developed by Prof.L. Underhill on the Sperry 1100 series mainframe computer of the University of Cape Town, the algorithm used being that described by Underhill and Peisach (1985).

Concentrations of the chloride and sulphate ions were not measured during the study period. The reasons for this were principally logistic, specifically in relation to the additional information that would be gained. Unpublished water analyses had been performed by the Water Chemistry section of the Divisional Council for the Cape, during 1978 and 1979 for the Cape Point vleis, and for most years since 1975 for Rondevlei. The analyses were generally performed monthly and included all the major cations and anions, except in Rondevlei where no analysis of calcium or magnesium was performed. A mean chloride concentration was calculated by determining the Na/Cl ratio for all sodium levels that fell within the range measured during the study period. The product of the mean Na/Cl ratio and mean sodium concentration was assumed to represent a reasonable mean of the chloride concentrations. Although sulphate levels can be more variable, a mean concentration was similarly calculated using both the Cl/SO_4 and K/SO_4 ratios.

The levels of soluble reactive phosphorus, nitrate, nitrite and ammonium were determined using the automated procedures of the Technikon Auto Analyser. These are described with minor modifications by Mostert (1983). Stock solutions of standards were made up from KH_2PO_4, KNO_3, $NaNO_2$ and $(NH_4)_2SO_4$, oven dried at 105 C for one hour (except $(NH_4)_2SO_4$, which was dried in a desiccator), to a concentration of 0.2 g PO_4-P l^{-1}, 0.1 g NO_3-N l^{-1}, 0.1 g NO_2-N l^{-1}, and 0.2 g NH_4-N l^{-1} respectively. These were stored in darkness at 4 C in sealed glass containers and working standards were diluted freshly for each analysis. The sequence of samples in each run was as follows: three double-distilled water blanks followed by three replicate standards, repeated until the readings were stable, two double-distilled water blanks followed by two or three unknown samples, repeated five times, and the whole sequence then begun again. For the measurement of ammonia, blanks of ammonia-free double-distilled water (passed through a column of Amberlite resin) were used and samples were stored frozen, with no airspace in the container. However ammonia is difficult to measure accurately and even with these precautions, the fact that the samples were stored frozen longer than a few weeks probably caused some reduction in the measured levels. Since this is a comparative study, no attempt was made to quantify such reduction. Problems were experienced with the determination of nitrate. In the analysis, nitrate is reduced to nitrite by a copper-cadmium reduction column and the total nitrate plus nitrite is then measured as nitrite. In the humic water samples interference was noted, sometimes with the appearance of a precipitate, and reduced levels, often lower than the measured levels of nitrite alone, were recorded for many months of the sampling period. Little note is made in most methodological texts of this interference, which must be present to a varying degree in many fresh waters. Mackereth *et al.* (1978) do however refer to a study by Afghan and Ryan (1975) in which the interference is investigated and a modified procedure is suggested using an acidified copper sulphate solution to precipitate out the interfering organics before analysis. No such interference is suspected in the determinations of nitrite alone and the interference is thought to be related to the column, only present for nitrate determination, and to subsequent colour development (Afghan and Ryan 1975).

A matrix of Pearson correlation coefficients (r) was calculated as a measure of the intensity of association amongst the inorganic chemical variables, as well as between major organic chemical variables, physical variables and a biological variable.

RESULTS AND DISCUSSION

Oxygen. High levels of dissolved oxygen were generally maintained in all the vleis by the frequent mixing of the water column and in addition, in Rondevlei and Grootwitvlei by photosynthetic activity (see chapter 8). The level of oxygen in the water was on average close to 100% saturation in all the vleis, except in Suurdam where it was closer to 90%; the range was mostly between 70 and 130%. The slightly lower levels of dissolved oxygen in Suurdam are probably due to a combination of the almost negligible photosynthetic activity of phytoplankton, the presence of summer thermal stratification and a greater relative depth. In all the vleis there was very little vertical or horizontal variation in the levels of the dissolved oxygen, most variation occuring over time. I therefore conclude that oxygen is not a limiting element in these shallow frequently mixed systems. In Rondevlei a thick organic sludge (ca. 0.30m thick) covers the bottom sediment and conditions therein are likely to become anoxic. Dissolved oxygen was not measured in the organic sludge, but gas bubbles in the sediments (also in parts of Grootwitvlei) was taken as an indication of anoxic conditions.

pH. The variation in the pH of the water of each vlei is shown in fig. 5.1 and the calculated mean and range for each vlei is shown in table 5.2. The vleis differed considerably in their range of pH. Suurdam and Gillidam both had low pH waters (a mean pH of 3.80 and 4.15 respectively) and showed very little variation in pH through the year. The waters of Sirkelsvlei and Grootrondevlei were both acid but had considerably higher pH values than those of the first two vleis. Grootrondevlei had a mean pH of 5.85 and Sirkelsvlei a mean pH of 6.55. Both displayed a definite seasonal variation, with late summer to autumn pH maxima and mid-winter to spring minima. Grootwitvlei and Rondevlei both had alkaline waters in which the pH never dropped below 7. Rondevlei had the greater mean pH of 8.60 and Grootwitvlei a mean pH of 7.95. Both waters displayed seasonal variations in pH similar to those in Sirkelsvlei and Grootrondevlei (a late summer to autumn maximum and mid-winter to spring minimum), but far greater amplitudes of variation (an annual range of approximately two pH units).

The occurrence of the common mid-winter to spring minimum in the four vleis of higher pH is thought to result directly from the inflow of acid water also containing high levels of humic substances. In all four vleis water levels rose dramatically in July and remained high before beginning to decline at the end of October (see fig. 4.7). The levels of colour and humic substances rose correspondingly in the vlei waters of the Grootvleis and Rondevlei. In Sirkelsvlei, however, the water displayed an anomalous drop in both colour and levels of humic substances. The effects of rain falling directly into the vleis, although unlikely to be great, might contribute to a reduction in the pH of those waters with a pH greater than 5.6. Most precipitation entering the vleis, however, does so as catchment runoff and as such drains to a varying degree through well leached acid sandstone soils (see general discussion). These sandy podsols generally have a soil pH of less

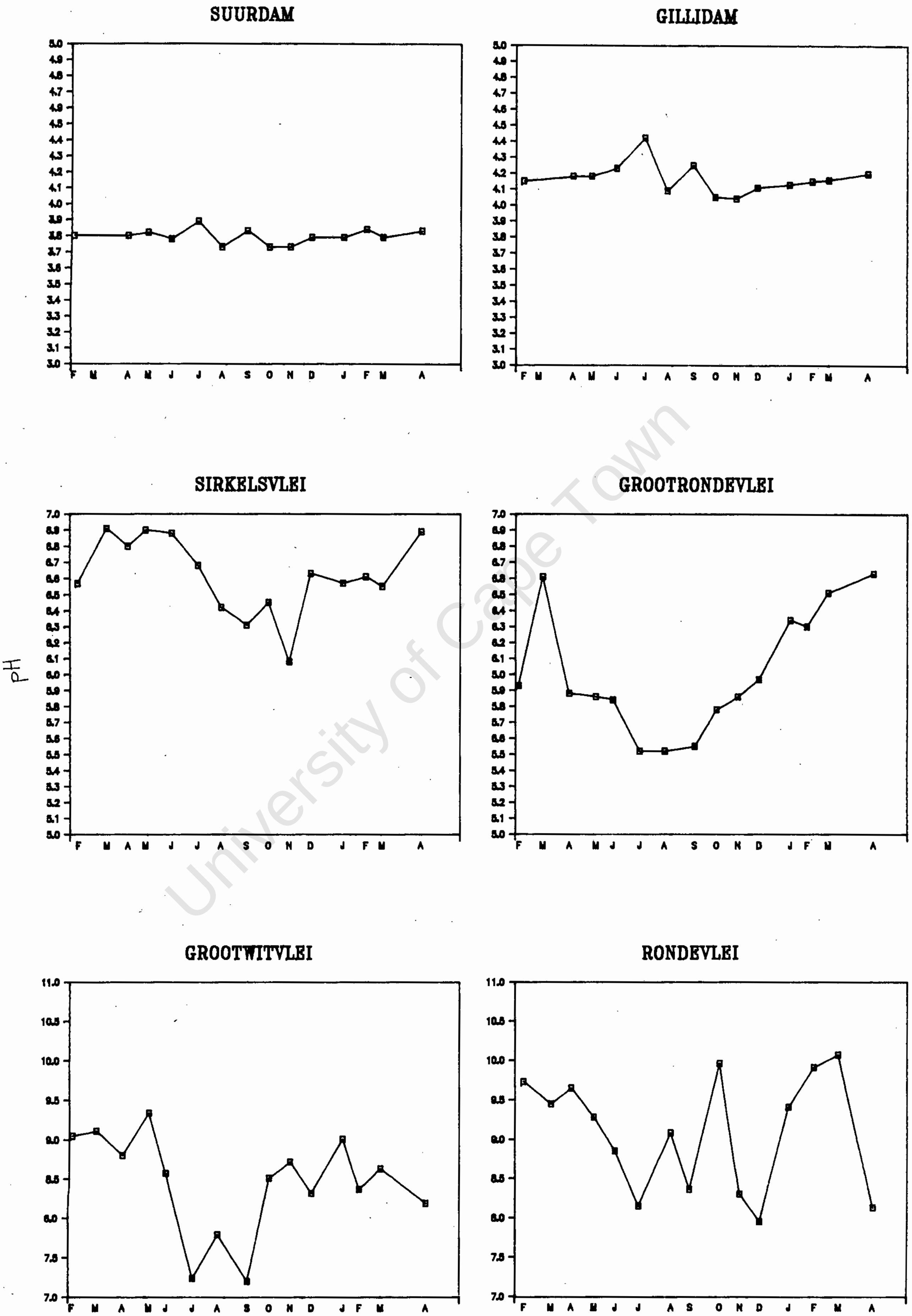

Figure 5.1 Seasonal variation in the surface pH of the waters of each of the six vleis.

	SU		GI		SI		GR		GW		RO	
	mean	max min	mean	max min	mean	max min	mean	max min	mean	max min	mean	max min
pH	3.80	3.90 3.70	4.15	4.40 4.05	6.55	6.90 6.30	5.85	6.65 5.50	7.95	9.35 7.20	8.60	10.05 8.15
Cond. mS m^{-1}	114.9	127.1 94.6	54.2	74.8 35.5	791.1	1310 449	24.9	41.5 18.8	47.8	99.4 22.4	146.1	239.9 74.1
Na	6.45	16.81 4.47	2.87	5.67 2.00	55.20	125.1 30.0	1.40	2.33 0.87	2.27	4.73 1.07	8.84	18.01 3.00
Ca	0.27	0.65 0.20	0.12	0.24 0.08	1.32	2.94 0.73	0.12	0.16 0.09	0.62	1.28 0.17	0.68	1.12 0.42
Mg	0.93	2.16 0.67	0.34	0.73 0.23	5.74	12.96 3.22	0.18	0.26 0.13	0.28	0.56 0.12	1.01	1.77 0.48
K	0.15	0.45 0.08	0.05	0.14 0.03	1.08	3.00 0.60	0.01	0.02 0.01	0.02	0.04 0.01	0.68	1.20 0.20
Fe µmol	5.82	9.49 4.12	6.15	10.21 3.04	9.28	14.15 5.73	7.15	10.21 4.66	2.59	5.37 0.72	0.72	1.43 0.54
Cl*	7.7	20 5	3.5	7 3	56.7	128 31					10.0	20 3
SO_4*	0.3	0.8 0.2	0.2	0.6 0.1	2.9	8.1 1.6					1.0	1.7 0.3
Acid.	0.80	1.10 0.46	0.46	0.68 0.30	-		-		-		-	
Bicarb Alk.	-		-		p	0.49 0.23	p	0.14 0.05	1.16	1.82 0.46	1.70	3.01 1.30
Carb. Alk.	-		-		-		-		0.04	0.17 0.00	0.13	0.55 0.00

Table 5.2 Mean, maximum and minimum values of the inorganic chemical variables measured in each of the six studied vleis, Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO). All values are given in mmol l^{-1} except pH, conductivity (mS m^{-1}), and Fe (µmol l^{-1})

* denotes values obtained from analyses performed by the Divisional Council for the Cape (unpubl. data from P. King) over the three years preceding the study period.

than 4 and thus the water entering the vlei is likely to be more acid than the resident water. In the case of Suurdam and Gillidam the pH of the water is consistently very low and thus the acid water entering the vlei has little effect on the pH of the resident water. In the other four vleis the low-pH, inflowing water should act to reduce the pH of the vlei water, causing the common mid-winter to spring minimum.

The late summer to autumn maximum is probably influenced by a number of seasonal changes. High rates of primary production in the summer months (as evidenced by high standing crop - chapter 8) should certainly act to increase the pH in Grootwitvlei and Rondevlei where phytoplankton biomass is greatest (cf. Talling 1985 and see chapter 8). Decreased water levels in late summer result in increased salinities and thus in a more highly buffered water in Sirkelsvlei. In addition, increased heterotrophic activity and incident (uv) radiation should result in increased rates of degradation of humic substances, which contribute to the acidity of the water. Suurdam and Gillidam contained little phytoplankton and experienced reduced summer circulation, while heterotrophic activity was probably low as a result of the low pH. Thus the negligible variations in the pH might be expected (see also Discussion in chapter 6).

Acidity. Measurable acidity was present only in Suurdam and Gillidam. Variations in the levels of acidity are displayed in fig. 5.2 and the mean and range of levels in table 5.2. Suurdam water had the highest acidity levels (a mean of 0.80 mmol l^{-1}) and Gillidam markedly lower levels (a mean of 0.46 mmol l^{-1}). In contrast to pH, the acidity levels showed marked seasonal variations in these two vleis. Suurdam had lowest values in winter and highest in summer, varying over a range of approximately 0.6 mmol l^{-1}. Gillidam showed a lesser variation, but a similar trend of lower winter and higher summer values. Although there is no statistically significant correlation between acidity and the levels of humic substances ($P > 0.10$, table 5.4), they both showed low winter and high summer levels (see figs. 5.2, 6.3 and 6.12). A relationship might be expected between acidity and humic substance levels because of the contribution to acidity the weak organic acids of the humic fraction are expected to make (even though acidity measurement is not in general very accurate). The lack of any corresponding trends in acidity and pH in either vlei indicates a large reservoir of undissociated weak organic acids maintaining a constantly low pH (see Discussion in chapter 6).

Alkalinity. A report by Kemp (1977) states that the brown humic materials, commonly found in vlei water, show an appreciable change in charge coefficient as the pH varies. Thus the acidic organic material causes the water to show an

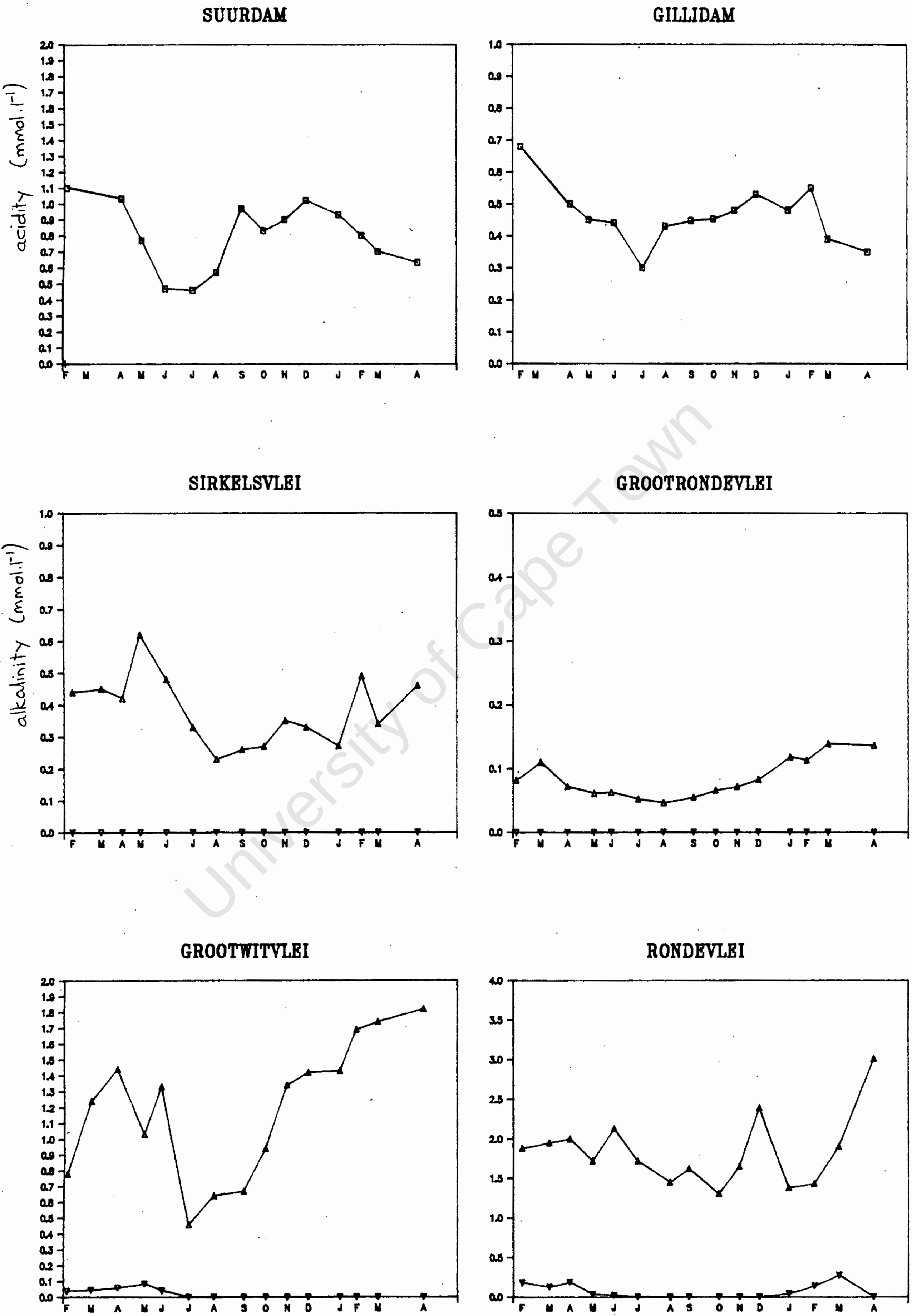

Figure 5.2 Seasonal variation in the surface acidity (□), total alkalinity (△) and phenolphthalein alkalinity (▽) of the waters of each of the six vleis. All values are in mmol l^{-1}.

SUURDAM	Na	Mg	Ca	K	Fe	Cond	pH	Acid	F-C	Col	A250	SRP	NO_2	NH_4	DEP	TMP
Na																
Mg	****															
Ca	****	****														
K	****	****	****													
Fe	***	***	**	****												
Cond	****	****	****	*	●											
pH	●	●	●	●	●	●										
Acid	*	*	●	●	**	**	●									
F-C	***	**	●	****	****	●	●	●								
Col	***	**	●	**	****	●	●	●	****							
A_{250}	●	●	●	●	**	●	*	●	**	****						
SRP	●	●	●	●	●	●	●	●	***	***	**					
NO2	**	**	**	***	****	●	●	●	*	**	●	●				
NH4	*	*	*	*	*	●	●	●	●	●	●	●	***			
DEP	(***)	(***)	(***)	(****)	(****)	●	●	●	(**)	(*)	●	(**)	(**)	●		
TMP	●	●	●	●	●	**	●	****	●	●	●	●	●	●	●	
CHL	●	●	●	●	●	●	●	●	●	(**)	(*)	(****)	●	●	●	●

**** = 99.9%
*** = 99%
** = 95%
* = 90%
● < 90%
( ) = -ve

GILLIDAM	Na	Mg	Ca	K	Fe	Cond	pH	Acid	F-C	Col	A250	SRP	NO_2	NH_4	DEP	TMP
Na																
Mg	****															
Ca	****	****														
K	****	****	****													
Fe	***	***	***	**												
Cond	***	***	****	**	***											
pH	●	●	●	●	●	(***)										
Acid	*	●	●	●	●	●	*									
F-C	***	***	***	**	****	****	(*)	●								
Col	***	**	**	**	****	***	●	●	****							
A_{250}	**	**	**	**	****	****	(**)	●	****	****						
SRP	**	**	**	**	****	*	●	●	****	****	***					
NO2	●	●	●	●	****	*	●	●	***	***	**	*				
NH4	**	**	**	**	***	**	●	●	***	***	**	**	***			
DEP	●	●	●	●	(**)	●	●	●	(**)	(***)	(**)	(****)	●	●		
TMP	●	●	●	●	****	***	(**)	**	****	****	****	*	***	●	●	
CHL	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●

SIRKELSVLEI	Na	Mg	Ca	K	Fe	Cond	pH	T.Alk	F-C	Col	A250	SRP	NO_2	NH_4	DEP	TMP
Na																
Mg	****															
Ca	****	****														
K	****	****	****													
Fe	●	*	*	●												
Cond	**	**	****	**	●											
pH	●	●	**	●	●	**										
T.Alk	●	●	**	●	●	****	***									
F-C	(***)	(***)	(*)	(***)	●	●	●	●								
Col	●	*	●	●	****	●	●	●	●							
A_{250}	●	●	●	●	●	●	●	●	●	***						
SRP	●	●	●	●	*	●	●	●	***	*	●					
NO2	●	●	●	●	●	●	(**)	●	●	●	●	●				
NH4	●	●	●	●	●	●	●	●	(**)	●	●	(**)	●			
DEP	(****)	(****)	(****)	(****)	(*)	(****)	(**)	(**)	*	●	●	●	●	(**)		
TMP	●	●	●	●	●	●	●	●	●	●	●	●	**	●	●	
CHL	****	****	****	****	*	**	●	●	(*)	●	●	●	●	**	(***)	●

GROOTRONDEVLEI	Na	Mg	Ca	K	Fe	Cond	pH	T.Alk	F-C	Col	A250	SRP	NO_2	NH_4	DEP	TMP
Na																
Mg	****															
Ca	****	****														
K	●	●	*													
Fe	***	***	***	*												
Cond	****	****	****	●	**											
pH	***	****	***	●	●	***										
T.Alk	****	****	****	●	*	****	****									
F-C	(****)	(***)	(*)	●	●	(***)	(**)	(***)								
Col	(**)	(**)	●	●	●	(**)	(**)	(*)	****							
A_{250}	●	●	●	●	●	●	●	●	***	***						
SRP	*	*	*	●	***	●	●	●	●	●	●					
NO_2	●	●	*	(**)	***	●	●	●	●	●	***	(*)				
NH_4	*	*	**	(**)	***	*	●	●	●	●	●	●	***			
DEP	(****)	(****)	(****)	**	(***)	(****)	(***)	(***)	**	**	●	(*)	(*)	(**)		
TMP	●	●	●	(*)	●	●	●	*	●	●	●	***	*	●	●	
CHL	(*)	(**)	(**)	**	(**)	●	●	●	●	●	●	●	(**)	(*)	**	●

GROOTWITVLEI	Na	Mg	Ca	K	Fe	Cond	pH	T.Alk	P.Alk	F-C	Col	A250	SRP	NO_2	NH_4	DEP	TMP
Na																	
Mg	****																
Ca	****	****															
K	****	****	****														
Fe	***	***	****	**													
Cond	****	****	****	****	***												
pH	•	•	•	•	•	•											
T.Alk	****	****	****	**	****	****	•										
P.Alk	•	•	•	•	•	•	**	•									
F-C	(*)	(*)	(**)	•	****	(*)	(**)	(****)	•								
Col	(****)	(****)	(****)	(**)	****	(****)	•	(****)	•	****							
A_{250}	(***)	(***)	(***)	•	***	(***)	(*)	(****)	•	***	•						
SRP	**	**	(**	•	(*)	**	•	*	•	(**)	(**)	•					
NO_2	(**)	(**)	(**)	•	**	(*)	•	(**)	•	**	*	**	(**)				
NH_4	•	•	•	•	•	•	•	•	•	•	•	•	•	•			
DEP	(****)	(****)	(****)	(****)	(****)	(****)	•	(****)	•	**	****	***	•	***	•		
TMP	•	•	•	•	•	•	**	•	•	•	•	•	•	(**)	•	•	
CHL	•	•	•	•	(**)	•	•	*	•	(***)	(*)	•	•	(**)	•	(*)	***

RONDEVLEI	Na	Mg	Ca	K	Fe	Cond	pH	T.Alk	P.Alk	F-C	Col	A250	SRP	NO_2	NH_4	DEP	TMP
Na																	
Mg	****																
Ca	•	•															
K	****	****	•														
Fe	•	•	•	•													
Cond	****	****	•	****	•												
pH	•	•	(***)	•	•	•											
T.Alk	*	**	*	**	•	**	(*)										
P.Alk	**	**	•	***	•	*	***	•									
F-C	•	•	•	•	•	•	•	•	•								
Col	•	•	•	•	•	•	**	•	•	•							
A_{250}	****	****	•	***	•	****	•	**	•	•	•						
SRP	*	*	•	**	•	•	•	•	•	•	•	•					
NO_2	•	•	•	•	•	•	•	•	•	•	•	•	•				
NH_4	•	•	•	•	•	•	(**)	*	•	*	•	•	•	•			
DEP	(****)	(****)	•	(****)	•	(****)	•	(*)	(**)	•	•	(****)	(**)	•	•		
TMP	•	•	•	•	•	•	•	•	•	•	•	•	•	(***)	•	•	
CHL	•	•	•	•	*	•	•	•	*	•	•	•	**	•	•	(*)	•

Table 5.4 The levels of significance of the Pearson correlation coefficient (r) calculated as a measure of the intensity of association between the major inorganic chemical variables [Na, Mg, Ca, K, Fe, conductivity (Cond), pH, total and phenolphthalein alkalinity (T.Alk and P.Alk), soluble reactive phosphorus (SRP), NO_2-N, NH_4-N], organic chemical variables [dissolved humic substances (A_{250}), polyphenols (F-C)], and physical variables [temperature (TMP), water level (DEP), colour (Col)]. Where $P < 0.001$ = ****, $P < 0.01$ = ***, $P < 0.05$ = **, $P < 0.10$= * and ( ) indicates a negative correlation.

anomalous titration curve. He suggests a procedure involving the flocculation of the organic material and redetermination of the titration curve. The paper in which this procedure was described was not uncovered before the analyses, so no attempt was made to remove the acidic organic material present in the vlei waters before alkalinity was measured. Thus measured alkalinities of Sirkelsvlei, and to a lesser extent of Grootrondevlei, will be inaccurate as a result of an anomalous titration curve. Grootwitvlei and Grootrondevlei had similar levels of interfering organics from mid-winter to spring, but for the remaining months Grootwitvlei had very low levels, closer to those of Rondevlei (see fig. 6.3). The measured alkalinities of Rondevlei, and for the late summer months of Grootwitvlei, would therefore not suffer from these interferences. The extent of inaccuracy of the results of Sirkelsvlei, Grootrondevlei and Grootwitvlei is not known. The results are presented in fig. 5.2 and the mean and range of the calculated bicarbonate and carbonate alkalinity in table 5.2. No hydroxide alkalinity was present in any vlei. Sirkelsvlei and Grootrondevlei both registered measurable total alkalinity but zero phenolphthalein alkalinity. The alkalinity can thus be ascribed entirely to bicarbonate ions. During the periods of highest pH, both Grootwitvlei and Rondevlei contained phenolphthalein alkalinity as well as high levels of total alkalinity and thus contained both carbonate and bicarbonate ions during late summer. For the rest of the year only total alkalinity, and therefore only bicarbonate ions, were present. Rondevlei displayed the highest levels of alkalinity, but no obvious seasonal trends. The levels do however correlate broadly with both pH (negative) and calcium concentration at levels of significance of $P < 0.1$ ~~and $P < 0.5$~~ (table 5.4). This is to be expected in highly productive waters where photosynthetic activity creates a large demand for inorganic carbon, with consequent effects on the pH and the levels of calcium in solution. Grootwitvlei had lower levels of alkalinity, with a marked winter minimum corresponding to an increase in colour and in levels of humic substances in the water. Alkalinity correlated well with Ca throughout the study period ($P < 0.001$, table 5.4) but with pH only when values for July to October are omitted (low phytoplankton standing crop and a large influx of humic compounds). The levels displayed in Sirkelsvlei and Grootrondevlei are low and probably inaccurate, but the real levels are unlikely to be much higher.

Conductivity. Variation in the conductivity of the water in each vlei is displayed in fig. 5.3 and the mean and range of measured conductivity in each vlei is shown in table 5.2. Sirkelsvlei had very high conductivities throughout the year, well in excess of the maxima of any of the other vleis. The greatest conductiviy recorded was approximately 25% that of seawater (1310 mS m^{-1} at 25°C). In contrast, the

Grootvleis show very low conductivities, on average 3% and 6% of that of Sirkelsvlei water. Conductivity in Gillidam was also low, whereas that in Suurdam and Rondevlei was intermediate. The values measured thus differed widely between the vleis and the mean values ranged through all three of the arbitrary classes described by Talling and Talling (1965). Class I (060 mS m^{-1}) includes both the Grootvleis and Gillidam; Class II (60-600 mS m^{-1}, the moderately saline lakes) includes Suurdam and Rondevlei, and Class III (over 600 mS m^{-1}, the very saline waters), includes Sirkelsvlei. Conductivity varies seasonally in all the vleis and appears closely linked to water level, the major ions being concentrated under low water conditions and diluted at high water levels. The conductivity in Rondevlei, Grootwitvlei, Sirkelsvlei and Grootrondevlei shows a strong negative correlation with water level (in all cases $P < 0.001$, table 5.4). Suurdam, however, experiences minimal change in the water level, but a significant variation in conductivity and Gillidam an extremely large change in the water level, but little greater variation in the conductivity. The reasons for the seasonal variations in these two vleis are thus obviously complex and may relate to changes in mineral cycling and biological activity throughout the year (see sodium (Results) and General Discussion). Certainly the effects of metal complexation by humic substances in these vleis are not completely known (see Discussion and chapter 6). The levels of humic substances are greatest in Suurdam and Gillidam, and pH is the lowest, and thus greater complicating effects may be expected. In addition the concentrations of ions in both rainfall and streamflow in the south-western Cape vary during the year (D Britton, B A Byren and J A Day pers.comm.).

The sum of the total equivalence of the major cations, sodium, magnesium, calcium and potassium (ie. (2 [divalent ions] + [monovalent ions]), is also illustrated in fig. 5.3.. In general it reflects closely the seasonal variation in conductivity, thus indicating the dependence of the conductivity on the levels of the major ions. In Suurdam and Gillidam the proportion of conductivity to the total equivalence of cations is greater than in the other four vleis (ie. conductance:total equivalence of the cations is greater). Thus an additional ionic fraction is contributing to the specific conductance. The consistently low pH values in Suurdam and Gillidam indicate relatively high concentrations of H$^+$ ions (mean hydrogen ion concentrations of 0.158 and 0.071 mmol l^{-1} respectively), generally greater than potassium concentrations, and thus form an additional and significant fraction of the conductivity. In the waters of higher pH, most of the difference between the conductivity and the combined levels of major cations is probably due to the contribution of the cations bound in the particulate and colloidal suspensoids (measured by a.a. spectrophotometry, but not reflected as conductivity). At high

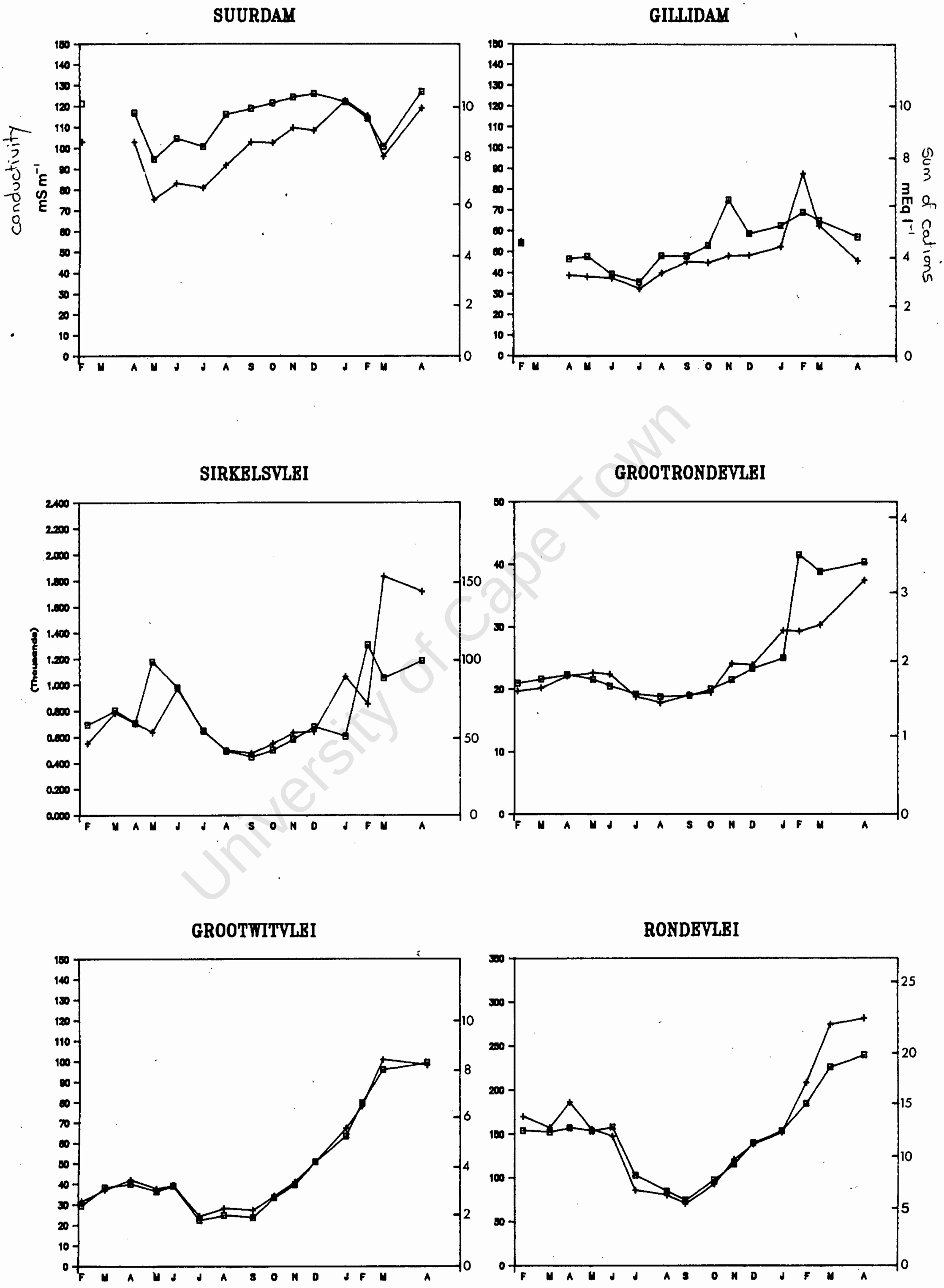

Figure 5.3 Seasonal variation in the surface conductivity (mS m^{-1}; □) and sum of the major cations (meq l^{-1}; +) of the waters of each of the six vleis.

pH, humic substances probably remain largely undissociated and thus contribute little to the conductivity of the vlei waters.

Cations. The major cations sodium, magnesium, calcium and potassium differed considerably in concentration between the vleis. In addition the levels fluctuated seasonally and varied proportionally in each vlei. The mean and range of concentration of each cation is shown in table 5.2 and the seasonal variation is displayed in figures 5.4 (Na), 5.5 (Mg), 5.6 (Ca), and 5.7 (K). Molar percentages plotted as ionic polygons show the mean relative proportions of the ions in each vlei in fig. 5.8. Concentrations of all the major ions are presented as molar quantities (mmol l^{-1}).

Sodium was the dominating cation, constituting over 70% of the molar percentage of cations in all the vleis. Mean levels ranged from 55 mmol l^{-1} in Sirkelsvlei to less than 1.5 mmol l^{-1} in Grootrondevlei. All the vleis other than Sirkelsvlei had mean levels of less than 10 mmol l^{-1}. Seasonal variations in sodium concentrations are closely correlated to the variation in conductivity ($P < 0.001$, table 5.4). There was thus a marked minimum from winter to spring or early summer in Sirkelsvlei, Grootrondevlei, Grootwitvlei and Rondevlei, and a maximum in late summer to autumn. The variations are also strongly negatively correlated with water level ($P < 0.001$, table 5.4). Suurdam and Gillidam showed little obvious seasonal variation in sodium concentration. Both displayed a slight winter minimum and raised summer levels, but no correlation with water level. Concentration at low water level and dilution at high water level thus appear to play an important role in seasonal fluctuation of sodium levels in all but the last two vleis. Concentrations of sodium in rainfall and in mountain stream water in the south-western Cape are almost always less than 0.1 mmol l^{-1} and 1.0 mmol l^{-1} respectively (data from Van Wyk 1982, Davies *et al.* 1987 and J A Day pers. comm.). The concentrations (of sodium) in the incoming water are thus generally well below the normal range of sodium levels present in the vleis and a dilution effect should result. Conversely high rates of evaporation should contribute to higher concentrations in summer. The very limited seasonal variation in the levels in Suurdam and Gillidam may be the result of a size effect (or edge effect) combined with the fact that both receive all their inflow as seepage inflow. The small volume of water in both, and the seepage inflow, suggest a close relationship between soil water concentrations and the vlei water and little dilution resulting from lower concentrations in rain or stream water. Sodium is a relatively conservative ion. It is also highly soluble and occurs in such abundance that concentrations are not normally altered by biological activity or changes in chemical equilibria.

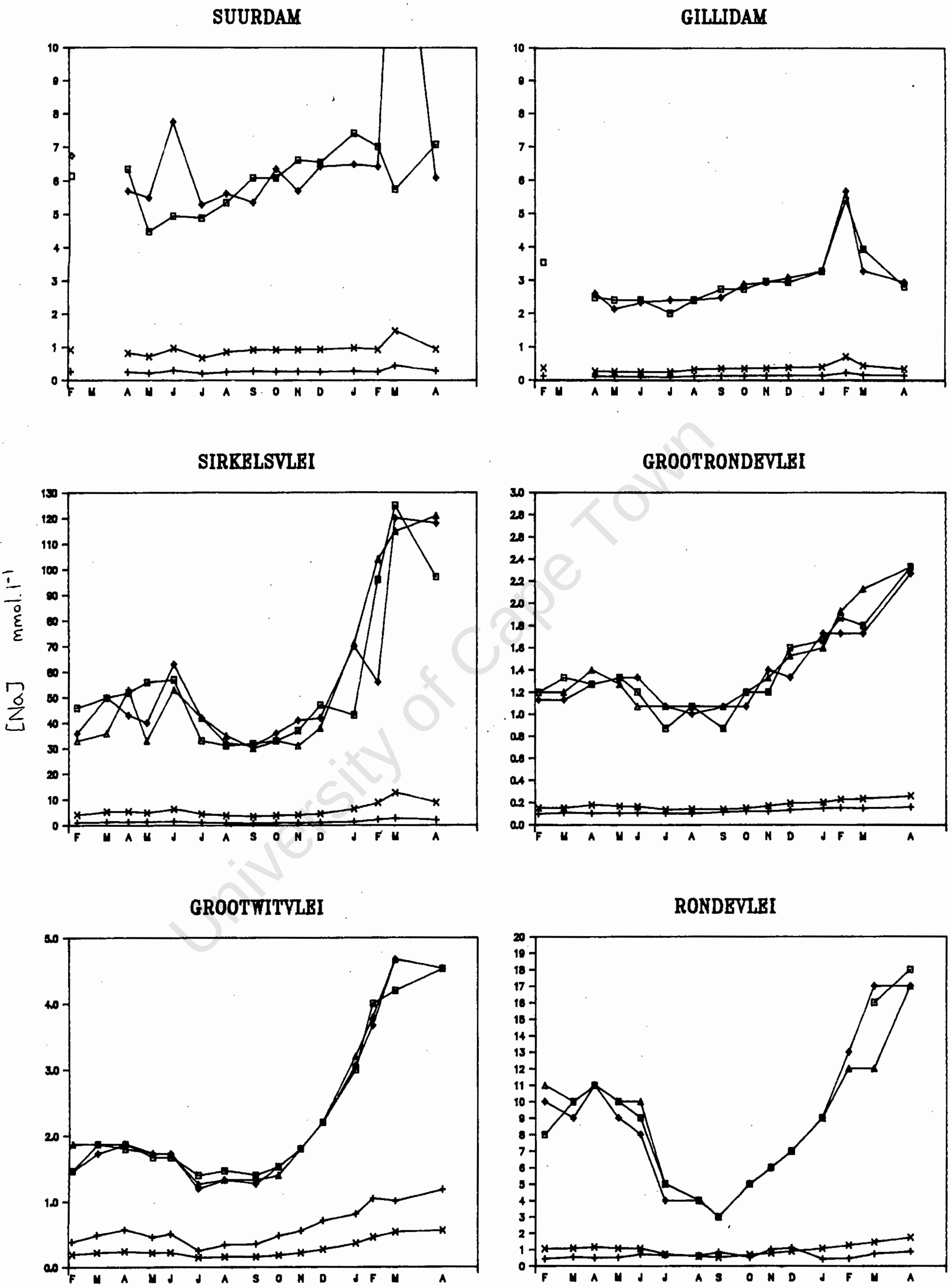

Figure 5.4 Seasonal variation in the surface [Na] of the waters of each of the six vleis. All concentrations are in mmol l^{-1}. Station 1 - □ , station 2 - ◇ , station 3 - △ , station 4 - ▽ , mean [Mg] - × , [Ca] - + .

Magnesium was the next most abundant cation in both mass and number in the four acid vleis, normally constituting at least nine percent of the molar percentage of the cations. In the two alkaline waters calcium concentrations were sometimes greater. Sirkelsvlei had the greatest mean level at 5.7 mmol l^{-1}, and Grootrondevlei the lowest, at 0.2 mmol l^{-1}. Other than Sirkelsvlei, all vleis had mean levels of close to, or less than, 1 mmol l^{-1}. Seasonal variations in magnesium levels are closely correlated to the variation in sodium levels ($P < 0.001$, table 5.4) in all vleis and are hence closely correlated to conductivity as well. Magnesium is also a highly soluble and relatively conservative ion. Although it is an essential element for plant growth, concentrations are normally far in excess of metabolic demand (Wetzel 1983). Compounds of magnesium are much more soluble than those of calcium and thus are rarely precipitated (Mickle and Wetzel 1978). As such the levels would be expected to respond to the same factors forcing seasonal fluctuations in the levels of sodium.

Calcium constituted between two and four percent of the molar percentage of the cations in the waters of the Cape Point vleis; in Grootrondevlei it constituted between six and nine percent, in Grootwitvlei between 16 and 22 percent and in Rondevlei anything between 3 and 19 percent. Only in Grootwitvlei, and in some months in Rondevlei, were calcium levels greater than those of magnesium. Mean concentrations ranged between 1.3 mmol l^{-1} in Sirkelsvlei and 0.1 mmol l^{-1} in both Grootrondevlei and Gillidam; only in Sirkelsvlei was the mean greater than 0.7 mmol l^{-1}. In the Cape Point vleis and in the Grootvleis the variations in the calcium levels are closely correlated with those of sodium and magnesium as well as with those of conductivity ($P < 0.001$ for all, table 5.4). Even though calcium is less soluble and a more dynamic ion, levels are well below saturation at the respective pH of the waters and seasonal variations thus appear to be determined by the same factors that affect the levels of sodium and magnesium. In Rondevlei the variation in calcium level does not correlate with that of the other cations, but rather is negatively correlated with pH ($P < 0.01$, table 5.4). The levels were lowest in the late summer and autumn months and highest in the winter and spring months. The solubility of $CaCO_3$ decreases rapidly as pH rises (at constant P_{CO2}) and above a pH of approximately 8.7 the measured levels of calcium are all in excess of the theoretical maximum soluble concentration of $CaCO_3$ (from Stumm and Morgan 1981). As noted earlier the variation in pH is probably due to the fluctuations in primary production of the dense phytoplankton community. In addition, in the late summer and autumn months increased primary production should cause reduced levels of CO_2, resulting in an equilibrium shift and the precipitation of $CaCO_3$ (from Berner 1971). Thus $CaCO_3$ can be precipitated from the water both as a result of

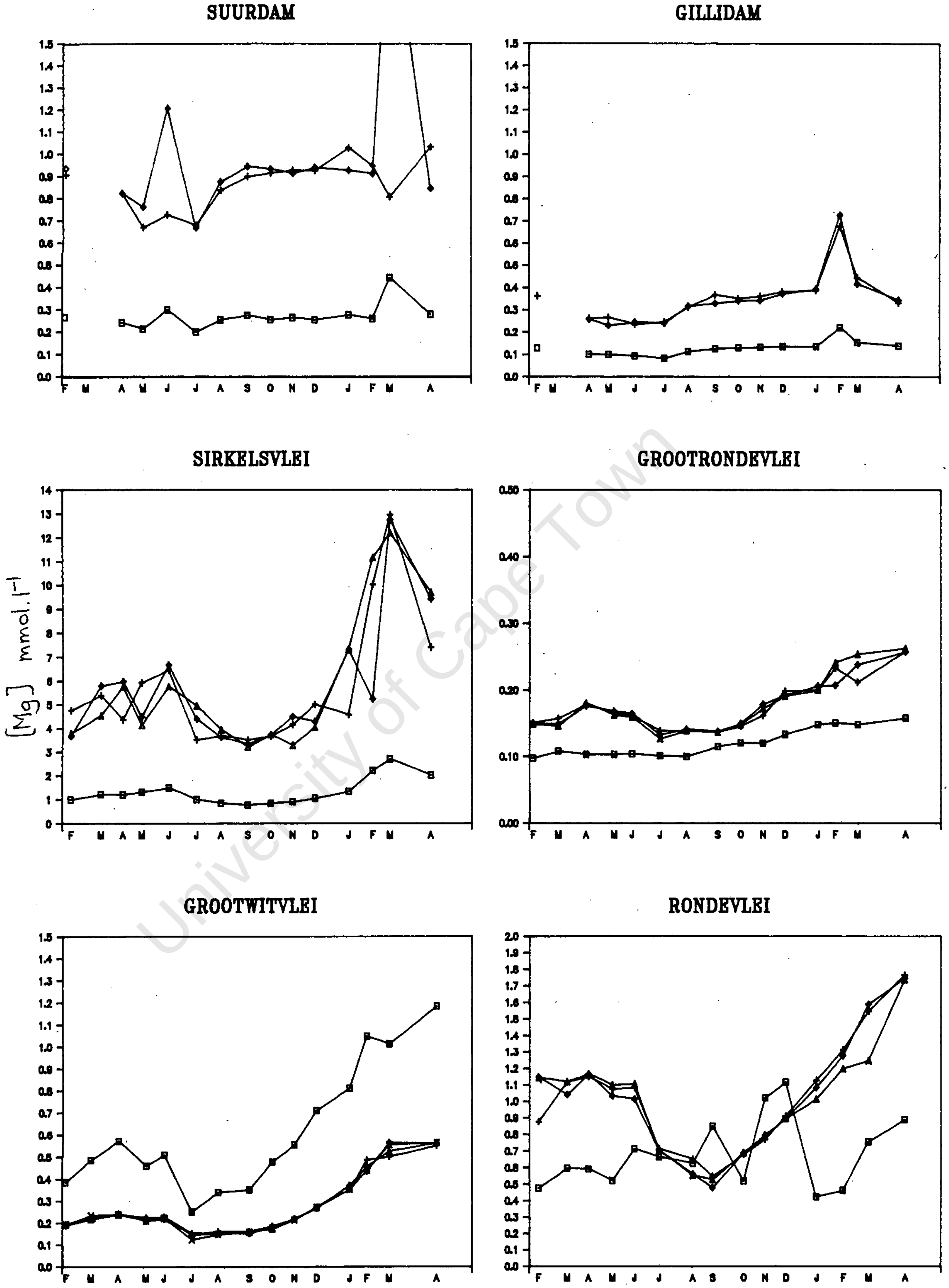

Figure 5.5 Seasonal variation in the surface [Mg] of the waters of each of the six vleis. All concentrations are in mmol l^{-1}. Station 1 - × , station 2 - ◇ , station 3 - △ , station 4 - ▽ , mean [Ca] - □ .

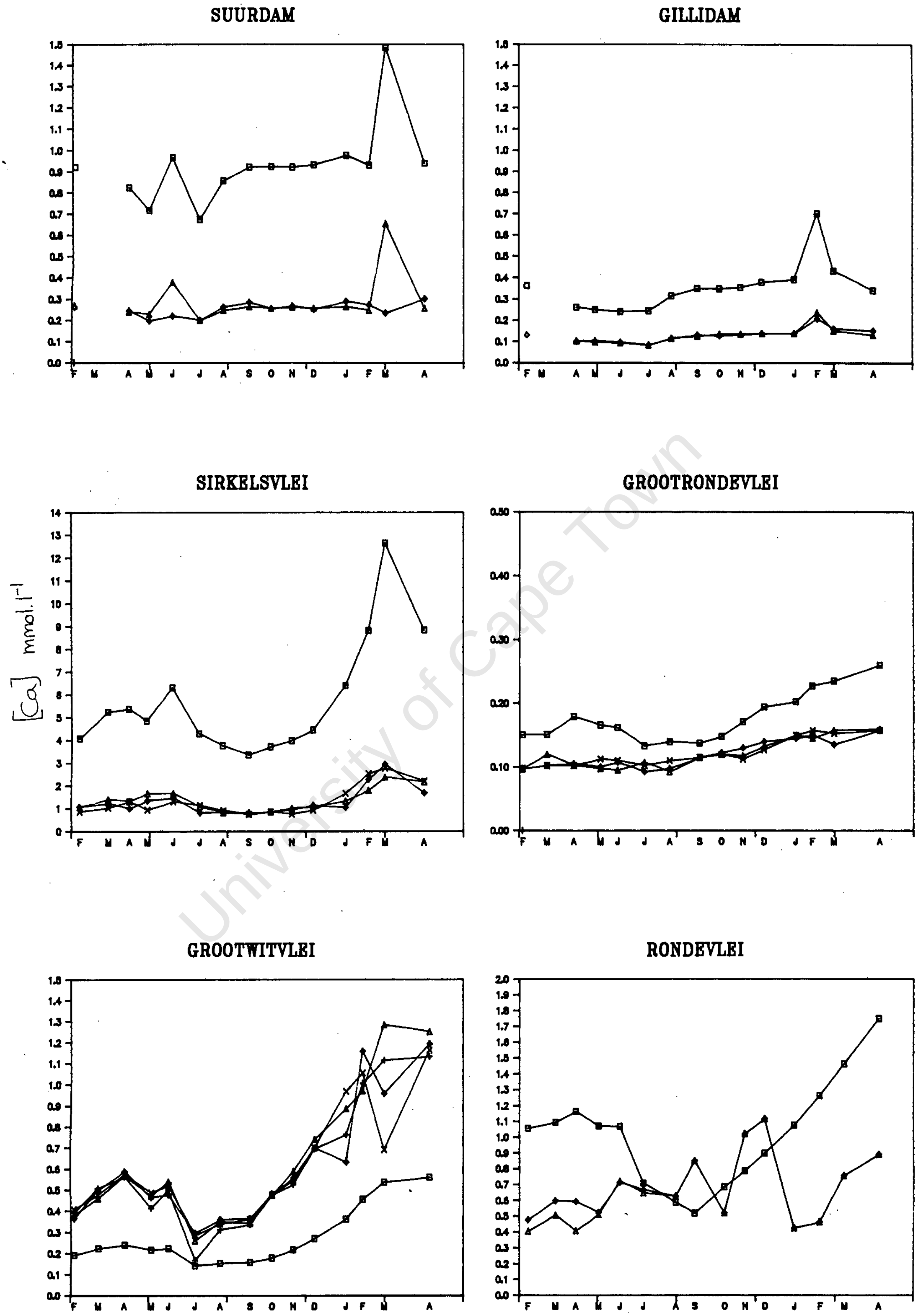

Figure 5.6 Seasonal variation in the surface [Ca] of the waters of each of the six vleis. All concentrations are in mmol l^{-1}. Station 1 - ◇ , station 2 - △ , station 3 - × , station 4 - + , mean [Mg] - □ .

the high pH and as a result of the equilibrium shift caused by active photosynthesis. The dynamics of the dense phytoplankton community influence both the levels of calcium and the pH. There was a marked difference between the calcium levels of the four stations in Grootwitvlei in the late summer months of 1982 . This was concurrent with the maximum biomass of phytoplankton and might also have resulted from local differences in CO_2 demand (see chapter 8).

The measured calcium levels appear on occasion to have exceeded the theoretical maximum concentration (see Stumm and Morgan 1981). This may be because, as noted earlier, calcium levels were measured by A A spectrophotometry and hence colloidal $CaCO_3$ not removed by filtration, and calcium adsorbed to humic compounds, may have contributed.

Potassium was the least abundant of the major cations constituting two percent or less of the molar percentage of the cations in the Cape Point and the Grootvlei waters. In Rondevlei, however, the molar percentage was far greater, constituting between four and seven percent of the cations. In the late summer and autumn months in Rondevlei the levels of potassium in fact exceeded those of calcium as a result of the decalcification of the water. The mean levels of potassium ranged from 1.08 mmol l^{-1} in Sirkelsvlei to the exceedingly low level of 0.01 mmol l^{-1} in Grootrondevlei. Seasonal variations are again very closely correlated with variations in the levels of sodium and magnesium in all the vleis except in Grootrondevlei and, except for Rondevlei, in the levels of calcium ($P < 0.001$, table 5.4). The reason for the anomalous variation in Grootrondevlei probably resulted from the reduced sensitivity of measurement at such very low levels rather than from a real (significant) difference.

In contrast to the concentrations of the cations, the molar proportions changed relatively little over the seasons in most of the vleis. Rondevlei waters were the obvious exception, with the precipitation of calcium in late summer causing a marked change in the cation composition. The close correlation in the seasonal variation of the major cations reflected the almost constant composition in most of the waters. The molar percentages have been discussed briefly above and mean molar percentages and range of each are displayed in the ionic polygons in fig. 5.8. and in appendix 5.1. As noted earlier, the composition was markedly dominated by sodium, the four low pH water vleis (fig 5.8 a-d) showing the highest proportions of sodium and the proportions closest to that of seawater. Owing to the geology of the catchment and the input of bird exreta (see Discussion and chapter 2), both the Grootvleis and Rondevlei had greater proportions of calcium than did the Cape Point vleis . The proportions of calcium in the Cape Point vlei waters, on the other

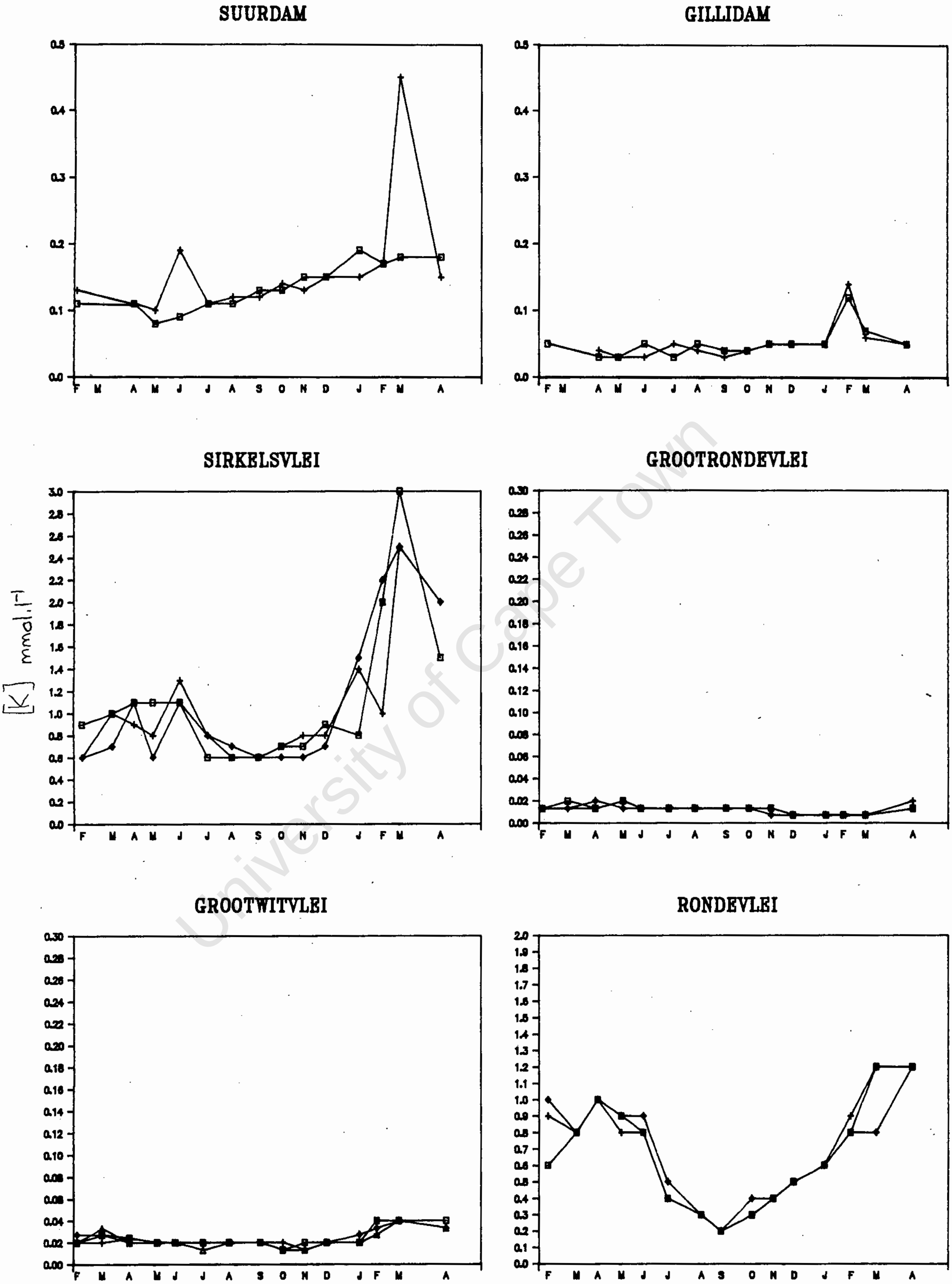

Figure 5.7 Seasonal variation in the surface [K] of the waters of each of the six vleis. All concentrations are in mmol l^{-1}. Station 1 - □ , station 2 - + , station 3 - ◇ , station 4 - △ .

hand, closely approached the low proportion of calcium in sea water. The proportion of potassium was consistently low in the waters of all the vleis except Rondevlei. The higher proportions in Rondevlei might have resulted from the input of dissolved fertilizers and from bird excreta (table 2.6). Variations in the proportion of potassium, as well as of sodium, should merely be responses to independent fluctuations in the levels of calcium. The range of potassium proportions are very similar in the Grootvleis and noticeably lower even than those of the Cape Point vleis (appendix 5.1). A possible cause of this reduction is uptake by the extensive marginal macrophyte beds (chapter 2). Mickle and Wetzel (1978) have shown removal of more than 30% of potassium flowing through a *Myriophyllum* complex and Howard-Williams and Junk (1977) have a plant/water ratio of approximately 8 for potassium concentration in Amazon aquatic macrophytes, the ratios of the other three cations all being less than one. Data from Bayly and O'Neill (1972) also show potassium concentrations in *Phragmites communis* shoots to be far greater than concentrations of the other major cations. Magnesium constituted a similar proportion of the total cations in all the vleis (ca. 10%), a proportion that closely approaches that of seawater. Even in Rondevlei the proportion of magnesium remained close to 10%, not altering much with changes in the levels of calcium, probably as a result of some similarity in the behaviour of the two elements.

The results of the correspondence analysis are displayed in fig. 5.9. Axis 1 accounts for 77% of the inertia or total information content of the data matrix and axis 2 a further 21%, thus together accounting for 98%. The two-dimensional plot thus provides an almost complete display of the data matrix. The sets of cation molar percentages for each of the different months form distinct clusters for each vlei, almost without overlap. Of these clusters, the most closely grouped are the three Cape Point vleis, which infers that the cation proportions of these vleis were most similar. The very loose clustering of Rondevlei samples reflects the changing cation composition during the year. The contrast or separation defined by axis 1 is mainly determined by the proportion of calcium and hence Grootwitvlei and the Cape Point vleis lie in opposite directions from the origin. Axis 2 is largely defined by the proportion of potassium and Rondevlei is therefore separated from the remaining vleis, which remain close to the origin. The remaining 2% of the inertia is accounted for by axis 3 and results in a small separation between Suurdam and Sirkelsvlei caused by the slightly greater proportions of magnesium in the former. Gillidam remains intermediate. Sodium accounts for very little inertia, thus causing minimal separation in relation to the other three cations. The analysis therefore serves as a useful plot of the variability over time of the cation composition of the

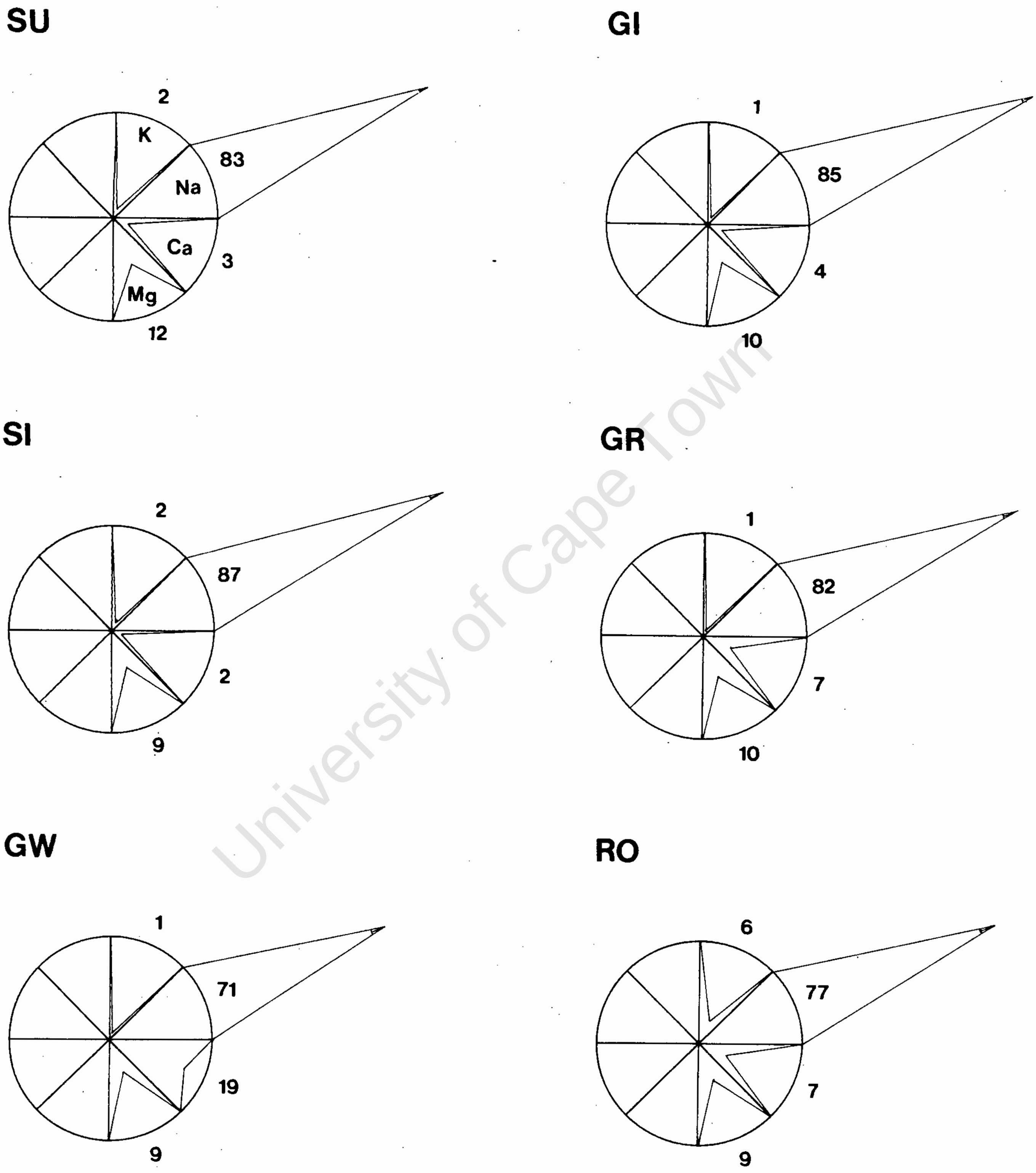

Figure 5.8 Ionic polygons for each of the six vleis displaying the mean molar percentages of each of the four major cations (K, Na, Ca and Mg). Mean molar percentages of seawater are : K 2%, Na 86%, Ca 2%, Mg 10% (Harvey 1955). For ranges see Appendix 5.1. Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO).

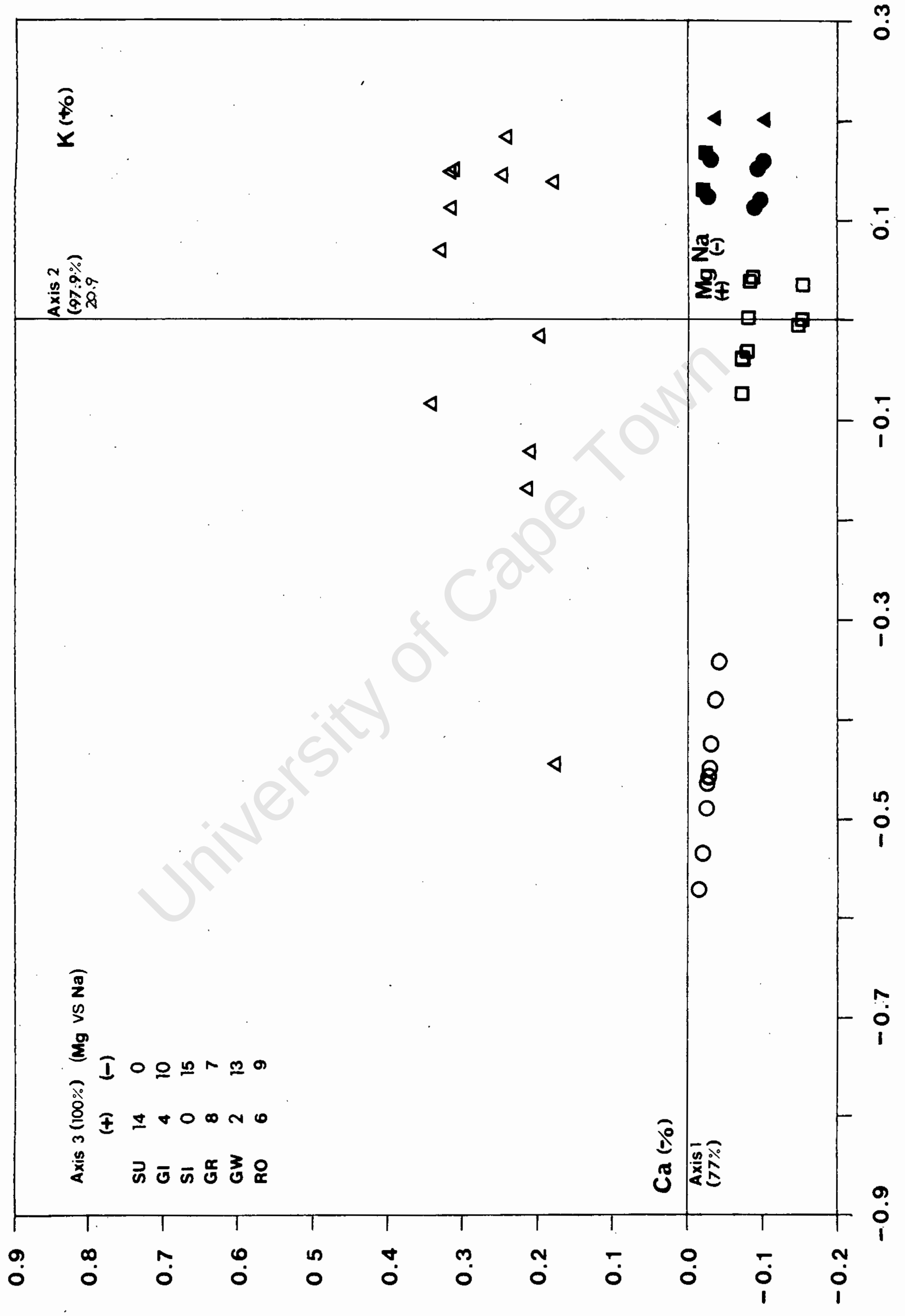

Figure 5.9 Variability in the cation composition displayed as a graphical plot using correspondence analysis. Suurdam (■), Gillidam ( ), Sirkelsvlei (▲), Grootrondevlei (□), Grootwitvlei (○) and Rondevlei (△).

vleis as well as of the similarity of composition outside the overriding dominance of the sodium ion.

The cation ratios of divalent/monovalent ions (D/M), calcium/magnesium and sodium/potassium are unlikely to offer much additional information on the cation composition of the waters. In the past they have been used as indicators of lake water character however, (see Introduction), and can therefore serve as a quick source of comparison. The mean and the ranges of each ratio are given in table 5.3.

	SU		GI		SI		GR		GW		RO	
	mean	max min	mean	max min	mean	max min	mean	max min	mean	max min	mean	max min
D/M	0.18	0.21 0.17	0.16	0.18 0.14	0.13	0.14 0.10	0.21	0.25 0.18	0.39	0.44 0.33	0.21	0.43 0.13
Ca/Mg	0.29	0.31 0.27	0.37	0.41 0.32	0.23	0.27 0.21	0.69	0.84 0.58	2.26	2.66 1.84	0.75	1.64 0.37
Na/K	46	55 36	62	76 43	51	61 45	134	273 74	95	138 65	13	15 11

Table 5.3 Mean, maximum and minimum cation ratios for the surface waters of each of the six vleis, Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO). The cation ratios for seawater are D/M =0.13, Ca/Mg =0.20, Na/K =46.

Anions. Bicarbonate and carbonate levels, measured as total and phenolphthalein alkalinity, are presented above. Approximate means, maxima and minima of the chloride and sulphate anions were determined for Rondevlei and the Cape Point vleis and the values are displayed in table 5.2. As far as I know, no analyses of chloride and sulphate have been performed on the waters of the Grootvleis, so that there are no data on the levels of these anions, except for a single set of analyses performed for this study in October 1987 (Grootrondevlei $[Cl^-]=1.0$, $[SO_4^{2-}]=0.2$; Grootwitvlei $[Cl^-]=1.9$, $[SO_4^{2-}]=0.1$ mmol l^{-1}).

As in seawater, chloride levels appeared to be uniformly higher than those of sodium, and it was the dominant anion in all the vleis. Sulphate is a more dynamic ion and as such should vary more. Concentrations tended to fall between those of magnesium and calcium and thus constituted a similarly low molar percentage of the anions. No attempt was made to balance electroneutrality, due to the unknown error in the determination of the carbonate and bicarbonate ions (see alkalinity). In the very acid waters of Suurdam and Gillidam, where the latter two species are not present, differences in the electrochemical balance should be due to the electrochemical contribution of the weak organic acids.

The chemistry of the complexation of iron and copper with humic compounds is relatively well understood and for this reason the concentrations of both metals were measured.

Iron. Levels of total dissolved iron were nearly three orders of magnitude lower than levels of the major cations. The variation in the concentration of iron in each of the vlei waters is illustrated in fig. 5.10 and the mean and range for each vlei is given in table 5.2. Suurdam, Gillidam, Sirkelsvlei and Grootrondevlei had mean levels of iron more than double those of Grootwitvlei and Rondevlei. Sirkeslvlei showed the greatest mean concentration (9.3 umol l^{-1}), but the levels in the other three vleis were not much lower. Rondevlei, in contrast, has a mean level (0.72 umol l^{-1}) much lower even than that of Grootwitvlei. Yoshimara (1931, in Hutchinson 1975) divided Japanese lakes into four categories corresponding to the total iron concentrations, three of which cover the range of lakes under study (and include most lakes worldwide). The categories are described as:

1. uncoloured neutral of alkaline lakes; iron generally undetectable but occasionally as high as 0.90 umol l^{-1} (includes most data for Rondevlei).
2. moderately coloured lakes, neutral or alkaline; iron often undetectable, but may be as high as 4.66 umol l^{-1} (Grootwitvlei).
3. lakes coloured by organic material, slightly acid (pH 4.2 - 6.6); total iron from 0.54 - 44.77 umol l^{-1} (Cape Point vleis and Grootrondevlei).
4. lakes containing sulphuric acid of volcanic origin; total iron 1.61 - 343.80 umol l^{-1}.

What allows this categorization is the form in which the iron is generally maintained under different conditions. The reactivity of iron to chemical conditions in the waters results in the relative mean concentrations of iron in suspension (as well as the seasonal variation) differing considerably from those of the major cations. Under acid oxidising conditions most of the uncomplexed iron occurs in a soluble reduced state (Fe^{2+}). On the other hand in alkaline oxidising conditions, most of this iron is maintained in the insoluble Fe^{3+} form, generally as $Fe(OH)_3$. The formation of iron complexes with dissolved organic compounds greatly alters iron solubility, however, and leads to an enrichment of iron in waters with high concentrations of humic compounds. In the brown acid waters of the Cape Point vleis and Grootrondevlei the formation of these organic iron complexes is probably the most important mechanism resulting in the high total iron levels. Seasonal

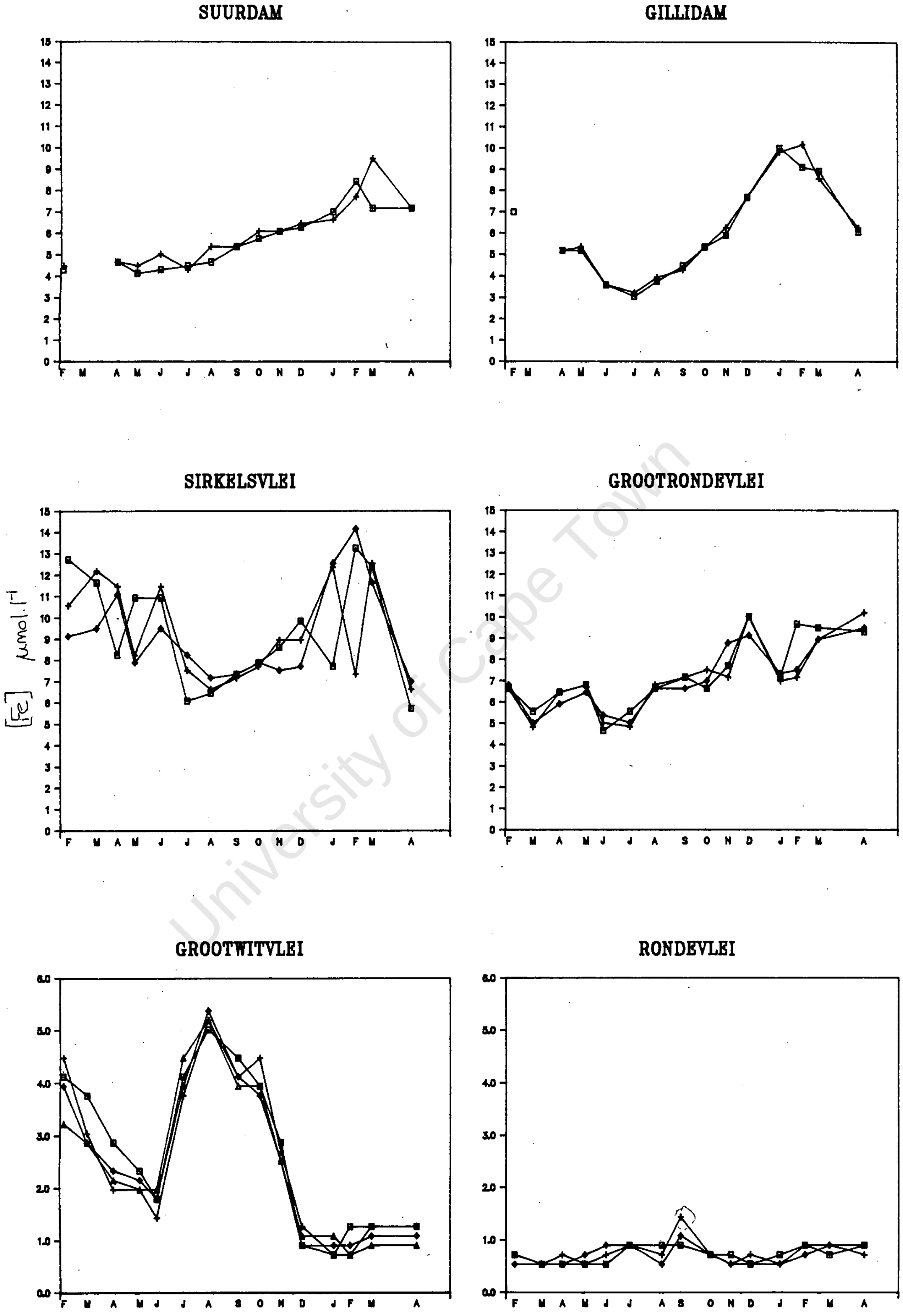

Figure 5.10 Seasonal variation in the surface total dissolved [Fe] of the waters of each of the six vleis. All concentrations are in µmmol l^{-1}. Station 1 - □ , station 2 - + , station 3 - ◇ , station 4 - △ .

variations in levels of total iron correlate closely ($P < 0.001$, table 5.4) with variation in water colour and levels of humic substances (see chapter 6) for Suurdam, Gillidam, Sirkelsvlei and Grootwitvlei. The water in Rondevlei is less intensely coloured than the other vleis (in most cases the levels are an order of magnitude lower) and there is little correlation between colour and iron levels, suggesting a significant presence of other forms of iron. The high pH and elevated oxygen levels, as a result of photosynthesis, suggest a dominance of $Fe(OH)_3$ The reason for the lack of correlation between colour and total iron in Grootrondevlei is not understood, but may be linked to the limited seasonal variation in colour. Seasonal variations in total iron levels differ between the Cape Point vleis, which exhibit late summer to autumn maxima, and Grootwitvlei and to a limited extent Rondevlei, with winter to early summer maxima. The maxima correspond to the colour maxima of the vlei waters, which result from the levels of humic substances present. The levels of iron seasonally present in the water appear, therefore, to be controlled by the influx of coloured dissolved organic compounds. The causes of these fluctuations will be discussed in chapter 6 (humic compounds).

Copper. Copper was determined for the month of September only since the levels measured were close to the detection limit for the method and further analysis would have required preconcentration procedures. The results are presented in table 5.5. Copper may be present as ionic, organic or sestonic fractions, the first two of which were jointly measured. Copper may also form organic complexes with dissolved organic compounds thus increasing its concentration in the water (Riley 1939, in Hutchinson 1975).

SU	GI	SI	GR	GW	RO
0.24	0.16	0.36	0.17	0.27	0.16

Table 5.5 Total dissolved copper concentrations measured in September (1981). All values are in $\mu mol\ l^{-1}$ and are close to the detection limit of the method.

If the levels of copper are assumed to vary seasonally in a similar way to those of iron it might be suggested that there is in fact a marked difference in the concentrations of copper present in the brown waters relative to that present in the moderately clear alkaline waters. This would result from the fact that in September iron reaches peak levels in Grootwitvlei and Rondevlei whereas in the other brown water vleis it is still close to the minimum level at that time. The past additions of copper to Gillidam and Sirkelsvlei (see chapter 2) have not resulted in noticeably higher concentrations in solution, but high concentrations may well occur in the sediments.

Major Nutrients. Results of the anlayses of soluble reactive phosphorus, ammonium and nitrite are presented in figures 5.11, 5.12 and 5.13 respectively. The mean concentration and range of each nutrient are listed in table 5.6. Concentrations are presented by mass (ug l^{-1}) rather than by number (umol l^{-1}) in accordance with the units used in most other freshwater studies.

Levels of soluble reactive phosphorus (SRP) were on average similar (35-73 ug P l^{-1}) in all the vleis except in Suurdam, where they were significantly higher. The mean level in Suurdam was more than 310% greater than those of the other vleis all of which were below 100 ug P l^{1}. Of the remaining vleis, Gillidam and Sirkelsvlei displayed slightly greater mean levels (59 and 73 ug P l^{-1}) and the two Grootvleis the lowest mean levels (both 35 ug P l^{-1}). There was a marked seasonal variation in the levels in Suurdam and Gillidam, with a minimum from winter to early summer and a maximum from late summer to autumn.

	SU		GI		SI		GR		GW		RO	
	mean	max min	mean	max min	mean	max min	mean	max min	mean	max min	mean	max min
SRP	227	287 158	59	104 30	73	160 34	35	45 22	35	98 8	48	142 12
NO_2-N	426	857 129	68	201 30	114	243 30	38	59 15	9	19 2	17	92 3
NH_4-N	290	441 115	107	176 40	186	325 81	92	199 20	67	150 12	279	896 63

Table 5.6 Mean, maximum and minimum levels of nutrients in the surface waters of the six vleis, Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO). All values are in µg l^{-1}.

The variation in SRP in these two vleis is closely correlated with that of the levels of humic substances (in both cases $P < 0.01$, table 5.4). SRP is readily complexed by humic compounds (often SRP-Fe-humic complexes- chapter 6) and these correlations indicate the likelihood of complexation of the phosphorus and a resultant concentration of the dissolved phosphorus as a consequence of the high levels of humic substances. Sirkelsvlei displayed a less marked seasonal variation in SRP levels, although the levels are also correlated with those of the humic substances ($P < 0.05$). For the remaining three vleis seasonal variations in SRP

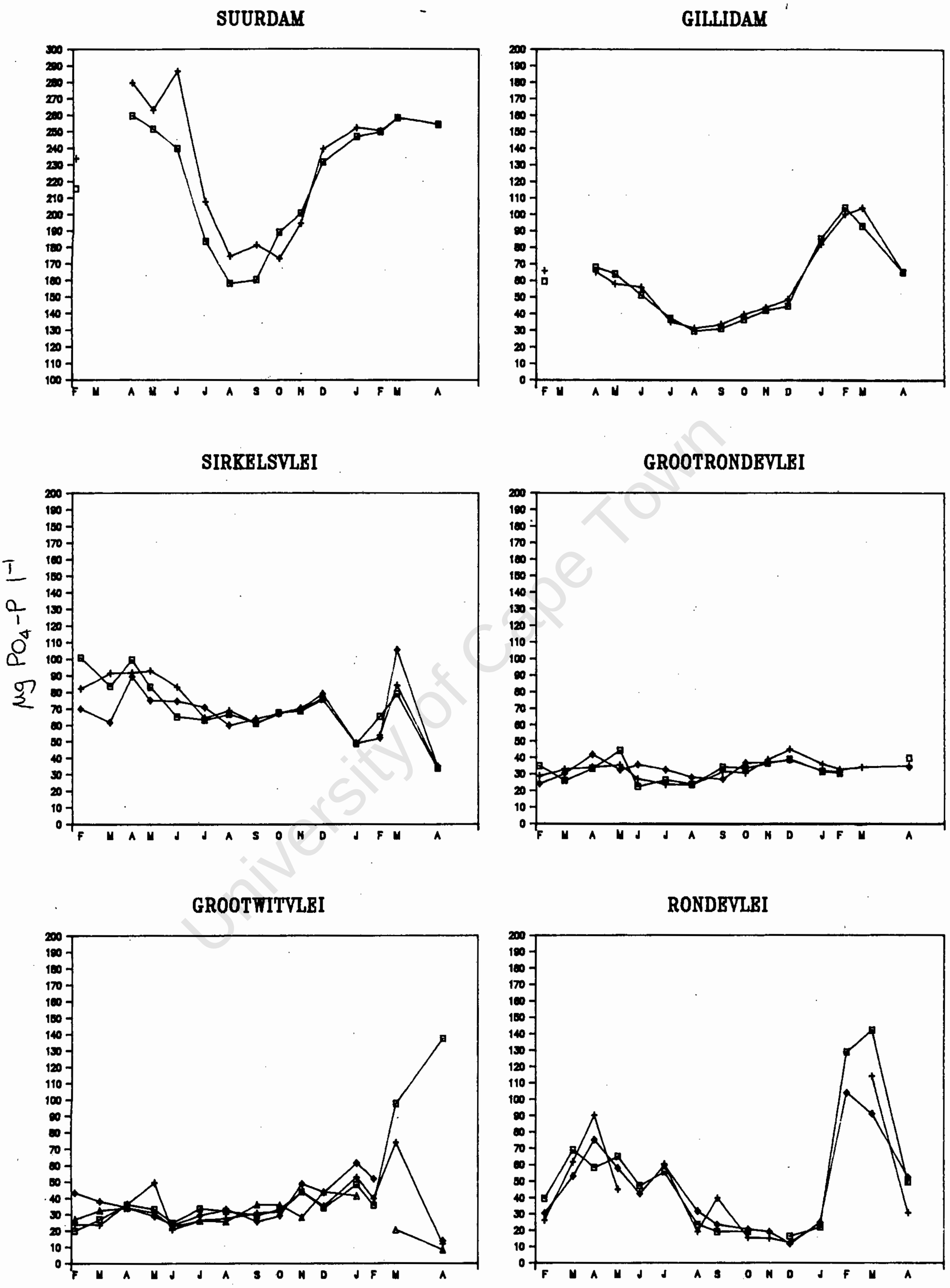

Figure 5.11 Seasonal variation in the soluble reactive phosphorus (SRP) levels of the surface waters of each of the six vleis. All concentrations are in µg PO$_4$-P l^{-1}. Station 1 - □ , station 2 - + , station 3 - ◇ , station 4 - △ .

levels are not positively correlated with those of the levels of humic substances found in these waters. The SRP levels in the Grootvleis showed little distinctive seasonal variation, except for a peak in late summer to autumn in Grootwitvlei. What seasonal variation did exist correlates with the iron levels in Grootrondevlei ($P < 0.01$, table 5.4) and the sodium, magnesium and calcium levels in Grootwitvlei ($P < 0.05$, table 5.4). The SRP may thus reflect a complexation of iron or of calcium with the phosphate anion. Rondevlei showed a marked seasonal variation in SRP levels, with a distinct minimum in spring to early summer and maxima in late summer to autumn. The variations in SRP levels do not show any close correlations with those of any other inorganic chemical variables (table 5.4). This does not discount any association of the phosphorus with the other inorganic and organic chemical species however, but it does emphasise the complex fluxing and the high loading of phosphorus in this vlei. The concentrations of chlorophyll *a* (see chapter 8) closely follow the variation in SRP. The spring to early summer minimum of phosphorus is reflected by a delayed drop in the chlorophyll *a* concentrations and a similar rapid increase in late summer. The cycling of the SRP, NO_2-N and NH_4-N species will be discussed together below.

Measurements of the levels of nitrate were considered inaccurate as a result of humic interference (see Methods), however mean combined nitrate and nitrite measurements are included in fig. 5.14 to illustrate winter nitrogen maxima.

Mean nitrite-nitrogen levels varied to a greater extent between the vleis than did the SRP levels. Suurdam again had far greater levels than the other vleis, with a mean level more than 370% greater than the next highest vlei, Sirkelsvlei. The remaining four vleis all had mean levels of less than 100 ug N l^{-1}. The lowest mean levels were found in Grootwitvlei and Rondevlei, where the levels remain below 20 ug N l^{-1} for most of the year . Seasonal variations in the levels of nitrite-nitrogen are not easily interpreted without knowing the complementary variation in the levels of nitrate-nitrogen. Higher levels in Suurdam, Sirkelsvlei and Grootrondevlei occurred in the spring to early summer months. In Gillidam there was a distinct midsummer maximum and a minimum from winter to spring, the causes of this variation are unclear however, particularly with respect to the differences between Gillidam and the other acid brown water vleis. Grootwitvlei and Rondevlei both displayed distinctive peaks in the nitrite levels from mid-winter to spring. Analysis of nitrate levels over the same period (fig. 5.14) indicates even greater peaks of nitrate-nitrogen, especially in Rondevlei even though levels might have been underestimated by interference of humic substances. The maxima of combined nitrite and nitrate were 66 ug N l^{1} in Grootwitvlei and 930 ug N l^{1} in Rondevlei.

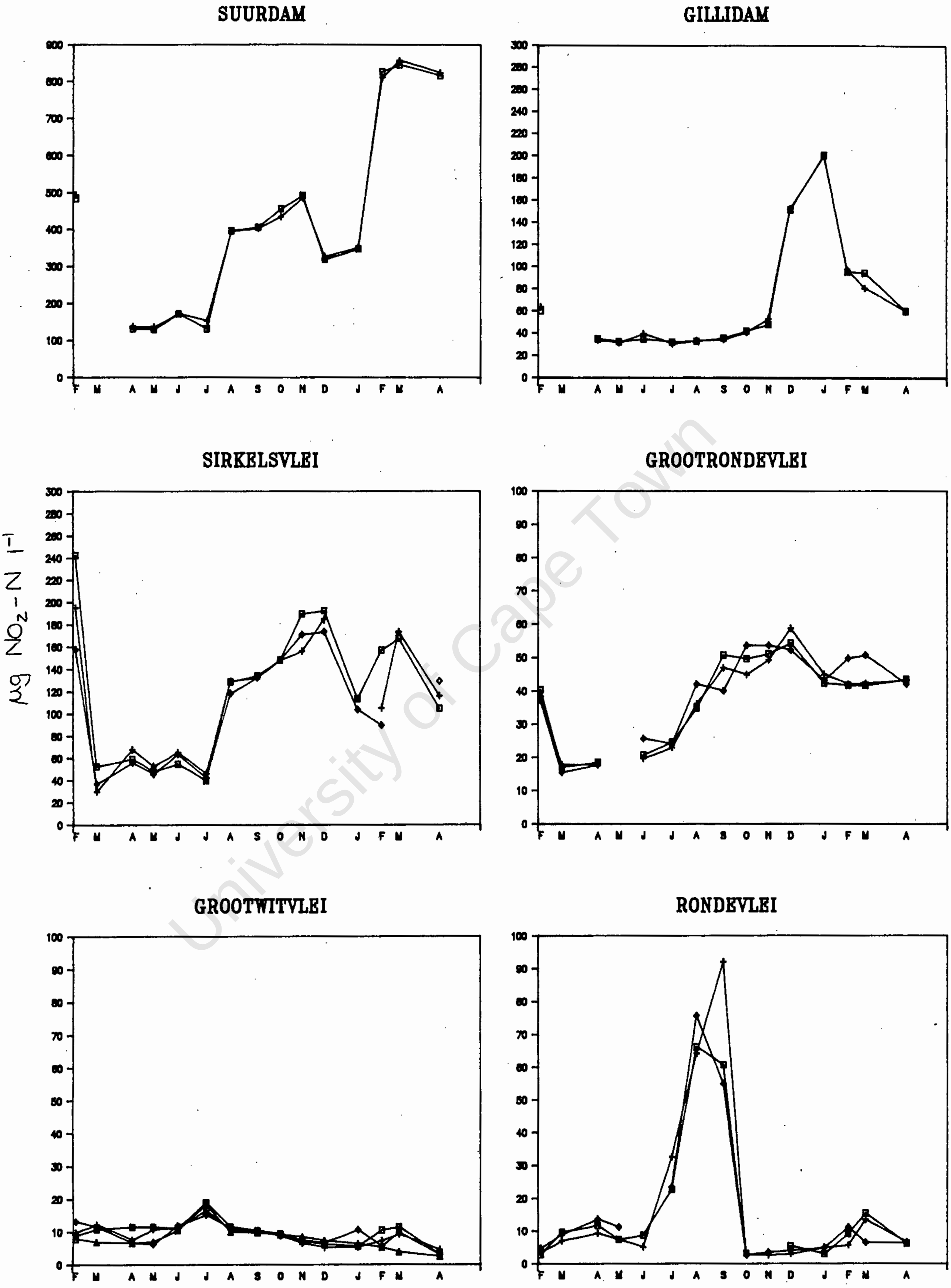

Figure 5.12 Seasonal variation in the nitrite-nitrogen (NO_2-N) levels of the surface waters of each of the six vleis. All concentrations are in µg NO_2-N l^{-1}. Station 1 - □ , station 2 - + , station 3 - ◇ , station 4 - △ .

These marked nitrite and nitrate maxima corresponded to the three months of highest rainfall and appear to result from a very high nitrogen loading as a result of run-off over this period.

Mean ammonium-nitrogen levels also vary noticeably between the vleis. Suurdam and Rondevlei have the highest mean levels, both close to 300 ug N l^1, followed by Sirkelsvlei with a mean level close to 200 ug N l^1. Gillidam, Grootrondevlei and Grootwitvlei show mean levels closer to 100 ug N l^1. Seasonal variation in the levels of ammonium is once again not easily interpreted, but an attempt will be made to explain part of the variation in a discussion of the cycling below. There does appear to be a period of minimum ammonium levels common to all the vleis in the very late summer to autumn of the first year. The minimum is followed by higher levels during the winter in all the vleis. Similarly low levels of nitrite-nitrogen occur over the same late summer to autumn period, but increase only in mid-winter in Grootwitvlei and Rondevlei or in spring or early summer in the remaining vleis. There is thus some common variation in the levels of ammonium and nitrite which is reflected in a positive correlation between these two variables in the three least productive vleis, Suurdam, Gillidam and Grootrondevlei ($P < 0.01$, table 5.4). There is little correlation between ammonia and the other inorganic and organic chemical species, except in Gillidam and Grootrondevlei where the correlation is probably due to a common conservative variation in the levels.

Nutrient cycling. It is not the intention of this study to attempt to analyse the details of nutrient cycling in each vlei. However, as a result of examining the seasonal variation of the three nutrients, some comments can be made on the causes of the changes in nutrient levels (see fig. 5.14).

Rondevlei: For the major part of the year nitrite and nitrate levels in the surface waters are low. During July, August and September, however, levels rise sharply. The reason for the sudden increase is most likely to be the sudden influx of nitrogen-rich storm water runoff. Rainfall over these three months accounted for 63% of that year's total (fig.4.3) and caused water levels to rise sharply to the vlei maximum in July (fig.4.7). The nutrient content of the water entering the vlei via the Italian road canal was analysed in August and showed levels corresponding to those in the vlei waters (table 5.7). This suggests an allochthonous input of nitrite and nitrate caused by the large volume of inflow rather than increased authochthonous generation of nitrite and nitrate .

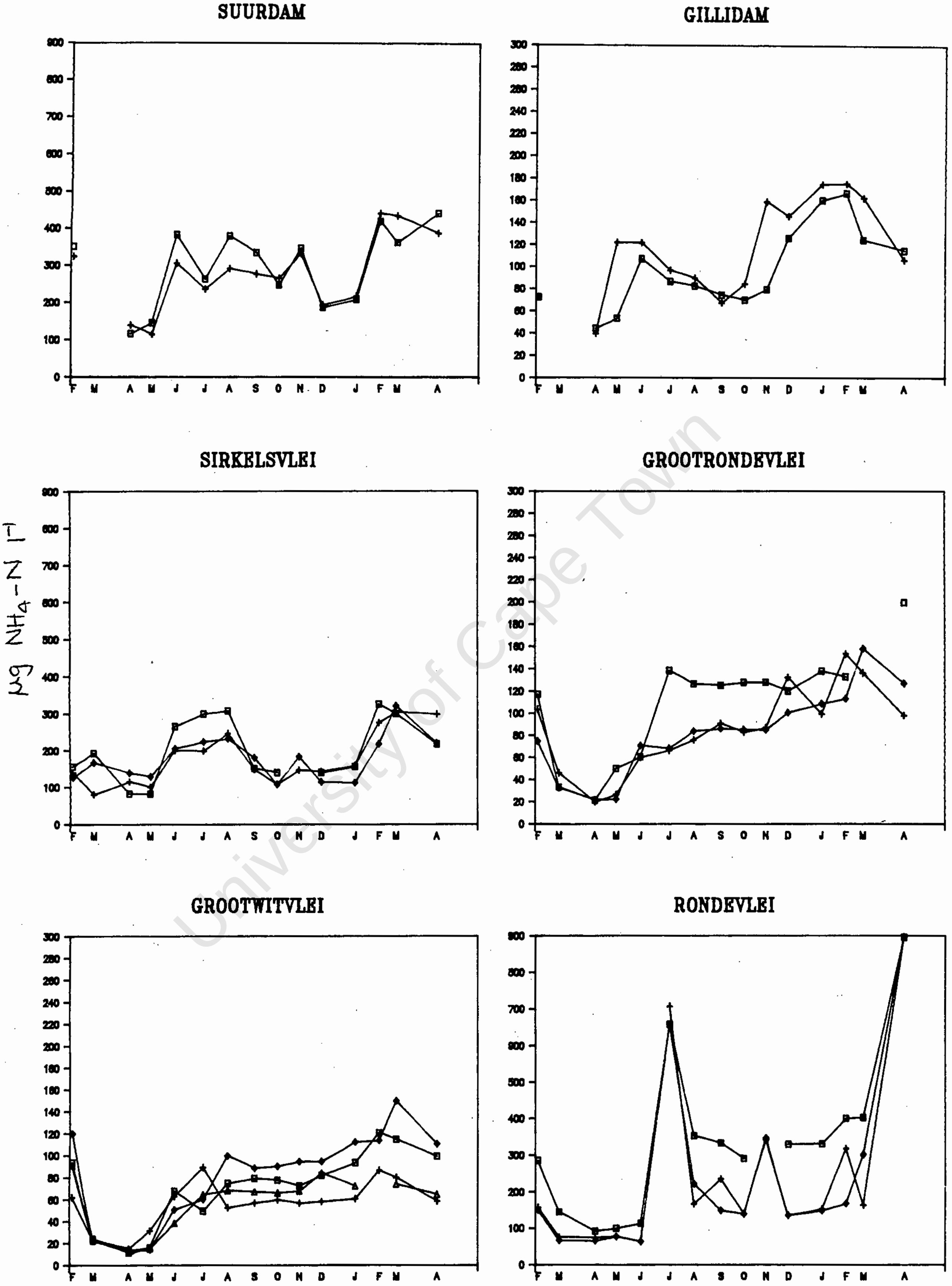

Figure 5.13 Seasonal variation in the ammonium-nitrogen (NH_4-N) levels of the surface waters of each of the six vleis. All concentrations are in µg NH_4-N l^{-1}. Station 1 - □ , station 2 - + , station 3 - ◇ , station 4 - △ .

	Fe	Colour	SRP	NO2-N	NH4-N
Inflow	1.43	0.049	31	91	248
Vlei	1.07	0.037	51	72	195

Table 5.7 Levels of nutrients (µg l^{-1}), total dissolved iron (µmol l^{-1}) and colour (absorbance at 400nm) measured in inflowing water (Italian Rd canal) and vlei water in Rondevlei in August (high rainfall).

SRP levels over the same period decreased between July and August and remained low until mid-summer. SRP levels in the water entering the vlei in August were similarly low (table 5.7).

Chlorophyll *a* concentrations remained high in the surface water over this period however. A likely interpretation of the consequence of this winter influx of nitrogen is as follows. The high levels of nitrate and nitrite maintained a high level of primary production, while a relatively low supply of SRP (the ratio of inorganic N:P << Redfield ratio (16:1)) and reduced microbial regeneration (temperature minimum: see fig. 4.5) caused SRP levels in the water to decrease.

In October the rainfall decreased to 5% of the mean figure of the previous three months and the water level dropped. The sudden reduction in nutrient supply as a result of the extremely reduced inflow, and light limitation as a result of suspension of the sediments (caused by the throughflow of water and strong winds) were probably the main causes of the rapid phytoplankton dieback (as indicated by very low levels of chlorophyll *a*) in October. A result of the dieback was the small increase in ammonium levels in November. In mid-summer SRP levels rose rapidly and were followed by a large increase in the chlorophyll *a* concentrations, but no immediately noticeable increase in the levels of dissolved inorganic nitrogen. This probably reflects increased microbial regeneration of nutrients from the sediments as a result of the higher temperatures and lower water levels.

Grootwitvlei: A similar but reduced increase in nitrogen occurred during the rainy season, probably as a result of both direct stream flow and indirect inflow *via* Grootrondevlei. Chlorophyll *a* levels remained low during this period of reduced temperature and light, however, and only in early to mid summer did both SRP and chlorophyll *a* levels rise. Again this may have been a result of increased microbial regeneration of nutrients from the sediments as a result of increased temperature

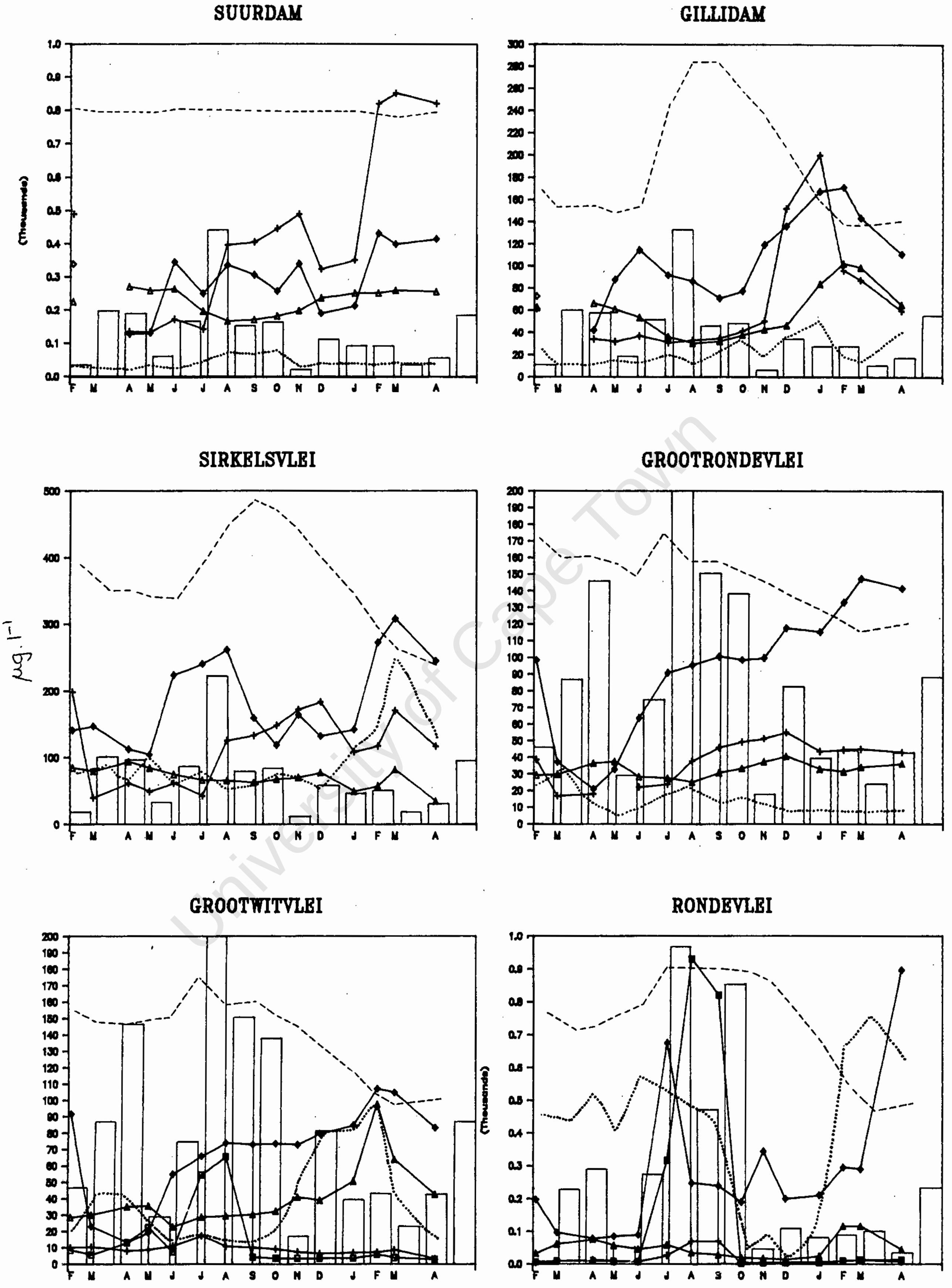

Figure 5.14 Seasonal variation in the mean levels of SRP (△), NO$_2$-N (+), NO$_2$-N+NO$_3$-N (□) and NH$_4$-N (◇) all in µg l^{-1}, in relation to rainfall (⊓), water depth (----) ~~(m)~~ and chlorophyll *a* (·········) (relative values only) in each of the six vleis.

and lowered water levels. The effect of the extensive macrophyte beds may also be important especially as August to November was the period of maximum growth of *Phragmites* and *Typha*.

It is difficult to comment much on the cycling of the nutrients in Suurdam, Gillidam, Sirkelsvlei and Grootrondevlei. All have low levels of phytoplankton production and shallow sediments. Except in Grootrondevlei, SRP levels seemed to be controlled by the levels of humic substances in the water column.

GENERAL DISCUSSION

An important characteristic of the chemical enviroment common to all six vleis is the generally high levels of **dissolved oxygen**. This is not unexpected in shallow lakes exposed to high average wind speeds and therefore experiencing frequent mixing of the water column. The important consequence is the lack of seasonal stratification or anoxia in the water column with its concomitant effects on both the biota and the chemical environment. Suurdam and Gillidam were both found to experience thermal stratification but appeared to lack any associated anoxia. Although the water column was thus consistently well oxygenated, the character of the sediment and its state of oxygenation probably varied considerably. Rondevlei, and to a lesser extent parts of Grootwitvlei, have thick layers of organically rich sediment experiencing anoxic, and thus reducing, conditions, with solubilization of precipitates and reversal of the oxidation reactions of the water column. These diagenetic chemical reactions can exert a significant effect on the composition of the overlying waters. The remaining four vleis do not receive the same amounts of sedimenting organic material (see chapter 7), and the sediments are thus more skeletal, and less important in the fluxing or recycling of the chemical constituents of the vlei.

As mentioned in the introduction, three mechanisms have been suggested as controlling the salinity of the inland waters of the world (Gibbs 1970, Feth 1971). All three of these mechanisms, namely **rock dominance, atmospheric precipitation** and **evaporation-precipitation** processes, appear to play some role in the determination of the chemical composition and its variation in the vleis under discussion. Below I attempt to separate the effects of the three mechanisms with particular regard to the pH, acidity, alkalinity and base composition of the vlei waters. This division of the control of input has been used by, amongst others, Sutcliffe *et al.* (1982), Sutcliffe (1983), Gorham *et al.* (1983), Sutcliffe and Carrick (1983), Rippey and Gibson (1984) and in group studies of lakes while others have chosen to examine inputs in the form of watershed and airshed inputs (Likens and Borman 1979) or inflow, atmospheric precipitation and atmospheric gaseous exchange (Talling, 1983).

Rock dominance refers to the influence of the geology and the soils of the catchment on the chemical compositon of the water. The soils and bedrock of each catchment are described in chapter 2. In general terms, however, they can be described as skeletal quartzitic sandstone-derived soils or wind-blown regic sands. Of these regic sands, some are calcareous and others are acidic and decalcified. Both the acidic sands and the quartzitic sandstone-derived soils have formed well leached podsols. As a result of the podsolization the soils contain a diagnostic ferrihumic horizon and have suffered severe base cation depletion. The net result is soils of low pH. Table Mountain Sandstone-derived soils supporting montane fynbos communities show soil pH values between 3.2 and 4.5, while acidic sand supporting a sandplain lowland fynbos community registered a pH of 5.2 (Witkowski and Mitchell 1987). A further consequence of these soils is the slow rates of chemical weathering (Stumm and Morgan 1981) and limited export of chemical constituents, as reflected in the very low conductivities of ground water and stream flow (Van Wyk 1982, Davies *et al.* 1987). In contrast the younger dune sands are not as well leached and lack the ferrihumic horizon. The sands are generally calcareous or associated with limestone deposits, resulting in a richer supply of base cations and anions and thus a greater soil alkalinity and pH. Aeolian sands supporting strandveld communities have yielded soil pH values of 6.6 to 7.5 and in calcareous sands overlying limestone pH's of 7.1 to 8.0 have been measured (Witkowski and Mitchell 1987).

The mean pH (and the conservative property of alkalinity) of each vlei water appears to be strongly influenced by the balance of the soil pH values of each catchment, although there are other contributing factors. Suurdam and Gillidam are both small closed-basin seepage vleis with water pH values very similar to those expected in the surrounding TMS-derived podsols. Sirkelsvlei is surrounded by similar soils, but displays a higher pH, as well as possessing some acid-neutralising capacity (ANC) as a result of the high total salinity of the water. The catchments of the Grootvleis incorporate TMS-derived podsols on the steep mountain slopes, acid sands and some sands associated with lime-rich deposits. The pH of the water in Grootrondevlei reflects the pH of the acid sandy soils immediately surrounding the vlei, neutralized to some extent by the closely associated lime-rich deposits. The alkaline waters of Grootwitvlei do not match the pH of the acid sands immediately surrounding the vlei. The high pH and relatively great ANC stem to some extent from similar lime-rich deposits, but probably mostly from the input of bird excreta with a high percentage composition of calcium (see chapter 2). Rondevlei waters are surrounded by both acid sands and calcareous dune sands, but also receive direct urban runoff. The high rate of input of bird and hippopotamus excreta, and the quality of the urban runoff, both of which contribute to high rates of primary production (as evidenced by a high standing crop of phytoplankton - chapter 7), all contribute to an even higher pH and ANC or alkalinity than might be expected from the surrounding soils. In contrast to the strong influence on the pH and alkalinity of the vlei waters (except in the case of Rondevlei), the total salinity and its cation composition are less strongly influenced by the soils and rock of the catchment. As noted, the slow rates of chemical weathering and high degree of leaching result in limited chemical input to ground and surface water. The lime deposits are, however, a rich source of base cations and thus have some effect on the chemical composition of the Grootvleis and Rondevlei.

Atmospheric precipitation, both wet and dry, is well documented as a source governing the levels of certain of the chemical constituents of lakes (Gorham 1961, Wright and Henriksen 1978, Ogden 1982, Sutcliffe 1983, Sutcliffe and Carrick 1983). In maritime regions the sea acts as a major source of ions, which are picked up as aerosols from the sea surface and deposited on the land by both rainfall and cloud condensation. In the south-western Cape, with a weather pattern of strong winds from both the south-east and the north-west for many months of the year (see chapter 4.), atmospheric precipitation of marine salt appears to be a primary determinant of the ionic composition of the vleis. The cation compositions of the three vleis in Cape Point are all very similar to that of seawater throughout the year. Those of Grootrondevlei and Grootwitvlei differ to a varying degree, largely as a result of calcium enrichment, and that of Rondevlei varies as a result of enrichment by calcium and potassium both, of which cations are present in high proportions in bird excreta (see table 2.6). Some analysis has been conducted on the ionic composition of atmospheric precipitation in the south-western Cape and it also has a composition suggesting a marine source of such ions (Van Wyk 1982, Davies *et al.* 1987 and J A Day pers. comm.).

The presence of a ferrihumic soil horizon in most of the acid podsols might be expected to have some effect on the ionic composition of precipitated water as it drains through these soils. As noted humic substances have a strong tendency to form complexes with metal ions (see chapter 6) thus constituting polyelectrolytic weak acids. Calcium and magnesium in particular have a tendency to coordinate with the carboxyl and hydroxyl functional groups of humic substances, causing them to precipitate (Stumm and Morgan 1981). In fact Stumm and Morgan (1981) state that "surface waters with high Ca^{2+} and Mg^{2+} (eg. > 10^3M) contain almost no humic substances." The levels of humic substances and their behaviour are described in chapter 6; it suffices here to state that the Cape Point vleis have high colour levels, Grootrondevlei is considerably less coloured, Grootwitvlei loses most of its colour in the mid to late summer months and Rondevlei is virtually uncoloured. Thus high levels of calcium and magnesium do co-exist with high levels of humic substances in the water column in Sirkelsvlei, whereas in the Grootvleis and Rondevlei calcium enrichment may be an important factor causing the reduction and removal of colour by coagulation.

While no other obvious alterations in ionic composition result from humic substances in these vleis, the levels and the variations in the levels of total iron are closely tied to the concentrations of humic substances in the lakes. The chelation of iron by humic substances carrying carboxyl and hydroxyl functional groups and the formation of organic iron complexes allows enhanced concentrations of total iron in the water column.

Rainwater is naturally acid, and drainage through acid podsols further lowers the pH. 'Acid rain' of anthropogenic origin (also termed acidification) is now a well documented phenomenon which further acts to lower the pH of, and to remove alkalinity from, natural waters. The effects of precipitation on the pH of the vlei water are not known, but some research on acid rain has been conducted at Jonkershoek (approximately 45 km east of the city centre of Cape Town) (Böhm 1985), where low pH rain was recorded in three winter maritime frontal storm events (pH's of 5.29, 5.39 and 4.95). In only one event was there sufficient sulphate and nitrate measured to indicate acid rain of anthropogenic origin. Jonkershoek and the vleis are all within 65 kms of the centre of Cape Town so the vleis are not too remote to receive acid rain. However Jonkershoek is located approximately downwind of Cape Town and the north-westerly and westerly frontal storm events, and might therefore be more exposed to acid-polluted rain than are the vleis (certainly more than are the Cape Point vleis to the south). Thus although based on limited data there is no reason to suppose that 'acid rain' is presently having any significant effects on the pH of the vleis.

The final mechanism of **evaporation-precipitation** concerns the balance between the processes of evaporation and precipitation. The balance is largely determined by the climate, with factors such as temperature, wind, solar radiation, and cloud cover strongly influencing the rate of evaporation. The most direct effect is the seasonal variation of the conservative base cations and anions as a result of concentration and dilution in the water. Seasonal variation in cation concentrations has been described, and where possible explained, in the results section. Other effects result from the varying residence time of groundwater and its constituent organic and inorganic species in the soil. The very high total salinity of Sirkelsvlei is an obvious consequence of a closed basin vlei with a small relative depth and subject to high average wind speeds and therefore evaporation. The winter drop in pH is likely to be a consequence of the influx of acid soil water and a dilution of the neutralizing effect of the high base cation concentrations, rather than an input of organic acids (humic substances). In Rondevlei the concentration of calcium and increasing water temperature would contribute to the summer decalcification of the waters.

The **nutrient fractions** SRP, NO_2-N and NH_4-N are dynamic both in their chemical reactivity and in biotic demand. Nitrogen especially is a highly mobile element, moving rapidly from one form to another. In addition both phosphorus and nitrogen are normally moved at a relatively fast rate between the different compartments of a freshwater system (such as the sediments and the biota)(Wetzel 1983). The level of the dissolved fraction of each nutrient is thus a balance of the allochthonous input, regeneration and removal in the lake, and the outflow or output from the system. Allochthonous sources of the nutrient fractions include some of the same sources controlling the salinity, namely the catchment geology and soils, and atmospheric precipitation, as well as biological sources. In a lake itself there are uptake and regeneration by the sediments, the macrophytes, the phytoplankton and the heterotrophs, as well as interaction with inorganic and organic chemical species and suspensoids and input by nitrification and the fauna. Output includes river outflow and denitrification, as well as export by some components of the fauna. Thus the cycling within a lake is complex; in this discussion I attempt to comment on the levels of the dissolved nutrient fractions in relation to what is known of the nutrient input and uptake in the vleis. The soils of the south-western Cape are generally of low nutrient status, which is a characteristic determinant of the heathland type of vegetation found on these soils (Kruger *et al.* 1983). Most studies on soil nitrogen and phosphorus in this region have been conducted on coastal acidic sands, although Witkowski and Mitchell (1987) have also surveyed the soil phosphorus of other TMS derived soils and calcareous sands. Studies by Stock and Lewis (1986) and Stock *et al.*(1988) have described low concentrations of soil total nitrogen, exchangeable NH_4N and NO_3-N. Stock and Lewis (1986) further show a small seasonal change in the three nitrogen fractions in the surface soil, with low concentrations of exchangeable NH_4-N and NO_3-N associated with the low total nitrogen. They attribute the low concentrations to climatic influences, such as low rainfall (381mm) and high temperature, and the parent material of the soil, which is well leached with a low clay content.

Campbell (1983), working on montane fynbos, has shown a strong positive correlation between total soil nitrogen and rainfall. Mean annual rainfall is greater at Betty's Bay and Rondevlei, while in Cape Point, although the rainfall is less, the soils are shallow and seasonally waterlogged. On the basis of soil moisture, the undisturbed soils of the catchments are thus likely to have slightly greater soil nitrogen concentrations than those found by Stock and Lewis (1986), although the levels should still be low. Atmospheric nitrogen input was also measured by Stock and Lewis (1986) at the same site, 62 km north of Cape Town. The input was described as low, especially when compared to the north temperate latitudes, and this was thought to be a result of a mainly oceanic source with little influence from anthropogenic activities. Values of 1.79-1.99 kg N ha^{-1} y^{-1} total nitrogen and 1.12 kg N ha^{-1} y^{-1} of NO_3-N and NH_4-N were measured with a NH_4N : NO_3N ratio of 1:1. A value of 1.0 kg N ha^{-1} y^{-1} is given by Wetzel (1983) as an average for the United States, although the distribution is described as highly irregular. The possible influence of anthropogenic activities on rainwater entering the vleis is discussed in the results section (pH) and is not likely to be much greater than that found to the north of Cape Town. Although NO_3-N and NH_4-N concentrations decreased with increasing precipitation volumes, the period of greatest rainfall still accounted for the period of greatest input. The combined effect of atmospheric nitrogen input and soil nitrogen transport could well be the cause of the noted increase in NH_4-N levels in the vleis that occurred at the beginning of the rainy period (see fig. 4.3) in June or July. NO_2-N increased similarly in the Grootvleis and Rondevlei, but showed a delayed increase in Suurdam and Sirkelsvlei. Waterlogging of the soil causes reducing conditions to prevail and the reduction of NO_3-N to NO_2-N is a common reaction occurring under these conditions. The delayed flush of nitrite in Suurdam and Sirkelsvlei was probably a result of the waterlogging that occurred over this rainy period and the reduction of NO_3-N that followed. In October, at the end of the rainy season, measurement of the NO_2-N and NH_3-N levels at the inflow to Grootrondevlei and at the outflow of Grootwitvlei respectively showed inflow concentrations 4.0 and 1.8 times higher than the outflow concentrations. In Rondevlei the exceptionally high levels of NH_4-N, NO_2-N, and NO_3-N are almost certainly the result of terrestrial anthropogenic sources such as urban runoff, fertilizers and possibly purified sewage in the disturbed catchment.

Soil phosphorus in the south-western Cape has been studied by Mitchell *et al.* (1984) and Witkowski and Mitchell (1987), who have described low total soil phosphorus concentrations. The analyses of Witkowski and Mitchell (1987) show soil phosphorus levels to be lowest in the well leached, acidic sands and TMS-derived soils supporting lowland sand fynbos and montane fynbos, as opposed to relatively higher levels in the calcareous sands or sandy soils associated with lime-rich deposits supporting strandveld or limestone fynbos. The total soil phosphorus in the well leached soils consisted of 68-77% organically-bound phosphorus, while the smaller fraction of inorganic or available phosphorus was mostly iron- or saloid-bound. The calcareous sands, on the other hand, contained a high fraction of inorganic or available phosphorus (85-90%), most of which was either calcium- or saloid-bound. Sandy soils overlying lime-rich deposits were found to contain approximately 58% organically-bound phosphorus and the inorganic phosphorus was again found to be calcium- or saloid-bound. There is thus a furth~~u~~er separation of the soils in relation to the amount of available or inorganic phosphorus, with the acid, well leached soils containing very low concentrations of iron- or saloid-bound phosphorus and the alkaline soils containing higher levels of calcium- or saloid-bound phosphorus. The effects of the varying soil phosphorus concentrations and their associations on the vlei waters are not obvious, which is to be expected from a source generally low in soil phosphorus. The supply from the undisturbed soils of the Rondevlei catchment and parts of the Grootvlei catchments may be greater than that from the Cape Point catchments, but the levels of dissolved SRP are strongly affected by other factors.

Atmospheric phosphorus input has been measured by Brown *et al.* (1984) as 0.19 kg P ha^{-1} y^{-1} at the same site as atmospheric nitrogen. The input is described as significant in that it supplies 4.5% of the soluble soil phosphorus pool of the acidic sands in a year. Again, although phosphorus concentrations decrease with increasing rainfall volumes, the period of greatest rainfall still accounts for the period of greatest input. Unlike nitrogen, however, the combined effect of atmospheric phosphorus input and soil phosphorus transport causes little noticeable change in the SRP concentration of the water, except possibly for a small increase in July in Rondevlei. The inflow and outflow levels of SRP measured for the Grootvleis in October (at the end of the rainy season) showed only a 26% decrease in concentration in the effluent, as opposed to the 75% decrease in NO_2-N and 43% decrease in NH_4-N noted above. As with nitrogen, the input of phosphorus from anthropogenic terrestrial sources can be great. Thornton and Walmsley (1982) found phosphorus exports exceeding 50 mg m^{-2} y^{-1} from catchments in South Africa receiving municipal wastewater discharge. Rondevlei is the only vlei which receives input of this nature. An additional source of nutrient input in Grootwitvlei and Rondevlei is the input of faunal excreta. Bird excretion can act as a major source of nutrients in both vleis as studies by Coterill (unpub.), Serruya and Pollinger (1983) (both in Thornton 1986) and others suggest, and hippopotamus excreta (Viner and Smith 1973, Kilham 1982, both in Thornton 1986) can contribute to the nutrient load of Rondevlei.

There are thus some major differences in the nutrient loading of the different vleis, largely as a result of biological input. It is however difficult to relate these differences to the levels of the measured nutrient fractions. Internal cycling and the chemical environment appear to compensate for the differences in loading and one of the few noticeable effects is the increased levels of available nitrogen due to increased transport in the rainy months. Extensive beds of marginal macrophytes, varying development of the sediments, and differing levels of primary production regulate the higher loading of Rondevlei, Grootwitvlei and possibly of Grootrondevlei. In the Cape Point vleis, high levels of humic substances, the endorheic nature of the systems and possibly a greater interfacing with the soil chemical environment, in conjunction with limited influence from the factors affecting the other vleis, act to allow an enrichment of the dissolved fractions. This reaches an extreme in Suurdam, where the high levels of humic substances, the extremely low pH and levels of phytoplankton primary production, as well as the small lake volume, contribute to cause an enriched dissolved nutrient fraction. The relative levels and range of levels in each vlei are summarised in the notched box-and whisker plots of fig. 5.15. In ~~this~~ figure 6.16 the SRP values presented by Talling and Talling (1965) and Thornton (1986) for African lakes and reservoirs are included as a comparison to the levels of the Cape vleis. The levels in the Grootvleis generally fall within the bottom 25% of values for African lakes (measured since 1961), and the levels of Gillidam, Sirkelsvlei and Rondevlei in the lower 50% of the values. Suurdam as noted is exceptional and falls within the upper 50% of values. The range of values measured in African lakes prior to 1961 (Talling and Talling 1965) lie mostly in the lower 50% of the range of post 1961 values and encompass the values of all the vleis except Suurdam. In the very broad scale of African lakes and reservoirs, the range of SRP values found in all of the vleis except Suurdam are low, but not exceptionally so.

SUMMARY

The chemical environments differed markedly between the six vleis. In Cape Point, Suurdam and Gillidam both contained waters of very low pH, and consequently of high acidity and zero alkalinity. In both cases proportions of the cations were very similar to those in seawater, indicating a marine origin, and the

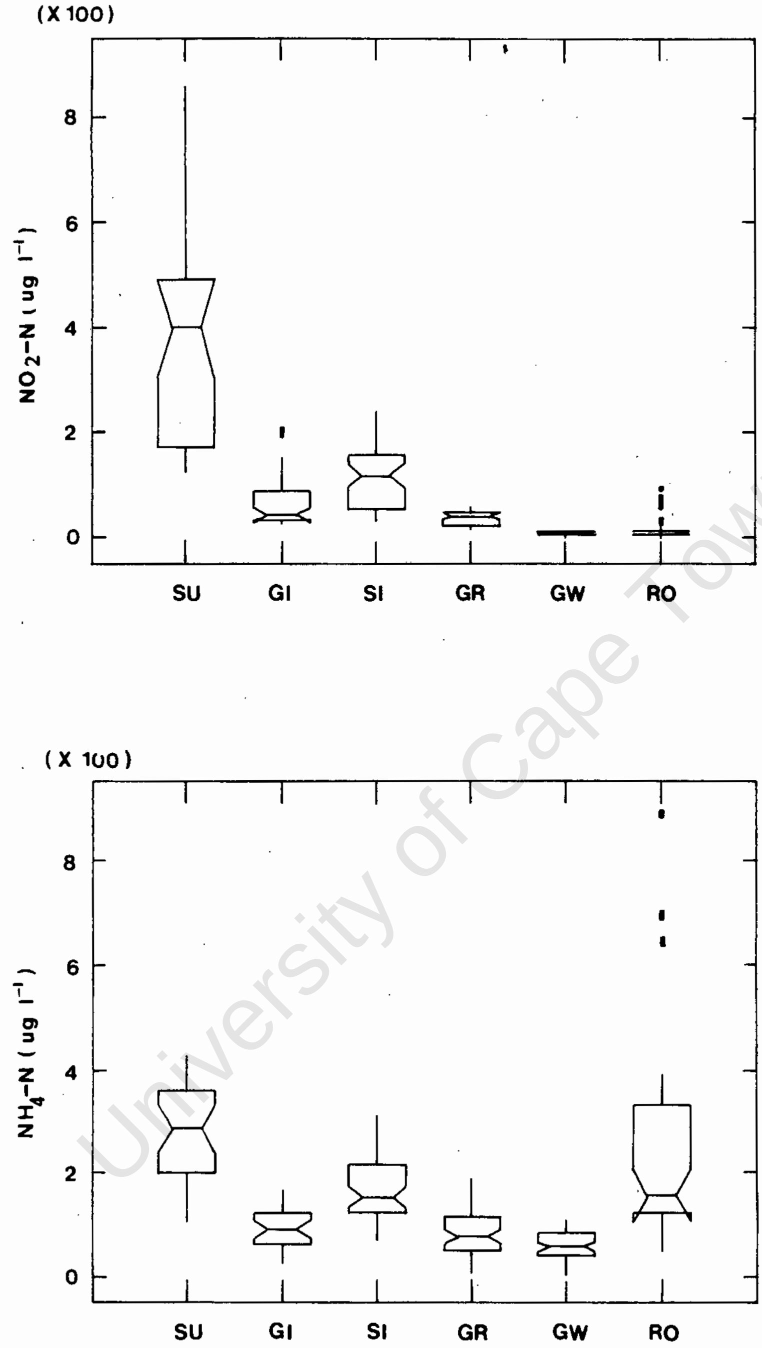

Figure 5.15 Nitrite (a) and ammonium (b) concentrations (in ug l^{-1}). Notched box and whisker plots illustrating the median, the upper and lower quartiles, the range and the confidence interval of the median in Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootwitvlei (GW) and Rondevlei (RO).

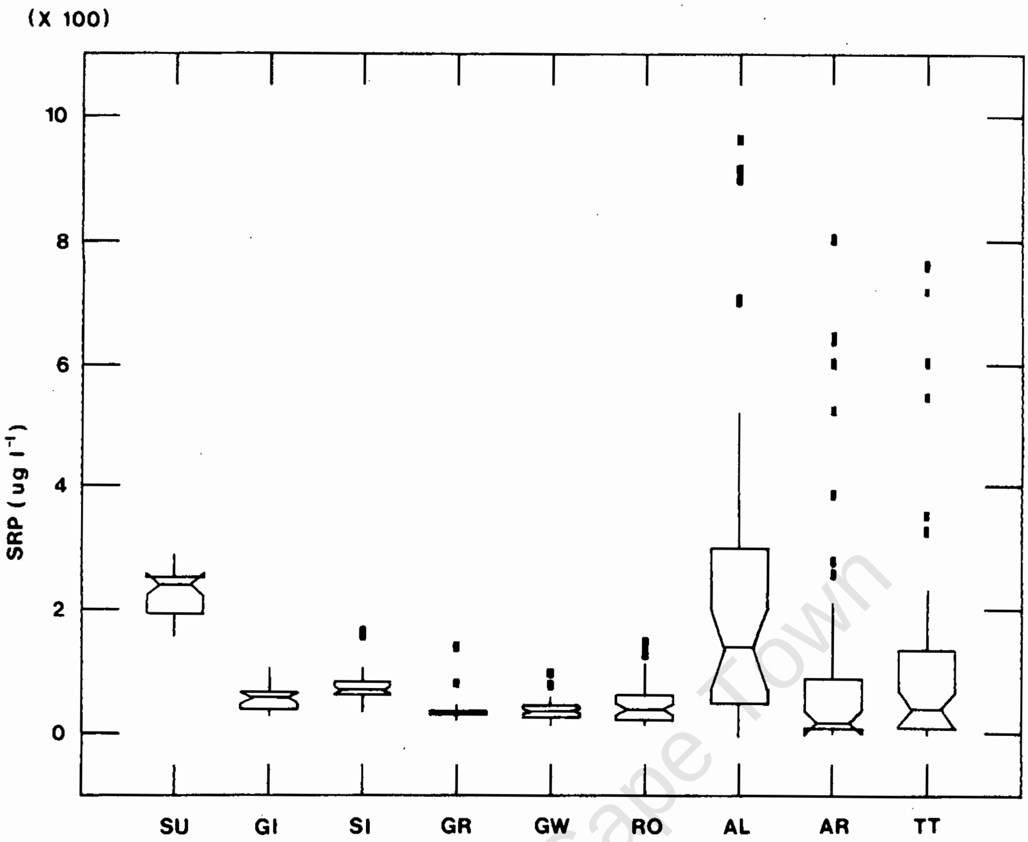

Figure 5.16 A notched box and whisker plot displaying the range of soluble reactive phosphorus concentrations (ug l^{-1}) in comparison to those documented by Talling and Talling (1965) and Thornton (1986) for African lakes and reservoirs pre and post 1961 respectively. SU-Suurdam, GI-Gillidam, SI-Sirkelsvlei, GR-Grootrondevlei, GW-Grootwitvlei, RO-Rondevlei, AL-African lakes post 1961, AR-African reservoirs post 1961, TT-African lakes prior to 1961.

Outlying concentrations (>1650) have been omitted for ease of comparison. The omitted values are from Thornton (1986) for lakes Abaya (4480), Albert (12600), Arangaudi (25580), Bogoria (3500), Kilotes (42640), Magadi (11000), Manyara (20000), Mariut (2560), Nakuru (13600), Pretoria Salt (7000) and Turkana (1650) and for Kainji reservoir (4000).

levels also displayed little obvious seasonal variation. In both, levels of total dissolved iron, and in Suurdam levels of SRP, were however, relatively high and displayed distinct seasonal variations closely correlated with variation in the levels of humic substances. Nitrite and ammonium levels in Suurdam were also markedly higher than in the other vleis, but in Gillidam were similar to levels in the other brownwater vleis.

Sirkelsvlei and Grootrondevlei both contained acid waters, not as low in pH as Suurdam and Gillidam, and total alkalinity was detectable. Sirkelsvlei was distinguished by a relatively high salinity (approx. $8^{\circ}/_{\infty}$) and a cation composition very similar to that of marine salts, while Grootrondevlei had a particularly low salinity throughout the year. Both vleis contained high levels of total dissolved iron, but in neither did seasonal variation correlate closely with that of the humic substances. SRP levels in Sirkelsvlei were similar to those in Gillidam, but correlated less closely with humic substances. In Grootrondevlei levels were lower and the variation was independent of humic substance concentration. Similarly nitrite and ammonium levels in Sirkelsvlei were well below those in Suurdam, but greater than those of the remaining four vleis.

The waters of Grootwitvlei and Rondevlei, in contrast, were of high pH and contained both total and phenolphthalein alkalinity. Seasonal variation in the pH of Sirkelsvlei, Grootrondevlei, Grootwitvlei and Rondevlei showed a common mid-winter to spring minimum. Seasonal variation in the concentrations of the major cations in the four vleis, on the other hand, varied seasonally as a result of fluctuating water levels, following a cycle of winter dilution and summer concentration. In comparison to the Cape Point vleis both the Grootvleis displayed increased proportions of calcium, and Rondevlei displayed increased proportions of both calcium and potassium. Levels of total dissolved iron were low in Grootwitvlei and Rondevlei, as were levels of SRP and nitrite. Ammonium levels, however, were high in Rondevlei. Both vleis showed a marked winter peak in nitrate and nitrite levels coinciding with the period of greatest inflow.

The geology and soils of the catchments exert a strong influence on the chemistry of the waters. Water draining through well-leached, acid sands and TMS-derived soils, results in the low pH waters of Suurdam and Gillidam and causes the seasonal minima common to the other vleis. Calcareous outcrops and lime deposits in the catchments of the Grootvleis and Rondevlei contribute to the higher pH, alkalinity and greater proportions of calcium in the vlei waters. The TMS-derived podsols and acid sands are generally of low nutrient status and are depleted of base cations, but contain a well developed ferri-humic horizon, which results in the enhanced iron and SRP levels in the more darkly stained and acid waters. Atmospheric precipitation of marine salt appears to be the primary determinant of the ionic composition of the vleis. Atmospheric input of nutrients may be significant in the case of P, but has little impact on the nutrient status of the waters. In Rondevlei, significant nutrient input occurs from anthropogenic terrestrial sources and faunal excreta. The excreta also contribute to the calcium and potassium proportions of the waters and thus contribute to a higher pH and relatively great ANC. High rates of evaporation and the endorheic nature of Sirkelsvlei appear to be the cause of its high salinity (in contrast to the smaller and more recently formed Suurdam and Gillidam).

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Appendix 5.1 The ranges of the mean molar percentages of each of the four major cations.

	SU	GI	SI	GR	GW	RO
Na range	81-84	84-87	86-90	79-84	69-75	66-83
Ca range	3-4	3-4	2-3	6-9	16-22	1-19
Mg range	11-13	9-11	7-9	10-11	8-9	8-11
K range	2-2	1-2	2-2	0-1	1-1	4-7

CHAPTER 6 : ORGANIC CHEMICAL ENVIRONMENT

INTRODUCTION

The dissolved organic matter (DOM) found in water and soil consists of a mixture of the products of plants, animals and micro-organisms in various stages of decomposition, and of substances synthesized chemically and biologically from these degradation products. The organic compounds can be divided into two broad categories, namely non-humic and humic substances (Schnitzer and Khan 1972). Non-humic substances include compounds such as carbohydrates, proteins, peptides, amino acids, fats, waxes, resins, pigments and other low-molecular-weight organic substances, each of which exhibits specific chemical characteristics, and thus forms a distinct class of compounds. These substances are generally easily utilized or degraded by the biota, display relatively rapid turnover times, and are normally low in concentration at any particular instant. Humic substances constitute by far the greater proportion of the dissolved organic matter (Schnitzer and Khan 1972, Reuter and Perdue 1977). They consist of amorphous, yellow, brown or black, hydrophilic, acidic, polydisperse, partly aromatic, chemically complex substances, which range in weight from a few hundred to a few hundred thousand daltons. These compounds display some important common characteristics such as a general resistance to microbial degradation, the ability to form stable water-soluble and water-insoluble salts and complexes with metal ions and hydrous oxides, and the ability to interact with clays, other minerals and organic compounds including alkanes, fatty acids, dialkyl phthalates, pesticides, herbicides, carbohydrates, amino acids, peptides and proteins (Schnitzer and Khan 1972, Schnitzer 1978 in Kerndorff and Schnitzer 1979). In addition they act as surface active materials (Hyase and Tsubota 1973). Otherwise they form a heterogenous group of complex polymers, the character of each mixture depending largely on the contribution of the major allochthonous and autochthonous sources and the inorganic chemical environment of the water. Humic substances in the soil have traditionally been divided into three fractions based on their solubility in acid and base :

-Humic acids (HA), precipitated by acidification to pH 2
-Fulvic acids (FA), which remain in solution at pH 2, and
-Humin, which is insoluble.

Aquatic humic substances can be divided into the first two fractions. The principal difference between HA and FA is the molecular weight, although the two fractions are also found to differ in the proportions of the major functional groups. FA forms the lower molecular weight fractions (Ghassemi and Christman 1968, Gamble 1970, Buffle *et al.* 1978, Visser 1984), but contains a higher content of oxygen-containing groups (COOH, OH and C=O) (Kerndorff and Schnitzer 1979). FA also constitutes the bulk of aquatic humic substances in surface waters, commonly comprising 80 90% of the concentration by weight (McKnight *et al.* 1983, Visser 1984). FA and HA are chemically similar in their behaviour, but part of the higher-molecular-weight fraction may exhibit a colloidal structure, important in the physical behaviour of the humic substances (Pennanen 1975, Buffle *et al.* 1978). In simple terms the structure of the humic compounds consists of a polymeric skeleton or core of varying amounts of aromatic and aliphatic components with attached functional groups. The major functional groups are the oxygen containing functional groups - the carboxyl, phenolic and alcoholic hydroxyl, and the ketonic and quinoid carbonyl groups. Through these groups humic substances react with trace metals, cations, anions and other organic ligands.

A number of ideas have been presented concerning the process of formation of humic substances both in the soil and in aquatic environments. In soils, humic substances are thought to be formed from the contributions of various natural polymers such as lignin, polysaccharides and protein, which then undergo oxidation, polymerization and the degradation of the easily degradable fraction. A high phenol content in humic compounds results from phenolic plant constituents such as lignin, tannin, phenolic acids and flavanoids (Tsutsuki and Kuwatsuka 1978, 1979). In the aquatic environment the most abundant sources of organic matter are often the plankton and thus lignin, which is highly aromatic and a major precursor to soil humic substances, is often lacking. The formation process is thought to involve sugars and amino acids or amines in the "Maillard reaction", resulting in brown nitrogenous polymers (Ertel and Hedges 1983, Poutanen 1985). Harvey *et al.* (1983) suggest a pathway *via* the oxidative crosslinking of polyunsaturated lipids, catalyzed by ultra-violet (uv) light and transition metals, with amino acids and sugars as appendages to the main structure. Poutanen (1985) supports both the Maillard-type reaction and the inclusion of phytoplankton-derived lipids, forming the highly branched network of aliphatic structures. The aromatic content of humic substances formed in the aquatic environment (autochthonous HS) is thus normally much lower than that of humic substances formed in the soils of the terrestrial environment (allochthonous or terrigenous HS). In marine systems, very little, if any aromaticity is found in humic substances, with unsubstituted aliphatic structures dominating (Kalle 1966, Poutanen 1985, Hatchers *et al.* 1983). In terrestrial systems, humic substances are largely aromatic, derived from lignin and other residues which are predominantly aromatic in structure and which occur only in the terrestrial vascular plants. The degree of aromaticity can thus be used as a measure of the terrigenous humic content in an aquatic system. In freshwater systems emergent macrophyte decomposition will contribute to the aromatic content of autochthonous humic substances, particularly in very small ponds. Within any system additional factors may be important in determining the character of the humic compounds. Geochemical and geographical factors, the nature of the parent plant material, the degree of microbiological activity and the climate are all contributing factors (Gjessing 1976, Gillam and Wilson 1983). In soils, moisture and temperature are particularly important factors regulating decomposition (Millar 1974, in Wallis 1979), with excess moisture causing reducing conditions which limit microbial activity and thus retard the rate of decomposition and probably affect the character of the humic compounds. The initial rate of formation of humic substances from dead plant material appears to be high in all cases. Phytoplankton cells (Poutanen 1985), macrophyte leaves (Stewart and Wetzel 1980, 1981) and leaves of terrestrial fynbos shrub species (Dudley 1983, Raubenheimer 1987) all rapidly produce humic substances after death and on immersion in water. Decomposition of the structural components of the plant material proceeds more slowly and thus the incorporation of much of the aromatic and less labile content is likely to occur later in the process of formation. This latter, slower, process of formation is also referred to as humification and an increasing degree of humification of the organic matter has variously been reported to involve increases in the aromatic character of the material, the condensation of unsaturated aliphatic chains with each other, increases in the carboxyl and methoxyl and to a lesser extent carboxyl content, decreases in the content of alcoholic hydroxyl groups and decreases in the H:C and O:C ratios of the compounds (Schnitzer and Resjardins 1965, Jackson 1975, Gjessing 1976, Visser 1983b). The initial rapid formation of humic substances and the slower humification process appear to reflect the ideas of aquatic and terrestrial production respectively of the humic substances mentioned earlier. The process of humification is generally reported in soil environments as a continuous and very slow process. No reference was found to the process of humification in aquatic environments, other than seasonal changes in the degree of humification (De Haan 1983, Visser 1983a, 1983b) in lake and river waters. The processes of uv and microbial degradation and changes in the rate of production of autochthonous humic substances will all act to alter the degree of humification of the water, so that the extent of humification reactions occurring in the aquatic environment is not easy to establish.

The importance of humic substances in determining many of the limnological features of aquatic systems has long been realized. Classically, 'brown-water' or dystrophic lakes were known to have low to moderate plankton productivity (Wetzel 1983 and see chapter 1). Limited light penetration, complexation and adsorption reactions of a variety of inorganic and organic chemical species, and the depression of the pH and redox potential, all affect the planktonic community to some degree and are discussed in more detail later. Most studies on humic substances in aquatic environments have appeared in the last two decades but few of these deal with the temporal and spatial distribution of aquatic humic substances. This has largely been the result of the lack of adequate methodologies for routine measurement. In this chapter an attempt has been made to measure both the temporal and spatial variation in the quantity, as well as to gain some knowledge of the variation in the character, of the mixture of humic compounds present in the water column of each of the six vleis studied. The discussion then aims to relate the variation in humic substance to the major environmental variables of each catchment and the inorganic chemical environment of each vlei. Further discussion on the importance of the variation in levels of humic substance is presented in Chapter 9.

OVERVIEW OF METHODS

Due to the broad heterogeneity in the structure of humic substances, and their importance in the environment, a large body of literature has appeared in recent years on the structure and characterization of these compounds. Structural analyses have been conducted by means of infra-red absorption spectrometry, electron-spin resonance, gas chromatography/mass spectrometry and nuclear magnetic resonance (^{1}H and ^{13}C). For all these techniques sophisticated instrumentation are required, as are thorough preseparation and pretreatment steps. In addition, in most cases chemical degradation techniques are required to break the macromolecules into fragments that are more easily studied. From these methods valuable information has been obtained on the amounts of different functional groups present, the free radical groups present and the carbon structure (Schnitzer and Khan 1972, Gjessing 1976, Sposito *et al.* 1976, Holtzclaw and Sposito 1979, Holtzclaw *et al.* 1980, Choudhry 1981, Liao *et al.* 1982, Gillam and Wilson 1983, Hatcher *et al.* 1983, Reuter *et al.* 1983, Steelink *et al.* 1983, Thurman and Malcolm 1983 and Becher 1987). Analyses of this type are time-consuming however, and require both sophisticated equipment and special manipulative skills. What is required in broad ecological studies, including this one, is a technique that allows a rapid characterization and quantification of the humic substances present in water. No one such technique exists at present. Many studies have employed separation techniques such as solvent extraction (Eberle and Schweer 1973, Wagner and Hoyer 1975, Tipping and Woof 1983), acid precipitation (Black and Christman 1963, Telang *et al.* 1976) and resin absorption (Thurman and Malcolm 1983, Visser 1983) to separate fractions which are then defined according to the nature and properties of the technique used. Disadvantages of this approach result from differences in methodologies making it difficult to compare the results from different studies. Buffle *et al.* (1982) pointed out the importance of attempting to characterize humic substances either quantitatively or with respect to their properties with as little modification as possible to the medium under study, thus avoiding coagulation, adsorption or aggregation reactions. To do this a number of sensitive techniques should be used together. The same approach has been used in this study, where relatively easily available equipment, and a number of techniques that are both sensitive to humic substances and allow the relatively rapid processing of samples, have been employed in an attempt to characterize and quantify the dissolved humic fraction of natural waters.

The spectrophotometric measurement of absorbance (optical density) in both the visible and uv regions of the spectrum has been employed in many studies to quantify and to characterise the levels of humic substances present. In almost all cases, the uv-visible spectra of neutral, alkaline or acidic aqueous solutions of humic substances are featureless, with no characteristic maxima or minima (Schnitzer and Khan 1972, Gjessing 1976, Visser 1984). The absorbance is caused largely by the presence of multiple bonds and unshared electron pairs in the humic molecules (referred to as chromophores) (Atherton *et al.* 1967, Orlov 1972). The virtually undifferentiated spectra are thus thought to result from the large numbers of chromophores in the humic compounds which result in many overlapping excitation levels (Visser 1984). Various functional groups (C-OH, C-NH_2 etc) do not confer colour but further increase the colour of the chromophores (and are referred to as auxochromes)(Schnitzer and Khan 1972). Absorbance increases almost exponentially with decreasing wavelength (800 - 200 nm), but occasionally an indication of a 'shoulder' in the curve can be discerned near 280 nm (Ziechmann 1964, Sato Kumada 1967, Schnitzer and Skinner 1968, Brown 1974, 1977). Brown (1974) related this shoulder to the presence of simple aromatic rings, "especially those conjugated with carboxyl, carbonyl and phenolic oxygen" and Buffle *et al.* (1982) to the presence of "phenolic and benzene carboxylic functional groups". The lack of any common characteristic feature in the spectra has resulted in absorbance normally being characterized by measurement at an arbitrarily fixed wavelength and by absorbance ratios, which are a measure of the spectral slope between two set wavelengths. Absorbance has been measured at a multitude of fixed wavelengths between 250 nm and 550 nm (see table 6.1), and also at higher wavelengths.

wavelength (nm)	reference
220	Ogura and Hanya (1967,68).
250	Mickle and Wetzel (1978), Stewart and Wetzel (1980, 81a, 81b), De Haan (1972a, 72b, 82, 83), Dorsch and Bidleman (1982), Melcer and Hassett (1986).
254	Geller (1985), Aho and Lehto (1984) Dobbs, Wise and Dean (1972).
260	Banoub (1973).
270	Davies-Colley (1983).
280	Brown (1974, 77), Mrkva (1969).
285	Buffle and Deladoey (1982), Buffle *et al.* (1982).
300	Wilson (1959).
310	Brown (1974,77) (E_{285}/E_{310}).
320	Mackereth (1963), Pennanen (1975), Buffle *et al.* (1982) (E_{285}/E_{320}).
330	Moore (1985).
350	Melcer and Hassett (1986) (E_{250}/E_{350}), Carlson and Shapiro (1981).
365	De Haan (1972a, 72b, 83), De Haan *et al.* (1983) (E_{250}/E_{365}).
380	Jerlov (1986).
400	WRC (1979), Larson (1978).
420	Pennanen (1975, 82), Pennanen and Frisk (1984).
430	Gjessing (1976).
440	Kirk (1976, 79, 80, 81), Bowling *et al.* (1986).
465	Underdown *et al.* (1981), Langford *et al.* (1983).
540	Visser (1984).

Table 6.1 Some of the wavelengths between 220 and 550 nm that have been used to measure the absorbance of humic substances

Measurement between 400 and 440 nm is normally used in studies on photosynthetically available radiation (PAR) (Kirk 1976, 1979, 1980, 1981, Bowling *et al.* 1986) and in studies on water colour. The wavelengths are close to the peak of the action spectrum of algal photosynthesis in the blue region, and there is a close statistical relationship with colour measured on the platinum (Hazen) scale. Measurement in the uv region of the spectrum is normally a consequence of the greater absorbance at these wavelengths and thus greater accuracy of measurement in waters of low colour concentration. Attempts to relate uv absorbance to the concentration of dissolved organic carbon (DOC) in the water appear in many cases to have been successful. Stewart and Wetzel (1981) found that absorbance correctly predicted DOC concentration only in the more labile materials in their studies using both macrophyte leachates and lake waters, and cautioned that this relationship might not be generally applicable. De Haan *et al.* (1982), however, found the absorbance at 250 nm (A_{250}) to be closely correlated to DOC for the humic lake Tjeukemeer (over a six year period) as well as for oligotrophic and humic Finnish lake waters. In their view A_{250} is an accurate predictor of DOC concentration in the routine analysis of humic lake waters. At wavelengths of 365 nm and greater the linear correlation varied in slope and decreased in significance. Buffle and Deladoey (1982) similarly established a close correlation between uv absorbance at 385 nm and DOC concentration in Swiss natural waters, and studies by Banoub (1973), Lewis and Tyburczy (1974), Lewis and Canfield (1977), Sheppard (1977) and Moore (1985) have also established relationships at similar wavelengths. Schnitzer and Khan (1972) have listed four important variables causing increased absorbance in humic substances - (a) the degree of condensation of the aromatic rings which they contain (Kononova 1966), (b) the ratio of carbon in aromatic nuclei to carbon in aliphatic or alicyclic side chains (Kasatochkin *et al.* 1964), (c) total carbon content (Kleist and Mucke 1966) and (d) molecular weight (Kleist and Mucke 1966).

A number of different absorbance ratios have been proposed in various studies. The ratios are usually independent of the concentration of humic substances and their values are thought to be determined largely by the particle size or molecular weight, and thus linked to variables such as the degree of humification, molecular condensation, pH, the number of carboxyl groups and others (Chen *et al.* 1977, De Haan 1983, Visser 1984). Ratios such as E_{465}/E_{665} (Kononova 1966, Chen *et al.* 1977), E_{420}/E_{665} (Kalle 1961, 1962, 1963, 1966), E_{285}/E_{665} (Buffle *et al.* 1982), E_{285}/E_{310} (Brown 1977) and E_{250}/E_{365} (De Haan 1983) have been used. The ratio E_{465}/E_{665} has been more popular in use than most, particularly in the characterization of extracted soil humic substance. It does however have limitations in the measurement of humic substances in natural waters, the chief being the extremely small absorbance values measured in the visible wavelength region (Brown 1974). For this reason I decided to use the ratio proposed by De Haan (1983) for the study of humic waters. By fractionation, using gel filtration procedures (Sephadex gel) he established the E_{250}/E_{365} ratio as an easy measure of the relative humification of coloured lake waters. Thus relatively low ratios (low spectral slope) were characteristic of strongly humified and oligotrophic waters, a relatively high molecular weight and a high content of phenolic polymers. An increase in the ratio indicated degradation of the humic substances and a decrease in the mean molecular weight, characteristic of more productive coloured lakes. De Haan (1972, 1975, 1983), while investigating the applicability of the E_2/E_3 ratio, found values in the alkaline humic lake Tjeukemeer to range between 4.95 and 7.62 (17.1 to < 4.0 Hazen units). In other Friesland (Netherlands) lakes with colour varying between 2 and 14 Hazen the ratio ranged from 6.42 to 7.71, while in the Finnish lakes the ratios measured were 7.50 in Saanjarvi (10 Hazen), 5.98 in Saimaa (35 Hazen), 4.34 in Kaakonlampi (200 Hazen) and 4.98 in the epilimnion of Harkojarvi (170 Hazen) and 4.72 in the hypolimnion (240 Hazen) (from Pennanen 1975).

Size fractionation, by membrane ultrafiltration and gel filtration chromatography, has been performed in many studies in attempts to characterize the mixtures of humic substances present in any humic lake waters (Ghassemi and Christman 1968, De Haan 1972, 1984, Pennanen 1975, 1982, Gjessing 1976, Buffle *et al.* 1978, Larson 1978, Stewart and Wetzel 1980, 1981, Buffle and Deladoey 1982, Buffle *et al.* 1982, Aho and Lehto 1984, Cole *et al.* 1984, Visser 1984). Once fractionated, absorbance (visible and uv), fluorescence, and other techniques have been used to examine the relative contribution of each fraction to the overall spectra of the unfractionated water. Humic substances, as noted, range widely in molecular weight with fulvic acids forming the lower molecular weight fraction and humic acids the larger molecular weight fraction. There is some uncertainty over the actual molecular weights as a result of the different and often unreliable methods used for their estimation, but they appear to range from a few hundred to a few hundred thousand daltons (Buffle and Deladoey 1982, Visser 1984). The high-molecular-weight component is more intensely coloured (stronger absorbance), but fluoresces weakly, whereas the low-molecular-weight component is pale in colour (weaker absorbance) and fluoresces strongly (Stewart and Wetzel 1980, Pennanen 1982, Visser 1984). However in many waters, especially more productive waters, the fulvic acid component accounts for by far the greatest fraction of the humic substances and thus is responsible for most colour production, absorbance and of course fluorescence (Dempsey and O'Melia 1983, Oliver *et al.* 1983).

The measurement of fluorescence has also been widely employed in the characterization of humic substances. Humic substances in general fluoresce strongly and are probably only second to photosynthetic pigments as fluorescent materials in natural waters (Underdown *et al.* 1981). Data confirm that the fluorescence is due to the properties of the humic substances themselves (L'evesque 1972, Gosh and Schnitzer 1980). Fluorescence is usually exhibited by aromatic, cyclic or closed-ring structures, although some aliphatic compounds can also show fluorescence. Certain functional groups (electron donating groups) such as hydroxyl, methoxyl and some amines further increase the fluorescence of aromatic compounds and shift it to higher wavelengths (Schnitzer and Khan 1972, Visser 1983). Distinct fluorescence maxima are found in both the excitation and emission spectra. The wavelengths of the maxima vary with the character of the humic substances, however. The structural features that contribute to these shifts in wavelength include the phenolic content, which has been shown to be positively correlated with the excitation maximum (Visser 1983), and the molecular weight, which is inversely related (Stewart and Wetzel 1980, Visser 1983). The origin of the humic material has also been shown to be important, with autochthonous aquatic humus showing maxima at lower wavelengths than its terrigenous humic counterpart (Ertel and Hedges 1983). Ewald *et al.* (1983) ascribes this to the lack of phenol derivatives in marine autochthonous humic substances. The maximum excitation or emission wavelength can thus be used to characterize aquatic humic substances. Some of these maxima recorded in various studies are listed in table 6.2.

The relative intensity of the fluorescence is determined more by the basic aromatic structure of the molecules than by the functional groups (Visser 1983). The molecular weight is also inversely related to the intensity (Ghassemi and Christman 1968, Hall and Lee 1974, Stewart and Wetzel 1980, 1981, Visser 1983) and autochthonous aquatic humic substance generally shows a greater intensity than terrigenous humic substance (Jackson 1975), although no apparent relationship was found between the intensity and the source of the humic substances or any other polymer characteristics by Ertel and Hedges (1983). Attempts to relate intensity of fluorescence to the concentration of dissolved organic carbon concentration have met with limited success. Smart *et al.* (1976) found a strong linear correlation between DOC and relative intensity. Stewart and Wetzel (1981) however, found fluorescence intensity to be a consistently poor predictor of DOC concentration, which they relate to greater levels of internal quenching and shielding in compounds of larger apparent molecular weight. Various other studies, such as those of Black and Christman (1963), Ghassemi and Christman (1968), and Buffle and Deladoey

(1982) have also reported the lack of a constant DOC:fluorescence ratio for waters of differing origin.

Emission (nm)	Excitation (nm)			
	(a)		(b)	
370-550	320-370		372-461	Visser (1983).
420-500		345-420		Buffle *et al.*(1982).
420-490		-		Dorsch and Bidleman (1982).
426-510		346-427		Hall and Lee (1974).
400-460	250-270		340-350	Smart *et al.*(1976).
420	325			Plechanov *et al.* (1983).
445-450	350			Saar and Weber (1982).
450	365			Ghassemi and Christman (1968).
450			470	L'evesque (1972).
465		375		Larson (1978).
450-520		325-427		Ertel and Hedges (1983).
480		370		Underdown *et al.* (1981).
490	365	404	436	Christman and Ghassemi (1966).
490	365	404	436	Carlson and Shapiro (1981).

Table 6.2 Fluorescence maxima (excitation and emission) recorded for a variety of different humic substances

Brun and Milburn (1977) report an automated fluorometric determination that has worked well on a variety of estuarine waters, but has not been applied to fresh waters, which contain mostly terrigenous humic substances. Buffle and Deladoey (1982) further report the DOC:fluorescence ratio to be a good indicator of the nature of the organic matter, but only at DOC concentrations of less than 10 mg l^{-1}.

Factors that affect the absorbance and fluorescence of humic substances in the aquatic environment are pH, metal ion concentration and temperature. The pH has no noted effect on the maximum wavelength of emission or excitation (Choudry 1981, Schnitzer and Khan 1972) but it does affect the relative fluorescence intensity of both. Between pH 6 and pH 8 there is little change in fluorescence intensity, but with increasing pH the excitation band often intensifies and the emission band intensity often weakens, while with decreasing pH the opposite occurs (Visser 1983). The pH dependence is further thought to vary with the type of humic substance. Studies by Smart *et al.* (1976) and Stewart and Wetzel (1980) showed the intensity of emission to decrease at pH less than 5 and to either increase or decrease at pH greater than 7. Absorbance, and thus colour, is also pH dependent and increases with increasing pH (Tsutsuki and Kuwatsuka 1979, Gjessing 1981), although Stewart and Wetzel (1980) found an increase of less than 3.5% (A_{250}) between pH 4.5 and 10.1. Temperature affects both the fluorescence intensity and the maximum wavelength of emission and excitation. Visser (1983) found lowered excitation and emission wavelengths with lowered temperature and increased fluorescence intensity of both emission and excitation with lowered temperature, as did Smart *et al.* (1976).

The metal ion concentration is well known to affect the fluorescence and absorbance of humics substances by the formation of metal-humic complexes. The fluorescence of humic substances is generally quenched by the complexation of trace metal ions (Parker 1968, Chen 1976, Langford *et al.* 1983) and absorbance is generally enhanced by complexation (Lawrence 1980, Gjessing 1981, Underdown *et al.* 1981, Langford *et al.* 1983).

Another method that has been less widely used, but which may be more specific in what it measures, is the use of the Folin-Ciocalteu phenol reagent. The reagent was developed by Folin and Ciocalteu (1927) for the determination of tyrosine and tryptophane in proteins and has since been suggested as a suitable measure of humic substance concentration in soils (Sharma and Krishnan 1966, Tsutsuki and Kuwatsuko 1978), tannin and lignin levels (Kloster 1974) and polyphenolic compounds in lake sediments (Povoledo and Gerletti 1968). In the reaction, phosphomolybdic and phosphotungstic acids are reduced by the aromatic hydroxyl or phenolic groups to a heteropoly blue in alkaline solutions. De Haan (1975) investigated its use on dissolved humic substances in fresh waters, using tyrosine as a reference standard. He concluded that the determination underestimated the humic substance content (and that absorbance at 278 nm was an overestimate), possibly as a result of fewer phenolic groups occurring on large molecular weight humic substances. This relates to the findings of Visser (1983) that an increase in the maximum excitation wavelength correlates with both an increased mean molecular weight and a decrease in phenolic content. De Haan concluded that the E_2/E_3 ratio (as a measure of humification) was positively correlated with the Folin-Ciocalteu reaction calculated per colour unit (at 365 nm) at each station, and that this method thus supplied useful additional information about the nature and amount of the humic substances. More recently Box (1983) investigated the performance characteristics of this method. The method was found to have definite advantages over other methods measuring phenolic compounds, although varying absorbances given by equal concentrations of substituted phenols suggest that the method be used to monitor variations in the humic substance levels in natural waters rather than to determine their absolute concentrations. Randtke and Larson (1984) questioned the sensitivity of the method and the possibility of interference, and cautioned the interpretation of results due to temporal and spatial variation in the character of the humic substances. In reply, Box (1984) stated that interference from non-phenolic substances is negligible in unpolluted waters, whereas absorbance and fluorescence methods do suffer from such interference, and that spatial and temporal variation in the character is a problem faced by any nonspecific method in the determination of a "large amorphous grouping, such as humic substances".

METHODS

Since I wanted a rapid quantification and characterization, fractionation procedures were omitted and absorbance and fluorescence techniques and the Folin-Ciocalteu reagent were used. The methods are summarized in table 6.3. All the chemical standards and reagents were made up in double distilled water (see methods in chapter 5). The humic standard was made from Ega-Chemie (H1,675-2) Aldrich humic acid (sodium salt), the tannin standard from Sigma (T-0125) tannic acid and the Folin-Ciocalteu phenol reagent was from Merck (Art. 9001). All the remaining chemical standards and reagents were made up using analytical grade chemicals. Sample containers and all glassware were precleaned as described in chapter 5 and samples were collected, stored and processed as described in chapter 3.

Since both absorbance and fluorescence intensity are pH-dependent, a portion of each sample was buffered in phosphate buffer (KH_2PO_4/Na_2HPO_4) of pH 6.88. In each case 5 ml of buffer were added to 10 ml of sample and the final pH checked to measure 6.88. Phosphate buffers have been used by De Haan (1972), Lawrence (1980), Tipping and Woof (1983) and Geller (1985), with apparently no interfering

Variable	Procedure	Measurement*
	Absorbance	
untreated samples		
Colour	absorbance measured at 400nm.	A_{400}
Humic substances	absorbance spectrum 230-500nm Feb.(1), July, September, December and Feb.(2) samples.	E_{250}/E_{365} A_{290}
buffered samples		
Colour	absorbance measured at 400nm.	A_{400}
Humic substances	absorbance spectrum 230-500nm measured for all 15 samples (every month).	E_{250}/E_{365} A_{290}
Fulvic acids	Lawrence (1980) semi-quantit. multiple wavelength approach, using an expanded form of Beers Law.	A_{290}, A_{320} A_{360}
	Fluorescence	
buffered samples		
Humic substances	Excitation spectrum 200-500nm measured at a constant emission of 470 nm for Feb.(1), July, September, December and Feb.(2) samples.	μ_{ex} I_{ex}
Humic substances	Emission spectrum 330-700 nm measured at a constant excitat. of 340 nm for Feb.(1), July, September, December and Feb.(2) samples.	μ_{em} I_{em}
	Folin-Ciocalteu	
untreated samples		
Phenolic content	As per Box (1983) using the phenol reagent of Folin and Ciocalteu (1927)	as mg l^{-1} of phenol

*A_{250} = absorbance of 250 nm

μ_{ex} = maximum wavelength of excitation

μ_{em} = maximum wavelength of emission

I_{ex} = relative intensity of excitation

I_{em} = relative intensity of emission

Table 6.3 Summary of the methods used for the quantitave and qualitative analysis of humic substances.

effects, whereas 0.01M NaOH was found by Lawrence to produce time-dependent instability.

All absorbance measurements were made using a Beckman Model 25 double-beam uv/visible spectrophotometer with samples measured in matched 1 cm path-length quartz cuvettes. Dilutions were necessary in the case of Suurdam, Gillidam and Sirkelsvlei samples, and double distilled water was added to dilute these samples 1 in 5, 1 in 2 and 1 in 2 respectively.

Colour was measured at an absorbance wavelength of 400 nm, as suggested by the Water Research Centre (1979), at the ambient environmental pH of the vlei water. Absorbance at this wavelength is highly positively correlated ($P < 0.001$, Pearson correlation coefficient) with absorbances at 420, 430 or 440 nm, which have been used by other authors (see table 6.1) as standard wavelengths for colour measurement. In the PAR attenuation studies of Kirk (1976, 1979, 1980) and Bowling *et al.* (1986) and the optical study of Davies-Colley (1983), absorbance (as optical density) is expressed as the absorption coefficient at 440 nm of humic substances ('gilvin'), which is calculated as absorbance over a one metre pathlength (corrected for scattering by water). Thus absorbance at 400 nm can similarly be expressed as an absorption coefficient (m^{-1}). Absorbance at all four wavelengths is also closely correlated to colour measured as Hazen units and Bowling *et al.* (1986) have calculated the regression equation for Tasmanian waters as

$$2.303.\text{absorption coefficient} = 0.081 \text{ Hazen} + 0.40 \ (r^2 = 0.984)$$

Colour was also measured in the buffered samples at 400 nm for comparison with the true colour measurements. The absorbance ratio of E_{250}/E_{365} (De Haan 1983), absorbance at 290 nm, and absorbance at 400 nm, were measured in order to characterise and monitor the variation in the quantity and quality of the humic substances. Absorbance spectra of 50 and 100 mg l^{-1} humic acid standards and 25 mg l^{-1} tannic acid standards (buffered where applicable) were measured with each batch of samples, and in addition the absorbance spectra of 200 mg l^{-1} phenol and 100 mg l^{-1} L-tyrosine solutions were measured. Sample blanks were prepared using double distilled water and where applicable, phosphate buffer.

The method of Lawrence (1980) is a semi-quantitative simultaneous determination of fulvic acid, tannin and lignin concentration using absorbance measured at three or more different wavelengths and having a reported deviation from known concentrations of $<15\%$ for fulvic acid, $<30\%$ for tannic acid and $<50\%$ for lignin. The gram extinction coefficients calculated by Lawrence (1980) were used in the calculations and may contribute to the error, although some comparison was possible between tannin determination and the concentration of the tannic acid standards. The separation of these three groups of compounds is possible because of large differences in their absorbance spectra. There is no characteristic difference between the spectra of humic and fulvic acids and thus the concentrations of fulvic acid are actually the combined concentrations of fulvic and humic substances and will be referred to as such.

Fluorescence was measured using an Aminco SPF 500 spectrofluorometer. Samples were all buffered and standards (also buffered) of humic acid (100 mg l^{-1}) and tannic acid (100 mg l^{-1}) were used. Sample blanks were prepared from double-distilled water (10 ml) and phosphate buffer (5 ml). No dilutions were necessary, since the gain control of the machine could be altered and sample fluorescence was corrected relative to the fluorescence spectra of the standards. Excitation and emission spectra were measured for samples taken during five different months in each vlei (see table 6.~~3~~4).

Correspondence analysis (see Methods in chapter 5) was used to present the three measures of relative intensity of fluorescence (emission, excitation (F1) and excitation (F2)) in two-dimensional space. The rows and columns of a 31 x 3 data matrix were plotted in the two-dimensional plane and rows with similar profiles were identified as a function of how closely together they were positioned. Thus samples which are similar are clumped and dissimilar samples are well separated.

The Folin-Ciocalteu phenol reagent was used to determine the polyphenolic content of the humic substances. The method was extracted from Box (1983), except for the alkaline supporting medium which was the Na_2CO_3.Na tartrate solution of Kloster (1974) and APHA (1976). The method involved the addition of 1,5 ml of the Na_2CO_3.Na tartrate solution and 0,5 ml of Folin - Ciocalteu phenol reagent to 10 ml of sample. The mixture was left for 60 minutes at 20°C for colour development and the absorbance was then measured at 765 nm. Standards of humic acid (100 mg l^{-1}), tannic acid (25 mg l^{-1}) and phenol (20 mg l^{-1}) and L-tyrosine (10 or 20 mg l^{-1}) were measured with each batch of samples to correct for any between-batch variation. The total relative standard deviation was 2.3% for humic acid, 1.1% for tannic acid, 1.1% for phenol and 1.4% for L-tyrosine. In addition calibration curves for all four standards were prepared - for humic acids (0-250 mg l^{-1}, $r=0.996$ $n=5$), tannic acids (0-25 mg l^{-1}, $r=0.999$ $n=5$), phenols (0-20 mg l^{-1}, $r=0.999$ $n=5$) and L-tyrosine (0-20 mg l^{-1}, $r=0.999$ $n=5$). De Haan (1975) determined the linear relationship for tyrosine up to 20 mg l^{-1} with a lower limit of detectability of 1 mg l^{-1}. The other three standards also displayed strongly positive linear relationships, up to 20 mg l^{-1} for tannic acid and phenol, and up to 250 mg l^{-1} for humic acid. Phenol was preferred as the reference standard by Box (1983) due to limited variation between different batches and different sources and it was also used in this study. All results are thus expressed as mg phenol l^{-1}. A lower limit of detectability of 6 mg phenol l^{-1} was demonstrated. Sample blanks consisted of both reagents with 10 ml of double-distilled water in the place of the sample. Dilution of the samples was only necessary for Suurdam samples, which were all diluted 1 in 2 with double-distilled water before the addition of the reagents.

A matrix of Pearson correlation coefficients (r) was calculated as a measure of the intensity of association between the different organic chemical variables.

RESULTS

Colour levels of the untreated water samples (**ambient colour** levels, where ambient refers to the colour of the water in its natural state), are shown in fig 6.1, the mean ambient colour values and their ranges are listed in table 6.4, and the box and whisker plot in fig 6.2 summarizes the median, the upper and lower quartiles, the range and the confidence interval of the median (see Results in chapter 5). Suurdam contains extremely dark coloured water: almost three times more intensely coloured than the next two most coloured vlei waters, namely, Sirkelsvlei and Gillidam. These three Cape Point vleis, in addition to containing the darkest water, showed a characteristic minimum in late winter and late summer maxima in colour levels. In comparison the colour levels in the two Grootvleis were on average less than half of those of Sirkelsvlei or Gillidam. The seasonal variation in colour levels was also markedly different, both displaying a late winter to spring maximum in water colour and late summer to autumn minima, in complete contrast to the Cape Point vleis. A noticeable difference between the two Grootvleis was the degree of seasonal variation in each, with colour levels in Grootrondevlei remaining higher on average throughout the year. Rondevlei had colour levels almost an order of magnitude below those of the Grootvleis. The seasonal variation was not marked, but there did appear to be maxima in late winter to spring, and in late summer. Variation in the colour levels between sampling points in each vlei was minimal except in Sirkelsvlei, where summer colour levels displayed distinct local variations, probably as a result of salinity, temperature and depth effects.

Colour levels in buffered samples (pH 6.88) (referred to as **buffered colour**) are presented in comparison to the mean monthly ambient colour levels in fig 6.3,

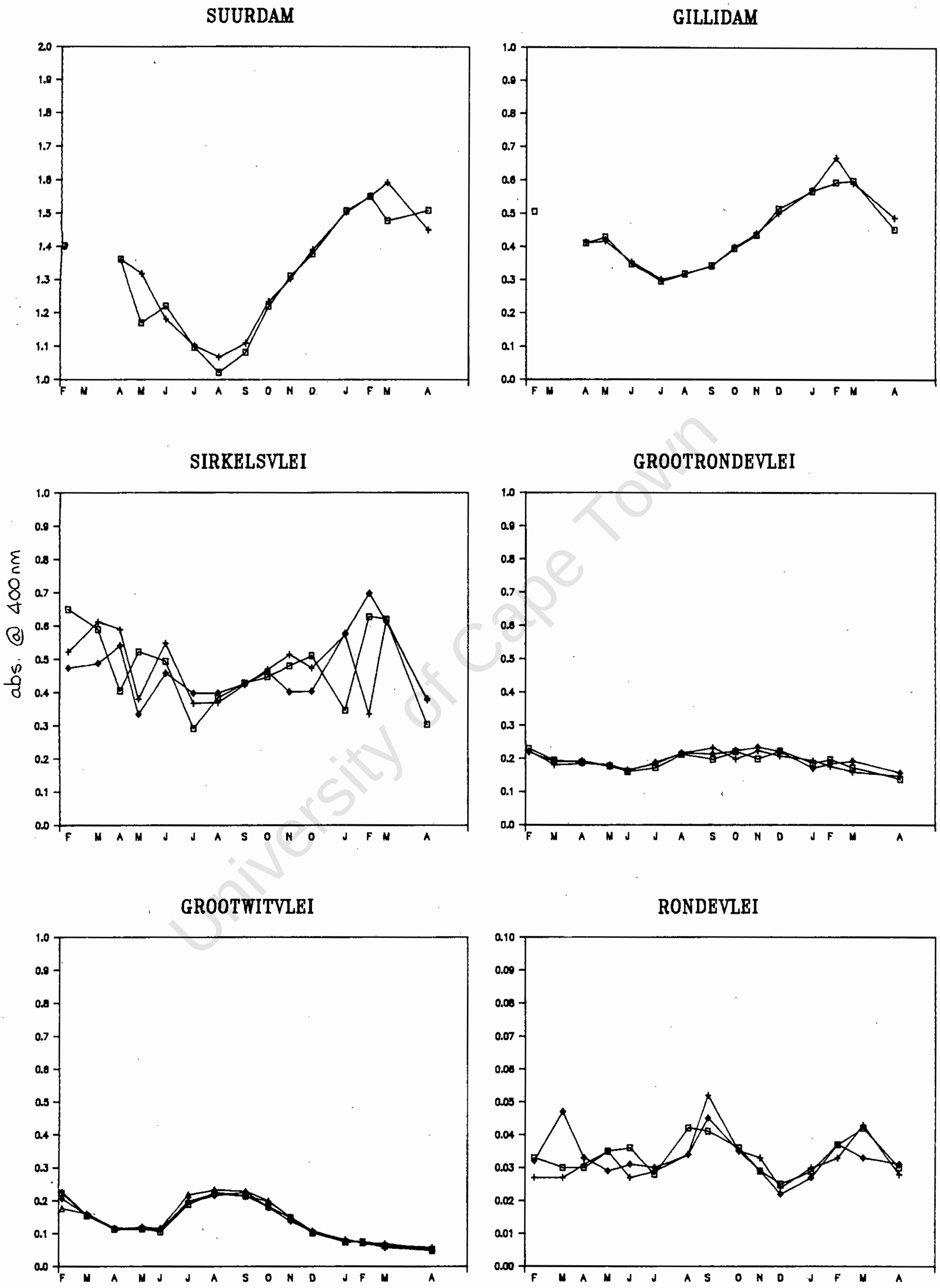

Figure 6.1 Colour in unbuffered water (ambient colour) measured as absorbance at 400 nm (optical density units) in each of the six vleis. Station 1 - □ , station 2 - + , station 3 - ◇ , station 4 - △ .

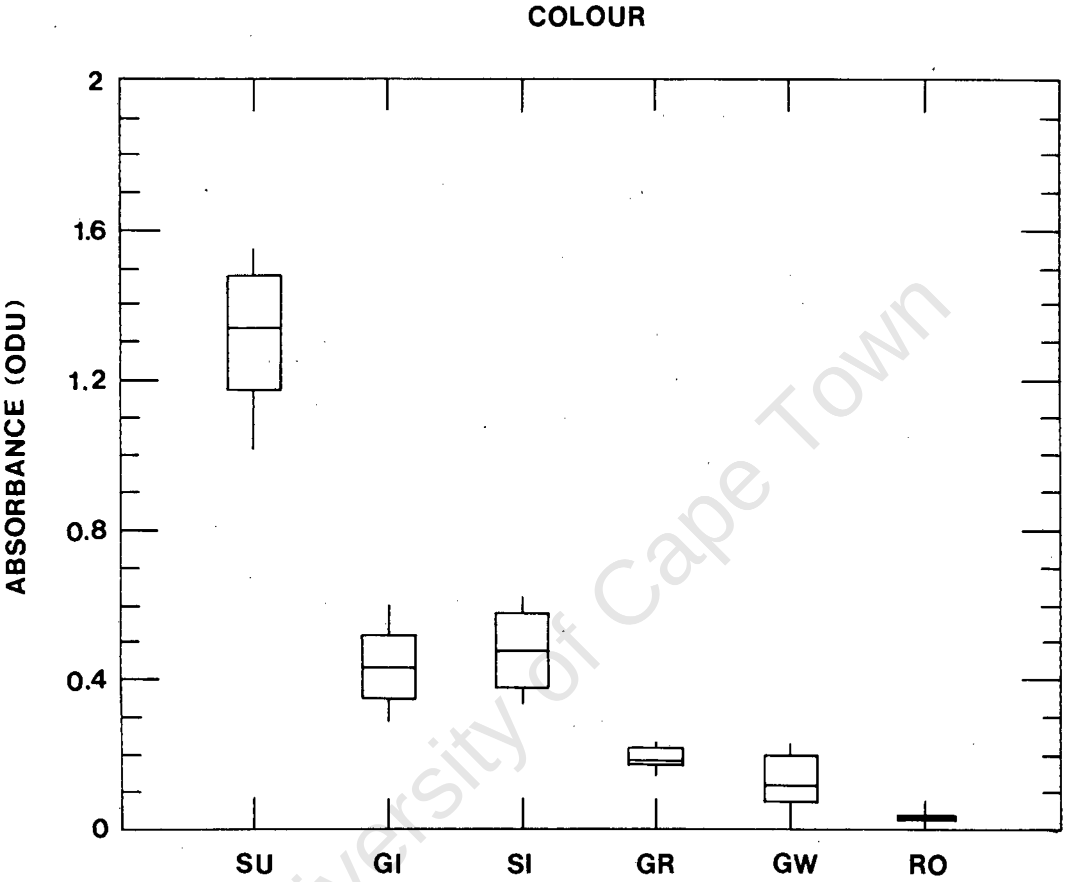

Figure 6.2 Colour in unbuffered water (ambient colour) measured as absorbance at 400 nm (optical density units). Box and whisker plot illustrating the median, the upper and lower quartiles and the range in Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO).

	SU		GI		SI		GR		GW		RO		HA
	mean	max min	mean	max min	mean	max min	mean	max min	mean	max min	mean	max min	mean
ABSORBANCE													
Colour *Hazen	1980	2400 1540	670	1000 435	710	1050 435	290	350 200	200	350 70	40	70 30	
Colour *A_{400}	1.316	1.591 1.021	0.444	0.667 0.295	0.473	0.697 0.292	0.192	0.233 0.137	0.137	0.233 0.047	0.033	0.052 0.022	0.612
Colour A_{400}	1.586	1.882 1.215	0.523	0.693 0.315	0.489	0.780 0.147	0.219	0.287 0.168	0.123	0.255 0.036	0.022	0.028 0.015	0.418
A_{290}	6.561	7.763 5.190	2.301	2.982 1.410	2.878	4.635 2.022	0.996	1.242 0.776	0.750	1.260 0.360	0.284	0.475 0.206	1.337
E_2/E_3	3.65	3.83 3.53	3.90	4.06 3.80	5.69	7.69 5.08	4.06	4.31 3.87	5.85	8.45 4.24	11.79	15.31 6.07	2.69
Fulvic acid	7.63	8.89 6.02	2.55	3.35 1.56	2.31	3.06 1.30	1.07	1.38 0.81	0.62	1.28 0.15	0.05	0.22 0.02	
FLUORESCENCE													
ex^1 max.	263	265 260	252	255 250	269	278 255	250	250 250	250	250 250	248	250 248	252
ex^2 max.	386	390 383	353	358 348	353	360 348	342	345 340	340	343 338	347	353 338	365
em max.	486	490 483	469	470 468	463	465 460	463	465 460	454	460 443	440	443 438	485
Iex^1 max.	32.2	48.1 19.9	126.4	161.2 96.2	136.1	184.0 91.3	129.2	146.5 117.0	187.8	215.1 160.8	142.3	169.3 130.5	146.1
Iex^2 max.	131.0	179.4 97.9	115.4	125.2 95.7	188.3	218.9 173.3	78.9	85.6 71.0	90.2	94.2 85.3	58.5	68.5 48.2	82.4
$\frac{Iex^1}{Iex^2}$	0.25		1.10		0.72		1.64		2.08		2.43		1.77
Iem max.	130.6	180.3 96.5	155.0	173.0 130.0	514.0	605.5 470.4	101.6	109.7 92.0	119.8	140.2 100.1	93.9	106.9 81.8	112.5
FOLIN-CIOCALTEU													
Phenol	21.8	26.1 18.2	9.3	12.5 5.7	8.3	10.5 7.1	4.2	5.2 3.1	2.2	3.9 0.6	0.4	0.9 0.2	5.9

Table 6.4 Mean, maximum and minimum values of the organic chemical variables measured in each of the six studied vleis, Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO), and for a 100 mg l^{-1} humic standard (HA). Values are expressed as follows - Colour as Hazen units (mg Pt l^{-1}), A_{400} as absorbance at 400nm over a 1cm pathlength (* -unbuffered samples), Fulvic acid as calculated from Lawrence (1980) in mg l^{-1}, Fluorescence excitation (ex) and emission (em) wavelength ( ) maxima in nm and intensities (I) as relative intensity units (standardised against tannic acid and humic acid), and polyphenolic content (Folin-Ciocalteu) as mg l^{-1} of Phenol. Iex^1/Iex^2 represents the ratio of the relative intensities at the two excitation maxima.

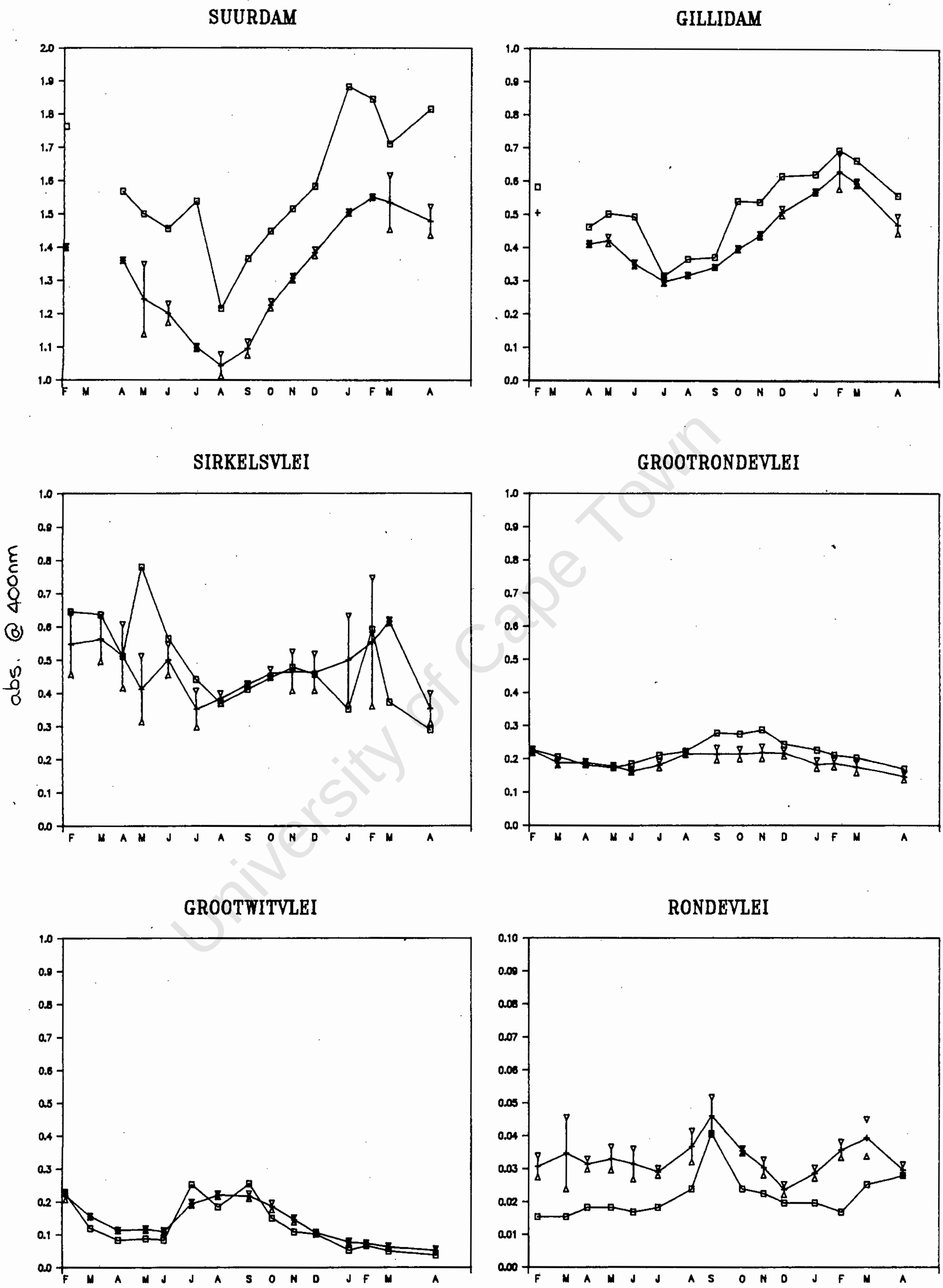

Figure 6.3 Colour in buffered water (buffered colour) measured as absorbance at 400 nm (optical density units) in each of the six vleis. Buffered colour - □ , and ambient colour - + (± sd).

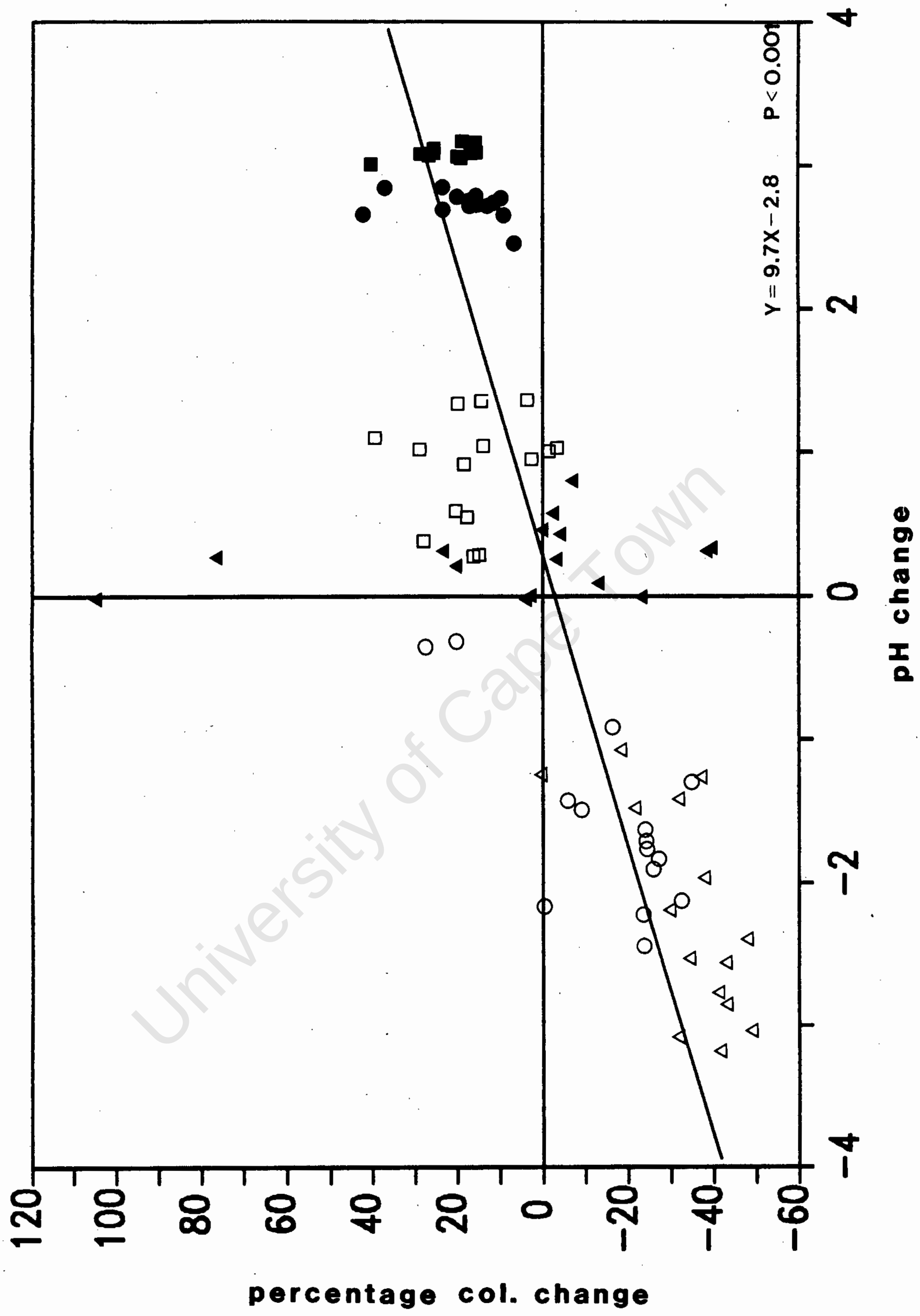

Figure 6.4 Percentage colour change plotted against the change in pH on buffering to pH 6.88. Colour measured as absorbance at 400 nm (optical density units). Suurdam (■), Gillidam (●) , Sirkelsvlei (▲) , Grootrondevlei (□) , Grootwitvlei (○) and Rondevlei (△).

SUURDAM	A_{400}unbf.	A_{400}bf.	A_{290}bf.	F-C	F.A.
A_{400}(unbuffered)					
A_{400}(buffered)	****				
A_{290}(buffered)	****	****			
Folin-Ciocalteu	****	***	**		
Fulvic acid	****	****	****	**	
E_{250}/E_{365}	•	•	•	•	•

**** =99.9%
*** =99.0%
** =95%
* =90%
() =-ve

GILLIDAM	A_{400}unbf.	A_{400}bf.	A_{290}bf.	F-C	F.A.
A_{400}(unbuffered)					
A_{400}(buffered)	****				
A_{290}(buffered)	****	****			
Folin-Ciocalteu	****	****	****		
Fulvic acid	****	****	****	****	
E_{250}/E_{365}	•	•	•	•	•

SIRKELSVLEI	A_{400}unbf.	A_{400}bf.	A_{290}bf.	F-C	F.A.
A_{400}(unbuffered)					
A_{400}(buffered)	**				
A_{290}(buffered)	**	****			
Folin-Ciocalteu	•	****	**		
Fulvic acid	**	****	****	****	
E_{250}/E_{365}	•	(*)	•	(****)	(*)

GROOTRONDEVLEI	A_{400}unbf.	A_{400}bf.	A_{290}bf.	F-C	F.A.
A_{400}(unbuffered)					
A_{400}(buffered)	****				
A_{290}(buffered)	****	****			
Folin-Ciocalteu	****	****	****		
Fulvic acid	****	****	****	****	
E_{250}/E_{365}	(***)	(**)	(**)	(****)	(**)

GROOTWITVLEI	A_{400}unbf.	A_{400}bf.	A_{290}bf.	F-C	F.A.
A_{400}(unbuffered)					
A_{400}(buffered)	****				
A_{290}(buffered)	****	****			
Folin-Ciocalteu	****	****	***		
Fulvic acid	****	****	****	****	
E_{250}/E_{365}	(****)	(****)	(****)	(***)	(****)

RONDEVLEI	A_{400}unbf.	A_{400}bf.	A_{290}bf.	F-C	F.A.
A_{400}(unbuffered)					
A_{400}(buffered)	****				
A_{290}(buffered)	•	*			
Folin-Ciocalteu	•	*	•		
Fulvic acid	***	****	•	•	
E_{250}/E_{365}	•	**	*	(*)	(****)

Table 6.5 The levels of significance of the Pearson correlation coefficient (r) calculated as a measure of the intensity of association between organic chemical variables - absorbance at 400nm (**A_{400}**) and 290nm (**A_{290}**) (buffered to pH 6.88), polyphenols as mg l^{-1} Phenol (**Folin-Ciocalteu**), fulvic/humic acid as determined by Lawrence (1980)(**Fulvic acid**) and the **E_{250}/E_{365}** ratio. Where $P < 0.001$ = ****, $P < 0.01$ = ***, $P < 0.05$ = **, $P < 0.1$ = * and ( ) indicates a negative correlation.

and the mean levels of buffered colour and their ranges are presented in table 6.4. As noted in the previous section, absorbance increased with increasing pH. In fig 6.3 the greatest pH increase on buffering was in Suurdam water followed by Gillidam, and the greatest pH decrease was in Rondevlei water followed by Grootwitvlei. The changes in water colour following buffering reflect the relative pH change. The mean change in absorbance, expressed as a percentage of the ambient colour level, was as follows: Suurdam 21.7 (± 7), Gillidam 18.4 (± 10), Sirkelsvlei 6.6 (± 39), Grootrondevlei 15.2 (± 12), Grootwitvlei -15.2 (± 18) and Rondevlei 34.0 (± 13). The relationship between colour change expressed as a percentage and the change in pH is displayed in fig 6.4 and shows a highly significant positive correlation ($P < 0.001$, table 6.5) with a linear regression of $y=9.7x-2.8$. Thus an increase in pH caused a related increase in colour and a decrease in pH caused a related decrease in colour. It is interesting to note that the darkest coloured waters were therefore made darker and the less coloured waters became lighter on buffering to a neutral pH. Seasonal variation in the buffered colour samples reflected the variation in the ambient colour ($P < 0.001$, table 6.5) except in Sirkelsvlei in the late summer and autumn months, when variables such as salinity, temperature and depth again probably caused interfering effects (see Discussion).

Variation in the E_{250}/E_{365} (E_2/E_3) ratio in each vlei is shown in fig. 6.5, the mean E_2/E_3 value and range in table 6.4 and a box and whisker plot in fig. 6.6. Relatively low ratios (4.0) are characteristic of strongly humified and oligotrophic waters, a relatively high molecular weight (75 000) and a high content of phenolic polymers, whereas higher ratios are characteristic of lower molecular weight and greater degradation of the humic compounds. The lowest E_2/E_3 ratios were for Suurdam waters, with values for Gillidam waters not very much higher. The ratios calculated for both vlei waters showed negligible seasonal variations and remained between 3.5 and 4.0 for almost all the months. Grootrondevlei waters also had low ratios, with a mean value just greater than 4.0, but showed a more distinct seasonal variation. The ratio dropped during spring and early summer and increased slightly in late summer and autumn. Although not apparent in fig. 6.5, the significance of the variation is borne by the strong negative correlation with both colour and polyphenolic concentration ($P < 0.01$ and $P < 0.001$, table 6.5). Sirkelsvlei waters had ratios which were markedly greater than those of any of the above three vleis, which varied seasonally, and which correlated negatively with polyphenol levels ($P < 0.001$). Grootwitvlei waters had a mean value similar to that of Sirkelsvlei, but showed large and very distinct seasonal variations. Ratios dropped to just over 4.0 during the rainy months and rose sharply at the end of spring as rainfall decreased.

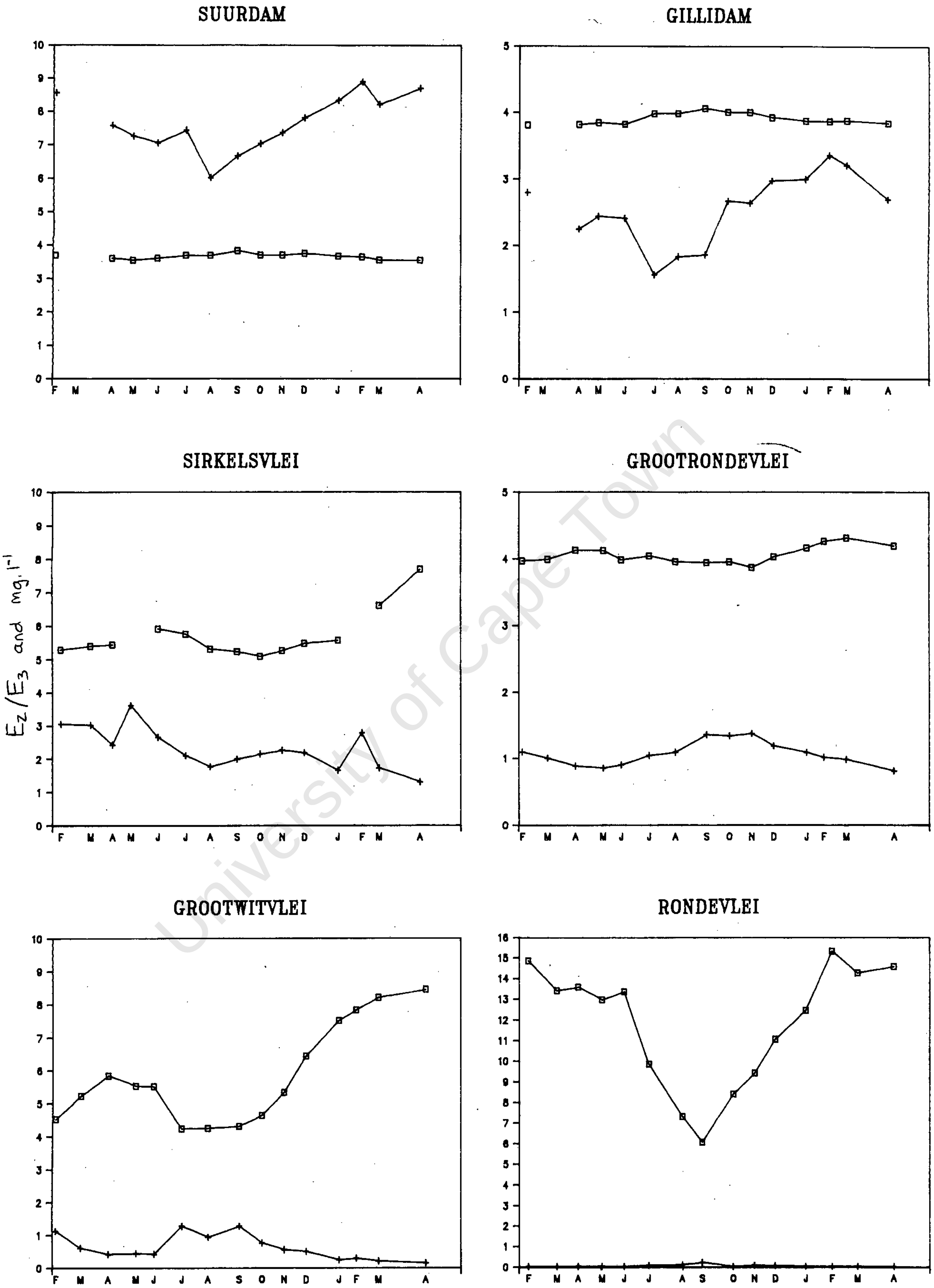

Figure 6.5 E_{250}/E_{365} ratios (absorbance) and Fulvic/Humic acid concentrations (in mg l^{-1}, as calculated with the method of Lawrence 1980) in each of the six vleis. E_{250}/E_{365} ratio - □ , Fulvic/Humic acid concentration - + .

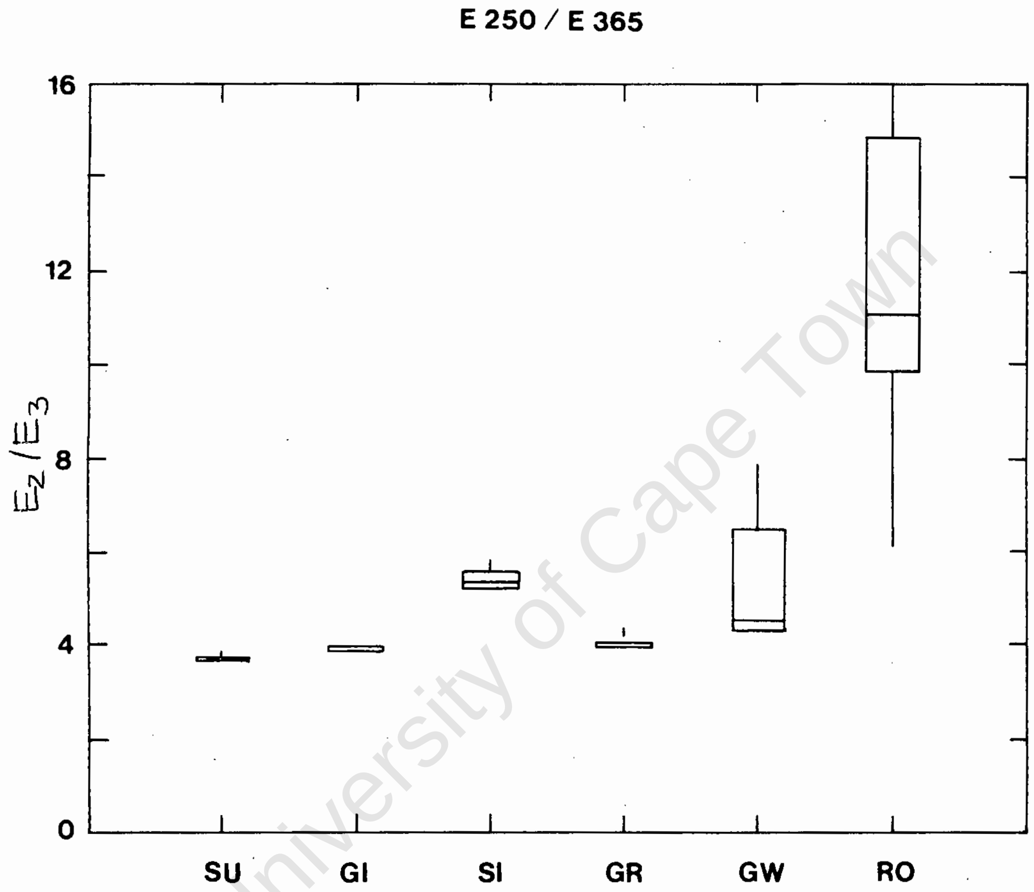

Figure 6.6 E_{250}/E_{365} ratios (absorbance). Box and whisker plot illustrating the median, the upper and lower quartiles and the range in Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO).

The ratios then remained high (approx. 8) during the summer months. The variation in the ratio is strongly negatively correlated with ambient and buffered colour, A_{290} values and polyphenol levels ($P < 0.001$ for all, except Folin-Ciocolteu where $P < 0.01$, table 6.5). Rondevlei waters had ratios significantly greater than those of any of the other five vleis (see fig. 6.6) with a very steep minimum in late winter to spring, again corresponding to the period of greatest rainfall and hence inflow. Subsequently ratios slowly increased to about 15.0 during the mid- to late-summer and autumn months. Interpretation of the variation in the ratios will be discussed jointly with the other measurements in the synthesis of results below.

Absorbance measured at 290 nm (A_{290}) in buffered samples is shown in fig. 6.7 in comparison to absorbance at 250 nm (A_{250}). De Haan *et al.* (1982) found the A_{250} value to be closely correlated with DOC concentration and Buffle and Deladoey (1982) similarly found A_{285} to yield a close correlation with DOC. In addition the appearance of a characteristic shoulder between 250 - 295 nm and its development may yield additional information on the characteristics of the humic substances. The height of the shoulder in (almost) all cases, however was small in relation to the projected curve of the absorbance spectrum and therefore no attempt was made to establish the relative height as a characteristic feature of the mixture of dissolved humic compounds. The variation in absorbance at 250 nm and 290 nm was in all cases very closely correlated to the variation at 400 nm ($P < 0.001$, table 6.5) except in Rondevlei where a correlation of only 90% was found (ie $P < 0.1$, table 6.5). The lower correlation probably reflects the large change noted in the E_2/E_3 ratio in Rondevlei during the study period and resulted from a lower maximum in late winter to spring and greater maxima in late summer.

A representative **absorbance spectrum** for each of the six vleis is plotted in fig. 6.8 to illustrate the lack of any feature except for the characteristic small shoulder at 250295 nm.

The concentrations of fulvic/humic acid, calculated using the **semi-quantitative method of Lawrence** (1980), are shown in fig. 6.5. Calculated concentrations of tannins and lignins were in all cases very close to zero and were thus not included. The mean concentrations of fulvic/humic acid, and the ranges, are included in table 6.4. Between the vleis the values varied similarly to the variations in the absorbance values, with Suurdam concentrations the greatest and Rondevlei concentrations the lowest. Seasonal variation, too, is very closely correlated to buffered absorbance values at 400 nm and 290 nm (in all cases $P < 0.001$, table 6.5). The calculated values of fulvic/humic acid thus yield very little additional information to the absorbance values other than a milligram per

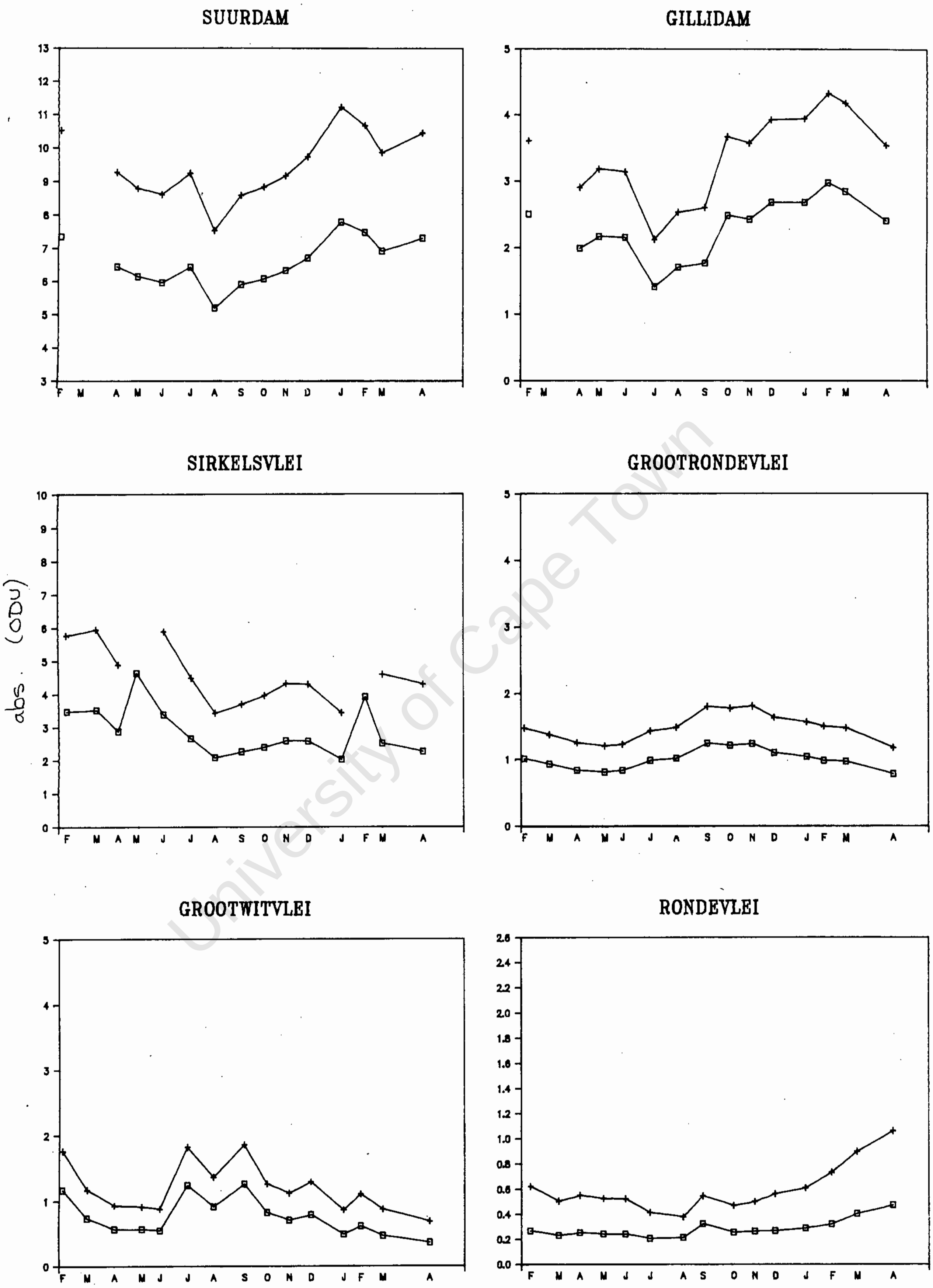

Figure 6.7 Absorbance measured at 290 nm (A_{290}) and 250 nm (A_{250})(as optical density units) in buffered water in each of the six vleis. A_{290} – □ and A_{250} – + .

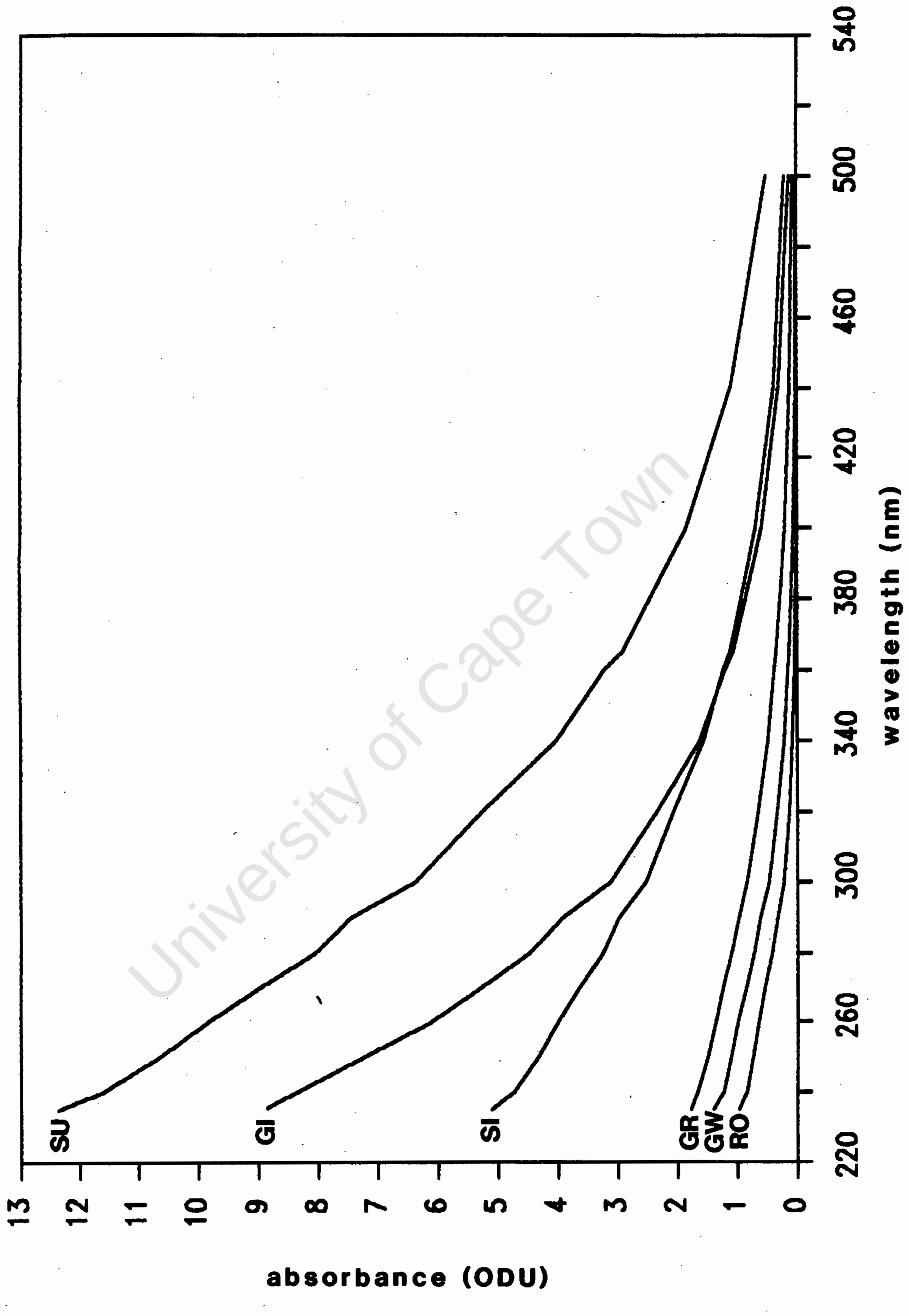

Figure 6.8 Representative absorbance spectra of buffered water (pH=6.88) from February (1982) samples. Absorbance measured as optical density units (ODU) over a 1cm pathlength. Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO).

litre quantity based on three extracted fulvic acids and the fact that tannins and lignins do not appear to contribute significantly to the absorbance values.

Fluorescence was only measured in five samples from each vlei and thus seasonal variation can be commented on, but not adequately plotted. A representative fluorescence emission and excitation spectrum for each of the six vleis is displayed in fig. 6.11, illustrating the similarity of the broad emission maxima and the difference between the excitation maxima.

The positions of the **excitation and emission maxima** are displayed in fig. 6.9 and the mean position of each maximum and the range are noted in table 6.4. The emission spectra for all six vleis between 330 nm and 700 nm consisted of one broad maximum in the region of 438 to 490 nm. The greatest emission wavelength was shown by Suurdam waters (480-490 nm) with Gillidam, Sirkelsvlei and Grootrondevlei clumped in the region of 460 to 470 nm, and Rondevlei waters close to 440 nm. Grootwitvlei waters showed a change of humic character during the year, with winter samples of similar character to the 460-470 nm group, and summer samples similar to Rondevlei waters. Additional maxima in the emission spectra at wavelengths of 346 nm and 685 nm were caused by the presence of the phosphate buffer or some other interference. The emission spectrum of the humic acid standard showed a similar broad peak with the centre of the maximum of 485 nm, but in addition with a shoulder positioned at approximately 460 nm. Tannic acid, however, shows little similarity, with a very broad maximum peaking around 415 nm. The excitation spectrum between 200 and 500 nm is quite different, displaying two maxima, the first positioned between 248 and 278 nm and the second between 338 and 390 nm. The relative positions of the two maxima are less distinctly different in the different vleis than the emission maxima, although there are some apparent differences in position. The region of the first maximum (F1) extends up to 278 nm for Sirkelsvlei and for Suurdam just above 260 nm. The remaining vleis all have a peak position close to 250 nm. The region of the second maximum (F2) occurs between 380 and 390 nm for Suurdam, between 350 and 360 nm for Gillidam and Sirkelsvlei, and close to 340 nm for Grootrondevlei, Grootwitvlei and Rondevlei. The most obvious difference in the excitation spectra is the relative intensities of the two maxima, which will be discussed later. Additional maxima in the excitation spectrum occurred at wavelengths of 236 nm and 468 nm, but were both caused either by the phosphate buffer or resulted from some other interference. The excitation spectrum of the humic acid standard displayed two maxima in similar positions to those of the vlei waters, at 252 nm and at approximately 365 nm. Tannic acid again showed little similarity, with a single maximum at 388 nm. Ertel

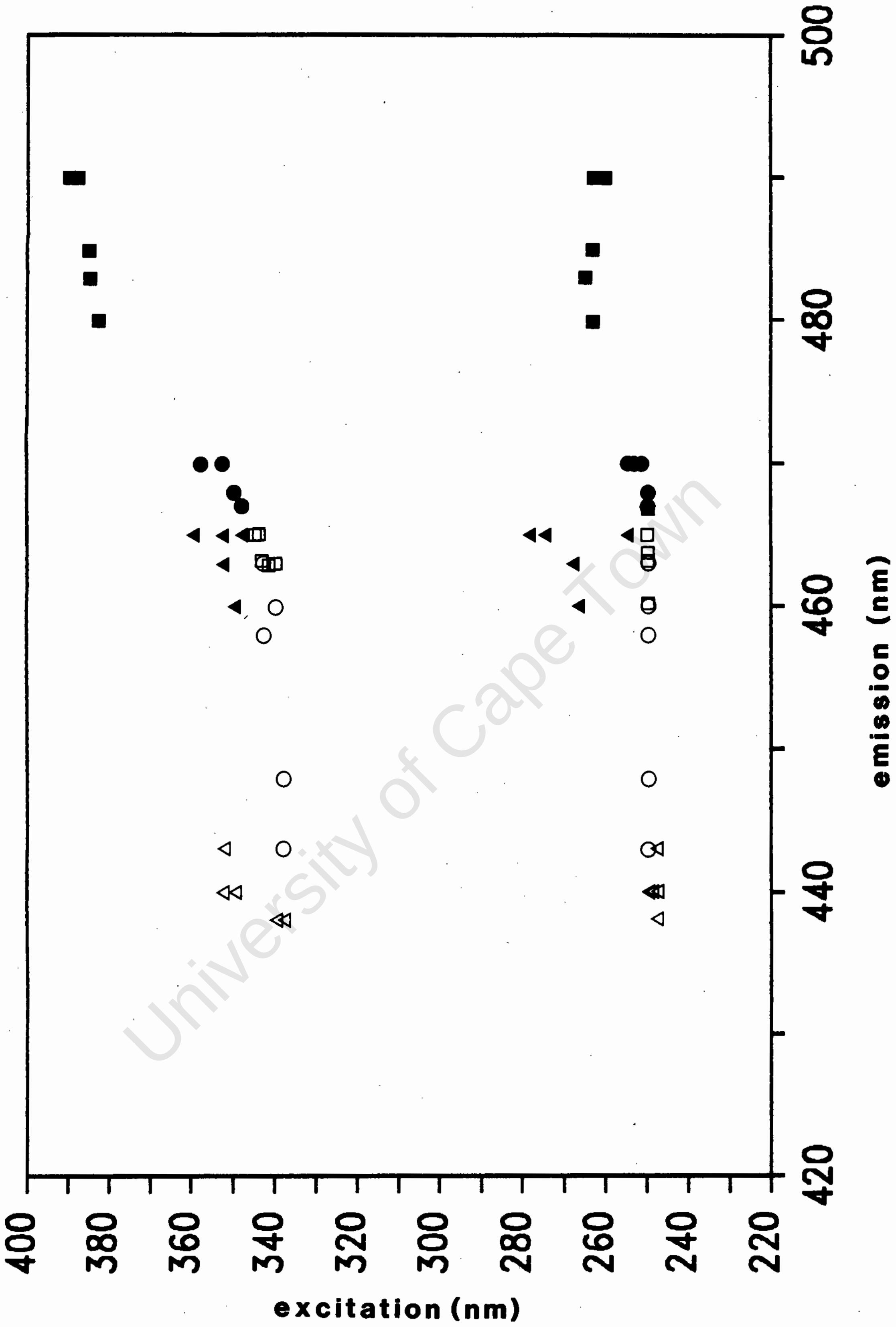

Figure 6.9 Fluorescence excitation maxima (F1 and F2) and emission maxima for five samples (Feb.(81),Jul.,Sep.,Dec., Feb.(82)) from each of the six vleis. Suurdam (■), Gillidam (●), Sirkelsvlei (▲), Grootrondevlei (□), Grootwitvlei (○) and Rondevlei (△).

and Hedges (1983) investigated marine humic acids, a model marine acid (melanoidin humic acid), terrestrial humic acids, and a model terrestrial humic acid (phenolic humic acid). The emission and excitation maxima positions were plotted similarly to those given in fig. 6.9. The most obvious similarity between the two figures was the position of the Suurdam maxima, which corresponded directly with the positions of the phenolic humic acids. Marine, terrestrial and melanoidin humic acids occupied the same region as Gillidam, Sirkelsvlei, Grootrondevlei and Grootwitvlei (winter) humic substances.

The **relative intensities** of the fluorescence maxima are presented as mean values and ranges in table 6.4. Correspondence analysis of three measures of relative intensity (emission, excitation (F1) and excitation (F2)) is displayed in fig. 6.10. Axis 1 and axis 2 of the plot accounted for all 100% of the "inertia" of the data matrix (80.8% and 19.2% respectively) and thus fig. 6.10 includes the full information complement of the analysis. The separation along axis 1 was due chiefly to the intensity of the first excitation maximum and separation along axis 2 chiefly to the intensity of the second excitation maximum. Most separation occurs along a line running between F1 and F2 however. Grouping along this line reflects the relative change in excitation peak height (see fig. 6.11) which is expressed in the Iex(F1)/Iex(F2) ratio in table 6.4. Samples within each vlei show the greatest similarity (clumping), with Grootwitvlei samples once again separating into summer samples, similar to Rondevlei waters, and winter samples, similar to Grootrondevlei waters. At one extreme Suurdam waters display a dominant second excitation peak (F2) and at the other Rondevlei waters display a dominant first excitation peak (F1). A further interesting separation occurs as a result of emission intensity, with Sirkelsvlei samples well separated as a result of very high emission intensities. The humic acid standard was most similar to the Grootrondevlei samples.

The results of the **Folin-Ciocalteu determination** of polyphenol content of the waters are displayed in fig. 6.12. The mean values and the ranges of the values are included in table 6.4 and fig. 6.13 displays the values in a box-and-whisker plot. Suurdam waters had the greatest levels of polyphenols, more than twice those of Gillidam or Sirkelsvlei, which contained the next greatest concentrations. Grootrondevlei had levels generally half those of the latter two vleis, but normally markedly greater than those in Grootwitvlei. Rondevlei had very low levels, generally much lower even than those of Grootwitvlei waters. Seasonal variation of the polyphenol levels is very closely correlated to the variation in buffered colour (and A_{290} and fulvic/humic acid) in all the vleis except Rondevlei (table 6.5), and thus is also very closely correlated to the variation in ambient colour in all the vleis,

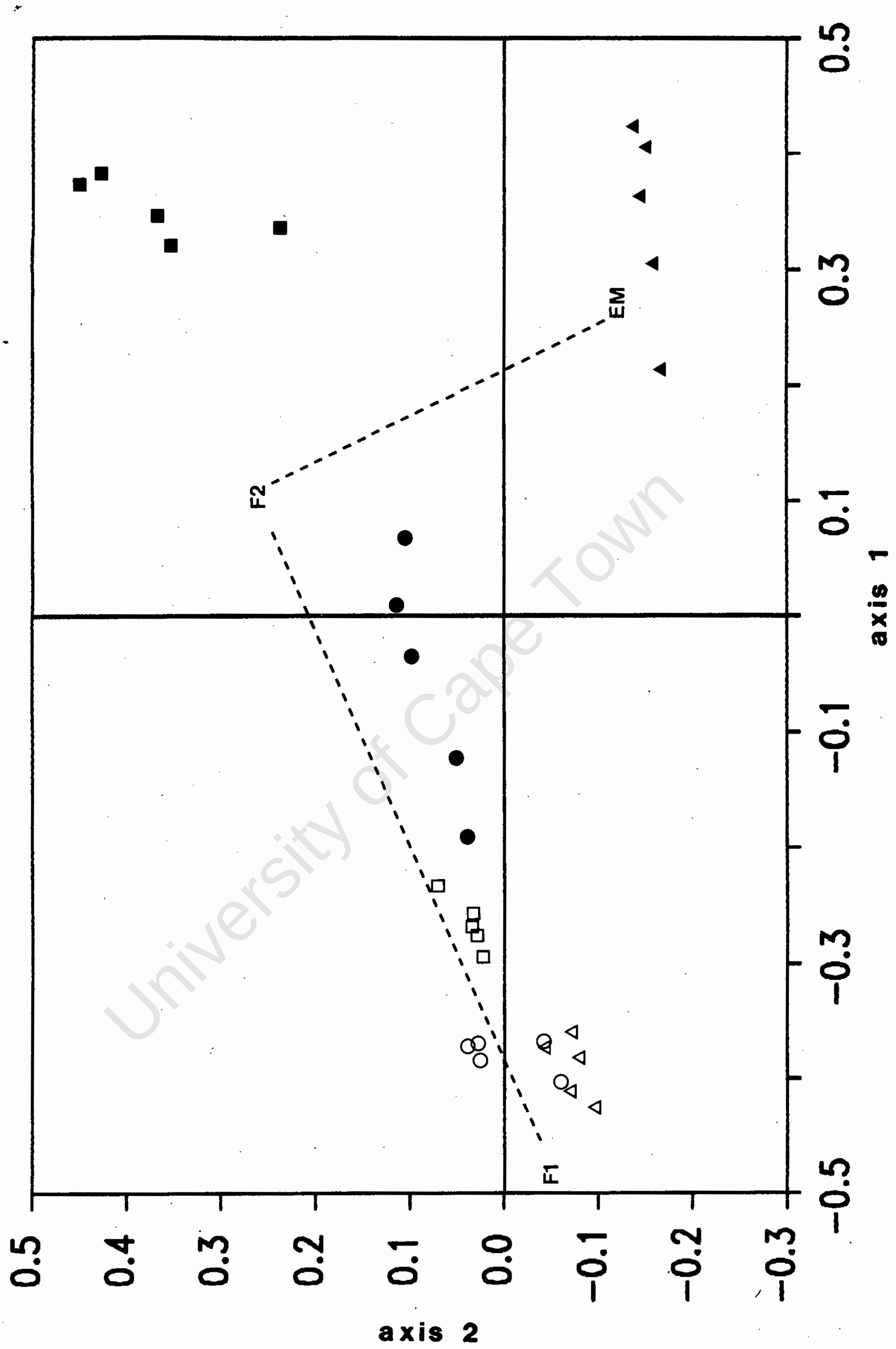

Figure 6.10 Variability in the relative intensity of fluorescence excitation (F1 and F2) and emission (EM) displayed as a graphical plot using correspondence analysis. Suurdam (■), Gillidam (●), Sirkelsvlei (▲), Grootrondevlei (□), Grootwitvlei (○) and Rondevlei (△).

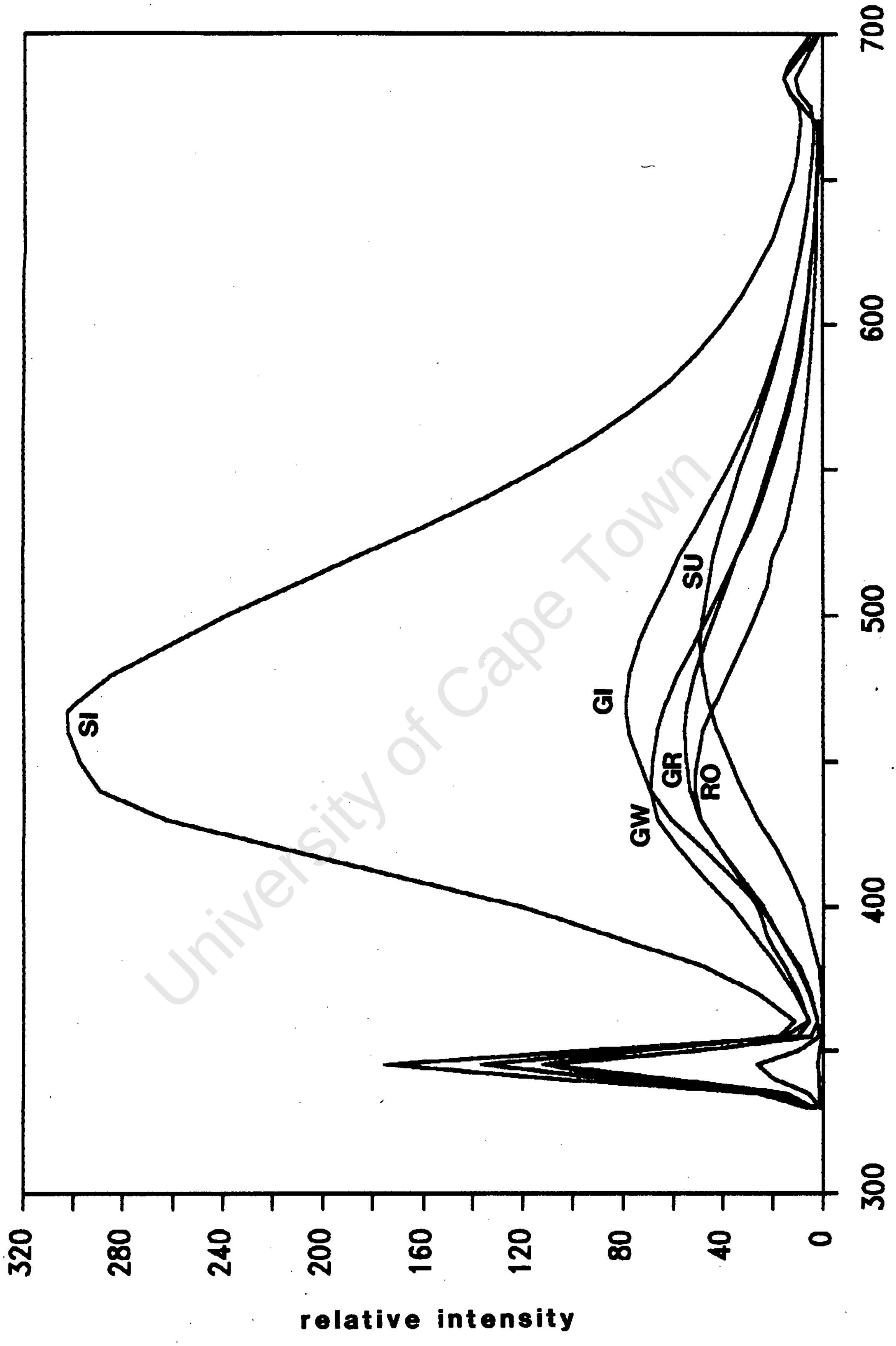

Figure 6.11a Representative fluorescence emission spectra of buffered water (pH=6.88) from February (1982) samples. Measured at a constant excitation wavelength of 340 nm. Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO).

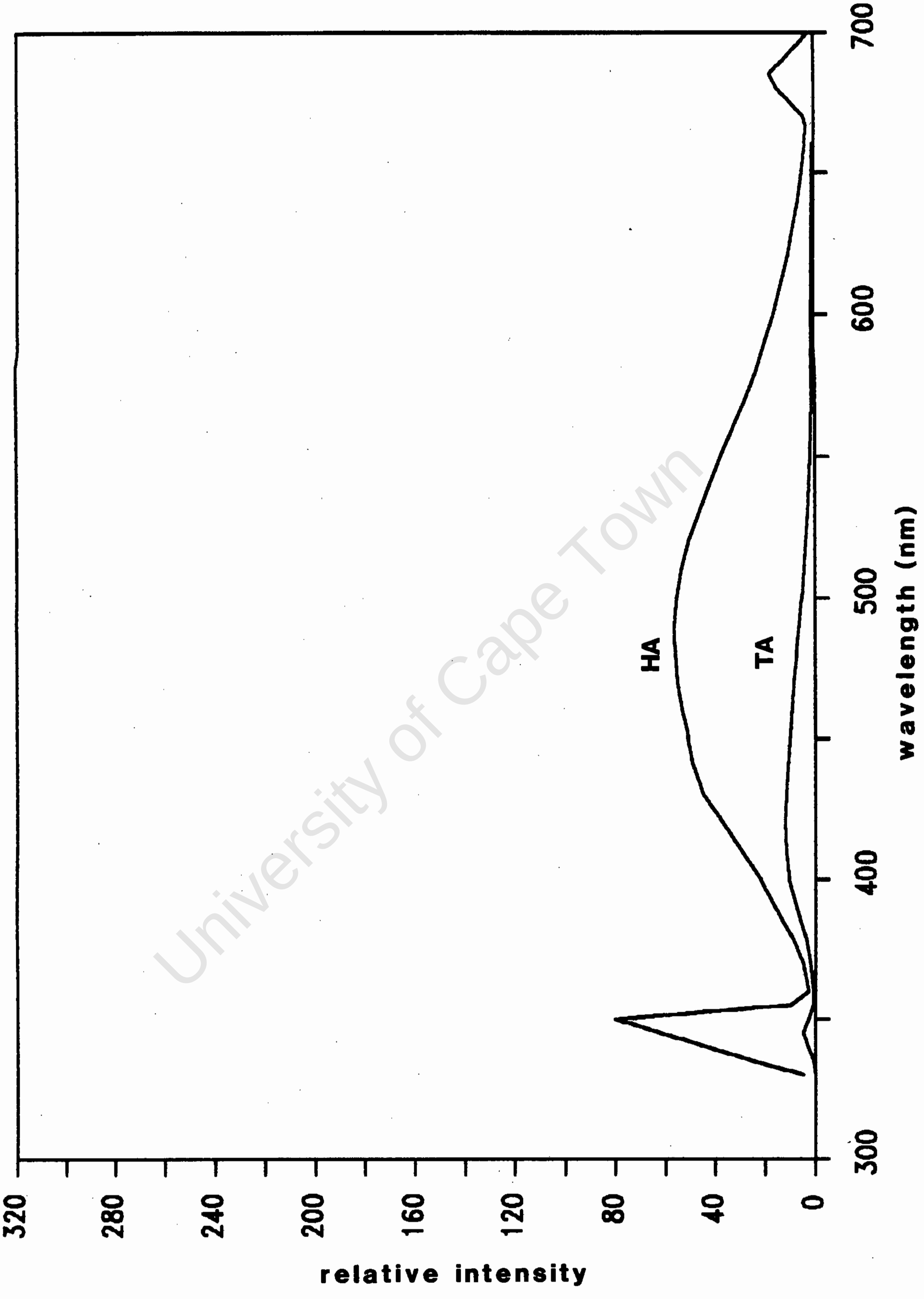

Figure 6.11b Representative fluorescence emission spectra of humic acid (HA) and tannic acid (TA) standards (both 100 mg l^{-1}). Measured at a constant excitation wavelength of 340 nm.

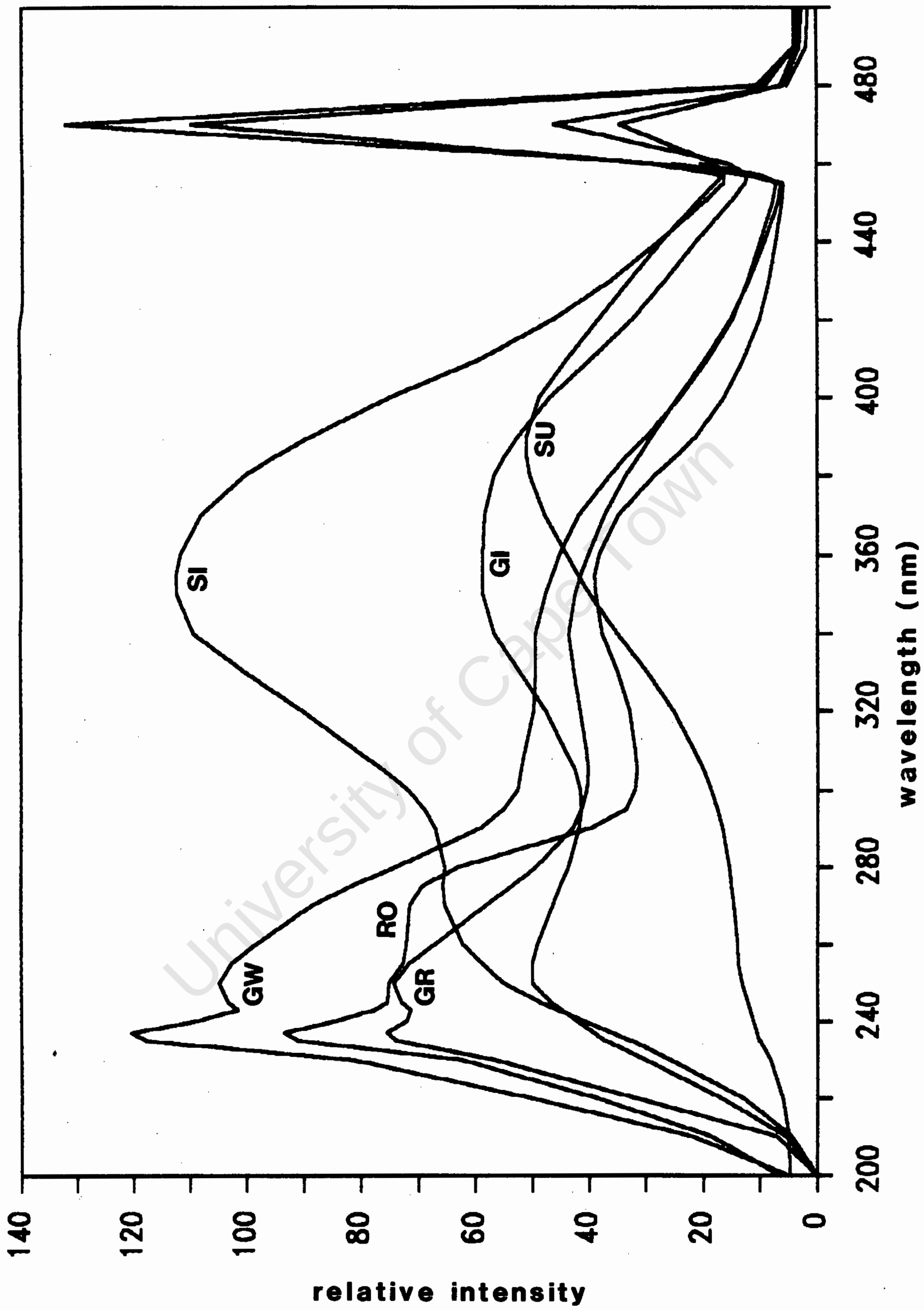

Figure 6.11c Representative fluorescence excitation spectra of buffered water (pH=6.88) from February (1982) samples. Measured at a constant emission wavelength of 470 nm. Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO).

except Rondevlei and Sirkelsvlei (reflecting the lack of correlation between ambient and buffered colour in Sirkelsvlei). The reason for the lack of correlation in Rondevlei between colour and polyphenol levels may result from the greater contribution of autochthonous humic substances, which lack the aromaticity of the terrigenous humic substances that dominate the other vlei waters. The variations in level of the polyphenols between the vleis (fig. 6.13) also corresponds very closely to that of the colour (fig. 6.2). The differences that do occur are relatively greater levels in Gillidam and Grootrondevlei waters, with no overlap between levels in Grootrondevlei and Grootwitvlei. The large difference between the levels in the Grootvleis is also probably related to the greater proportion of autochthonous humic substances of a less aromatic nature in Grootwitvlei.

SYNTHESIS OF RESULTS

Suurdam had by far the greatest concentrations of DOC (A_{250}), always more than twice as great as any of the other vleis. The character of the humic compounds appears to have changed little during the year. The dominant fractions of the humic substances are likely to be of relatively high molecular weight and high phenolic content (E_2/E_3 ratio). The very low pH, low productivity and apparent lack of change in the character of the humic substances through the year indicates that seasonal variation in the humic levels is unlikely to be regulated from within the vlei. There was an almost negligible change in water volume throughout the year and thus dilution effects within the vlei were also unlikely to have controlled the humic levels. The seasonal change in concentration is most likely to have been a result of the changing amount of water entering the vlei *via* seepage flow, with the stronger winter flow resulting in depleted soil levels of dissolved humic substances. In summer, reduced seepage flow and increased soil microbial activity caused higher concentrations in any seepage entering the vlei. In litter-fall studies conducted on coastal fynbos (Mitchell *et al.* 1986), the main period of litter fall occurred in summer and in autumn. This aspect of the phenology should hold true for the mesic mountain fynbos of Cape Point and the initial rapid formation of humic substances (leached from the leaf fall) would occur with the first rains of winter and further decomposition (and humification) would be retarded by the onset of waterlogging in the soils. This would contribute to the local depletion of soil humic substance and the mid-winter to spring minimum in concentration. The overall effect therefore probably resulted from the small size of the catchment area, resulting in the seasonal depletion of soil humic substances coupled with limited degradation of the compounds within the vlei.

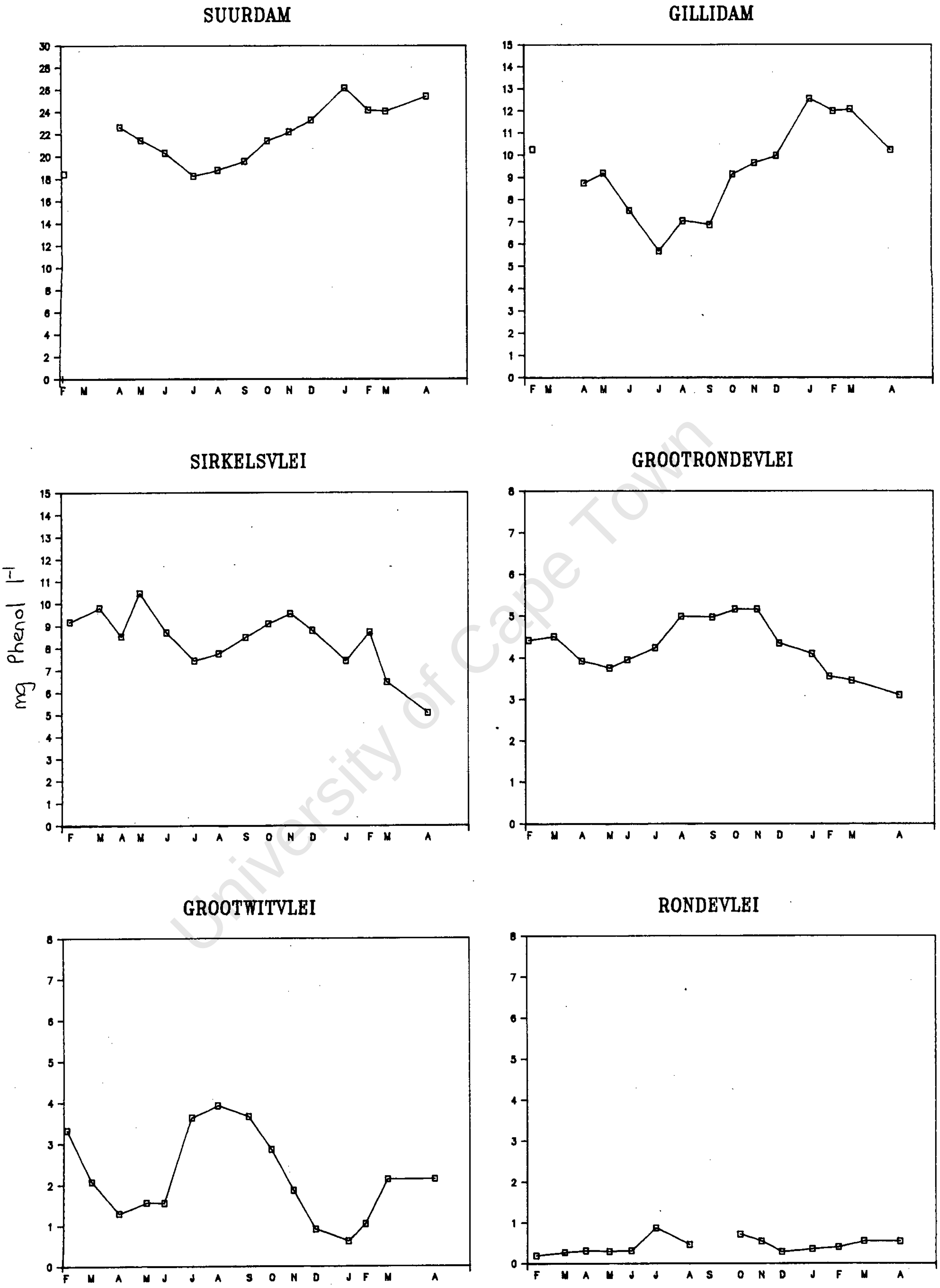

Figure 6.12 Folin-Ciocalteu determination of the polyphenol content of the water in each of the six vleis. Concentrations are expressed as mg Phenol l^{-1}.

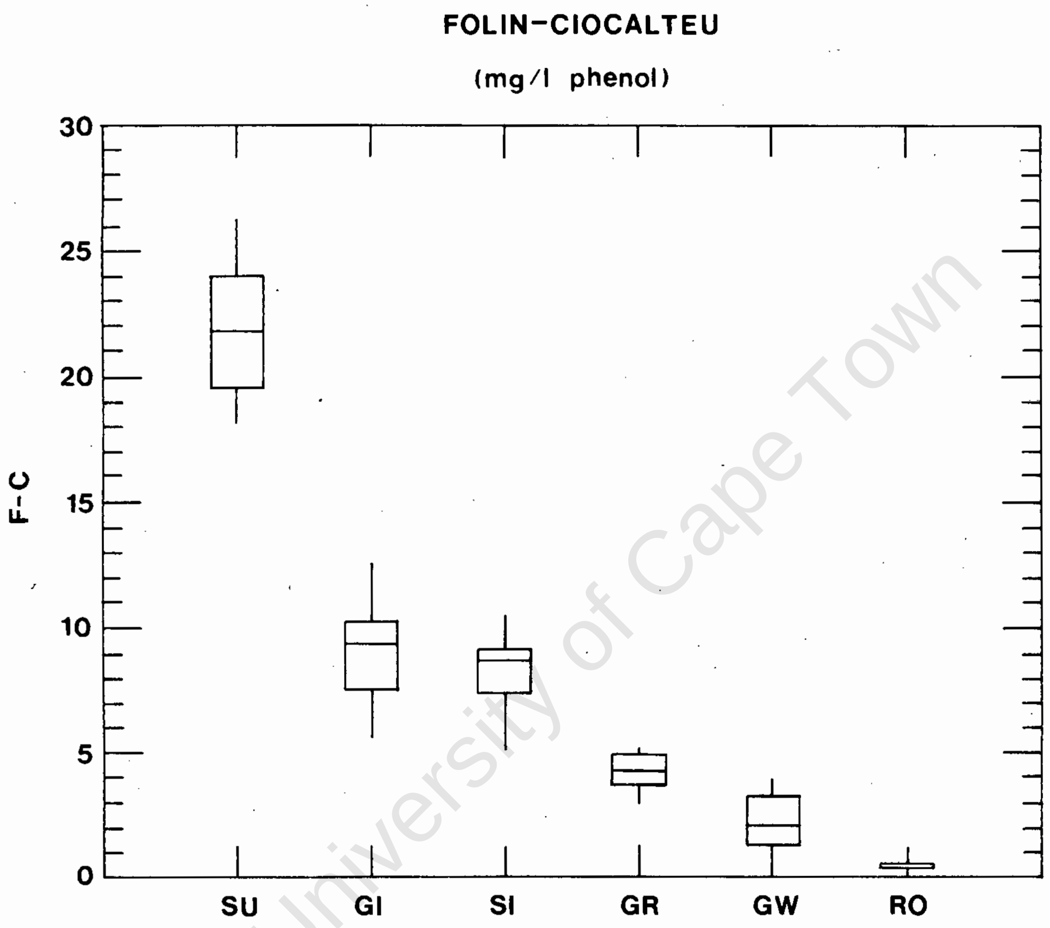

Figure 6.13 Folin-Ciocalteu determination of the polyphenol content of the water in each of the six vleis. Box and whisker plot illustrating the median, the upper and lower quartiles and the range in Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW) and Rondevlei (RO). Concentrations are expressed as mg Phenol l^{-1}.

Gillidam and Sirkelsvlei both had high concentrations of DOC. From the E_2/E_3 ratios, Gillidam appears to contain humic substances of similar character to those in Suurdam, in other words of relatively high molecular weight and high phenolic content. Fluorescence data (fig. 6.9 and 6.10) however separate humic substances from Gillidam indicating a lower phenolic content and possibly lower mean molecular weight than Suurdam, but greater than those of the remaining vleis. Again there appears to have been little change in character of the humic substances during the year. Gillidam water did have a slightly higher pH than Suurdam and a slightly greater productivity, and it experienced a large change in total volume. However the similar small surface area of the vlei, and the fact that it is also endorheic with a small catchment area, indicates that the seasonal variation in the levels of the humic substances was probably determined by the same factors as for Suurdam.

The character of the humic substances in **Sirkelsvlei** appears to be quite different from that of the other vleis. The E_2/E_3 ratio was intermediate in value, indicating a lower mean molecular weight and a lesser phenolic content than the humic substances in the other two Cape Point vleis. Fluorescence intensity data (fig. 6.10) indicate a very different humic character to the other vleis, however. The position of the first excitation maximum was greater than that for the other vleis, also indicating a difference in character. Lower values of the E_2/E_3 ratio might be expected in relation to the greater productivity and higher pH of the Sirkelsvlei waters, which would result in some autochthonous production of humic substances and greater microbial degradation. The fluorescence characteristics are however not easily interpreted. The most obvious factor that might have affected the behaviour of the humic substances is the high salinity, causing a high degree of complexation or association with the humics. Humic-metal (trace) complexes are known to quench fluorescence (see Overview of methods), but not to increase the emission fluorescence intensity, although the high salinity might have interfered with these complexes (see Discussion). There was seasonal variation in the character of the humic substances (see fig. 6.5) which should have resulted from the seasonality of the primary production and microbial degradation as well as the variation in salinity. Seasonal variation in the levels of the humic substances was less marked, but showed a similar pattern to the other Cape Point vleis. Sirkelsvlei is also endorheic, with a relatively small catchment. The surface area is much greater however and there are fairly extensive shallow areas in the summer months. The broad seasonal pattern probably resulted from the same factors determining the variation in Suurdam and Gillidam, but was complicated in the summer months by local salinity and temperature effects in the shallows, and emphasized in winter by the additional diluting effect of precipitation. The high salinities and temperatures should have affected the levels of humic substances in solution as a result of complexation and precipitation and may have been responsible for horizontal patchiness in colour.

Grootrondevlei had DOC or colour levels a lot lower than those of the Cape Point vleis, but the character of the humic substances was very similar. The E_2/E_3 values were almost as low as in Gillidam, and hence the compounds were also of relatively high molecular weight and high phenolic content. Fluorescence data confirm the similarity in the character of the compounds to those of Gillidam, with Grootrondevlei samples grouped in close proximity to those of Gillidam. Seasonal variation in the character of the compounds occured and was inversely related to the variation in the concentrations of the compounds. Both the Grootvleis have a relatively large and steep catchment area (compared to the Cape Point vleis) and receive a greater volume of precipitation as well as surface and ground flow, particularly during the winter months. As a result the variation in the levels of humic substances was quite different to that of the Cape Point vleis. The generally lower levels were probably determined mainly by the nature of the catchment area, in particular by the rate of throughflow and the degree of flushing that occurs. The rates of formation of humic substances in relation to the rates of removal (*via* leaching) should be very different in the catchment with steeper slopes receiving a higher rainfall. As a result the concentrations of humic substances in the inflow waters never rose close to the levels found in the Cape Point vleis. Within this range of lower concentrations, the seasonal variation in the inflow waters was probably determined similarly to that in other south-western Cape mountain stream waters. Levels of humic substances in mountain stream waters have been found to be very closely correlated to levels of discharge during the year (D Britton (Swartboschkloof) pers.comm., J A Day (Langrivier) pers.comm.). The winter maximum in the vlei levels of humics and the correspondingly low E_2/E_3 values occured during the period of greatest rainfall and hence discharge. During the remaining months of the year, processes within each vlei acted to reduce the levels. Grootrondevlei waters were low in productivity, but were not very acid and thus microbial degradation may have played some role in controlling the levels. The seasonal variation was not great however and much of the increase was likely to be due to increased rates of discharge.

Grootwitvlei waters were productive and high in pH. Consequently in the summer months there was probably a high rate of degradation of humic substances as well as a significant contribution of autochthonous humic substances. The high

E_2/E_3 values in these months confirm the presence of a large fraction of relatively low molecular weight molecules which are also low in phenolic content. In contrast, in the rainy months the ratio values dropped sharply as a result of the increased input of relatively high molecular weight, high phenolic content, humic substances originating from the surrounding catchment soils. The seasonal variation of the character was once again inversely related to the levels of the humic substances. Fluorescence data confirm the marked seasonal change in the character of the humic substances as a result of their origins. Summer samples were closer in character to Rondevlei waters and winter samples were very close in character to Grootrondevlei waters.

Rondevlei waters contained very low levels of DOC in relation to those of the other vleis. In addition the character of the humic substances was also very different from that in the other vleis. The E_2/E_3 values indicate coumpounds of low mean molecular weight and low phenolic content as the dominant fraction for most of the year. Fluorescence data confirm the difference in humic character with distinctly lower wavelengths of maximum emission and less well separated, but also lower first excitation maximum (F1) wavelengths. Excitation and emission at lower wavelengths are thus probably indicative of an autochthonous origin and a low molecular phenolic content. Grouping of Rondevlei fluorescence intensity measurements may be the result of lower mean molecular weight. Seasonal variation in the E_2/E_3 values occured as a marked decrease during the rainy months resulting from an influx of terrigenous humic substances with the large volume of inflow water. The influx was reflected in the small winter maximum in absorbance at 400 nm. There were however increases in ambient colour in late summer as well as increased absorbance at 250 nm, indicating increased DOC levels although the late summer increases were not reflected in the buffered colour measurements. The reason probably lies in the nature of the humic compounds. Autochthonous humic compounds should absorb less than larger molecular weight terrigenous compounds, especially in the visible region of the spectrum. Thus increased ambient colour resulted from the higher ambient pH and increased absorbance at 250 nm (in buffered samples) resulted from the greater accuracy of DOC measurement at that wavelength. The reasons for the generally very low levels of humic substances in the Rondevlei waters probably stem very much from the nature of the catchment and the catchment vegetation (see chapter 2). Much of the inflow is urban runoff and much of it drains through developed or disturbed areas; in addition much of the natural vegetation of the catchment lies on calcareous sands as opposed to acid podsols. The supply of terrigenous humic substances is thus likely to have been low and only in the rainy months did the influence of the podsolic soils of the Zandvlei catchment or of the acid sands reach the vlei. The vlei was also highly productive and autochthonous production of humic substances is expected to have been a significant source of DOC, while high rates of microbial degradation are expected to have been a significant sink.

As noted by De Haan (1983), the E_2/E_3 ratio "coincides with" changing molecular weight and aromaticity of humic substances and is a "measure of the relative humification of coloured lake water". However, as noted in the introduction, changes in aromaticity and humification do not necessarily infer a change in molecular weight. By using two further ratios we can attempt to separate the changes in aromatic content from those of molecular weight.

The relative phenolic content (as a measure of the aromaticity) of the compounds can be examined by calculation of the Folin-Ciocalteu:A_{250} ratio. Assuming A_{250} to be an accurate measure of the DOC, the ratio should indicate the mean relative aromatic hydroxyl content of the HS. As noted by Stewart and Wetzel (1981), some variation in the relationship between A_{250} and DOC may occur as a result of absorbance quenching in the high molecular weight materials, although quenching should also occur in the determination of the phenolics of the higher molecular weight materials. Interestingly, Grootrondevlei and Gillidam had the highest mean ratios followed by Suurdam (see table 6.6 and fig. 6.14).

	F-C : A_{250} ratio	
	Mean (±sd)	Range
SU	2.32 (±0.21)	1.75 - 2.49
GI	2.76 (±0.21)	2.39 - 3.18
SI	1.85 (±0.38)	1.19 - 2.30
GR	2.88 (±0.32)	2.34 - 3.36
GW	1.81 (±0.70)	0.70 - 3.12
RO	0.80 (±0.50)	0.30 - 2.10

Table 6.6 Mean, maximum and minimum values of the Folin-Ciocalteu : A_{250} ratio for each of the six vleis. The ratio is calculated as an index of relative aromatic content of humic substance.

Sirkelsvlei and Grootwitvlei both showed intermediate mean values. The ranges differed considerably however, with the ratios in Grootwitvlei waters varying far more than in Sirkelsvlei. Values for Grootwitvlei correlate closely with the variation in chlorophyll *a* levels ($P < 0.001$) through the year, indicating the strong influence of the autochthonous component (low aromatic content) during the periods of greatest primary production. During the rainy season the influence of the influx of terrigenous humic substance was marked by the increase in the ratio to values similar to those for Grootrondevlei. Rondevlei humic substances had low ratios, which rose during the rainy months (corresponding to a decrease in E_2/E_3 values), again indicating the influence of terrigenous humic compounds at this time of year, and the dominance of the autochthonous component during the rest of the year.

The ratio of fluorescence intensity to absorbance (at 250 nm) has been found by Stewart and Wetzel (1980) to be useful in indicating humic compounds of differing molecular weight (high values representing low molecular weight and vice versa). In their study the total fluorescence was measured and the intensities standardized against quinine sulphate, whereas in this study emission intensities were used without the same standardization. Their ratios are thus not comparable with the results obtained here, which should still be a useful index of mean relative molecular weight. The ratio when applied to a mixture will indicate an increase in both the proportion of higher molecular weight compounds and the relative molecular weight: ie an increase in average molecular weight by number and mass. Suurdam waters showed the lowest values, indicating compounds of greatest mean molecular weight (table 6.7 and fig. 6.15). Gillidam and Grootrondevlei also contained compounds of high mean molecular weight, although clearly lower than in Suurdam. Sirkelsvlei waters appeared to contain humic compounds of unexpectedly low mean molecular weight, considering the similar origins of humic substances in the Cape Point vleis. Stewart and Wetzel (1981) found a significant positive relationship between the ratio and calcium concentration and suggested a selective adsorption and precipitation of higher molecular weight humic materials onto particles of clay or calcium carbonate. Neither of these should be present to any degree in Sirkelsvlei water, and yet the idea of a selective removal of the higher molecular weight fraction as a result of the high salinity does seem a likely explanation. Grootwitvlei showed the same dichotomy as before between water of high primary production and water of great terrigenous influence, with low and high mean molecular weights respectively. Rondevlei showed a similar dichotomy, but with all values significantly greater than in Grootwitvlei, indicating much lower mean molecular weights. Both Rondevlei and Grootwitvlei waters may also have

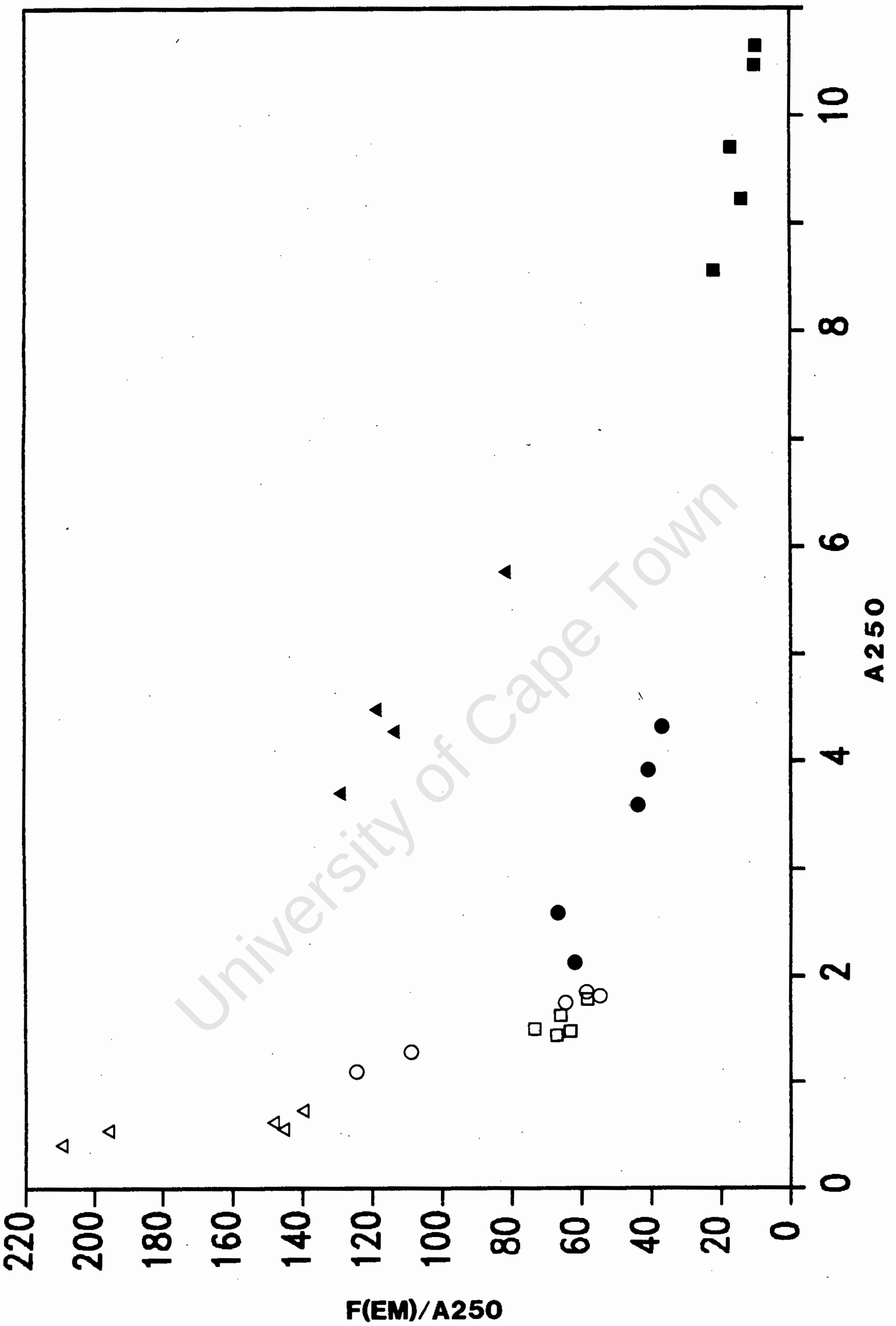

Figure 6.15 Relative molecular weight of the humic substances as expressed by the ratio fluorescence (emission):A_{250} (F(EM)/A_{250}) plotted against A_{250}.Suurdam (■), Gillidam (●), Sirkelsvlei (▲), Grootrondevlei (□), Grootwitvlei (○) and Rondevlei (△).

experienced selective removal of the higher molecular weight fraction by calcium carbonate particles during periods of high primary production.

	$F_{em}:A_{250}$ ratio	
	Mean (±sd)	Range
SU	14 (± 5)	9- 21
GI	50 (±13	36- 66
SI	111 (±20)	82-129
GR	65 (± 6)	58- 73
GW	82 (±32)	55-124
RO	167 (±32)	139-209

Tables 6.7 Mean, maximum and minimum values of the fluorescence intensity (emission) : A_{250} ratio for each of the vleis. The ratio is calculated as an index of relative molecular weight of humic substance.

Figure 6.16 summarizes the distribution of aromatic hydroxyl content and mean relative molecular weight (from tables 6.6 and 6.7). Both factors correspond except in the case of Suurdam and, to a lesser extent, Grootwitvlei. The relatively low content of aromatic hydroxyl groups in Suurdam may have been the result of quenching due to the high mean relative molecular weight of the compounds. The large change in aromatic hydroxyl content relative to molecular weight stems from the change in source noted earlier. The distributions of both ratios also correspond broadly with the E_2/E_3 ratio presented above.

DISCUSSION

Having discussed the seasonal variation in the levels of colour and HS (or DOC) in each vlei, and having drawn together, in the synthesis of results, information of the character of each mixture of humic substances and its variation through the seasons, the discussion now focuses on these changes in relation to the inorganic chemical environment and the interactions of the humic substances with the inorganic variables. Humic substances, as noted, contribute to acidity as weak organic acids and interact with trace metals, cations, anions and other organic ligands, often causing elevated levels of the various chemicals in the water column.

The acidity of humic substances is generally assumed to arise from the assemblage of carboxyl and phenolic hydroxyl groups, although the carboxyl groups dominate the acidic properties of these compounds (Burch *et al.* 1978, Oliver *et al.* 1983). The diversity of structure in the humic polymers results in few carboxyl groups being "chemically identical" (Burch *et al.* 1978). The total contribution to the acidity is thus variable and is a weighted average equilibrium function that is dependent on both the character of the compounds in solution and on their concentrations. The carboxyl groups are also involved in cation complexation and thus the cation concentrations relative to those of the humic substances are also important. Quantification of the contribution to acidity is generally by measurement of the carboxyl content of the humic substances (Perdue *et al.* 1980, Oliver *et al.* 1983). The contribution of the humic substances to the total acidity of Suurdam and Gillidam is not obvious from the seasonal variations of both variables (see fig. 5.2). There is no statistical correlation, although there was a similar late winter low and summer high in the levels of both (see acidity results in chapter 5). The effects of the changing levels of the humic fraction on pH are more obvious. Brossert (1979) has shown that humic substances at high concentrations have a strong buffering capacity at a pH of about 3.5. Both Suurdam and Gillidam displayed fairly constant pH values throughout the year, probably largely as a result of this buffering capacity at low pH. pH in Sirkelsvlei is almost certainly directly influenced by the high salinity and therefore the high buffering capacity of the water. The Grootvleis both had lower levels of humic substances than did the Cape Point vleis, but both experienced a pH drop with the winter inflow of water from acid soils with increased concentrations of humic substances. The pH drop in Rondevlei waters in September may also have been a response to the influx of humic compounds. Low pH therefore appears to be a consequence of both high levels of humic substances and acid, well leached soils; all the vlei waters are influenced to some extent by both factors.

The ability of humic substances to form metal-humic complexes with metal ions, oxides, hydroxides and minerals has been well studied. The metal-humic complexes differ widely in their chemical and biological stabilities and can be either water-soluble or water-insoluble depending on the environmental conditions. The transition metals in particular interact strongly with humic compounds. Within the group the trivalent ions of Fe and Cr, as well as Cu and Al, show the strongest association with humic compounds, the type of interaction and the solubility of the complex in water depending on the pH and the concentrations of HS and metal (Schnitzer and Kerndorff 1981). The alkaline earth metals (commonly Ca and Mg) are also chelated by the humic compounds, although not as strongly as the trace metals, whereas the monovalent cations such as Na and K can only form weak electrostatic bonds with single anionic groups (Gamble 1973). The main factors that control the extent of metal-humic interactions then are i) the value of the stability constants ii) the pH and iii) the concentrations of the major ions (Mantoura *et al.* 1978, Saar and Weber 1982). The most important functional groups involved in the metal ion chelation are thought to be the acidic carboxyl and phenolic hydroxyl groups (Gamble *et al.* 1980, Dempsey and O'Melia 1983, Gamble *et al.* 1983). Langford *et al* (1983) suggest four ways in which bidentate sites of chelation are provided by these functional groups and define an equilibrium function (K_4) as an expression of the mixture of chelating sites. They propose a variable stoichiometry of binding in terms of the variable equilibrium function (K_4). Strongly bound ions (such as Cu^{2+}) compete well for initial selective sites, but at high coverage K_4 is smaller and selectivity is greatly reduced. The later sites do not bind any ions sufficiently strongly (neither Cu^{2+} or Fe^{3+}) to exclude the less strongly bound ions (such as Mg^{2+} or K^+). Thus increasing ionic strength and decreasing total HS concentration, as well as decreasing pH (increased protonation of binding sites), decrease the K_4 and reduce the selectivity of binding. Various other studies have also shown a decrease in the proportion of complexed trace metals with increasing concentrations of the major cations (Mantoura *et al.* 1978, O'Shea and Mancy 1978, Sanders and Bloomfield 1980). In general terms the displacement of the more strongly bound trace metals and the formation of more weakly bound complexes with the major cations can be viewed as a competitive interaction between the two for the anionic ligand sites. In the same way decreasing pH results in increased competition from the H^+ ion.

The effect of this complexing capacity of HS is apparent in the enhanced concentrations and the seasonal variation of some of the ions monitored in the six vleis. As noted in chapter 5, the three Cape Point vleis and Grootrondevlei contained high levels of iron in the water column, most likely as a consequence of iron-humic complexes, in contrast to the less humic waters of Grootwitvlei and Rondevlei.

Variations in the levels of iron in Suurdam and Gillidam are closely correlated with variations in the levels of humic substances (table 5.4), indicating that most iron was present in a strongly complexed form.

In Sirkelsvlei and Grootrondevlei, however, there is no correlation between the variations in iron and HS levels. Grootrondevlei waters contained the second highest mean level of total iron after Sirkelsvlei and the lowest mean salinity of the six vleis, as well as being well stained with humic compounds. A high degree of iron complexation should thus be expected. The factor most likely to be responsible for the lack of correlation is the pH regime, which over the range of redox potentials expected for humic waters, allows the presence of a ferric hydroxide fraction (Stumm and Morgan 1981, Wetzel 1983) in addition to that complexed by humic compounds. Furthermore, the iron content of higher aquatic plants averages about an order of magnitude greater than that of terrestrial plants (average aquatic plant iron content of 5 mg g^{-1} dry mass (Oborn 1960 in Wetzel 1983)) and thus a fluxing of dissolved iron between the water and the aquatic macrophyte beds may maintain a significant uncomplexed fraction of iron in solution. Sirkelsvlei waters displayed a similar pH regime to Grootrondevlei, the highest levels of iron, high levels of humic compounds and an average salinity an order of magnitude greater than the other vleis. The pH regime should again result in the presence of a ferric hydroxide fraction contributing to the lack of correlation between the variations of iron and HS, although the salinity level is likely to play a determining role in the general complexation of the humic compounds. The high salinity should result in weakly bound complexes with high proportions of the major cations (Ca, Mg, Na, K) at the expense of displaced trace metals such as Fe and Cu. The presence of high concentrations of these weakly bound complexes in the water column could explain the unusual fluorescence and absorbance characteristics noted in the results. Fluorescence of humic substances is well known to be quenched by increasing concentrations of paramagnetic transition metal ions (such as Cu^{2+}) *via* intramolecular energy transfer, yet the emission fluorescence intensity of Sirkelsvlei was higher than for any other vlei. The displacement of these metal ions by the alkali earths and alkali metals, and the formation of weak, often electrostatic bonds, may be conjectured to play some role in reversing the fluorescence-quenching effect. Absorbance increases with increasing concentrations of the same paramagnetic transition metal ions (Gamble *et al.* 1980, Langford *et al.* 1983), yet absorbance in Sirkelsvlei waters was less than that of the other Cape Point vlei waters, even though all drain similar catchments. In addition, a relatively small pH shift by buffering to pH 6.88 (<0.6 pH units) resulted in a large shift in the absorbance measured in the late summer and autumn months, such that there is no correlation between the variations in ambient colour and buffered absorbance measurements (table 6.5 and fig. 6.4). The greatest percentage change in colour (absorbance) occurred in the months when salinities were greatest, implying a salinity effect and thus a consequence of the type of complexation.

Grootwitvlei waters contained levels of humic compounds often close to those of Grootrondevlei, yet the levels of iron were on average less than half those of the more humic vleis. The iron that was present in the water column is likely to have been strongly bound to the humic fraction as there is a strong correlation between the variations in both (table 5.4). However the high pH and the high levels of particulate matter in the water column are thought to limit the levels of the dissolved iron present. The formation of metal-humic complexes is not as favoured at high pH as at intermediate or low pH. In addition, iron is more rapidly transformed to insoluble forms at higher pH and in the presence of high particulate matter loads the ferric hydroxide colloidal particles can be neutralized and join together to form a rapidly settling precipitate (Wetzel 1983). The reduced iron levels thus result from a competitive removal of iron.

In Rondevlei there were very low levels of iron and of humic substances. Metal-humic complexation may have been present, but did not significantly enhance iron concentrations. Most iron was probably removed from solution by the same processes as noted for Grootwitvlei: in fact the levels of iron in Rondevlei remained at the same concentrations as found in Grootwitvlei during the period of greatest particulate load and highest pH (summer to autumn).

Complexation of other cations, such as Ca^{2+}, is not apparent due to the high concentrations relative to the complexation capacity of the humic substances, but is likely to occur in the waters other than Sirkelsvlei. Iron-humic complexation has a further consequence, in that under acidic, aerobic conditions these complexes can sorb ionic orthophosphate, thus enhancing the epilimnetic concentrations of phosphorus (Koenings 1976, Koenings and Hooper 1976, Francko and Heath 1983). In the absence of humic substances, ferric iron (Fe^{3+}) and phosphate combine, under oxidising conditions, to form insoluble ferric phosphate. The iron-humic complexes may be readily photo-reduced by uvlight, causing the release of orthophosphates and the formation of ferrous iron-humic complexes, which are stable in acidic, aerobic water, but cannot bind orthophosphates (Koenings and Hooper 1976). The (ferric) iron-humic complexes thus act as a chemically reactive store of phosphorus, not biologically available but abiotically controlled by a uv light-induced release (Francko 1986). The reaction forms one of three distinct orthophosphate regenerative mechanisms in the epilimnion. Levels of SRP in Suurdam and Gillidam, and to a lesser extent in Sirkelsvlei, are noted in chapter 5 to show a strong correlation with the levels of humic substances. Thus in these three vleis, complexation of the SRP by the iron-humic complexes appears to be occurring. This is further borne out by the high mean concentrations of SRP in these vleis in comparison with those in the Grootvleis. Reasons for the lack of association between SRP and HS in Grootrondevlei in particular are not understood, whereas in Grootwitvlei it is possibly a consequence of the higher trophy of the water and thus competitive demand for phosphorus. Stewart and Wetzel (1981b) were unable to demonstrate orthophosphate binding in an epilimnion with relatively low concentrations of iron and high values of alkalinity, calcium and pH (no figures given), but affirm its importance in systems of lower alkalinity. Hence the conditions in both Grootwitvlei and Rondevlei were presumably not conducive to the binding of orthophosphate.

The ability of the humic substances to complex or adsorb many different chemical species leads to the question of the role these enhanced concentrations of trace elements, nutrients and toxic compounds may play in the chemical and biological functioning of the limnetic environment. The idea of "a kitchen" of micro-elements is suggested by Gjessing (1981), who states that it is probable that a number of associated micro-elements are exchangeable and available for organisms in the surroundings. Certainly humic substances at low concentrations are well known for their stimulatory effects on primary producers, but at high concentrations humic substances inhibit phytoplanktonic growth due to, amongst other effects, the increased metal complexation capacity which reduces the availability of essential ions to the phytoplankton (see Prakash *et al.* 1975, Prakash and MacGregor 1983). The accumulation of both essential (nutrients, trace metals) and toxic (heavy metals, organic pollutants) species by humic compounds occurs readily, but the bio-availability of the complexed species is not reflected in their concentrations. Other effects of the humic compounds on the primary productivity of the water may be due to specific toxic characteristics, such as the phenolic constituents (see Buikema *et al.* 1979), as well as the obvious effects of light attenuation due to the high absorption coefficients of most of the waters; these are discussed in chapters 1 and 9. Even though most humic substances are notably resistant to both chemical and biological degradation there are certain bacteria, fungi and other microorganisms that utilize humic compounds as an energy source (Prakash and MacGregor 1983). De Haan (1974, 1977, 1983) proposes that the microbial degradation of humic substances is stimulated by co-metabolism or by a priming effect of the bacteria in the presence of easily degradable substrates. Thus in lakes of higher trophy (productivity) with high rates of release of easily degradable substrates, increased rates of degradation of the humic substances should occur. The large decrease in the levels of humic substances in Grootwitvlei during the periods of greatest productivity may in part be due to increased rates of microbial degradation and similarly the very low levels of humic substances in Rondevlei are most likely maintained at these levels in part by microbial degradation. Ultra-violet radiation is also responsible for the degradation of humic substances, as well as mediating the release of orthophosphates from iron-humic complexes.

SUMMARY

Suurdam waters were very dark in colour as a result of high concentrations of relatively high molecular weight humic substances. The relative phenolic content of the humic compounds was, on average, high, indicating a primarily allochthonous source. Gillidam and Sirkelsvlei both had waters less intensely coloured than Suurdam, but considerably darker than the Grootvleis. Although concentrations in the two vleis were similar, the overall character of each of the two mixtures differed, with humic compounds in Gillidam more similar to those in Suurdam and Grootrondevlei. All three mixtures appear to consist of relatively high molecular weight compounds of relatively high phenolic content. Sirkelsvlei on the other hand, appears to contain humic compounds of relatively lower molecular weight and lower phenolic content, closer in character to the 'average mixture' of Grootwitvlei. Seasonal variation in the levels of humic substances in the Cape Point vleis displayed a broad similarity, with a mid-winter to spring minimum. This minimum is probably the consequence of interaction between a number of factors, the most important of which are summer and autumn litterfall, winter waterlogging of the soil and small catchment size. These result in a winter depletion of soil humic substance as a result of flushing and reduced rates of formation.

Water in the Grootvleis is moderately brown coloured, still well within the range of 'brown waters'. Concentrations in the two vleis were similar in winter, but were lower in Grootwitvlei in summer. The character of the humic mixture also differed in Grootwitvlei between winter and summer. Both vleis displayed a winter maximum in concentration with humic compounds of moderately high molecular weight and high phenolic content. In summer, however, the humic compounds in Grootwitvlei were lower in molecular weight and phenolic content. This was probably the result of high rates of degradation, as well as a significant contribution of autochthonous humic substances. The winter maxima consisted of allochthonous input, resulting from increased surface and subsurface flow through large catchments, in contrast to low summer levels.

Rondevlei waters were not obviously stained and registered low colour values. Humic compounds were mostly authochthonous in origin and thus low in relative molecular weight and phenolic content. However, a limited influx of allochthonous compounds as a result of winter inflow caused a small increase in colour and a small increase in mean molecular weight and phenolic content.

Humic substances appear to affect pH of the vleis both by buffering at low pH and high concentrations, in Suurdam and Gillidam, and by reducing pH at lower concentrations in the Grootvleis and Rondevlei. Complexation of iron and SRP appears to be most pronounced in Suurdam and Gillidam, whereas in Sirkelsvlei, high salinities may result in the weak electrostatic binding of the major cations and precipitation of the higher molecular weight fraction. Grootrondevlei has relatively high levels of iron, which show little association with the humics and which may be present as a ferric hydroxide fraction. The SRP levels are low and also show little association with the humics. The lower molecular weight of the compounds and the greater productivity in Grootwitvlei and Rondevlei probably results in more rapid microbial degradation of the humics in these vleis.

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CHAPTER 7 : PARTICULATE ORGANIC MATTER

INTRODUCTION

Particulate organic matter (POM) suspended in the water column can, like dissolved organic matter, be broadly divided into that of allochthonous origin and that of autochthonous origin. The sources of allochthonous particulate material are primarily terrestrial plants. This POM may enter a lentic system as wind-blown material or as POM from streams, which can vary from very fine complexed humic compounds (the insoluble humin fraction) to coarser leaf and stem particulates. The allochthonous particulate organic fraction in lakes is usually much smaller by mass than the allochthonous dissolved organic fraction, constituting only about 10% of the total allochthonous organic matter (Wetzel 1983), and this may well be similar in most of the vleis under study. The particulate matter is usually soon leached of its easily degradable (non-refractory) compounds. It thus has a relatively low percentage of nitrogen and a relatively high C:N ratio. Wetzel (1983) gives a ratio of "about 50 : 1" and Visser (1983) gives mean C:N ratios for aquatic and terrestrial humic and fulvic acids of between 19 and 39. The refractory nature of humic materials, and their contribution to both the particulate and dissolved fractions, is an important consideration in the more humic lake waters.

Autochthonous particulate material originates from two primary sources (i) the littoral and (ii) the phytoplankton of the pelagic zone. The macrophytes and the algae of the littoral zone exude organic compounds (as DOM) during growth and the macrophytes generally display a significant seasonal dieback (see chapter 2), introducing a large quantity of plant material into the water over a number of months. This littoral production is recognised as one of the most important sources of particulate organic matter in small lakes (Wetzel 1983). Primary production in the open water is of variable importance as a source of POM but, depending on its quality or palatability, it is often a driving variable in limnetic 2° production,. The nitrogen content of this living fraction is obviously high and C:N ratios vary from about 5 to 10 (data from Banse 1974, Eppley *et al.* 1977, Abou Debs 1984, Hamilton-Taylor *et al.* 1984 and Fielding 1987). Wetzel (1983), grouping algae and macrophytes, gives an initial value of about 12. Upon death a rapid loss (leaching) of proteinaceous and other easily degradable materials occurs with a consequent increase in the ratio, but it still remains largely below 20.

The detrital particulate organic matter thus forms an important metabolic base of carbon and energy (Wetzel 1983). It is almost always present in excess of demand and drives the microbial decomposer cycle at rates dependent on the refractility and resistance of the matter. In comparison the living phytoplankton fraction, which drives the limnetic 2° production, may be limiting. Reasons for measuring the particulate organic carbon and nitrogen content of the seston were (i) to examine the overall quality of the particulate fraction in each vlei (C:N ratios) as a food base for microheterotrophs or secondary consumers; (ii) to estimate the contribution of the phytoplankton to the seston as a whole (see POC:Chl a ratios - chapter 8); and (iii) to observe any seasonality in quantity or quality of the seston. Thus the data presented in this chapter are supplementary to chapters 8 and 9.

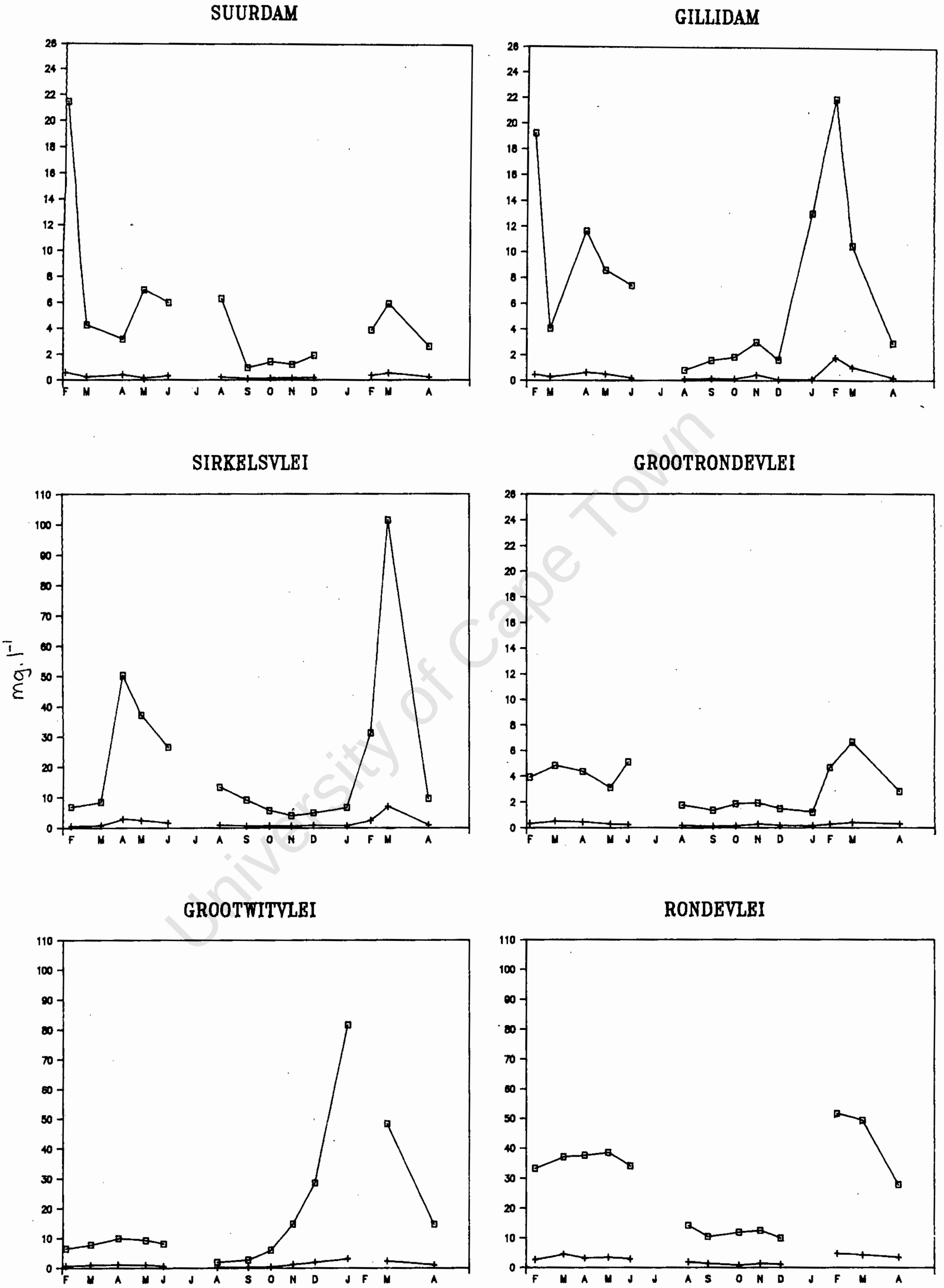
METHODS

Sample collection, filtration and storage is described in chapter 3. Discs of 5mm in diameter were punched in the filter-papers, placed in tin boats and combusted in a Heraeus CHN - Mikro universal combustion analyser which had been calibrated with cyclohexanone (Monar 1972). Sample blanks of pre-ashed filter papers were also combusted and the values subtracted from the sample values. Total particulate carbon and nitrogen (as mg l^{-1}) and the C:N ratio (where $N=1$) of the particulate matter were calculated for each vlei over the 15 month study period.

RESULTS AND DISCUSSION

Seasonal variation in the levels of suspended particulate carbon (POC) and nitrogen (PON) are displayed in fig. 7.1 and the mean and range of values are summarised in table 7.1. Rondevlei, Grootwitvlei and Sirkelsvlei displayed high mean values of POC and PON, whereas Suurdam, Gillidam and Grootrondevlei had mean levels an order of magnitude lower.

A significant feature is the large amount of variance about each mean in all vleis except Grootrondevlei. The three high mean values thus result from the greater seasonal maxima in Rondevlei, Grootwitvlei and Sirkelsvlei and the lower part of each range of values overlap to a large extent with the ranges of Suurdam and Gillidam, and to a lesser extent of Grootrondevlei. Due to the overlap there is no statistical difference between the means of all the vleis, except Rondevlei (Newman-Keuls multiple range test, $P < 0.05$). Large variations, particularly in the POC levels, are expected in shallow systems where wind-induced mixing is a frequent occurrence and may cause large changes over relatively short periods of time (days as compared to months). These changes obviously result from the resuspension of detrital material and thus patterns of 'seasonal' variation must be



SUURDAM

GILLIDAM

SIRKELSVLEI

GROOTRONDEVLEI

GROOTWITVLEI

RONDEVLEI

Figure 7.1 Seasonal variation in the suspended particulate organic carbon (□) and particulate organic nitrogen (+) levels (mg l^{-1}) in the six vleis.

treated with caution. The contribution of autochthonous POC increases with increasing phytoplankton abundance and thus is more seasonally controlled. The relative contribution of phytoplankton carbon is discussed in chapter 8, where investigation of the relationship between POC and chlorophyll *a* indicates a relatively high contribution in Rondevlei, Grootwitvlei and Sirkelsvlei, and relatively low contributions in the remaining three vleis. The high seasonal maxima of POC and PON correspond well with the maxima of chlorophyll *a* in Rondevlei, Grootwitvlei and Sirkelsvlei. In Suurdam, Gillidam and Grootrondevlei, as a result of the relatively low contribution of phytoplankton carbon, POC and PON levels were most strongly influenced by factors such as water depth, wind and allochthonous input. Certainly lowest levels occurred during the general period of high water level and low average wind speeds in the three vleis (late winter to spring) and high levels occurred generally in the summer months with low water levels and often strong winds. The possible impact of allochthonous input is difficult to distinguish from and/or to relate to macrophyte seasonal die-back (chapter 2), although the higher levels in Suurdam over June, July and August may have resulted from die-back of *Scirpus* over that period.

	POC mean (±SD)	 range	PON mean (±SD)	 range
SU	5.07 (± 5.34)	0.94- 21.46	0.27 (±0.16)	0.09-0.58
GI	7.73 (± 6.82)	0.80- 22.00	0.43 (±0.48)	0.06-1.79
GR	3.16 (± 1.71)	1.33- 6.66	0.26 (±0.12)	0.11-0.39
SI	22.53 (±26.89)	3.98-101.50	1.59 (±1.75)	0.52-6.98
GW	18.49 (±22.76)	1.90- 81.63	1.11 (±0.89)	0.15-3.18
RO	28.37 (±15.03)	9.87- 51.75	2.73 (±1.37)	0.74-4.78

Table 7.1. Mean particulate organic carbon (POC) and nitrogen (PON) levels and the range of levels in mg l^{-1} - Suurdam (SU), Gillidam (GI), Grootrondevlei (GR), Sirkelsvlei (SI), Grootwitvlei (GW), Rondevlei (RO).

Seasonal variation in the C:N ratio of the suspended particulate matter is displayed in figure 7.2 and the means and ranges of values in table 7.2. Both Suurdam and Gillidam had POM of a high mean C:N ratio, although there is a large variance about both means as a result of large fluctuations in the ratio. The remaining four vleis contained POM of similar mean C:N ratios with much lower

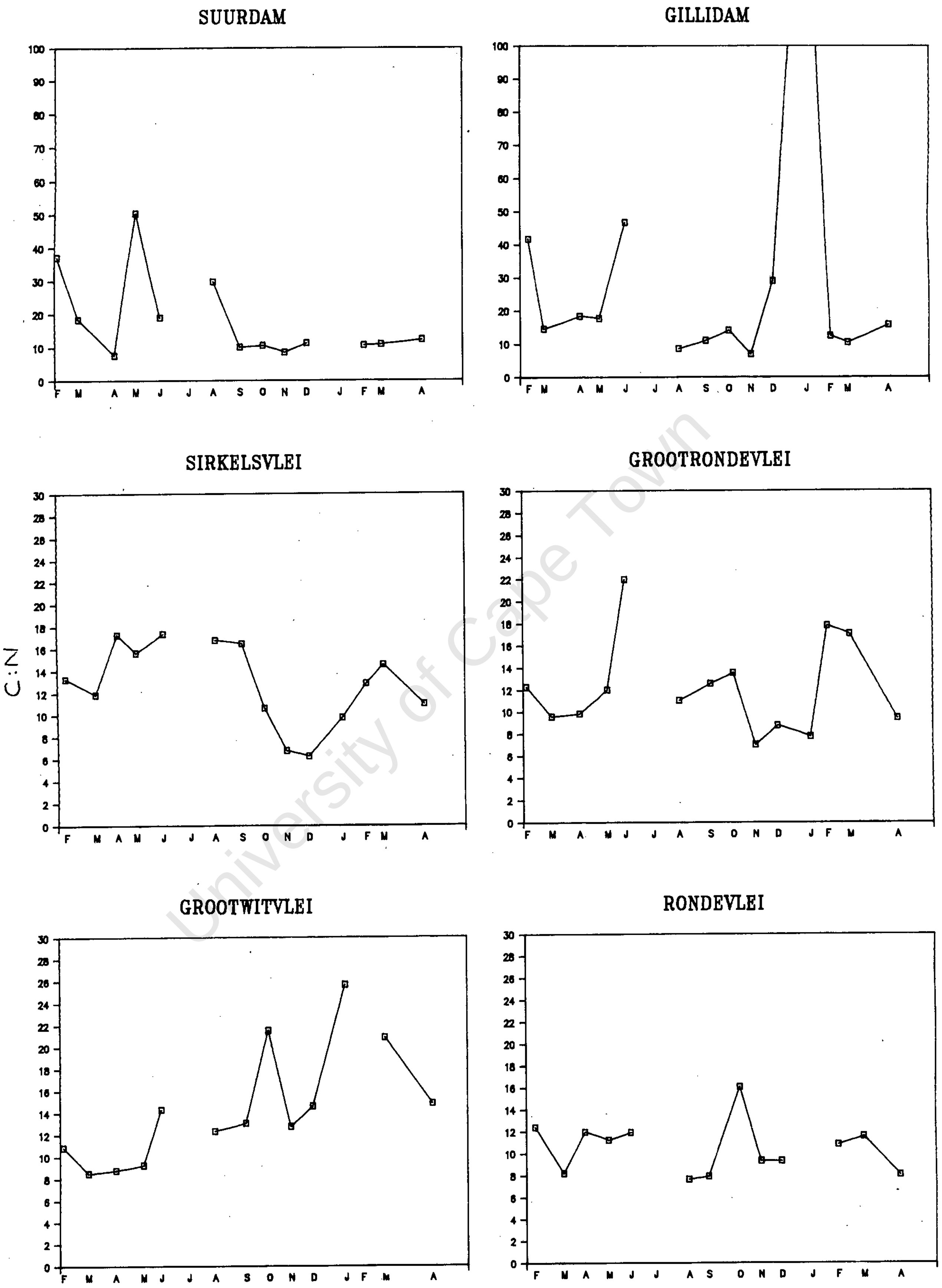


Figure 7.2 Seasonal variation in the C:N ratio of the suspended particulate organic fraction in the six vleis.

variance about the means. There is no statistical difference between the means (Kruskal-Wallis, $0.05 < P < 0.25$). The lowest values of all six vleis are characteristic of natural phytoplankton assemblages, although the highest values differ considerably. The very high C:N values in Suurdam and Gillidam may result from breakdown of *Scirpus* litter in the vlei or from resuspended 'dye' - the fine black bottom sediment found in humic waters and probably in this case the sum of the humin and humic acid content. Both vleis are very small, both have large *Scirpus* beds in relation to total water surface area and both have bottom sediments covered with 'dye'. In Suurdam the high C:N values correspond to high POC values and *Scirpus* dieback. In Gillidam the very high C:N ratio in January is probably due to resuspension of dye in the very shallow water. Amongst the remaining C:N values and the remaining vleis there is not a great difference in the range of values (mostly around 12) and there is little obvious pattern in their variation.

	C:N mean (±SD)	range
SU	18.2 (±13.1)	7.6- 50.4
GI	30.0 (±43.0)	6.9-173.5
GR	12.2 (± 4.2)	7.0- 22.0
SI	12.9 (± 5.1)	6.2- 16.8
GW	14.2 (± 5.1)	8.5- 25.7
RO	10.5 (± 2.4)	7.7- 16.1

Table 7.2. Mean C:N ratios and their ranges in the vleis - Suurdam (SU), Gillidam (GI), Grootrondevlei (GR), Sirkelsvlei (SI), Grootwitvlei (GW) and Rondevlei (RO).

In conclusion, therefore, the contribution of humic precipitates to the total particulate organic matter is not obvious, except possibly in Suurdam and Gillidam. The quality of the seston as regards the C:N ratio is not obviously or statistically different between the vleis, except for the greater variability in Suurdam and Gillidam. The loading of particulate organic matter however does differ considerably and although the ranges of the vleis overlap, the maxima of Rondevlei, Grootwitvlei and Sirkelsvlei correspond closely to the respective chlorophyll maxima.

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CHAPTER 8 : PHYTOPLANKTON

INTRODUCTION

Phytoplankton biomass is an important measure of food availability for zooplankton, a base reference in primary production studies and, in general, an index of lake fertility and/or pollution; yet it is almost impossible at present to make any direct measurement of phytoplankton biomass. There are a variety of techniques available for the analysis and calculation of phytoplankton biomass, but all involve a number of steps and the final results can vary widely. The problem common to most methods is how to separate the living phytoplankton from the bacteria and zooplankton and, most importantly, from the non-living fraction of organic detritus, as well as the inorganic particulate material that together form the seston of the water column (see chapter 7). In this study phytoplankton photosynthetic pigments and their breakdown products were used as a measure of the standing crop and an indication of the primary productivity; an overview of methods is presented below.

Chlorophyll *a* is the photosynthetic pigment common to all algae, whereas chlorophyll *b* is found only in the chlorophytes and euglenophytes, where it makes up less than half of the total pigment content (Round 1973). Chlorophylls c_1 and c_2 are found in small amounts in the bacillariophytes (diatoms), chrysophytes, dinophytes, xanthophytes and cryptophytes (Round 1973, Wetzel 1975). Of these groups, the chlorophytes and bacillariophytes generally comprise the greatest proportion of algal biomass. The remaining groups each have a relatively small number of planktonic species which make up a significant proportion of the phytoplankton biomass only under certain favourable conditions (from Wetzel 1983). Concentrations of chlorophylls *b* and $c_1 + c_2$ can therefore be used to give an idea of the contribution of such groups to the phytoplankton community. High pressure liquid chromatography (HPLC) techniques can further separate the relative importance of each group on the basis of differences in their xanthophyll and carotene spectra.

The three chlorophyll breakdown products commonly recognized are chlorophyllide, phaeophytin and phaeophorbide (phaeophytin and phaeophorbide are collectively referred to as the phaeopigments). Phaeophytin is formed by the loss of the central Mg atom of the chlorophyll molecule, chlorophyllide by the loss of the phytyl chain, and phaeophorbide by the loss of both the Mg atom and the phytyl chain. The displacement of magnesium, with the formation both phaeopigments, is thought to be caused by the acidic stomach conditions of grazers (Sartory 1982, Welschmeyer and Lorenzen 1985). Chlorophyllide *a*, however, appears as a result of the action of the enzyme chlorophyllase and indicates the presence of senescent cells in the population (Monteiro *et al.* 1985). In highly productive regions chlorophyllide *a* may constitute a large proportion of the chlorophyll-related compounds (Mantoura and Llewellyn 1983).

Welschmeyer and Lorenzen (1985) have shown that phaeopigments are not produced in significant amounts by either cell senescence or dark exposure of the cells, or as a result of the bacterial conversion of chlorophyll, but are produced mostly by the activity of herbivorous grazers. They have further shown that zooplankton grazing is the dominant factor in the removal of chlorophyll from the system, algal sinking being inconsequential in comparison. Loss of phaeopigment occurs both by the rapid sinking of large faecal pellets and by photodegradation of those phaeopigments that remain in suspension. They predict that in a single day under sunny conditions, photodegradation will remove about 92% of the original phaeopigments. Of the two phaeopigments, phaeophorbide *a* is probably the dominant constituent in most waters with relatively small amounts of phaeophytin normally present (Pattison and Parsons 1963, Yentsch 1967, Jeffrey 1974, Hallegraeff 1976, 1977b, Scor-Unesco 1980, Riemann 1978b). Degradation studies by Shuman and Lorenzen (1975) have shown a complete stoichiometric conversion of chlorophyll *a* to phaeophorbide *a* (1:1) as a result of zooplankton grazing. However more recent studies by Conover *et al.* (1986) and Wang and Conover (1986) suggest that a significant fraction of chlorophyll and its derivatives is destroyed or absorbed during its passage through the gut. The excreted fraction may still be positively correlated with the ingested fraction.

Phaeopigments may thus provide an extremely useful reflection of zooplankton grazing activity and hence phytoplankton loss from the system.

In this study chlorophylls *a*, *b* and $c_1 + c_2$, and total phaeopigment levels have been used to separate vleis of different trophy and to reflect the seasonal variation in total phytoplankton biomass in each vlei. The levels of chlorophylls *b* and $c_1 + c_2$ have been used to indicate the importance of the algal groups containing these chlorophylls (especially the diatoms) in the vleis as related to the differing chemical character of the waters. The phaeopigment levels have been included as a measure of chlorophyll loss and zooplankton grazing pressure on the phytoplankton community. However examination of the relationship between zooplankton numbers and/or grazing activity and phaeopigment levels is beyond the scope of this study and only brief comment is included below and in chapter 9. In addition the ratios of chlorophyll *a* to particulate organic carbon have been investigated as measures of the quality of the total particulate load.

OVERVIEW OF METHODS

Phytoplankton biomass. In the past estimates were obtained by total counts. Numbers of individuals may be appropriate when considering population dynamics and diversity, but species vary widely in size, and thus total counts are unreliable as a measure of biomass. More recently the most popular method has involved counting the algae and measuring the dimensions of individuals of each species. Average cell volume is calculated for each species and converted to algal fresh weight using average conversion factors (Vollenweider 1969, Tolstoy 1977, Vilyamaa *et al.* 1978, Hecky and Fee 1981, Heinonen 1982). This method is, however, both tedious and time-consuming and errors can be both large and variable as a result of limited numbers of counts, variations in ratios of fresh weight to fresh volume and/or variations in ratios of carbon to fresh volume (Lund 1964, Nalewajko 1966, Mullin *et al.* 1966, Strathman 1967, Hallegraeff 1977a).

Chlorophyll *a* is unique to plant cells, is relatively easy to measure, and provides a good reflection of the relative change in size of phytoplankton communities. It does not provide the same detailed information on changes in the community obtainable from microscopic counts, but is advantageous in that a large number of samples can be processed in a relatively short period of time. Although chlorophyll *a* gives a reasonably good reflection of changes in phytoplankton biomass, difficulties can arise in attempting to relate chlorophyll *a* concentration to phytoplanktonic carbon. The ratio of chlorophyll *a* to phytoplanktonic carbon can vary as a result of a number of different factors. These include the species composition, the growth rate, the age of the cells, the availability of nutrients, the light intensity, the time of day and the water temperature (Strickland 1960, Steele and Baird 1961, 1962a, 1965, Caperon and Meyer 1972, Sournia 1974, Banse 1977, Eppley *et al.* 1977, Chan 1978, Laws and Wong 1978, Barrister 1979, Hunter and Laws 1981). Thus, for even a single species, the ratio of chlorophyll *a* to phytoplankton carbon can vary by an order of magnitude (Laws and Wong 1978).

ATP has also been used as a measure of phytoplankton biomass. As in the case of chlorophyll *a*, however, ratios of ATP to phytoplankton carbon can vary widely, depending again on growth rate and the factors limiting growth (Cavari 1976, Perry 1976, Weiler and Karl 1979). Hunter and Laws (1981) conducted a systematic study of the variation in the ratio of chlorophyll *a* and ATP to phytoplankton carbon and found the greatest variation at low growth rates. Lowest values of both ratios occurred when growth rates were nutrient limited (particularly by phosphates) and highest values when growth rates were light limited. They suggested that in the surface waters of lakes in general, where phosphate may be the factor limiting growth, both ratios could vary widely as a function of growth rate, while in shallow lakes, often highly coloured and probably with frequent turnover, light may also be a limiting factor.

Steele and Baird (1961, 1962b, 1965) have attempted to calculate a measure of phytoplankton biomass using the relationship between chlorophyll *a* concentration and total particulate organic carbon content of the water column. This method plots the regression of total particulate organic carbon on chlorophyll *a* using the equation constant (the y-intercept) as a measure of detrital particulate carbon (non-chlorophyll carbon) and the slope, the ratio of carbon to chlorophyll *a*, as an indication of the proportion of chlorophyll *a* in the living plant cells. The method appears to have limited application however. Best results are obtained with monospecific, as opposed to mixed, phytoplankton assemblages, relatively low levels of detrital organic carbon, and with small time-intervals between samples or groupings of samples to avoid temporal change (Lorenzen 1968, Banse 1977, Ahlgren 1978, 1983).

Some researchers have attempted to compare the methodologies available for the estimation of phytoplankton biomass (Hallegraeff 1977a, Ahlgren 1983), but still with little real success in establishing either a more accurate methodology or any relationship between the variable errors associated with each method. Ahlgren (1983) stresses the unreliability of microscopic counting when converted to phytoplankton carbon estimates, yet the variability of ATP or chlorophyll *a* in relation to phytoplankton carbon does not allow a more accurate estimate.

Granberg and Harjula (1982b) compared chlorophyll *a* concentrations with phytoplankton biomass as determined by microscopic counting. They found a correlation, but the shape of the regression curve and the significance of the correlation were highly variable, both spatially and temporally. They suggest that this wide variation is due solely to the variability of cellular chlorophyll *a* content. This conclusion seems simplistic, however, in that the authors fail to take into account the error in their estimates of phytoplankton biomass. They also suggest that, in general, a peak in chlorophyll *a* content precedes the biomass maximum. This is in accord with the fact that the chlorophyll *a* content of algal cells varies readily and responds relatively rapidly to changing environmental conditions (cf. Hunter and Laws 1981). Thus chlorophyll *a* measurement should remain a good indication of the physiological state of the phytoplankton and of the overall changes in growth rate of the community. As stated by Hallegraeff (1977a), the different techniques give different information and there is no single method for estimating phytoplankton biomass and no conversion factor that may serve for general purposes.

Chlorophyll measurement. Methods of routine measurement have gradually developed over the past 35 years. Lorenzen and Jeffrey (Scor-Unesco 1980) describe briefly the development of the methods. Most of these methods have involved spectrophotometric or fluorometric analysis of the pigments and, of the two, spectrophotometric analyses of extracts of the pigment have in general been found to be the more useful. If more detailed analysis of the photosynthetic pigments (including pigments other than the chlorophylls) is required, chromatographic methods are necessary, of which HPLC is favoured. For the purposes of this study spectrophotometric analysis was chosen as detailed information on the pigments other than the chlorophylls and chlorophyll breakdown products was not required, and a large number of samples needed to be processed.

All the **spectrophotometric methods** for the measurement of chlorophyll involve the concentration of the phytoplankton cells onto a filter paper, the extraction of the chlorophylls and chlorophyll breakdown products from the phytoplankton cells, and the spectrophotometric measurement of the absorbance of the extract at certain wavelengths. Further than this details vary, often widely, both in sample preparation and measurement (see Sartory 1982). For this reason a review of the literature was conducted prior to analysis and is reported below.

The storage time of the sample prior to filtration is generally kept to eight hours or less (at 0^{O} C in the dark). However, Herve and Heinonen (1982) have shown no significant statistical change over a period of one day and, in most cases, no change over two or three days. This is subject to samples being stored and analysed in darkness as exposure to light causes a significant decrease in measured chlorophyll *a* (Herve and Heinonen 1984).

Glass fibre filters are usually recommended, and of these, Whatman GF/C or GF/F filters appear to be the most popular. A number of studies have been made to compare the efficiencies and effects of membrane and glass fibre filters. Conclusions vary with some authors reporting higher retention efficiencies with membrane filters (Levy and Fritsche 1980), and others reporting equal or greater retention efficiencies with glass fibre filters (Sheldon 1972, Long and Cooke 1972, Holm-Hansen and Riemann 1978). Generally the composition of the phytoplankton population, and more specifically cell size and fragility probably affects the retention efficiency of the filters. Certainly Salonen (1979), comparing the retention of glass fibre filters, showed the Whatman GF/F filter able to retain almost all bacteria from water of an oligotrophic lake (average cell diameter 0.6um). Membrane filters have also been noted on occasion to provide interference in absorbance measurements and chromatographic techniques (Creitz and Richards 1955, Jensen and Sakshaug 1973). Advantages of glass fibre filters, as noted by Salonen (1979) and Sartory (1982), include the relatively high loading capacity and filtration speed, the abrasive nature of the material which assists in homogenisation or grinding of the phytoplankton cells, the fact that glass fibre filters are normally cheaper, and the lack of interference with absorbance measurement. Whatman GF/C filters were used in this study.

Many authors recommend that magnesium carbonate is added to the filter before filtering (Creitz and Richards 1955, Strickland and Parsons 1972, Talling 1974, APHA 1985, Kaatra 1982). Its effect is to maintain a relatively high pH, preventing the breakdown of the chlorophyll to phaeopigments, as well as to increase the retention efficiency of the filter. A number of studies have been conducted to test the efficacy of the compound with varying results. Some researchers have found a reduction in phaeopigments in the presence of $MgCO_3$ (Daley *et al.* 1973, Levy and Fritsche 1980). Others have found no difference in the chlorophyll levels due to breakdown, with or without $MgCO_3$ (Rai 1973, Holm-Hansen and Riemann 1978). Levy and Fritsche (1980) found that retention efficiency was not affected by $MgCO_3$. Thus, because the addition of $MgCO_3$ is an established practice and the possible benefits outweigh any disadvantages its' addition was included in the analysis.

Ideally pigment extraction should be carried out immediately after filtration. However, for practical reasons it is more often necessary to store the filters before extraction and further analysis. Filters can be stored, either freeze-dried or frozen, at -20°C (always in the dark) for several months (Holden 1976, Holm-Hansen and Riemann 1978 and Levy and Fritsche 1980). Filters freeze-dried and then stored dry, in darkness, at room temperature, showed a large reduction in chlorophyll *a* content, probably due to the drying which reduces subsequent pigment extraction (Levy and Fritsche 1980). Levy and Fritsche (1980) also showed filters stored deep frozen (-18 °C) in a wet-condition yielded reliable results even after six months.

The extraction solvent most commonly used has been 90% acetone with methanol and ethanol less popular, although more recently ethanol has gained some favour. Certainly it appears that ethanol and methanol are superior to acetone as extractants of photosynthetic pigments from green and blue-green algae (Rai 1973, Holm-Hansen and Riemann 1978, Marker and Jinks 1982, Sartory and Grobbelaar 1984). A mixture of acetone (90%) and dimethyl sulfoxide (DMSO) (1:1) is also reported to be a superior extractant to 90% acetone alone (Shoaf and Quinn 1976, Stauffer *et al.* 1979). In addition liquid/liquid partitioning procedures using aqueous acetonitrile and hexane, and aqueous acetone and hexane have been employed to separate chlorophyll *a* from other interfering pigments (Wun *et al.* 1980, Swart and Barlow 1981).

There appears to be a paucity of literature on the specific extinction coefficients of chlorophyll in methanol, and many of these are contradictory (Stauffer *et al.* 1978). Also, according to Kaatra (1982) and Sartory (1982), methanol is classified as a toxic chemical (as is DMSO) and is thus to be avoided in routine determinations. There is even less literature on the specific extinction coefficients of chlorophyll with ethanol as an extractant and thus more research into its use is necessary. Furthermore methanol, and to a lesser extent ethanol, demonstrates a shift in its absorption spectrum on acidification making it unsuitable for the measurement of phaeopigments. Detailed literature is available on the specific extinction coefficients of photosynthetic pigments in 90% acetone and thus the most accurate trichromatic equations for the calculation of chlorophyll levels (Parsons and Strickland 1963, SCOR-UNESCO 1966, Jeffrey and Humphrey 1975). Thus 90% acetone was used in the present study, and the remaining discussion deals with extraction in 90% acetone.

Homogenisation or grinding is often used as an aid to extraction procedures. Again, there are different views as to the efficacy of grinding, probably because not all phytoplankton groups require mechanical cell destruction for good extraction. Mechanical breakdown is recommended by, amongst others, Parsons and Strickland (1963), Rai (1973), Youngman (1978), Chang and Rossman (1982), Youngman (1982), and Sartory and Grobbelaar (1984), while Holm-Hansen and Riemann (1978) report no improvement with grinding. Improved extraction, in particular from centric diatoms and filamentous blue-green algae, was noted by Chang and Rossman (1982). The main advantage of grinding/homogenisation is a reduction in extraction time, allowing samples to be processed more quickly.

Sonification is also used as an aid to extraction and to reduce extraction time. Improved extraction using sonification has been reported by Nelson (1960) and SCOR-UNESCO (1966); Daley *et al.* (1973) achieved complete extraction using a sonic probe rather than an ultrasonic bath, and Welschmeyer and Lorenzen (1985) used sonification, having found no difference between sonifying and grinding. Chang and Rossman (1982) reported no difference in extraction between sonified and non-sonified samples, but this was after 15 h of extraction.

There is a danger of conversion of the chlorophylls to their breakdown products if either grinding or sonification is continued for too long. Grinding for longer than three minutes with an electric grinder at 800 rpm causes heating (Sartory 1982), and extended grinding causes conversion into breakdown products (Kerr and Subba Rao 1966, Daley *et al.* 1973). Sonification for 30 minutes has been shown to cause chlorophyll breakdown (Daley *et al.* 1973), while periods of 10 to 20 minutes have shown no breakdown (SCOR-UNESCO 1966).

In these analyses homogenisation was performed by hand with a metal spatula, using the abrasive character of the glass fibres to break down the plant cells, followed by sonification for 20 minutes using the recommendations of SCOR-UNESCO (1966) and Swart and Barlow (1981). In this way extraction time was reduced to approximately one-and-a-half hours.

Centrifugation is used to separate the particulate cell material and fibres from the solvent and photosynthetic pigments. The speed and duration of centrifugation when specified, can vary between 2000 and 5000 rpm, generally for about 10 minutes (Parsons and Strickland 1963, Watling 1981, Chang and Rossman 1982, Sartory 1982, Van Breemen 1982, Herve and Heinonen 1984). Swart and Barlow (1981) centrifuged at 3800xg (15°C) for fifteen minutes which was approximately 9000rpm using the IEC B-20A centrifuge in this study. No literature was found reporting any detrimental effects as a result of the speed of centrifugation. Herve and Heinonen (1984) reported a slight decrease in measured chlorophyll *a* between centrifugation times of two and 10 minutes, but no difference between 10 and 20 minutes of centrifugation. Five minutes or less however was not long enough to remove turbidity and ten minutes was recommended.

Trichromatic equations are used to calculate the concentrations of the chlorophylls from their absorbance measurements. Various trichromatic equations have been proposed (Richards with Thompson 1952, Parsons and Strickland 1963, SCOR-UNESCO 1966 and Jeffrey and Humphrey 1975), as well as some monochromatic equations (Odum *et al.* 1958, Talling and Driver 1963). Monochromatic equations assume no interference due to absorbance by chlorophylls *b* and *c* at 663-665nm, whereas trichromatic equations attempt to correct for possible interference by these chlorophylls. It is for this reason that trichromatic equations are preferred. Of the available trichromatic equations, the Jeffrey and Humphrey (1975) equations supercede all the previous equations because they use the most accurate extinction coefficients available at present for chlorophylls *a*, *b*, c_1 and c_2. Chlorophylls *b* and especially c_1 and c_2 are incorrectly calculated using any equation other than Jeffrey and Humphrey (1975) (SCOR-UNESCO 1980). Humphrey (1978) has developed matrices to convert results from any of the few major sets of trichromatic equations to results from the Jeffrey and Humphrey equations and similarly, Wartenberg (1977) has developed an intercalibration technique which allows the conversion of results from any of the few sets of trichromatic equations to any other set.

None of the above equations take into account interference due to breakdown products of chlorophyll *a*, however. Both phaeophytin *a* and phaeophobide *a* are measured as chlorophyll *a* and can thus cause a large error if the levels of either are high. If the extract is acidified, however, chlorophyll *a* and chlorophyllide *a* are converted to phaeophytin *a* and phaeophobide *a*, as a result of the removal of the Mg atom in the porphyrin ring (Lorenzen 1967), with a consequent decrease in absorbance at 665 nm. This change in absorbance upon acidification allows for measurement of the phaeopigments. Vernon (1960) was the first to introduce an acidification step for phaeopigment analysis. Subsequently Lorenzen (1967), Moss (1967) and Marker (1972), after incorporating an acidification step into their methods, have published paired equations for the calculation of both chlorophyll *a* and phaeopigments.

The equations of Lorenzen (1967) are widely used and, in the intercalibration tests of SCOR-UNESCO (1980), appear slightly more accurate than those of Marker (1972). Thus they were used in preference to those of Moss (1967) or Marker (1972).

Absorbance measured at 665 nm is assumed to be due only to chlorophyll *a* and its breakdown products. Chlorophylls *b* and *c* and their breakdown products are not found to have a marked effect on absorbance at 665 nm (Talling and Driver 1963, Moss 1967, Marker *et al.* 1980). Thus using the trichromatic equations of Jeffrey and Humphrey (1975), it is possible to obtain a measure of chlorophylls *a*, *b*, and c_1 and c_2, including their breakdown products. By using the equations of Lorenzen (1967), it is possible to separate the level of phaeophytin *a* and phaeophorbide *a* from chlorophyll *a* and chlorophyllide *a*, although chlorophyllide *a* can only be separated from chlorophyll *a* by using chromatographic techniques (such as HPLC) .

A final acid concentration of ca.1 x 10^{-2}M HCl was used by Lorenzen (1967) and has since been used widely by many researchers. Riemann (1978a) and Sartory

(1982) however suggest a final acid concentration of 3×10^{-3}M HCl. The reduction in acid concentration is to prevent interference effects caused by other pigments as a result of over-acidification, shown by Riemann (1978a). If the acid concentration is too weak, however, there will be incomplete conversion of chlorophyll *a* and chlorophyllide *a* to phaeopigments *a*.

Although the acidification step of Lorenzen (1967) allows for the correction of interference by phaeophorbide *a* and phaeophytin *a*, it does not take into account interference due to chlorophyllide *a* or the various carotenoid pigments (Riemann 1978a) and should thus result in an overestimation of active chlorophyll *a*. **High pressure liquid chromatography** techniques permit the separation and accurate measurement of the plant pigments and their breakdown products without problems of mutual interference. A number of studies have been conducted to investigate the difference in chlorophyll measurement by HPLC, spectrophotometric and fluorometric techniques. Jacobsen (1978 and 1982) and Mantoura and Llewellyn (1983) both showed an overestimation by the latter two methods. Fielding (1987), however, showed no significant difference between the results of HPLC and spectrophotometric determinations according to Lorenzen (1967), although as expected he did find a significant difference between the results of HPLC and spectrophotometric determinations according to Jeffrey and Humphrey (1975). Jacobsen (1982) and Mantoura and Llewellyn (1983), when comparing the results of HPLC with Lorenzen spectrophotometric determinations found differences ranging up to just over one order of magnitude less. Fielding (1987) further showed that chlorophyll *a* values measured daily by HPLC and spectrophotometric methods over periods of 31-52 days showed very much the same trends, with no excessive differences in the values. The results will obviously differ most when high concentrations of degradation products are present.

Other techniques such as paper, column and thin-layer chromatography, as well as phase separation, also allow for the physical separation of pigments and their breakdown products, thus preventing mutual interference during the analysis (Holden 1962, Jeffrey 1968, 1974, 1981, Strain *et al.* 1968, Garside and Riley 1969, Daley *et al.* 1973, Hynnen and Ellfolk 1973, Hallegraeff 1976, Shoaf and Lium 1977, Jensen 1978, Brown *et al.* 1981, Swart and Barlow 1981, Riemann 1982). These techniques are often insensitive, however, and are generally slow and tedious, making them unsuitable for large numbers of analyses or for dealing with photolabile pigments.

HPLC was not available for use in the present study. However, with reference to the discussion above on the measurement of phytoplankton biomass, it is probably the most suitable method at present and thus some comment is included below. It is reported to eliminate the shortcomings of the other chromatographic techniques (Jacobsen 1978, 1982, Shoaf 1978, Geeskes and Kraay 1982, Mantoura and Llewellyn 1983, Monteiro *et al.* 1985). The ability of this method to separate the various photosynthetic pigments and their breakdown products from one another makes it a powerful tool in identifying the predominant algal taxonomic groups present at any time in the water column and as an indicator of the physiological state of the phytoplankton community as a result of the presence or abscence of different pigment breakdown products. Certain chlorophyll and carotenoid pigments are characteristic of different algal groups, and HPLC is capable of separating and quantifying all these key class-specific pigments in algae as well as their companion xanthophylls (over thirty algal chlorophyll and carotenoid pigments) (Mantoura and Llewellyn 1983).

METHODS

Sample collection, storage and filtration are described in chapter 3.

Before analysis the filters were allowed to defrost at room temperature and were then unfolded and placed in centrifuge tubes with 2ml of 90% (v/v) Analar grade acetone. Not more than three filters were used for each sample and not less than 120ml of lake water was filtered for each sample. Using a metal spatula the filters were reduced to a fibrous pulp in the centrifuge tubes, after which a further 10ml of 90% acetone was added to each and the tubes sealed and placed in crushed ice in darkness. The tubes were agitated ultrasonically in the dark for 20 minutes at 45 kHZ and then centrifuged at 9000 rpm (3800 x g) ($15^{o}C$) for 15 minutes, after which two 5 ml aliquots of supernatant were drawn off without disturbing the residue.

Each aliquot of supernatant was placed in a test tube and to one of each pair 0.10 ml of 1N HCl was added. The test tubes were then sealed and kept in darkness on crushed ice. The acetone extract was decanted into a 5cm path-length cuvette and the absorbances were measured against a 90% acetone blank in a double-beam Beckman model 25 spectrophotometer. Absorbance was measured at 750, 665, 664, 663, 647, 645, 630 and 480 nm for the non-acidified sample, and at 750, 665 and 663 mm for the acidified sample. The absorbance at 750 nm was subtracted from each of the other absorbances to correct for any interference due to turbidity. Chlorophyll concentrations were then calculated using the trichromatic equations of Parsons and Strickland (1963) and of Jeffry and Humphrey (1975) for chlorophyll *a* (including phaeopigments), chlorophyll *b* and chlorophyll c_1 and c_2, and the equations of Lorenzen (1967) were used to calculate chlorophyll *a* and phaeopigments separately. An attempt was made estimate the proportion of phytoplankton containing chlorophyll *b* and chlorophyll c_1 and c_2 in the different populations using chlorophyll *b*:chlorophyll *a* and chlorophyll *c*:chlorophyll *a* ratios.

RESULTS

CHLOROPHYLL A LEVELS

Seasonal variations in chlorophyll *a* levels and the mean and range of levels in each vlei are displayed in figure 8.1 and table 8.1 respectively. Suurdam was characterized by very low concentrations of chlorophyll *a* (< 3.7 ug l^{-1}). The annual range in chlorophyll *a* levels at the two sites varied from the negative value of -0.8 ug l^{-1} (an artefact resulting from estimation by trichromatic equations and viewed as approximately 0) to 3.7 ug l^{-1} . Of the little variation that did occur, there appears to have been a small peak in spring (September and October).

	CHLOROPHYLL *A*			PHAEOPIGMENT *A*		
	mean	±sd	range	mean	±sd	range
SU	0.9	±1.1	0.8- 3.7	2.9	±1.5	0.6- 6.5
GI	3.4	±2.7	0.4- 10.0	5.0	±4.5	0.9-11.5
GR	3.0	±2.7	-0.9- 10.7	3.4	±2.3	0.5-11.0
SI	11.6	±7.4	4.2- 38.0	12.0	±8.4	2.8-41.0
GW	30.8	±18.7	11.3- 84.7	11.4	±7.4	3.0-22.2
RO	60.4	±32.4	1.7-119.6	29.4	±18.6	4.5-74.1

Table 8.1. Mean chlorophyll *a* and phaeopigment levels and the range of levels in each of the six vleis - Suurdam (SU), Gillidam (GI), Grootrondevlei (GR), Sirkelsvlei (SI), Grootwitvlei (GW), Rondevlei (RO). All values in µg l^{-1} .

In Gillidam, the chlorophyll levels were low, but were in general higher than those in Suurdam. The shallower, more sheltered station (2) had the greater maxima: up to 8.3 ug l^{-1} in spring (September/October), 10.0 ug l^{-1} in early summer (December/January) and 9.0 ug l^{-1} in autumn (April/May). The more exposed

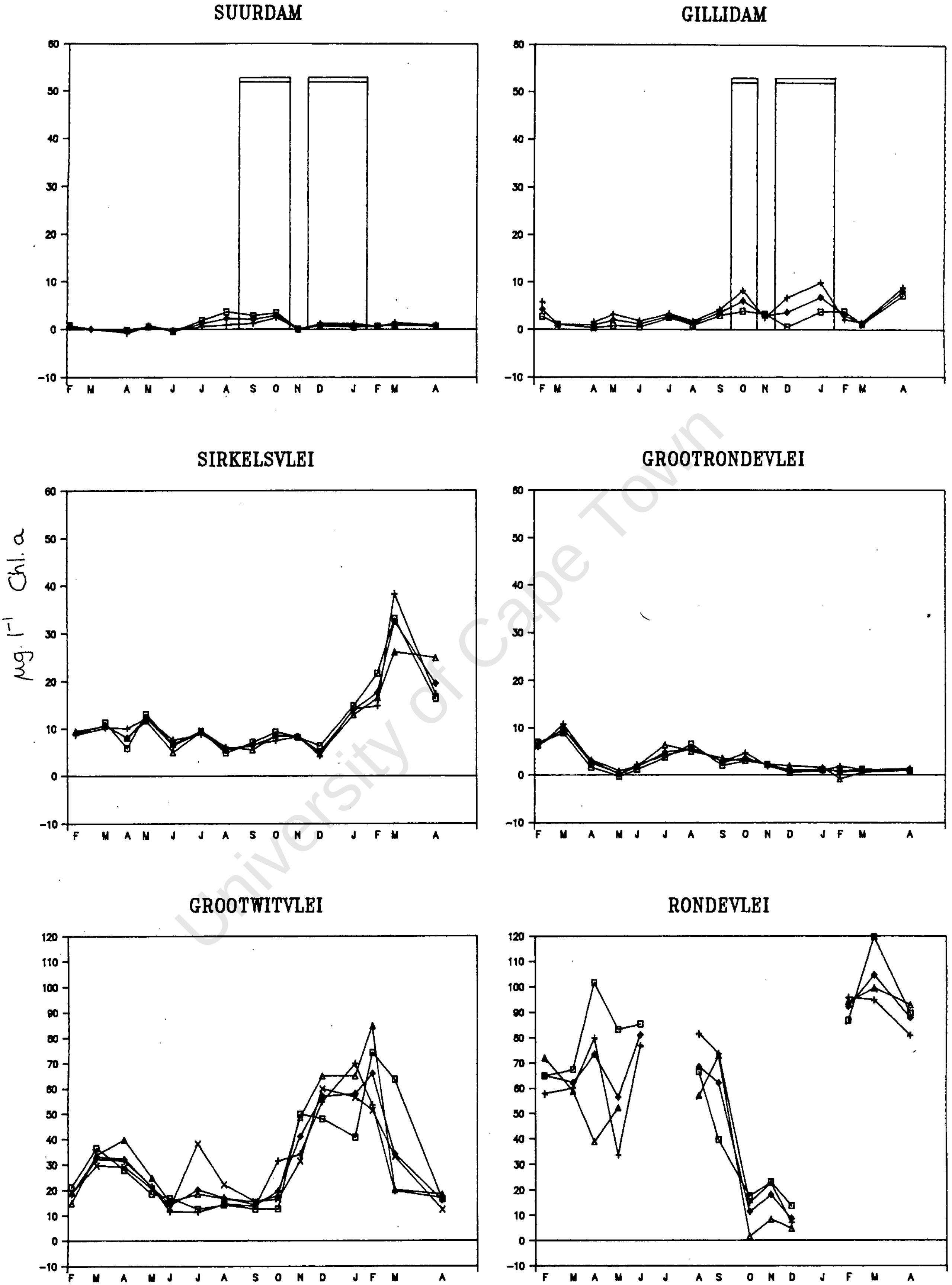

Figure 8.1. Seasonal variation in the chlorophyll *a* levels in each of the six vleis. All values in μg l^{-1}. Station 1 - □ , station 2 - + , station 3 - △ , station 4 - × and average - ◇ . Periods of stratification are indicated by ⊓.

station (1) had maxima at the same times, but with lower levels of chlorophyll *a* (up to 3.9, 3.9 and 7.3 ug l^{-1} respectively). Levels in winter (June/July/August) were all low and there was virtually no autumn peak in the first year (1981).

Grootrondevlei similarly had low levels of chlorophyll throughout the year although on average these were slightly higher than those in Suurdam or in the open waters of Gillidam (1). The chlorophyll *a* levels did not show an annual cycle, with only a single maximum (9-11 ug l^{-1}) in late summer (February/March) of the first year and a further slight increase (up to 6.5 ug l^{-1}) in mid-winter (July). Between these two blooms levels decreased to low autumn, early winter and summer levels of less than 2 ug l^{-1}.

Sirkelsvlei had considerably higher levels of chlorophyll *a* than did the previous three vleis. A major peak occurred in late summer (> 30 ug l^{-1}) (February/March/April) of the second year with a second, but lower maximum (approximately 12 ug l^{-1}) in late summer/early autumn (March/April/May) of the first year. Relatively low levels (4.2 - 9.5 ug l^{-1}) occurred from early winter through to early summer.

Chlorophyll *a* levels were highest in the alkaline waters of Grootwitvlei and Rondevlei. Both vleis showed a marked seasonal variation in chlorophyll *a* levels. Grootwitvlei had high chlorophyll *a* levels during summer and low levels during winter. Levels increased sharply in early summer (November) initially to an average of 57 ug l^{-1}, and eventually reached an average of 66 ug l^{-1} in the late summer of the second year. During midsummer there appears to have been a dip in chlorophyll *a* levels before the late summer maximum (February/March). An additional distinct late summer maximum occurred in the first year (March/April) reaching an average of 33 ug l^{-1}. Levels dropped sharply at the end of summer to just above 11 ug l^{-1} and remained at that level during the winter months.

Rondevlei is a eutrophic water body and as such had chlorophyll *a* levels well in excess of those of any of the other vleis. Mean annual chlorophyll *a* concentration was double that of Grootwitvlei and more than five times that of Sirkelsvlei (Table 8.1). As noted earlier, the water was normally green in appearance and commonly referred to as "pea soup". Chlorophyll *a* levels showed two broad maxima stretching over eleven of the fifteen months, but dropping sharply in spring and remaining low during early summer (between 1 and 23 ug l^{-1}) (October/November/December), before rising again steeply in mid-summer (February). High levels of chlorophyll *a* (between 34 to 120 ug l^{-1}) were therefore present from the end of summer, through autumn and winter, into spring.

Grootwitvlei and Rondevlei both showed more variation in chlorophyll *a* levels between stations during the year than did the other four vleis. This is probably related both to the greater size of the two vleis and the more variable basin morphology, as well as the greater primary productivity of the two (as indicated by the standing crop), both of which can cause greater horizontal patchiness of phytoplankton population events. On the other hand Sirkelsvlei and Grootrondevlei are of a similar, but smaller size and both have relatively uniform basin morphologies with few if any sheltered bays, so that chlorophyll *a* levels showed very little variation between-station.

The extent of the period of the chlorophyll *a* maxima over a seasonal cycle in each vlei appears to relate directly to the average standing crop (as indicated by chlorophyll a levels) present in that vlei. Thus with increasing average standing crop there was decreasing period of the chlorophyll *a* minimum and increasing period of chlorophyll *a* maximum and not merely an increase in the level of chlorophyll *a* during the maximum.

CHLOROPHYLL B LEVELS

Chlorophyll *b* levels were generally very low, often below 1 ug l^{-1}, but reaching 11 ug l^{-1} in Rondevlei. As noted in the Introduction, chlorophyll *b* is found only in the chlorophytes and euglenophytes, where it makes up less than half of the total pigment content. Seasonal variation in the chlorophyll *b* levels and the mean and range of levels in each vlei are presented in figure 8.2 and table 8.2 respectively.

Suurdam generally had chlorophyll *b* levels below 1 ug l^{-1}, with little seasonal variation. The chlorophyll *b*:chlorophyll *a* (*b*:*a*) ratio calculated for each month showed a mean approaching one (see fig.8.3). The high mean ratio results from a number of months in which chlorophyll *b* levels exceed chlorophyll *a*. During these periods chlorophyll *a* levels were exceptionally low, placing some doubt on the accuracy of measurement. However the general conclusion of a relatively high chlorophyll *b:a* ratio holds, thus suggesting a dominance of chlorophytes or euglenophytes in Suurdam.

Gillidam similarly had low chlorophyll *b* levels at the exposed station (1), generally less than 1 ug l^{-1}, with little seasonal variation, but at the sheltered station (2) levels were high and seasonal variation was similar to that noted for chlorophyll *a* (pulses in spring, early summer and autumn). The chlorophyll *b:a* ratio was still high, approaching 0.50, and did not differ much between stations. Therefore the proportion of chlorophytes or euglenophytes in the phytoplankton appears to be

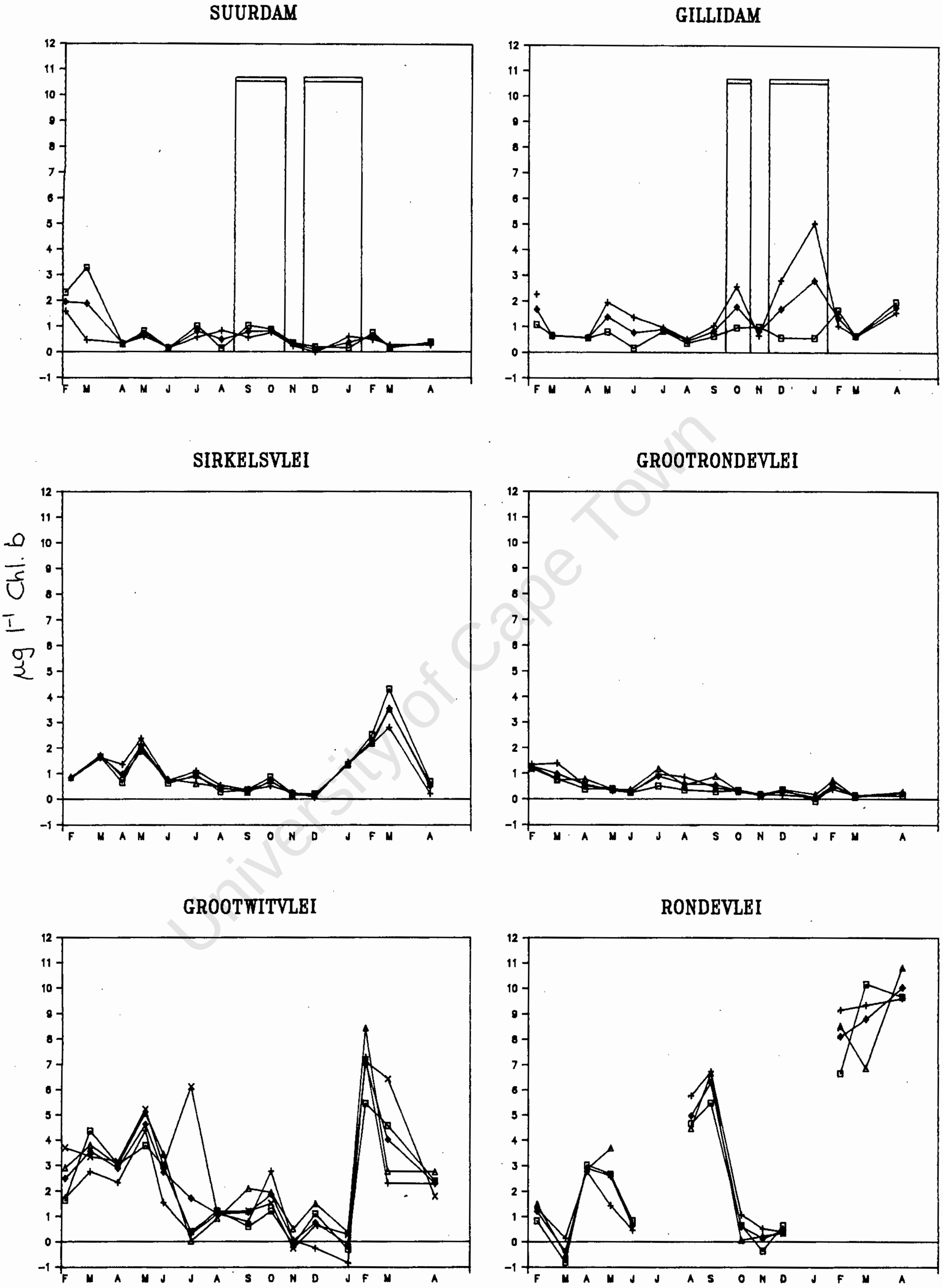

Figure 8.2. Seasonal variation in the chlorophyll *b* levels in each of the six vleis. All values in $\mu g\ l^{-1}$. Station 1 - □ , station 2 - + , station 3 - △ , station 4 - × and average - ◇ . Periods of stratification are indicated by ▭.

high, and similar at both stations, despite the difference in standing stock as measured by chlorophyll levels.

	CHLOROPHYLL *B*			CHLOROPHYLL *B/A*		
	mean	±sd	range	mean	±sd	range
SU	0.7	±0.7	0.0- 3.3	0.95	±1.16	0.04-4.81
GI	1.2	±1.0	0.2- 5.1	0.46	±0.30	0.15-1.53
GR	0.5	±0.4	-0.1- 1.4	0.23	±0.34	0.05-2.22
SI	1.1	±1.0	0.1- 4.3	0.09	±0.05	0.01-0.19
GW	2.4	±2.1	-0.9- 8.4	0.10	±0.07	0.00-0.25
RO	3.6	±3.6	0.8-10.8	0.05	±0.05	0.00-0.14

Table 8.2. Mean chlorophyll *b* levels and the range of levels and chlorophyll *b:a* ratios for each of the six vleis - Suurdam (SU), Gillidam (GI), Grootrondevlei (GR), Sirkelsvlei (SI), Grootwitvlei (GW), Rondevlei (RO). Chlorophyll *b* values in µg l^{-1} .

Grootrondevlei, like Suurdam, had very low chlorophyll *b* levels, generally below 1 ug l^{-1}, with very little variation between stations. Seasonally the levels showed the same maxima as chlorophyll *a* (late summer and mid-winter to spring), both of which were close to 1 ug l^{-1}. The chlorophyll *b:a* ratio was on average lower than in Suurdam or Gillidam (approaches 0.25), but was noticeably higher than in Sirkelsvlei, Grootwitvlei and Rondevlei. Thus, chlorophytes and/or euglenophytes appear still to be an important component of the phytoplankton. There was no obvious seasonal variation in the chlorophyll *b:a* ratio and therefore presumably in the proportions of the above taxa.

Sirkelsvlei, Grootwitvlei and Rondevlei all had mean chlorophyll *b:a* ratios of 0.1 or less, indicating a smaller proportion of chlorophytes or euglenophytes in the phytoplankton of these vleis. Nonetheless chlorophyll *b* levels were high in relation to those in the other vleis (excepting Gillidam station 2), in accordance with the greater standing crop of phytoplankton present. Seasonal variation of chlorophyll *b* in Sirkelsvlei paralleled that of chlorophyll *a*, with late summer to autumn maxima in both years and winter-spring and summer minima. Chlorophyll *b:a* ratios showed a similar, but less pronounced trend. Seasonal variation of chlorophyll *b* in

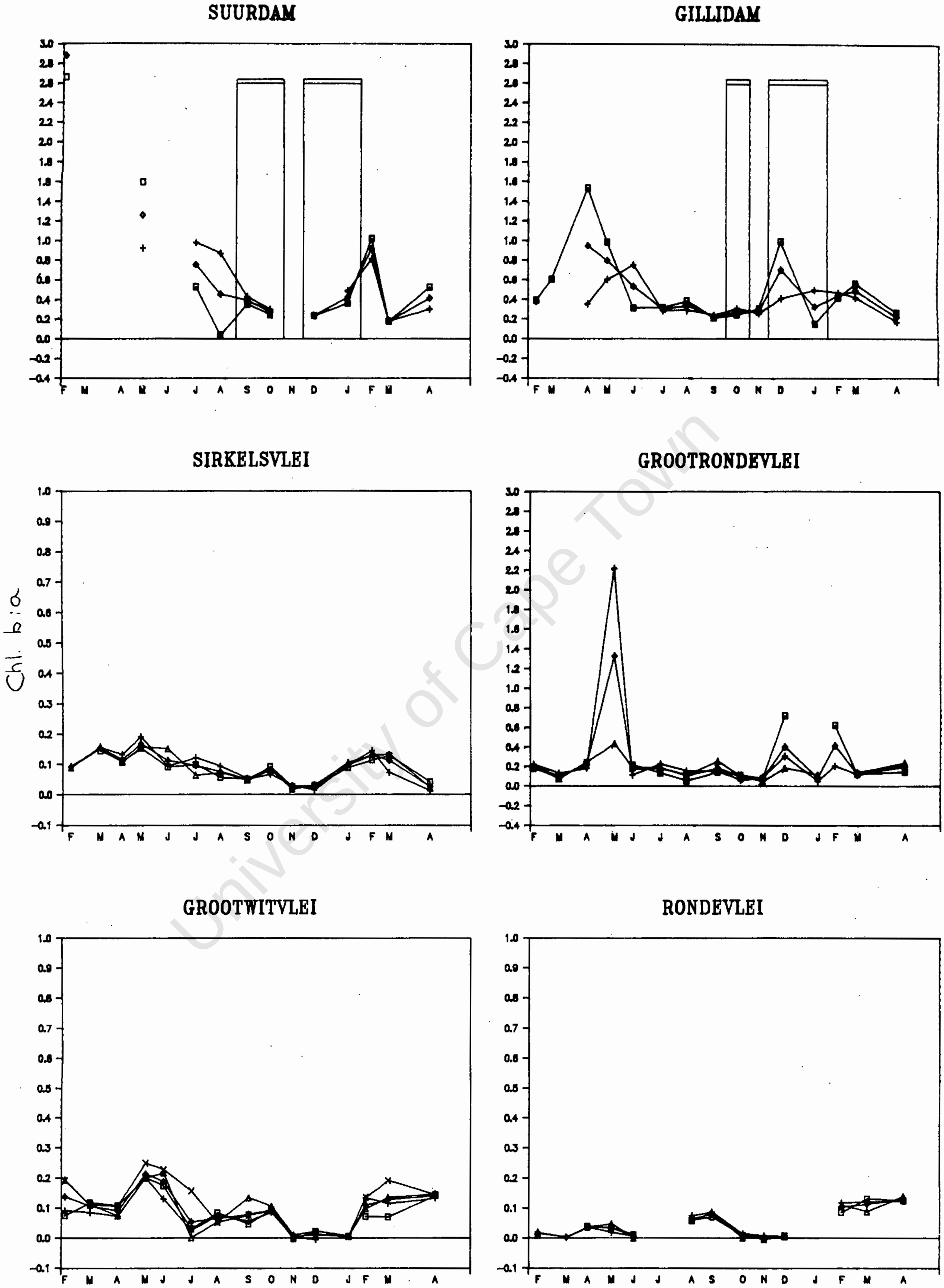

Figure 8.3. Seasonal variation in the chlorophyll *b:a* ratios in each of the six vleis. All values in µg l^{-1}. Station 1 - □, station 2 - +, station 3 - △, station 4 - × and average - ◇. Periods of stratification are indicated by ⊓.

Grootwitvlei and Rondevlei did not reflect variation in chlorophyll *a* throughout the year as found in the other vleis. In Grootwitvlei chlorophyll *b*-containing phytoplankton made up part of the late summer, but not of the early summer maxima as well as an additional autumn peak in the first year. For the rest of the year levels remained generally below 2 ug l^{-1}. In Rondevlei, the seasonal variation was more marked, but chlorophyll *b*-containing phytoplankton formed part of the broad maximum only in early spring and in late summer. For the rest of the year they remained less important (levels of chlorophyll *b* were usually below 2 ug l^{-1}). The chlorophyll *b:a* ratio showed a seasonal variation similar to chlorophyll *b* in both vleis.

Thus in Sirkelsvlei, Grootwitvlei and Rondevlei, the chlorophyll *b:a* ratio varied with chlorophyll *b* seasonally. This is to be expected in waters where chlorophytes and euglenophytes do not form the dominant or a large proportion of the phytoplankton community, but rather increase in proportion seasonally in relation to other chlorophyll *a*containing phytoplankton. In Suurdam, Gillidam and Grootrondevlei, because of the relatively high chlorophyll *b:a* ratio and little similarity between seasonal variation of the ratio and chlorophyll *b*, chlorophytes or euglenophytes are presumed to form the dominant or a large proportion of the phytoplankton.

CHLOROPHYLL C$_1$ + C$_2$ LEVELS

Chlorophyll c_1 + c_2 levels (referred to in this section as chlorophyll *c*) were in general slightly lower even than chlorophyll *b* levels. Chlorophyll *c* is found in the bacillariophytes (diatoms), chrysophytes, dinophytes, xanthophytes and cryptophytes in small amounts (see Introduction). Presence of chlorophyll *c* could thus indicate the inclusion of any one of these groups in the phytoplankton assemblage, although certain of the groups, such as the diatoms, are more commonly encountered than others. Levels of chlorophyll *c* were normally below 1 ug l^1, and the highest value was 6.8 ug l^{-1}, recorded in Rondevlei. Seasonal variation in the chlorophyll *c* levels and the mean and range of levels in each vlei are presented in figure 8.4 and table 8.3 respectively.

In Suurdam levels were once again mostly below 1 ug l^{-1} and no definite seasonal trends were apparent. Chlorophyll *c:a* ratios were high, on average approaching one, probably due again to the exceptionally low chlorophyll *a* values which were sometimes exceeded by the chlorophyll *c* values. However, the general conclusion of a relatively high average chlorophyll *c:a* ratio holds for the Suurdam phytoplankton assemblage.

	CHLOROPHYLL *C*			CHLOROPHYLL *C/A*		
	mean	±sd	range	mean	±sd	range
SU	0.5	±1.0	-0.3- 4.7	0.99	±1.35	0.01-4.69
GI	0.2	±0.4	-0.3- 1.3	0.24	±0.19	0.02-0.69
GR	0.2	±0.3	-0.3- 1.0	0.18	±0.21	0.00-0.93
SI	1.2	±1.3	0.1- 5.3	0.14	±0.07	0.04-0.28
GW	0.5	±1.1	-1.8- 3.2	0.04	±0.04	0.00-0.23
RO	1.9	±1.9	-1.0- 6.8	0.07	±0.07	0.00-0.43

Table 8.3. Mean chlorophyll *c* levels and the range of levels and chlorophyll *c:a* ratios for each of the six vleis - Suurdam (SU), Gillidam (GI), Grootrondevlei (GR), Sirkelsvlei (SI), Grootwitvlei (GW), Rondevlei (RO). Chlorophyll *c* values in µg l^{-1} .

Gillidam and Grootrondevlei had extremely low chlorophyll *c* levels, generally less than 0.5 ug l^{-1}. Levels in Gillidam showed little seasonal variation, and there was minimal difference between the two stations (in contrast to chlorophylls *a* and *b*). Grootrondevlei levels rose to a small maximum from midwinter to early spring (approximately 1.0 ug l^{-1}), but for the rest of the year remained very low at all three stations. On average chlorophyll *c:a* ratios for Gillidam and Grootrondevlei were considerably lower than for Suurdam, but higher than for Grootwitvlei and Rondevlei. As with the chlorophyll *b:a* ratio, the chlorophyll *c:a* ratio also showed little definite seasonal trend in Gillidam and Grootrondevlei and thus did not indicate any obvious change in the proportion of chlorophyll *c*-containing phytoplankton.

Sirkelsvlei had on average relatively high chlorophyll *c* levels which varied seaonally in the same way as chlorophylls *a* and *b*. The average chlorophyll *c:a* ratio fell between that of Gillidam and Grootrondevlei and that of Grootwitvlei and

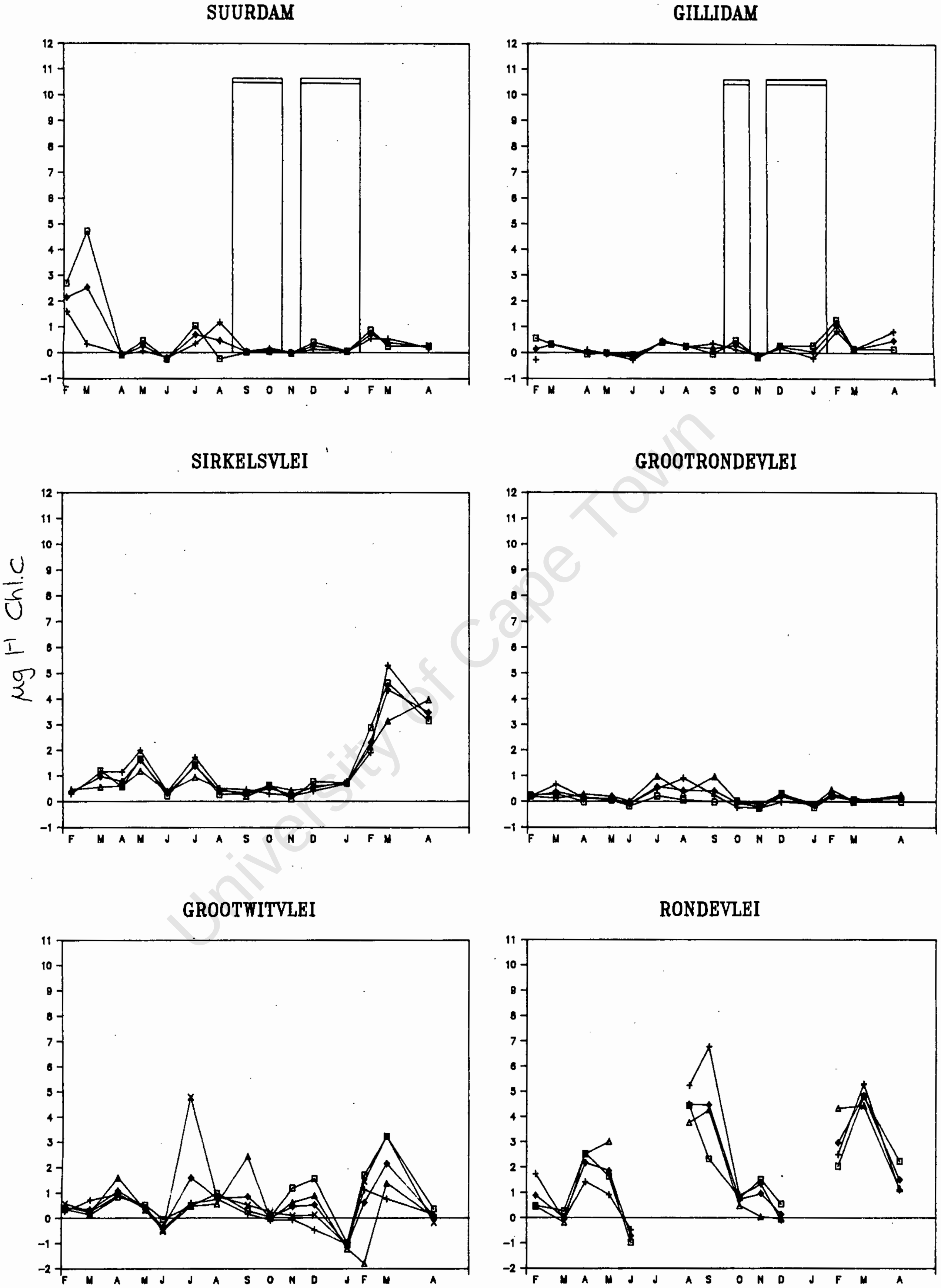

Figure 8.4. Seasonal variation in the chlorophyll *c* levels in each of the six vleis. All values in $\mu g\ l^{-1}$. Station 1 - □, station 2 - +, station 3 - △, station 4 - × and average - ◇. Periods of stratification are indicated by ⊓.

Rondevlei. Seasonal change of the ratio followed a similar, but less definite, trend to the chlorophyll *c* levels (as did the chlorophyll *b:a* ratio to chlorophyll *b*).

Chlorophyll *c* levels in Grootwitvlei were low and variable, with a small maximum occurring in the very late summer (March), at the end of the late summer peaks of chlorophyll *a* and *b*. In Rondevlei chlorophyll *c* levels were relatively high and formed part of the broad maximum in early spring and late summer. The variation was very similar to that in chlorophyll *b* levels, except in late summer of the second year where the chlorophyll *c* levels were lower. The chlorophyll *c:a* ratios were very low for both Grootwitvlei and Rondevlei, but in both cases there was some similarity in the seasonal variation of the *c:a* ratio and the levels of chlorophyll *c*.

In summary, there appears to have been a higher proportion of chlorophyll *c*-containing phytoplankton in Suurdam, Gillidam and Grootrondevlei, and in this case Sirkelsvlei as well, than in Grootwitvlei and Rondevlei. The fact that the first three vleis often had chlorophyll *a* values very close to zero might have resulted in artificially high chlorophyll *b:a* or *c:a* ratios, but there is no proof of this being so. The very low chlorophyll *c:a* ratios of Grootwitvlei and Rondevlei thus indicate a lower proportion of chlorophyll c-containing phytoplankton in the assemblage.

PHAEOPIGMENT A LEVELS

Phaeopigment levels were normally as high as the chlorophyll *a* levels in the vleis of low phytoplankton standing stock, but considerably lower most of the year in Grootwitvlei and Rondevlei, the two vleis with the greatest standing stock. Seasonal variation in the phaeopigment levels and the mean and range of levels are displayed in figure 8.~~6~~5 and table 8.1 respectively.

Phaeopigment levels in Suurdam were normally low, but slightly higher than the chlorophyll *a* levels, and there was very little variation between the two stations (mostly less than 1 ug l^{-1}). Seasonal variation was minimal, but a slight increase did occur during late summer and autumn of the first year. The greater phaeopigment levels are unlikely to have been due to grazing, because of the very low zooplankton numbers, but could have been due to other factors such as the extremely dark colour of the water, which reduces light penetration and thus reduces photodegradation of the phaeopigments in solution. Further summer stratification contributes to the reduced photodegradation and causes photo-oxidation in the phytoplankton cells trapped in the surface layers, while the extremely low pH of the water (3.7-3.9)

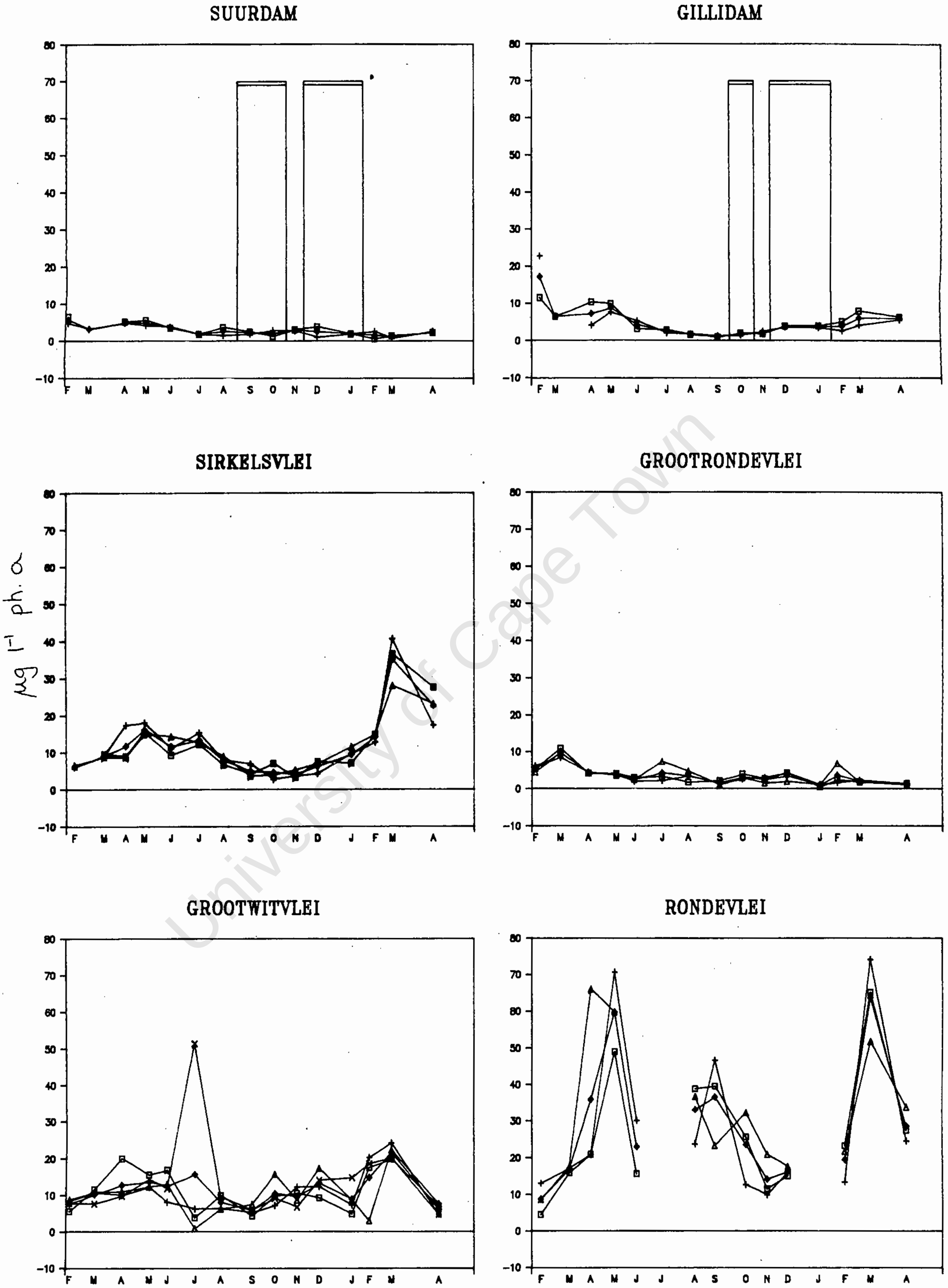

Figure 8.5. Seasonal variation in the phaeopigment *a* levels in each of the six vleis. All values in μg l⁻¹. Station 1 - □ , station 2 - + , station 3 - △ , station 4 - × and average - ◇ . Periods of stratification are indicated by ┌─┐.

might cause the natural degradation of the chlorophyll molecule in dead phytoplankton cells. Furth~~u~~ermore heterotrophic activity was most probably low (see chapter 6) with a consequent reduced rate of phaeopigment breakdown.

In Gillidam and Grootrondevlei phaeopigment levels were also low, but were on average higher than in Suurdam. The levels were similar to chlorophyll *a* levels (on average slightly higher) and both vleis showed little variation between stations, in contrast to chlorophyll *a* levels in Gillidam. In Gillidam phaeopigments exhibited quite a different seasonal variation from that exhibited by chlorophyll *a* levels. There was a broad minimum (1-4 ug l^{-1}) stretching through winter to early summer, with the highest levels in late summer to autumn in both years (up to 23 and 8 ug l^{-1}). The two stepwise increases that occurred after the winter/spring minimum and reflected the decrease in chlorophyll *a* after the spring and the early summer peaks. In Grootrondevlei phaeopigment levels showed the same maximum as chlorophyll *a* in late summer of the first year (8-11 ug l^{-1}), but only a slight increase during the midwinter chlorophyll *a* maximum. For the rest of the year, levels remained the same as, or rather slightly higher than, chlorophyll *a*, with little variation (1-4 ug l^{-1}).

Sirkelsvlei had high levels of phaeopigments, in a similar range to those of chlorophyll *a* and with little variation between stations. A distinct seasonal change in the levels of phaeopigments closely followed the variations in chlorophyll *a* levels. Phaeopigments were found in concentrations (7- 41 ug l^{-1}) greater than those of chlorophyll *a* during peak periods of both (late summer to winter) and in concentrations lower than chlorophyll *a* through the rest of the year (3-15 ug l^{-1}). Thus the variation in the phaeopigments - by emphasising the seasonal trends of chlorophyll *a* levels - reflected the state of the phytoplankton population.

Grootwitvlei, with an average chlorophyll *a* level three times that of Sirkelsvlei, had the same average phaeopigment level as Sirkelsvlei. The concentrations of phaeopigments were thus high, but considerably less than those of chlorophyll *a*. Seasonal change was far less marked, but does appear to be related to that of chlorophyll *a*. Concentrations of phaeopigments increased gradually to a maximum in autumn and late summer of each year (12-17 and 17-24 ug l^{-1}) before dropping sharply. The phaeopigment maxima appeared as the chlorophyll *a* levels declined following their summer peak. Low winter and autumn levels were found, as well as a mid-summer dip, the same seasonal features exhibited by chlorophyll *a* levels. The often large variability in concentration between sampling stations has been discussed above in relation to chlorophyll *a* levels.

Rondevlei had the highest levels of phaeopigments but, as with Grootwitvlei, the levels were considerably lower than the levels of chlorophyll *a* (on average approximately half). Phaeopigment maxima occurred in autumn and late summer of each year (up to 71 and 74 ug l^{-1}) with lowest levels in winter and in early summer (10-30 ug l^{-1}). The lowest chlorophyll *a* levels were similar to the low phaeopigment levels present over the same period. Both maxima occurred after noticeable increases in the chlorophyll *a* concentration, as might be expected, but unlike the chlorophyll maxima they were relatively short-lived.

THE RELATIONSHIP BETWEEN CHLOROPHYLL A AND PARTICULATE ORGANIC CARBON

The relationships between chlorophyll *a* and particulate organic carbon (POC) were examined. This was not an attempt to calculate phytoplankton biomass (using the method of Steele and Baird 1961, 1962b and 1965), due to the fact that there was very little likelihood of homogenous phytoplankton populations, and the fact that the samples were collected over a relatively long time interval of fifteen months. Instead the relationship between the two variables was investigated in order to indicate the dominance of either phytoplankton or detrital matter in the lake seston. The functional linear regression between each set of data points was calculated (Picker 1984) and the t-test was used to test for a significant positive relationship between each pair of variables. The degree of significance (the slopes of the regression significantly different from zero) of the positive relationship was used as an index of the dominance of phytoplankton or detrital carbon or nitrogen in each lake on average during the study period. A highly significant relationship indicates a strong link between chlorophyll *a* and POC.

Sirkelsvlei ($P < 0.001$, $n=14$), Rondevlei ($P < 0.02$, $n=12$) and Grootwitvlei ($P < 0.05$, $n=14$) all show highly significant positive correlations, indicating a strong link between chlorophyll *a* and POC and thus a dominance of living phytoplankton in the euphotic zone. Suurdam ($n=12$), Gillidam ($n=14$) and Grootrondevlei ($n=14$) do not show significant positive correlations between chlorophyll *a* and POC, indicating that most of the particulate matter suspended in the euphotic zone was detrital and not living phytoplankton. This conclusion is borne out by the very low chlorophyll levels, generally less than 4 ug l^{-1}, in these three vleis.

Steele and Baird (1961, 1962b, 1965) use the x intercept (ie., where chlorophyll $a = 0$) as a measure of the level of detrital particulate carbon. However in the three vleis that show a significant functional regression, the x-intercept is

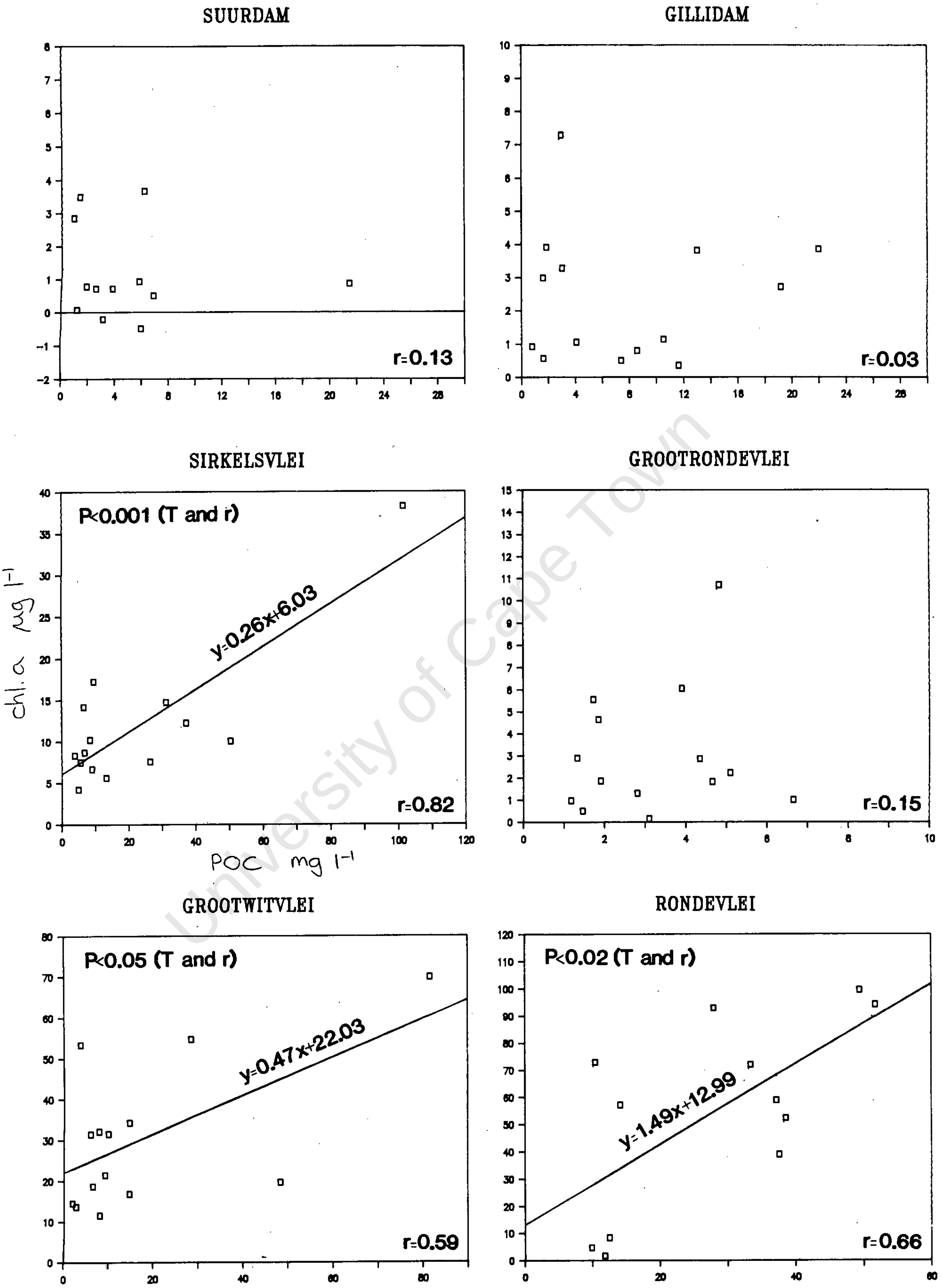

Figure 8.6. The relationship between chlorophyll *a* and POC levels in each of the six vleis.

negative. This is presumably as a result of too much scatter in the data points due to the variability of the phytoplankton populations over the long period of sampling.

The ratio of chlorophyll *a* to POC (chl a:POC) is less useful as an indication of chlorophyll dominance in the seston than is the slope of the regression. This is due to the fact that the ratio is variable both within the phytoplankton cell (see Introduction, this chapter), and in the seston. In the seston an increasing ratio can indicate either an increasing phytoplankton population or decreasing residual detritus levels or both, and thus may be used as an indication of the quality of the food available to herbivorous zooplankton. The use of the ratio as an index of food quality might be promoted by the assumption that an increasing phytoplankton population has a greater chl a:POC ratio within the cells than a senescing population thus biasing the index towards increasing food quality.

Of the six vleis the ratios were lowest on average in Suurdam and Gillidam (means of 0.60 and 0.73), both of which showed a small spring peak similar to that found in their respective chl a concentrations (fig. 8.7). Grootwitvlei and Rondevlei showed the highest ratio (on average 3.76 and 2.14), both also peaking in spring, although the spring peaks did not reflect the summer and late summer peaks shown by the respective chlorophyll *a* concentrations. Sirkelsvlei and Grootrondevlei had similar average ratios (0.97 and 1.13). The multiple range test of Newman and Keuls (Zar 1974) shows that the means of all six vleis are significantly different ($P < 0.05$), but the means of Sirkelsvlei and Grootrondevlei differ when $P < 0.001$ (note that even though food quality as shown by the chl a:POC ratio may be similar, availability, which depends on concentration, is very different). Grootrondevlei showed a small spring peak similar to that found in chlorophyll *a* concentrations whereas Sirkelsvlei showed no definite seasonal trend in the chl a:POC ratio. Thus the three vleis dominated in the seston by detritus (Su,Gi,Gr), probably of allochthonous origin as a result of their low annual chlorophyll *a* levels, were the three vleis which reflected their spring chlorophyll *a* peaks in the chl a:POC ratio.

DISCUSSION

Periodic changes in phytoplankton biomass occur in most lakes throughout the world. In temperate lakes these changes are normally caused by seasonal changes in abiotic factors and thus lead to generally predictable seasonal variations in biomass. In tropical lakes, changes in biomass (also a result of abiotic changes) tend to occur more frequently as a series of episodic changes, which may also be regular in their seasonality.

We noted in Chapter 4 that the vleis of the south-western Cape can be classified as tropical lakes in as much as the water temperature does not drop below a temperature of 4°C (Whipple in Pearse 1926, also Maitland 1978 and Moss 1982), yet all lie in a southern temperate latitude. The Cape vleis can therefore be regarded as intermediate between temperate and tropical. In truly temperate lakes, atmospheric temperature and the intensity and duration of solar radiation are too low in winter to allow net primary production, whereas in truly tropical lakes, temperature and illumination are normally adequate throughout the year and are not the major factors controlling seasonal levels of primary production (Beadle 1981). In the Cape vleis, atmospheric (and therefore water) temperatures display a distinct seasonality, which is not in general present in the tropics, as does illumination, yet it is unlikely that either is a major factor limiting primary production. In contrast to temperate lakes, then, primary production is therefore probably not controlled directly by temperature and illumination effects, but rather (or in addition) by water circulation and water chemistry variables. The fact that the Cape vleis are all very shallow and exposed to frequent and strong winds means that wind-induced mixing is common (except possibly in Suurdam and Gillidam), with concomitant redistribution of nutrients and resuspension of plankton. The importance of physical mixing on phytoplankton species succession or periodicity has been demonstrated by Reynolds (1982) and Reynolds *et al.* (1983) who regard it as the major cause, both directly and indirectly, of phytoplankton periodicity in lakes. The frequent water circulation or mixing thus plays an important role in the maintenance of net primary production. Variables such as the levels of major nutrients are unlikely to become (locally) limiting in the epilimnion due to the extremely short duration of near-surface density gradients and the high degree of interaction between the sediment and water column. In addition, periodic mixing can act to increase the depth of light penetration and provide a quite different set of conditions for algal growth and survival. Thus water chemisty is more important in determining the total phytoplankton biomass that can be supported at any one time rather than it is in influencing periodicity.

Having discussed in general terms the variables most likely affecting the seasonal periodicity of phytoplankton in the south-western Cape vleis (driving variables), we can now examine the points of similarity and difference in the seasonal variation of phytoplankton biomass (as reflected by chlorophyll *a*) of the vleis.

Seasonal variation. There appears to be no distinct pattern common to all of the six vleis. The three vleis with seston dominated by detritus, and with very low phytoplanton biomass, namely Suurdam, Gillidam and Grootrondevlei, have little in common in the periodicity of their chlorophyll *a* levels, apart from higher-than-average levels in spring (September/October). In Gillidam and Grootrondevlei there were also higher-than-average levels in mid to late summer (January/February/March). However the levels were so low that a fifteen-month sampling period was not long enough to recognise patterns of seasonality complicated by inter-annual differences in abiotic factors.

Sirkelsvlei, Rondevlei and Grootwitvlei each had a seston dominated by living phytoplankton rather than by particulate detritus, and a considerably greater phytoplankton biomass than in the other vleis. There was also a more distinct seasonal periodicity of the chlorophyll *a* levels in each vlei and a seasonal maximum common to all three vleis. The peak chlorophyll *a* levels in each vlei were recorded in mid to late summer (January/February/March) of the second year. Grootwitvlei showed an additional early summer maximum (November/December), probably caused by green algae, which was not present in Sirkelsvlei or Rondevlei. Also in early summer Rondevlei displayed the most distinct seasonal event in its chlorophyll *a* levels, dropping steeply to the extreme low of less than 25ug l^{-1}. Furthermore, Rondevlei exhibited no winter minimum, and it is thus difficult to establish whether the vlei is characterised seasonally by an extreme early summer crash or by a late summer peak (see nutrient cycling in chapter 5). Sirkelsvlei and Grootwitvlei both displayed distinct minima in winter to early spring. These three vleis had chlorophyll *a* levels (and thus phytoplankton biomasses) considerably greater than those in Suurdam, Gillidam and Grootrondevlei. Sirkelsvlei had maximum levels close to 35ug l^{-1} and an annual average of 12ug l^{-1}, Grootwitvlei had maximum levels close to 80ug l^{-1} with an annual average of 31ug l^{-1} and the eutrophic Rondevlei had maxima around 110ug l^{-1} and an average of 60ug 1^{-1} (see table 8.1). Thus these three vleis were by no means similar in their standing crops of phytoplankton, but did show some common trends in their gross seasonal changes. What may be related to standing crops and thus to the physical and chemical environments is the decreasing period of the chlorophyll *a* minimum (noted in the results) with increasing standing crop.

Driving variables. The fact that there is so little similarity in the seasonal variation of phytoplankton biomass between the six vleis suggests that indeed atmospheric temperature and illumination are not limiting and that other physical and chemical factors have a more direct effect. Temperature increases do however appear to be coupled, in some of the vleis, to seasonal increases in phytoplankton biomass. In Suurdam and Gillidam a spring rise in temperature and stratification of the surface water corresponds closely with the spring chlorophyll *a* peaks (also in Gillidam, in early summer). Further, the early summer and late summer biomass peaks in Grootwitvlei appear closely linked to the seasonal change in temperature. Sirkelsvlei, however, has a distinct seasonality of phytoplankton biomass, but it is offset from the temperature changes.

The other factors that are likely to be important in determining both the seasonality and phytoplankton biomass of the vleis are, as noted earlier, the water chemistry and the circulation of the water mass. All the factors - including biological factors - have been grouped conveniently by Hutchinson (1967) into three categories proposed to account for the seasonal variation of phytoplankton. These three categories are (i) partly independent physical factors - temperature, illumination, and water mixing or circulation, (ii) interdependent chemical factors - such as inorganic nutrients and organic compounds, and (iii) biological factors - such as predation, competition and parasitism. Reynolds (1984) separates the effects of the chemical and physical environment. He suggests that changes in gradients of resource ratios (chemical variables) regulate a unidirectional community succession (autogenic sequence), whereas periodicity is regulated by variability of the physical environment (allogenic change). Allogenic change may cut through any autogenic sequence, shifting it to a new position. On this basis Reynolds (1984) arranges the three categories (of physical, chemical and biological) in descending order, based on the extent of the community response they cause. The effect of the different chemical factors is discussed further in chapter 5 and the effects of predation in chapter 9.

It thus remains to discuss the differences in lake morphology size and situation as the major factors determining differences in water circulation and mixing between the vleis. The vleis are all very shallow with water levels never greater than two metres. The wind regimes are similar, but exposure to winds differs considerably as a result of the large differences in size and shape of the vleis (see chapters 2 and 4). Suurdam and Gillidam are both small and lie below the level of the surrounding land. As a result they developed a spring to mid-summer stratification (corresponding to the temperature maximum) which may or may not have been stable throughout the period. The chlorophyll *a* maximum, as noted earlier, appears to be coupled to this period of higher temperature and stable water and thus the phytoplankton communities should be different to those found in the unstable, or more turbulent waters of the other four vleis. Grootrondevlei, Sirkelsvlei, Grootwitvlei and Rondevlei are all relatively large and polymictic with no stratification other than unstable diurnal differences in temperature between surface and bottom waters. Rondevlei and Grootwitvlei are the two largest vleis and both have heterogeneous basin morphologies. Circulation of the water thus varies between different parts of the vleis under different wind strengths and directions. This is evident in the variation between chlorophyll *a* levels at the different stations of both vleis: due to the varied basin there is a greater degree of horizontal patchiness. Sirkelsvlei and Grootrondevlei are in the order of 5 times and 3 times smaller than the two large lakes and both have relatively homogeneous basin morphologies. Water circulation is therefore continuous throughout the basin to a greater degree and there was little between-station variation in the levels of chlorophyll *a* (ie. little horizontal patchiness) except during the late summer maximum in Sirkelsvlei. As a result of polymixis and lack of stable stratification in the four large vleis, there is limited seasonality of the water circulation. There is thus little effect on the seasonality of the phytoplankton apart from variation in the horizontal patchiness which appears to overlay the general seasonal trend. Suurdam and Gillidam are the two exceptions, in that stratification periods correspond with maxima in temperature and chlorophyll *a*.

The extreme differences between the vleis in both standing crop and periodicity result from their shallowness and differences in chemical character. Straskraba (1980) in relating phytoplankton production to abiotic variables emphasised the extreme variability in phytoplankton biomass found in shallow water bodies. Hutchinson (1967) also mentions a "more complex and diversified set of phenomena" in the periodicity of shallow lakes and often in the case of small ponds "a very slight and quite irregular seasonal variation" (Nygaard 1939, in Hutchinson 1967). The formation and collapse of stratification is regarded by Reynolds (1982) as the "major cause of phytoplankton periodicity in lakes". Shallow lakes with rapid and frequent mixing of the entire water column, generally lack seasonal stratification and display more erratic and variable changes caused by wind and rainfall patterns (see Hutchinson 1967, Beadle 1981 and Ashton 1985). Brylinsky (1980) attempted to relate phytoplankton production and biomass statistically to abiotic factors on a global scale. He concluded that latitude-related variables (or variables related to solar energy input) were most closely tied to production, especially at high latitudes, whereas water chemistry-related variables were less closely tied, but became more critical in the low latitudes. Because of the strong relationship between geographical location and phytoplankton biomass or production, as well as the variability of very shallow water bodies, there is little use in the comparison of phytoplankton biomass levels of humic waters in general. Straskraba (1980) shows a relationship in which, with sufficient nutrients, maximum biomass will be reliant on the extinction coefficient of light and the mixing depth.

Obviously humic or otherwise coloured waters would thus maintain a biomass well below that of similar clear waters. The complex interaction of the major variables (geography, morphometry, hydrology, nutrient status and biological balance of populations) however mask the direct effects of the coloured compounds. This is borne out to a certain extent by the results of Granberg and Harjula (1982a) who found the phosphorus-chlorophyll relationship of Dillon and Rigler (1974) to yield satisfactory results for humic as well as clear water lakes. The relationship, however, only makes use of the mean seasonal chlorophyll *a* concentration. Rai (1978a, 1978b), Rai and Hill (1980), Granberg and Harjula (1982a), Jones and Arvola (1984), Ilmavirta (1984), Ilmavirta *et al.* (1984), Varis (1984), and Meffert and Overbeck (1985) all present chlorophyll *a* values for humic waters, most of which fall in the range found for the black and brown Cape vlei waters.

Chlorophylls b **and** $c_1 + c_2$. Little use has been made in the ecological literature of estimations of chlorophyll *b* and c_1 and c_2. As stated by Lorenzen (1981), it is unclear whether this is because chlorophyll *a* is the universal photosynthetic pigment and many studies are concerned with production or food web considerations, or because these pigments are relatively insignificant and possible relationships are normally obscured, or even because present techniques are not adequate, especially when compared to new HPLC techniques. Certainly interference with significant levels of either chlorophyll *b* or c_1 and c_2 does occur with both spectrophotometric and fluorometric techniques (Jeffrey and Humphrey 1975, Gibbs 1979) and this affects the estimates of all the chlorophylls and their degradation products. For this reason estimates of all the chlorophylls have been treated with some caution. Also, if an accurate idea of the contribution of chlorophyll *b*- or *c*-containing phytoplankton is required, microscopical counts are generally used, but these are time consuming. Lorenzen (1981) has made use of chlorophyll *b:a* ratios in estimating occurrence and abundance of chlorophyll *b* in marine waters. Green algae grown in the laboratory were usually found to show a *b:a* ratio of 0.3 to 0.4. Combined with the chlorophyll *b:a* ratio of phytoplankton samples, an estimate of the percentage of green algae in a sample could therefore be calculated. The highest chlorophyll *b:a* ratio was 0.141, indicating that up to 47% of the chlorophyll *a* in the sample was associated with green algae, while the majority (95%) had ratios less than 0.09, indicating less than 30% of the chlorophyll *a* associated with green algae. Most (51%) showed a *b:a* ratio of less than 0.02 suggesting less than 5% was associated with green algae. Data from Shoaf and Lium (1976) for seven freshwater chlorophyte species yielded an average *b:a* ratio of 0.39 0.15 and data from Humphrey (1978) for two marine chlorophyte species yielded an average *b:a* ratio of 0.35 0.20. Both sets of data were determined spectrophotometrically and agree broadly with the values of Lorenzen (0.35 0.07). Marine algal assemblages are typically dominated by chlorophyll *a*- and *c*-containing species, whereas in freshwater, green algae containing chlorophyll *b* are often common. Thus chlorophyll *b:a* ratios on average greater than 0.02 (see Lorenzen) could be expected for the phytoplankton of the vlei waters. On average Suurdam, Gillidam and Grootrondvlei all had considerably higher chlorophyll *b:a* ratios (see table 8.2) which showed little obvious seasonal variation indicating little variation in the proportion of chlorophytes or euglenophytes. Indeed the ratios are closer in value to those obtained by Lorenzen for cultured green algae. Sirkelsvlei, Grootwitvlei and Rondevlei had lower chlorophyll *b:a* ratios (on average 0.1 or less), but even these were greater than the ratios for marine phytoplankton of Lorenzen (1981). As noted in results, the chlorophyll *b:a* ratio in these three vleis follows the seasonal variation of the chlorophyll *b* levels, indicating seasonal change in the proportion of chlorophytes or euglenophytes. In Sirkelsvlei the chlorophyll *b* levels reflected the chlorophyll *a* peaks in late summer and autumn, whereas in Grootwitvlei and Rondevlei chlorophyll *b* levels only formed part of the broad chlorophyll *a* maxima. The general indication of the chlorophyll *b:a* ratios is that the phytoplankton communities of Suurdam, Gillidam and Grootrondevlei have a large proportion of chlorophytes or euglenophytes while those of Sirkelsvlei, Grootwitvlei and Rondevlei have a considerably lower proportion which contributes to the phytoplankton biomass in a distinctly seasonal manner.

Regular mixing of the water column favours non-motile phytoplankton species such as the diatoms (Reynolds 1983, Reynolds *et al.* 1984) and thus a large proportion of diatoms might also be expected in the shallow waters of the vleis. In addition diatoms are 'well tailored' to the frequent large-scale fluctuations in irradiance common during the regular mixing of highly-coloured waters. High chlorophyll *c:a* ratios occurred in the phytoplankton communities of Suurdam, Gillidam, Grootrondevlei, and also in Sirkelsvlei (all highly-coloured), indicating a high proportion of diatoms or other chlorophyll *c*-containing algae in each (see table 8.3). In Grootwitvlei and Rondevlei however, chlorophyll *c:a* ratios were generally lower (on average less than 0.1) indicating a smaller proportion of diatoms or other chlorophyll *c*-containing algae. Chlorophyll *c* generally occurs in small amounts in relation to chlorophyll *a* (Round 1973) and thus the same value of *c:a* and *b:a* ratios indicates a higher proportion of chlorophyll *c*-containing algae. Small amounts of chlorophyll *c* also mean that estimations are more susceptible to error due to interference effects, and thus the conclusions from *c:a* ratios are drawn cautiously. Data from marine phytoplankton species containing chlorophyll *c* (from Humphrey 1978) yield an average *c:a* ratio of 0.23 0.12 (for four species of

Bacillariophyta, two Chrysophyta and two Dinophyta). The *c:a* ratios for Gillidam, Grootrondevlei and Sirkelsvlei were on average close to this figure (Suurdam values were artificially high), suggesting a very high proportion of chlorophyll *c*-containing phytoplankton, most likely diatoms. The chlorophyll *c:a* ratios in Rondevlei, Grootwitvlei and Sirkelsvlei displayed seasonal variations that paralleled chlorophyll *c* levels to some extent. This indicates some seasonal change in the proportion of chlorophyll *c*containing phytoplankton in these three vleis. In Suurdam and Gillidam, chlorophyll *a* and chlorophyll *b* levels displayed a seasonal increase corresponding closely to the period of stratification, whereas chlorophyll *c* levels showed no such increase. The increase probably results from the development of a stable-water community dominated by green algae replacing the diatom species, which suffer photoinhibition and sinking due to a lack of mixing (Reynolds 1983).

The lower *c:a* and *b:a* ratios in Rondevlei and Grootwitvlei suggest a greater proportion of phytoplankton species containing only chlorophyll *a*. Both the cyanophytes (blue-green algae) and xanthophytes are largely associated with the benthos, with only a few planktonic species (Wetzel 1983). It is likely then that one or more of the common blue-green species dominates the phytoplankton biomass, on average, in these vleis.

	PHYTOPLANKTON CONTAINING		
	CHLOROPHYLL *B* commonly green algae	CHLOROPHYLL *C* commonly diatoms	CHLOROPHYLL *A* ONLY commonly blue-green algae
SU	high (±40%)	high (±60%)	v.low (±0%)
GI	high (±55%)	high (±45%)	v.low (±0%)
GR	high (±45%)	high (±55%)	v.low (±0%)
SI	mod. (±30%)	high (±60%)	low (±10%)
GW	mod. (±30%)	low (±20%)	high (±50%)
RO	low (±15%)	mod. (±30%)	high (±55%)

Table 8.4. General composition of the phytoplankton communities as indicated by the average *b:a* and *c:a* ratios, expressed as a proportion, for each of the six vleis - Suurdam (SU), Gillidam (GI), Grootrondevlei (GR), Sirkelsvlei (SI), Grootwitvlei (GW), Rondevlei (RO).

Grootwitvlei, and in spring and late summer in Rondevlei. Chlorophyll *c*-containing species in Sirkelsvlei increase in proportion with increasing phytoplankton biomass thus indicating their dominance in the community.

A number of factors are noted as important in determining both the phytoplankton standing crop and its periodicity in the vleis. Temperature and illumination do not appear to be limiting, although the maxima in Suurdam and Gillidam and in Grootwitvlei correspond to seasonal change in temperature. Interdependent chemical factors are probably most important in determining the maximum standing crop in each vlei, with factors such as pH, acidity and the concentration and character of humic substances, the most limiting. Stratification occurs in Suurdam and Gillidam with consequent effects on phytoplankton periodicity (see above). The other vleis experience frequent mixing, and both as a result of this, and their shallow nature, phytoplankton biomass and periodicity are unlikely to be limited by surface depletions of the major nutrients or by the light transmittance characteristics of the water. The effects of nutrient loading in Grootwitvlei and Rondevlei (see chapter 5) should be the major causes of the high phytoplankton biomasses in these two vleis. Heterogeneous basin morphologies of the above two vleis further result in horizontal patchiness of the standing crop. Wind and rain are also noted as factors causing erratic and variable change in shallow water systems.

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CHAPTER 9 : ZOOPLANKTON

INTRODUCTION

Both the structure and abundance of zooplankton communities are influenced by a variety of different physical, chemical and biological variables. The community composition at any one time is the net result of a suite of conditions determined by the set of largely interrelated variables. Zooplankton communities are normally dominated by three major groups - the rotifers, the copepods and the cladocerans. The generation times of these zooplankters range from days for rotifers and small cladocerans, through weeks for small copepods and larger cladocerans, to months for large copepods (Allan 1976). The response time to environmental change is thus fairly short in most cases, and taxa can respond to short-term changes in variables that are normally limiting. Thus seasonal succession of zooplankton species occurs as it does in phytoplankton assemblages, and sometimes in conjunction with the changes in the phytoplankton. Underlying the seasonality of the different populations is a basic community structure set largely by the range of each abiotic variable and the biotic interactions of the species able to survive within those ranges. The most important factors determining both the seasonal (or short term) response and the community structure include the quality and quantity of phytoplankton and microbial production, size-selective predation by vertebrates and invertebrates, temperature, pH, salinity, mixing, the quality and quantity of humic substances, and lake size. Food is often limiting in both quantity and quality.

Resource partitioning on the basis of particle size, the efficiency of different co-exploiters at different food levels, and the unpalatability of some algal food sources as a result of shape and toxicity (particularly blue-green algae), have all been shown to be important factors determining the results of competitive interactions (Lampert and Schober 1980, Porter and Orcutt 1980, Smith and Cooper 1982, Bengtsson 1987). Predation often alters the prevailing balance of competition and therefore drives species succession (Hart 1985). Predation pressure can be separated into two contrasting types - visual predation, generally by vertebrates, removing large forms (Hall *et al.* 1976, O'Brien 1979, Zaret 1980) and tactile predation by invertebrates focussing on small prey species (Dodson 1974, Kerfoot 1974, Lynch 1979). In a number of studies predation pressure has been suggested as the major factor controlling zooplankton distribution and abundance (Brooks and Dodson 1965, Dodson 1970, Murdoch *et al.* 1984, Post and McQueen 1987).

Temperature has a variety of direct and indirect effects on the zooplankters. The thermal tolerance range of a species directly dictates its presence or absence, while temperature effects on development time, body size and energy requirements are more subtle (Gophen 1976, Burns 1979, Hart 1981). Indirectly temperature is a major cue in the seasonality of each system, an increase generally heralding increased rates of biological production and degradation, and chemical reactions. Factors such as pH and salinity have well-documented physiological effects, especially at low pH (<5) and high salinity (>3°/∞). Mixing, or stratification, and the levels of humic compounds both influence the effective underwater climate and the availability of nutrients, thus controlling phytoplankton growth and succession, and indirectly controlling zooplankton population dynamics. Some of the direct effects of humic substances, resulting from both quantity and quality of HS, are noted in chapter 1 and include both physiological effects and specific toxic effects, particularly when combined with low pH. Lake size plays a rather unexplained role in species presence or absence and in total species diversity (see Fryer 1985). Habitat diversity has some influence, in particular in the shallow vleis under study, and the development of the littoral may further influence the proportion of littoral/benthic species that are present in the limnetic community.

It is thus a large and complex set of variables that influence and ultimately determine the structure and abundance of the zooplankton community. The communities in the vleis under study are generally exposed to more extreme conditions than most, as a result in particular of the high humic levels and low pH (and in one case high salinity).

One of the aims of the study was thus to determine the community structure and zooplankton abundances of these unusual and unstudied systems and to assess the influence of the set of abiotic and biotic variables, mentioned above, on the structure and dynamics of the zooplankton community.

Another important objective of the study was to establish a comprehensive list of the crustacean species in the limnetic communities of these systems. The aquatic invertebrate fauna of southern Africa has been divided into two major groupings, the South Temperate Gondwanian and the Pan-Ethiopian (Harrison 1965, 1978). Most of the freshwater fauna of southern Africa is closely related to that of tropical Africa, forming a truly Pan-Ethiopian or Sub-Saharan grouping. It consists of elements resulting from long-distance dispersal from Palearctic and Oriental regions as well as elements resulting from allopatric speciation of the tropical Gondwanaland fauna. Patterns of zooplankton species distribution within this region are described by Dumont (1980). The South Temperate Gondwanian fauna constitutes the remains of the south temperate zone fauna of the early Jurassic times. It is now limited to the south-western Cape (in which it shows its greatest development) and to refugial montane regions distributed eastwards and then northwards along the Drakensberg and adjacent ranges (Stuckenberg 1962). The fauna is thus allopatric to other temperate Gondwana relict faunas of the southern continents and forms an unique and distinct grouping. Apart from the works of Sars (1916, 1924, 1927), Hutchinson *et al.* (1932), Harrison (1962), Coetzee (1986) and Coetzer (1987), no attempt has previously been made to document the zooplankton fauna of this region and its distribution. For this reason a synthesis of records of the distribution, taxonomy and ecology of the species encountered in this study has been included and it is hoped that this synthesis, together with the data presented, will go some way to filling the gap in the knowledge of the freshwater zooplankton fauna of the region.

METHODS

Sampling procedures and the preservation of the samples are described in chapter 3. Before sorting, the animals in each sample were stained by the addition of a few ml of rose bengal stain (a solution of approx. lg l^{-1} of distilled water). The buffered formalin preservative was filtered off using an 80 um mesh sieve and the samples were resuspended in distilled water.

Sample sorting was carried out in two stages. The first stage involved an examination of the entire sample under low power (10x magnification) of a binocular dissecting microscope. All animals greater than approximately 1 mm in length were counted and removed. In addition specimens of uncommon species were removed and their presence noted. Taxa removed at this stage thus included the Notonectidae (Hemiptera), Corixidae (Hemiptera), fish larvae, most specimens of the calanoid copepod genus *Lovenula* (Crustacea), the ostracod genus *Parastenocypris* (Crustacea), most *Chironomidae* (Diptera), some of the other insect larvae and some of the large adult *Daphnia* spp. (Crustacea) and their ephippia. Taxa with specimens of smaller size, of which presence or absence was noted, included many of the ostracod, cladoceran, and Hydracarina species. The sample composition was thus almost completely established in the first stage.

The second stage involved subsampling, before counting the animals under high power (40x magnification) using a 'Bogaroff' counting tray. The subsampling method used closely followed that of McCallum (1979). The sample was placed in a 500 ml measuring cylinder and made up to volume with distilled water. The sample was mixed by blowing through a straight-sided plastic-pipette, with a 5 mm bottom aperture diameter, for five seconds. The subsample was removed immediately after bubbling with a similar pipette, also with a bottom aperture diameter of 5 mm, to which a Gilson pipetman (P500) was attached. An aliquot was thus removed in the plastic pipette as it was withdrawn from the measuring cylinder. The size of the subsample and the volume to which the measuring cylinder was filled was determined both by attempting to maintain a similar number of animals per subsample and by the limited volume of the counting tray. On average the subsample size was 4 ml of a total volume of 300 ml. From each sample a minimum of four subsamples was removed and counted. Each subsample contained more than 150 animals, sometimes more than 1000 animals, but most often between 300 and 400. Thus in each sample a minimum of 600 animals was counted. Good replication of the common species in the subsamples was almost always obtained and more than four subsamples was only necessary to establish the frequency of occurrence of rare species. Suurdam samples were exceptional. As a result of the paucity of zooplankton, 4 ml subsamples out of a total volume of 60 ml were necessary in order to have subsamples containing more than 100 animals.

Animals were all identified and counted and the abundance of each taxon calculated (number.m^{-3}). The Copepoda, Cladocera, Ostracoda and Rotifera were all separated to species level, although for many of the Cladocera the use of group names was necessary due to the lack of collected material from this region. The limnetic Notonectidae and Corixidae were also identified to species level, whereas the more littoral and benthic hexapod groups were identified only to family. The water mites were separated into apparent species on the basis of obvious morphological differences since samples sent away for identification were unfortunately never named nor returned.

The copepod populations were separated into adult males, females with and without eggs, copepodites and nauplii, and the average body length of each group was measured for each month.

RESULTS AND DISCUSSION

As a result of the restricted ranges and paucity of biogeographical and ecological information on many of the taxa occurring in the south-western Cape, it was felt necessary to summarise the available information with particular regard to the abundant and the restricted taxa found in the net plankton in the six vleis.

Community composition and seasonal variation will then be described and discussed in relation to physical, chemical and biological factors in the sections following.

TAXONOMY, ECOLOGY AND DISTRIBUTION OF THE TAXA

Copepoda

Calanoida

All the freshwater calanoid copepod species present in southern Africa belong to the family Diaptomidae (Rayner in press). The two genera that occur in the studied vleis are *Metadiaptomus* and *Lovenula*.

The genus *Metadiaptomus* contains eleven species, six of which occur in southern Africa (*M.transvaalensis, M.meridianus, M.colonialis, M.purcelli, M.capensis* and *M. vandouwei*), and one in east Africa (*M.mauretanicus*). The two north African species (*M.chevreuxi* and *M.aethiopicus*) do not occur south of a latitude of 12-15°N (Dumont 1979, Dumont *et al.* 1981), being replaced by *Tropodiaptomus* and *Thermodiaptomus* species in tropical Africa. The southern African metadiaptomids are probably similarly restricted to the southern and possibly eastern regions of the continent. Of the southern African species, *M.capensis* is further restricted to the south-western Cape and *M.purcelli* to the south-western and southern Cape. *M.meridianus* is the most widely distributed of the southern species, found in most permanent impoundments (N Rayner pers.comm.), yet with the other three southern African metadiaptomids does not occur in the western or southern Cape (as far as is known). Only *M.capensis* and *M.purcelli* were found in the present study.

Metadiaptomus capensis (Sars, 1907)
(syn. *Diaptomus capensis*: Sars, 1927, *Paradiaptomus capensis*: Kiefer 1928a, 1929).

Adult female length : 1.20 - 1.90 mm
Adult male length : 0.75 - 0.90 mm

M.capensis is the larger of the two Cape species, although both are smaller than the other southern African metadiaptomids. Judging from the maxillipeds and the maxillae, *M.capensis* feeds on suspended particulate matter. The species is limnetic, occurring in high numbers throughout the water column and also extends its range into the marginal vegetation (Harrison 1962).

M.capensis has only been recorded in the south-western Cape. Sars (1927) records the species found "at five different places near Cape Town" and "on the Cape Flats" (see Fig. 9.1); Hutchinson *et al.* (1932) record the species in Lakeside

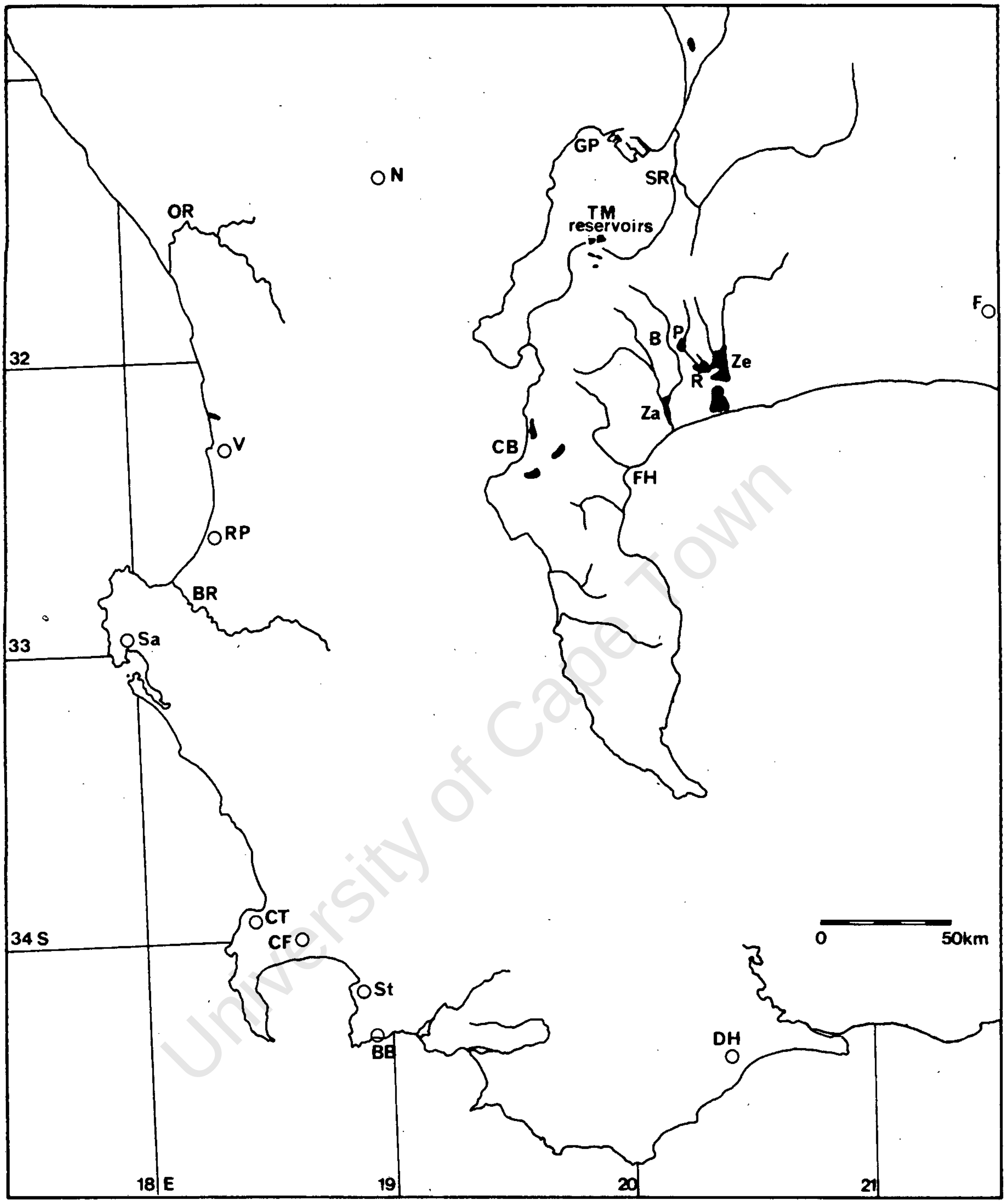


Figure 9.1 Previously recorded localities of both the abundant and restricted taxa found in the six studied vleis. See also Figure 2.1. B - Bergvliet, BB - Black Bass lake, BR - Berg River, CB - Chapmans Bay, CF - Cape Flats, CT - Cape Town, DH - De Hoopvlei, F - Faure, FH - Fish Hoek, GP - Green Point, N - Nieuwoudtville, OR - Olifants River, P - Princess vlei, R - Rondevlei, RP - Rocher Pan, Sa - Saldanha Bay, St - Steenbras reservoir, TM reservoirs - Table Mountain reservoirs, V - Verlorenvlei, Za - Zandvlei, Ze - Zeekoevlei.

vlei (syn. Zandvlei); Harrison (1962) records it in Sirkelsvlei (confirmed in this study); Harding and Smith (1967) in Zeekoevlei, Sirkelsvlei and a temporary pool on the Cape Flats; Coetzee (1986) in De Hoop vlei (also found there by the author) and Coetzer (1978, 1987) in Rocher Pan. These are the only known records of *M.capensis*; A Coetzer (pers.comm.) has reported this species in the vicinity of Verneuk Pan in the north-western Cape, but this record is uncertain.

There is little information on the physical, chemical or biological characteristics of the waters in which *M.capensis* has been found previous to this study. The salinity of Lakeside vlei was ca. $8^{\circ}/_{oo}$ (from Hutchinson *et al.* 1932) and pH was over 9, while Sirkelsvlei waters are unlikely to have changed much in salinity (or otherwise) since the late 1940's (see chapter 2). De Hoopvlei, with salinities between 6 and $13.5^{\circ}/_{oo}$ supported *M.capensis* populations only at salinities below ca. $12^{\circ}/_{oo}$ (data from Coetzee 1986) and Rocher Pan waters contained salinities between approximately 1 and $12^{\circ}/_{oo}$ (Coetzer 1978). Zeekoevlei waters in the 1940's are also likely to have been slightly saline (see chapter 2). Thus judging only from the available information, the distribution of *M.capensis* does seem to be tied to waters ranging in salinities between 1 and $12^{\circ}/_{oo}$ (this is discussed further below). Water pH, colour and phytoplankton vary more widely, pH from slightly acid to alkaline, and colour from brown to probably at least slightly brown most of the time, whereas phytoplankton asemblages, although not recorded, are variable judging from basin morphometries and water appearance.

Metadiaptomus purcelli (Sars, 1907)
(syn. *Diaptomus purcelli*: Sars 1927, *Paradiaptomus purcelli*: Kiefer 1928a, 1929).

Adult female length : 0.55 - 1.00 mm
Adult male length : 0.55 - 0.80 mm

M.purcelli has maxillae and maxillipeds of a similar structure to those of *M.capensis* and therefore also appears to feed on suspended particulate matter. It is also a limnetic species occurring in high numbers throughout the water column.

M.purcelli is more widely distributed than *M.capensis*. Sars (1927) records it found "at Bergvliet" and "in the Cape Flats"; Hutchinson *et al.* (1932) record it in all the Table Mountain reservoirs and also at Steenbras reservoir; Harding and Smith (1967) record it as characteristic of temporary pools on the Cape Flats; Sinclair *et al.* (1986) record it in Verlorenvlei and Rayner (pers. comm.) has identified it from the lower reaches of the Buffalo river.

Again there are few physical, chemical or biological data on the waters in which it occurs. The reservoirs sampled by Hutchinson *et al.* (1932) were all slightly acid (pH 5.2-6.1), brown-coloured waters with low salinities -characteristics common to Gillidam and the Grootvlei waters in which it also occurs (except that pH ranges more widely in these vleis). *M.purcelli* therefore appears to be associated with lower salinities than those in which *M.capensis* tends to occur and, judging only from the occurrences noted by Hutchinson *et al.* (1932) and in this study, also appears to be common in humic waters.

The genus *Lovenula* contains five species, three of which occur in southern Africa (*L.falcifera*, *L.excellens* and *L.simplex*), one in east Africa (*L.africana*) and one in north Africa (*L.alluaudi*) (Rayner in press). Of the four southern African species, only *L.simplex* occurs in the south-western Cape, and appears to be restricted to this area. Both *L.falcifera* and *L.excellens* are widespread further north, with *L.excellens* often occurring with *M.meridianus* in larger, permanent impoundments (Rayner pers.comm.).

Lovenula simplex Kiefer, 1929
(syn. *Lovenula falcifera*: Sars 1899, 1927, *Lovenula falcifera*: Harding and Smith 1967)

Adult female length : 3.0 - 4.0 mm
Adult male length : 3.0 - 3.5 mm

According to Sars (1927), this form is one of the largest known freshwater copepods. The posterior maxillipeds are very strongly developed (almost three times as long as the anterior pair) and constitute "very powerful preying organs" (Sars 1927), thus suggesting a predatory lifestyle. It is a limnetic species most probably preying on the metadiaptomids and cladocerans with which it normally co-occurs.

L.simplex is restricted to the south-western Cape. Sars (1927) records it on Green Point Common ("apparently in pure fresh water"); Kiefer (1934) records specimens collected between Fish Hoek and Chapmans Bay by the German South Polar expedition 1901-1903; Hutchinson *et al.* (1932) note a juvenile *Lovenula* in a sample collected in Lakeside vlei (Zandvlei) and Coetzer (1978, 1987) records it in Rocher Pan. Coetzee (1986) records a *'Lovenula falcifera'* in De Hoop vlei, but he also records *'Diaptomus capensis'*. Both are the names used by Sars (1927) to describe *Lovenula simplex* and *Metadiaptomus capensis* respectively (subsequently reassigned by Kiefer 1934) and thus the *L.falcifera* recorded by Coetzee (1986) can probably be referred to *L.simplex*.

The known physical and chemical characteristics of the waters in which *L.simplex* occurs vary more widely than those in which the metadiaptomids are known. The species co-occurs with *M.capensis* in the slightly saline waters of De Hoop vlei, Rocher Pan, Sirkelsvlei and possibly previously in Lakeside vlei and in addition co-occurs with *M.purcelli* in the non-saline waters of Grootrondevlei (this study). The pH of the waters range from slightly acid to alkaline and the water colour is variable.

Cyclopoida

The cyclopoid species are generally more widespread, some with world-wide distributions, although some are endemics with restricted ranges. Most species are raptorial, preying on smaller zooplankton such as copepodites, nauplii, rotifers and small cladocerans. The genera *Thermocyclops, Microcyclops, Tropocyclops* and *Paracyclops* occur in the open waters of the studied vleis.

The genus *Microcyclops* contains a number of species which occur in all parts of Africa, the central Americas and India. Five species occur in southern Africa (Rayner in press), of which only *M. crassipes* appears to occur in the south-western Cape.

Microcyclops crassipes (Sars, 1927)
(syn. *Cryptocyclops crassipes*: Sars 1927)

Length of adult female : 0.6 - 0.8 mm

This species, as the generic name suggests, is one of the smaller cyclopoids. It is probably raptorial and is a limnetic species occurring throughout the water column.

Its distribution appears to be restricted to the extreme south-western Cape. Sars (1927) records the species from "a pond on the Cape Flats"; Kiefer (1934) refers to the species, but records no localities; and Hutchinson *et al.* (1932) did not encounter the species in their collecting throughout South Africa. Dussart and De Faye (1985) list the species distribution as South African, citing Sars (1927), Kiefer (1929, 1934) and Lindberg (1957). Apart from the Lindberg (1957) reference which could not be traced, no other reported records of this species are known. I have made a further unconfirmed identification of material collected by B A Byren from Nuweberg Dam on the Palmiet River.

The present study provides the only record of the habitat requirements of this species, although once the identification from Nuweberg Dam is confirmed data from this locality is available.

Thermocyclops has numerous representative species in Africa south of the Sahara, yet very few in Europe. Dumont and DeCraemer (1977) describe the genus as consisting of thermophilic, pelagic species unable to advance into the cold climate of Europe and unable to survive the Sahara. Dumont *et al.* (1981) also describe *Thermocyclops* as herbivorous rather than carnivorous. Only one species occurred in the present study.

Thermocyclops oblongatus (Sars, 1927)
(syn. *Mesocyclops oblongatus*: Sars 1927, *Mesocyclops Schuurmanae*: Kiefer 1929, *Mesocyclops infrequens*: Kiefer 1934, *Thermocyclops schuurmanae*: Kiefer 1928a, *Thermocyclops infrequens*: Kiefer 1929, *Thermocyclops stephanidesi*: Kiefer 1938).

Length of adult female : 0.88 - 1.1 mm
The male is slightly smaller than the female.

T.oblongatus is a warm stenothermic species, also described as a tropical Ethiopian relict species by Dumont *et al.* (1979). It is a limnetic species and Seaman (1977) suggests a (raptorial) herbivorous and detritivorous feeding habit with the ability to extend its food choice, while Jarvis (NIWR 1985) refers to it as carnivorous.

The species is widely distributed throughout Africa, especially in southern and eastern Africa, being absent only from the Guinea-Congo basin. It is also recorded in Europe in Corfu, Portugal, the Balearic islands and West Anatolia (Turkey). In southern Africa it is widespread in the Transvaal occurring in both pans and impoundments (see Hutchinson *et al.* 1932, Seaman 1977, NIWR 1985). In the south-western Cape it has been recorded by Sars (1927) "from a small duck pond at Salt River" and "occasionally on the Cape Flats"; by Hutchinson *et al.* (1932) in Princessvlei and by Harrison (1962) and Harding and Smith (1967) in Zeekoevlei.

Hutchinson *et al.* (1932) note an association of this species with abundant phytoplankton or macroscopic vegetation. Certainly the Cape localities are eutrophic and many of the Transvaal impoundments and pans are eutrophic or turbid, or both. The presence of high densities of phytoplankton and/or allochthonous material may well favour the presence of this species. Zeekoevlei and Rondevlei were both slightly saline when Hutchinson and Pickford sampled, as evidenced by the presence of the brackish water species *Brachionus plicatilis* and *Cletocamptus trichotus*; since the weirs have been constructed (see chapter 2), salinities have dropped and *T.oblongatus* has colonised the vleis from Princessvlei.

The genus *Tropocyclops* consists of single species throughout Africa, Europe and North America - *Tropocyclops prasinus*, although a number of subspecies are recognized in east Asia, Africa and the Americas (see Dussart and De Faye 1985, Dumont 1981).

Tropocyclops prasinus (Fischer, 1860)
(many synonyms have been applied - those that have been used in the South African context are - *Leptocyclops prasinus*: Sars 1927 and *Eucyclops prasinus*: Kiefer 1928b).

Length of adult female : 0.5 - 0.9 mm

The species is also raptorial and may or may not be limnetic. Harding and Smith (1974) record it as non-planktonic in the United Kingdom, but Pennak (1978) refers to it as limnetic in North American waters. In the south- western Cape it is rare in the open water and thus most probably conducts a littoral existence.

Although cosmopolitan and, among the Cyclopoida, one of the most widespread species, certified records of its occurrence are rare south of the Sahara (Dumont 1981). It is found in the Transvaal (see Hutchinson *et al.* 1921) and in the Cape is recorded by Sars (1927) in a dam in Bergvliet and in ponds on the Cape Flats.

Paracyclops consists of a number of species, most of which are cosmopolitan.

Paracyclops poppei (Rehburg, 1880)
(many synonyms - that which has been used in the South African context is - *Platycyclops poppei*: Sars 1927).

Length of adult female : 0.54 - 0.76 mm

The species is raptorial and is littoral and benthic in habit (Pennak 1978).

It is cosmopolitan, occurring in Europe, America and Africa. In southern Africa it is recorded in the Transvaal by Hutchinson *et al.* (1932), and in the Cape from Fish Hoek in a pond (Sars 1927) and from Chapmans Bay (Hutchinson *et al.* 1932).

Cladocera

Daphniidae

Five species of *Daphnia* were found in the present study.

Daphnia pulex (Leydig) is a cosmopolitan species and probably the most common dominant limnetic species worldwide.

Daphnia obtusa (Kurz) is also a cosmopolitan species.

Daphnia laevis (Berge) is cosmopolitan, but the South African form is very different from its conspecifics elsewhere (ie North and Central America). In South Africa, Seaman and Kok (in press) record this species as present north of approximately 25°45' S and extending southward along the eastern coastal plateau as far as the eastern Cape; the present records thus extend its range.

Daphnia barbata (Weltner) is a species endemic to Africa. According to Dumont *et al.* (1981) the species occurs on the East African plateau, extends south to southern Africa, lives in the Nile and wedges into the Sahel area of West Africa. Together with the other *Daphnia* species, it is not found at all in the equatorial lowlands of Africa (the Guinea-Congo region and adjoining fringe of the Sudan/Zambezi regions). In southern Africa it is widespread (N A Rayner pers.comm.). Dumont notes its occurrence in the southern, western and eastern Cape and Harding (1961) records it in the Transvaal and the south-western Cape.

Daphnia hodgsoni (Sars) seems to be restricted to the south-western and eastern Cape. Sars (1916) records the species from a vlei outside Port Elizabeth and Coetzer (1978, 1987) from Rocher Pan (where, as in Sirkelsvlei, it co-occurs with *Metadiaptomus capensis).* Wagler (1936) suggests that it is synonymous with *Daphnia dolichocephala,* a suggestion with which Harding (1961) and Noble and Schaeffer (1967) agree. The author and Nancy Rayner (Univ. Natal) are not yet convinced, however, and are investigating fresh material.

All five species are limnetic and like most Daphnidae are herbivorous, feeding on the suspended particulate fraction of the water. Individuals of *D.pulex, D.obtusa* and *D.hodgsoni* are large, with adult females generally 2.5 mm or greater in length, while *D.barbata* and *D.laevis* are smaller, with adult females generally less than 2 mm in length. Other *Daphnia* species collected by Sars (1916) in the environs of the studied vleis, but not found in this study are, *D.dolichocephala* (Sars) (another African endemic), *D.propinqua* (Sars) and *D.tenuispina* (Sars).

Three species of *Ceriodophnia* - *Ceriodaphnia cornuta* (Sars) (syn. *Ceriodaphnia rigaudi* (Richard)), *Ceriodaphnia dubia* (Richard) and *Ceriodaphnia reticulata* (Jurine) - occur in the studied vleis . All three are cosmopolitan species, *C.reticulata* ranging through Europe, Central Asia, Africa and the Americas, *C.cornuta* through southern Asia, Australia, Africa and middle America and *C.dubia* through Europe, Africa, south-east Asia, Australia and New Zealand. In the south-western Cape *C.reticulata* has been recorded on the Cape Flats (Sars 1916), in temporary pools near Fish Hoek (J Green pers.comm.), in Rocher Pan (Coetzer 1978, 1987) and in the lower reaches of the Berg river (Harding 1961). *C.cornuta* has been recorded from a dam at Faure (Sars 1916) and in Princess Vlei (Hutchinson *et al.* 1932), and *C.dubia* has been recorded from Bergvliet (Sars 1916). All are limnetic and feed on the bacterial fraction of the suspended particulate matter rather than the phytoplankton (Gophen *et al.* 1974, Smyly and Collins 1975). *C.cornuta* and *C.dubia* are reported as pond species, in contrast to *C.reticulata*, which is common in large bodies of water (Seaman and Kok in press). Other species collected by Sars (1916) in the environs of the studied vleis were *C.laticaudata*, *C.quadrangula* and *C.producta*, the last of which may be restricted to the south-western Cape.

Moinidae

Only *Moina micrura* (Kurz) was found in the studied vleis. It is a cosmopolitan limnetic species and according to Dumont (1979) is one of the most widespread and successful species of Cladocera in the world. At least three subspecies are recognized (Goulden 1968), with *Moina micrura dubia* the form that extends through Africa and the mediterranean (Dumont 1979). It is found in temporary waters, ponds and lakes and in southern Africa is common in impoundments (Seaman and Kok in press). It has not previously been recorded in the south-western Cape.

Chydoridae

The Chydoridae are a large and complex group, with species groups and complexes now recognised in place of many of the 'cosmopolitan species' of the past. Southern African 'species' have been little studied since Sars (1916) and there is thus little comparison with forms from other parts of the world. The use of group names (gr.) is therefore necessary for many of the taxa until actual comparisons have been made between the taxa in South Africa and the nominate taxa elsewhere (D G Frey pers.comm.). Terms such as 'cf.' and 'near' indicate a close, but not true, identification and the need for a taxonomic revision of the group. In this regard there appears to be a number of species in the south-western Cape which differ from the nominate taxa and may therefore be restricted forms or species peculiar to this region.

The Chydoridae are mainly substratum-living animals common in the littoral and the benthos and generally only incidental or adventitious in the open water. As such they do not form a significant fraction of the limnetic community, except in the smaller vleis.

Chydorus gr. *sphaericus* (O.F.Muller) is a ubiquitous and cosmopolitan group found in a wide range of environmental conditions and is often the dominant littoral cladoceran (Smirnov and Timms 1983). Dumont (1979) records it throughout Africa (except the western and central Sahara) and in the south- western Cape. Harding (1961) records it from this region and Hutchinson *et al.* (1932) record it locally from the Steenbras reservoir.

Ephemeroporus gr. *barroisi* (Richard) is cosmopolitan and found throughout Africa (Dumont 1979). Sars (1916) records it from the southern Cape (as *Chydorus barroisi*). Both of the above species or groups are known to occur in markedly acid waters in Australia and *E.* gr. *barroisi* is the most likely to be found there (Smirnov and Timms 1983). At times of great abundance in the littoral *Ephemeroporus* gr. *barroisi* is planktonic (Timms and Midgley 1969, in Smirnov and Timms 1983).

Alona gr. *intermedia* (Sars) is also cosmopolitan and may also be an indicator of acid conditions (D G Frey pers.com.). Sars (1916) records it from a pond on the Cape Flats. The remaining species of *Alona* (apart from *Alona karua*) need to be compared to the nominate taxa to establish their exact taxonomic position. *Alona karua* (King) is recorded by Sars (1916) from South America, Ceylon and Australia, and in Southern Africa, from the south-western Cape. The Australian record is however regarded as 'incertae sedis' by Smirnov and Timms (1983).

The genus *Rak* consists of two species of limited distribution in Australia (Smirnov and Timms 1983). Both species tend to occur in acid habitats. The species of *Rak* found in Suurdam is a new species (D G Frey pers.comm.) and the first record outside Australia.

Pleuroxus gr. *aduncus* (Jurine) and *Oxyurella* gr. *tenuicaudis* (Sars) are both cosmopolitan groups known from a variety of water types. According to Dumont (1979) these two species are in general 'inferior' (competitively) to *Chydorus* in cold, temperate and tropical climates.

Of the three species of *Leydigia* recorded in this study, *Leydigia macrodonta* was described by Sars (1916) from a small pool on the Cape Flats and thus appears to be restricted to the south-western Cape. The taxa to which the last two species are presently referred, *Leydigia leydigii* (Schoedler) and *Leydigia acanthocercoides* (Fisch.), are both cosmopolitan.

Macrothricidae

Four macrothricid species are found in the studied vleis. The family is normally associated with vegetated littoral areas, often on or near the bottom sediments (Seaman and Kok in press). *Ilyocryptus sordidus* (Lievin) is a cosmopolitan, benthic species, recorded in the south- western Cape by Sars (1916) and Harrison (1962). *Macrothrix spinosa* (King) occurs in Australia, South America and Africa, while *Macrothrix hirsuticornis* (Norman and Brady) is in addition widespread throughout the northern hemisphere. Both are recorded in the south-western Cape by Sars (1916) (*M.hirsuticornis* as *M.propinqua*) and *M.spinosa* by Harding (1961).

Sididae

Only two species of the genus *Diaphanosoma*, are known from southern Africa (Seaman and Kok in press). *Diaphanosoma perarmatum* is found in Indonesia, and in southern Africa previous to this study has only been recorded from Brandvlei in Namibia (Seaman and Kok in press). Both littoral and limnetic species of *Diaphanosoma* are known, but I have found no record of the habit of this species.

Ostracoda

The Ostracoda of the vleis inhabit the littoral or benthos and are not truly limnetic, although some species (particularly the larval stages) are semi-planktonic and can form a significant fraction of the limnetic community. Most species of ostracod are relatively unselective scavengers. As a group the Ostracoda have received very little study and as a result of the work of Sars (1924) the Cape Province (South Africa) is probably the best known African region with regard to its ostracod fauna (Martens in press). The distribution records noted for the species below are the only records of which the author is aware.

Limnocytheridae

Gomphocythere (Sars)

Of the three species that occur in the Cape, two were found in the studied vleis. The adult forms lack natatory setae on the antennae and are thus largely benthic in habit, although the larvae appear to be semi-planktonic. *Gomphocythere* *expansa* (Sars) has been recorded by Sars (1924) on the Cape Flats and by Martens (pers.comm.) in Black Bass vlei (Malkopsvlei) and in a pool in the same area. Harrison (1962) also records a *Gomphocythere sp.* in Black Bass vlei and in Sirkelsvlei, in both cases probably *G.expansa*. *Gomphocythere obtusata* (Sars) seems to have a wider distribution, being recorded by Sars (1924) from Lake Victoria, Saldanha Bay area and Cape Town and by Muller (1914) in a pond near Chapmans Bay.

Martens (in press) considers *G.expansa* to be typical of saline conditions. This is true for Sirkelsvlei waters, but not for the Betty's Bay localities in which it occurs. *G.obtusata* may have some association with alkaline, eutrophic waters occurring in both "a small duck pond in Salt River" (Sars 1924) and in Rondevlei (co-occurred with *Thermocyclops oblongatus,* but there are not enough records to state this with any certainty.

Cyprididae
Parastenocypris (Hartman)
(syn. *Stenocypris*: Sars 1924)).

There are approximately 13 nominal species in this Indian genus (Martens in press.). *Parastenocypris pardalis* (Sars) is a species of large individuals (cf. 2.6 mm) with natatory setae, most commonly found in the littoral (Gardiner 1980). Sars (1924) records it from the Cape Flats and notes that the species is very active and fast swimming.

Potamocypris (Brady)
(syn. *Cyprilla*: Sars 1924)).

Three species of very small size occur in small numbers in the waters of Grootwitvlei. The presence of well developed natatory setae suggests a littoral mode of life, probably swimming amongst and in the proximity of the submerged *Potamogeton* beds. *Potamocypris mastigophora* (Methuen) is widespread through the whole of Africa (Martens in press), while *Potamocypris humilis* (Sars) and *Potamocypris gibbula* (Sars) are more restricted in range. *Potamocypris humilis* is recorded from the Cape Flats by Sars (1924), while Löffler (1967) and Martens (in press) note a record from Finland, and *P.gibbula* is recorded in the vicinity of Nieuwoudtville (western Cape)(McKenzie 1971).

Sarscypridopsis (McKenzie)
(syn. *Cypridopsis*: Sars 1924)).

At least twenty ill-defined nominal species of this genus occur in southern Africa (Martens in press) and of these, five occur in the studied vleis. Natatory setae are once again present and the animals are strong swimmers. All five species are probably present in greatest numbers in the littoral, particularly in the *Potamogeton* beds in Grootwitvlei (Gardiner 1980), but they can occur in reasonably large numbers in the open water. Sars (1924) records *Sarscypridopsis glabrata* (Sars) from the Saldanha Bay area (together with *Gomphocythere expansa), Sarscypridopsis elizabethae* (Sars) from Port Elizabeth (eastern Cape), *Sarscypridopsis spinifera* (Sars) from the Cape Flats and around Cape Town and *Sarscypridopsis tonsa* (Sars) from Green Point common. In addition *Sarscypridopsis aculeata* is recorded from Zeekoevlei (Muller 1908), in Langevlei (near Simonstown), in Zandvlei, and in a pond at Chapmans Bay (Muller 1914), from Brakpan (Transvaal) (Hutchinson *et al.* 1932) and through most of Europe (Löffler 1967). *S.spinifera* is also recorded in Sirkelsvlei by Harrison (1962) and by Martens (pers.comm.) from a pool in the vicinity of the Grootvleis.

Martens (in press) states *S.aculeata* to be typical of saline waters and its recorded presence in Sirkelsvlei and Zandvlei, and in Zeekoevlei before the 1940's, suggests that this is likely. It is widespread in Europe, where it is associated with temporary, brackish and saline waters (Löffler 1967).

Candonidae

Physocypria (Vavra)

(syn. *Cypria*: Sars 1924))

The species present in Suurdam and Gillidam is, according to Martens (pers.comm.), undoubtedly a new species. The only other *Physocypria* species known in South Africa, *P.capensis,* is common and is a free swimming, periphytic to semi-planktonic species. *Physocypria* sp.n. appears to have a similar lifestyle. It occurs in significantly high numbers in the open water compared to another species, *Paracypretta syngramma*, which is restricted almost completely to the *Scirpus* fringe. Virtually all the individuals of *Physocypria* sp.n in the open water are larval stages. The species may well be restricted to very acid, humic waters.

Rotatoria

Brachionidae

Only three species of rotifer, all belonging to the genus *Brachionus*, were found in the studied vleis. All three are cosmopolitan and among the most common species throughout the world. They are truly limnetic and are omnivorous, feeding on small organic particles. *Brachionus plicatilis* is noted as a brackish or saline water species by Ber$\overset{z}{g}$ins (1967) and Walker (1981), although according to Pennak (1978) it is confined to extremely alkaline ponds and lakes. Certainly in the south-western Cape the criterion is salinity, since Hutchinson *et al.* (1932) record it from Rondevlei and Zeekoevlei, but not from Princessvlei (with low salinity and *B.calyciflorus* present), and it appeared in Sirkelsvlei during the period of greatest salinity in the present study. *Brachionus calyciflorus* and *Brachionus rubens* are less specific as regards salinity. The genus *Brachionus*, according to Myers (in Pennak 1978), is confined to alkaline waters with a pH above approximately 7. Both *B.calyciflorus* and *B.rubens* occur in alkaline waters in the south-western Cape, although *B.plicatilis* is not limited in this respect, occurring in the acid waters of Sirkelsvlei.

Hemiptera

Notonectidae

Although occurring in relatively low numbers when compared to other limnetic species, the notonectids are both large animals (adults 6.5 to 7.5 mm) and voracious ~~ferocious~~ predators, and have been shown to strongly influence the structure and dynamics of zooplankton communities (Murdoch *et al.* 1984). Only a single species, *Anisops aglaia* (Hutchinson, 1929) was found in the vleis, with the exception of a single occurrence of *Anisops varia* in Gillidam. The genus *Anisops* is an Old World genus, absent from North America and Europe, and *A.aglaia* is endemic to southern Africa, occcurring in the Cape and southern Transvaal. In the south-western Cape it was recorded by Hutchinson (1929) from various localities on the Cape Flats and from the Wynberg and Woodhead Reservoirs (Hutchinson *et al.* 1932) on Table Mountain where these authors believed that it might be the cause of a drop in the numbers of *Metadiaptomus purcelli.* Harrison (1962) recorded *A.aglaia* from Zeekoevlei and Princessvlei. An interesting feature is that, although coloration in *A.aglaia* is variable and thus not an important taxonomic feature (Reichart pers.comm.), the Suurdam population was characterised by the presence of black marks on the pronotum in all the specimens. Notonectid adults are known to fly readily (Usinger 1956), yet there may be a resistance to dispersal and mixing with other populations. Hutchinson (1929) notes that *A.aglaia* was found only in standing waters (as opposed to moving waters or small pools) in contrast to the other *Anisops* species, which do not appear to be limited in this way. Another unusual fact is that *A.aglaia* is the only notonectid species present in the studied vleis, whereas a number of notonectid species commonly co-occur in other regions. *A.aglaia* and a subspecies of *A.varia* are two of only three notonectid species recorded by Hutchinson in water with a pH below 6.

Pleidae

The pleids are closely related to the notonectids, but are far smaller (generally less than 2.3 mm) and are swimmers of limited distances, normally associated with submerged vegetation. *Plea pullala* (Stal) was present only in March in Rondevlei but is common in many waters, especially temporary ones in the south-western Cape.

Corixidae

Micronecta winifreda (Hutchinson) occurs generally in very small numbers in some months in Rondevlei. Individuals are small in size (2.3 - 3.0 mm) and, like most corixids, are strong swimmers, probably largely herbivorous, but also ingesting small benthic organisms and some insect larvae. *Micronecta winifreda* is recorded by Hutchinson (1929) as endemic to the western and southern Cape. Another species, *Sigara meridionalis*, was recorded by Hutchinson (1929) and Hutchinson *et al.* (1932) from Zandvlei, Zeekoevlei, Rondevlei and Princessvlei and again by Harrison (1962) in Zeekoevlei and in Princessvlei. The latter species is confined to the western and central parts of South Africa and is common in brackish waters. Its absence in Rondevlei is probably (as with *Metadiaptomus capensis* and *Brachionus plicatilis* related to the decrease in salinity experienced by Rondevlei and Zeekoevlei since the 1940's (see chapter 2).

Diptera

Chironomidae

A planktonic existence by first instar larval chironomids has been recorded by many authors (Davies 1976). Later instars are also capable of entering the plankton temporarily and the planktonic phases are believed to be advantageous as a mechanism of passive dispersal of the larvae. This planktonic existence is enhanced by adaptation to feeding (in some cases), and positive phototaxis (in most cases) (Davies 1976). Both predacious and herbivorous/ detritivorous species occur in the zooplankton. Chironomid larvae are present in the zooplankton in all the studied vleis as a small, variable fraction, but the taxonomy of the group is unknown.

Hydracarina

Water mites were present in the zooplankton of all the vleis except Sirkelsvlei and Rondevlei. In most cases they formed a small, but often significant fraction, of the zooplankton. Swimming is variously developed among the genera and although they are largely associated with the substrate or littoral vegetation mites are not generally uncommon in the water column. The forms A-F constitute superficially similar animals and may or may not correspond to the same species in the same or in the different vleis. The form X refers collectively to miscellaneous less common forms. They are probably all carnivorous.

COMMUNITY COMPOSITION

The compositions of the limnetic communities in each of the six vleis are presented in tables 9.1 - 9.6. The tables included all taxa found in the surface 0.5 m of the water column which in many cases, as a result of the shallowness of the water, high average wind speeds and the small size of the vleis, included a significant component of littoral and benthic species. These benthic taxa were normally present in small numbers and are generally only recorded as present (or absent), but together constitute a small percentage of the total abundance of 'zooplankton'.

The community of each vlei was dominated by a single copepod species making up between 29.9% (in Rondevlei) and 97.3% (in Gillidam) of the mean total zooplankton numbers.

In Suurdam the copepod species was the cyclopoid, *Microcyclops crassipes*; in Gillidam, Grootrondevlei and Grootwitvlei it was the calanoid species *Metadiaptomus purcelli*; in Sirkelsvlei it was the calanoid species *Metadiaptomus capensis* and in Rondevlei the cyclopoid *Thermocyclops oblongatus*. In both Sirkelsvlei and Grootrondevlei the large calanoid *Lovenula simplex* also occurred, but had a relatively low numerical abundance, while the small cyclopoid, *Microcyclops crassipes*, similarly co-occurred in Gillidam, Grootrondevlei and Grootwitvlei. The cyclopoids *Tropocyclops prasinus* (Gillidam and Grootrondevlei) and *Paracyclops poppei* (Grootrondevlei) both only occurred as a few individuals once or twice during the study period. The rotifers were the next most abundant group, but they only occurred for a short period of the year in Sirkelsvlei, and both for a short period and in low numbers in Grootwitvlei. In Rondevlei, however, their numbers were high throughout the year and at maximum numbers *Brachionus rubens* was numerically more abundant than *Thermocyclops oblongatus*.

Cladocerans were present in the water column of all six vleis. The generally limnetic Daphnidae and Moinidae were, however, present only in Sirkelsvlei, the Grootvleis and Rondevlei, whereas the primarily littoral Chydoridae were found in all six limnmetic communities. The genus *Daphnia* occurred only in Grootrondevlei, Rondevlei, and in very low numbers in Sirkelsvlei. In both Grootrondevlei and Rondevlei the daphnids constituted the next most numerous group after the copepods and rotifers. The number of cladoceran species ranged from only a single species in Suurdamm to seventeen species in Rondevlei.

Although the Ostracoda are generally littoral/benthic in habit, the larvae of *Physocypria* sp.n. (Suurdam and Gillidam), *Gomphocythere expansa* (Sirkelsvlei and

SUURDAM **Limnetic community**

Group	Species (or lowest taxon)	Avg.	sd.	Max.	Min.	%
Cyclopoida	*Microcyclops crassipes*	1004	586	2139	316	56.3
Harpacticoida	*Nitocra sp.*	75	65	271	11	4.2
Cladocera	*Rak* near *labrosus*	226	172	546	0	12.7
Ostracoda	*Physocypria sp.n.*	94	95	331	0	5.3
Hydracarina	sp.A	165	260	1009	11	9.3
	sp.B	135	101	346	34	7.6
	sp.C	15	17	63	0	0.9
	sp.D	p		p	0	
	sp.X	38	35	105	0	2.1
Notonectidae	*Anisops aglaia*	3	7	21	0	0.2
Diptera	Chironomidae	17	18	60	0	1.0
Coleoptera	Dytiscidae	p		p	0	
Odonata	Libellulidae	p		p	0	
Tardigrada	Tardigrada	p		56	0	
Nematodes	Nematodes	p		p	0	
	Total	1783		5017	373	

Table 9.1 The mean numerical abundance (number.m^{-3}) and the mean percentage composition (by number) of the taxa of the limnetic community in Suurdam. p = taxa present in low numbers (normally less than a total of three animals in four subsamples).

GILLIDAM **Limnetic community**

Group	Species (or lowest taxon)	Avg.	sd.	Max.	Min.	%
Calanoida	*Metadiaptomus purcelli*	42696	28616	99394	11976	97.3
Cyclopoida	*Microcyclops crassipes*	147	136	505	0	0.3
	Tropocyclops prasinus	p		p	0	
Harpacticoida		p		p	0	
Cladocera	*Alona gr.intermedia*	448	322	1130	40	1.0
	Ephemeroporus gr.barroisi	60	187	721	0	0.1
Ostracoda	*Physocypria sp.n.*	41	66	173	0	0.1
Hydracarina	sp.A	p		144	0	0.0
	sp.B	78	92	264	0	0.2
	sp.C	48	80	264	0	0.1
	sp.D	p		216	0	0.1
	spp.X	p		p	0	
Notenectidae	*Anisops aglaia*	15	27	89	0	0.0
Diptera	Chironomidae	253	292	866	0	0.6
Coleoptera	Dytiscidae	p		216	0	0.0
Odonata	Coenagrionidae	p		p	0	
Trichoptera	Hydroptilidae	p		p	0	
		43885		104171	12017	

Table 9.2 The mean numerical abundance (number.m^{-3}) and the mean percentage composition (by number) of the taxa of the limnetic community in Gillidam. p = taxa present in low numbers (normally less than a total of three animals in four subsamples).

SIRKELSVLEI Limnetic community

Group	Species (or lowest taxon)	Avg.	sd.	Max.	Min.	%
Calanoida	*Lovenula simplex*	1081	925	2933	0	1.0
	Metadiaptomus capensis	56783	32476	119446	22484	53.8
Cladocera	*Daphnia hodgsoni*	p		200	0	0.0
	Ilyocryptus sordidus	p		339	0	0.0
Ostracoda	*Gomphocythere expansa*	10671	13994	57698	678	10.1
	Sarscypridopsis glabrata	585	698	2425	0	0.6
	Sarscypridopsis tonsa	p		p	0	
	Sarscypridopsis aculeata	p		p	0	
Notonectidae	*Anisops aglaia*	3	7	24	0	0.0
Diptera	Chironomidae	p		437	0	0.1
Rotifera	*Brachionus plicatilis*	36145	95836	310393	0	34.2
Platyhelminthes	Turbellaria	205	341	1130	0	0.2
		105641		495025	23162	

Table 9.3 The mean numerical abundance (number.m^{-3}) and the mean percentage composition (by number) of the taxa of the limnetic community in Sirkelsvlei. p = taxa present in low numbers (normally less than a total of three animals in four subsamples).

GROOTRONDEVLEI Limnetic community

Group	Species (or lowest taxon)	Avg.	sd.	Max.	Min.	%
Calanoida	*Lovenula simplex*	355	398	1165	0	0.7
	Metadiaptomus purcelli	41516	49345	185749	2952	82.6
Cyclopoida	*Microcyclops crassipes*	71	81	226	0	0.1
	Paracyclops poppei	p		p	0	
	Tropocyclops prasinus	p		p	0	
Cladocera	*Daphnia barbata*	1795	2671	7146	0	3.6
	Daphnia laevis	2270	8025	31222	0	4.5
	Daphnia pulex	641	1703	5574	0	1.3
	Ceriodaphnia dubia	2922	10166	39545	0	5.8
	Chydorus gr.sphaericus	p		p	0	
	Alona gr.intermedia	117	234	874	0	0.2
	Alona gr.karua	p		p	0	
	Diaphanosoma perarmatum	p		p	0	
Ostracoda	*Gomphocythere expansa*	462	497	1613	0	0.9
	Parastenocypris pardalis	p		p	0	
	Sarscypridopsis glabrata	p		p	0	
	Sarscypridopsis elizabethae	p		p	0	
Hydracarina	spp.X	p		904	0	0.1
Diptera	Chironomidae	p		p	0	
Coleoptera	Dytiscidae	p		p	0	
Protura	Protura	p		p	0	
		50292		274273	2997	

Table 9.4 The mean numerical abundance (number.m^{-3}) and the mean percentage composition (by number) of the taxa of the limnetic community in Grootrondevlei. p = taxa present in low numbers (normally less than a total of three animals in four subsamples).

GROOTWITVLEI **Limnetic community**

Group	Species (or lowest taxon)	Avg.	sd.	Max.	Min.	%
Calanoida	*Metadiaptomus purcelli*	80006	68897	205481	1288	81.9
Cyclopoida	*Microcyclops crassipes*	p		264	0	0.0
Harpacticoida	*Bryocamptus* sp.	182	428	1648	0	0.2
Cladocera	*Moina micrura*	12074	46255	179271	0	12.4
	Ceriodaphnia cornuta	p		p	0	
	Chydorus gr.*sphaericus*	813	2281	8898	0	0.8
	Alona near *harpularia*	84	204	791	0	0.1
	Ilyocryptus sordidus	296	537	1789	0	0.3
	Macrothrix near *goeldi*	802	826	2175	0	0.8
Ostracoda	*Gomphocythere expansa*	2525	2481	8097	15	2.6
	Parastenocypris pardalis	45	115	447	0	0.0
	Sarscypridopsis juveniles	105	194	687	0	0.1
	Sarscypridopsis glabrata	p		p	0	
	Sarscypridopsis spinifera	p		101	0	0.0
	Sarscypridopsis elizabethae	p		p	0	
	Potamocypris juveniles	p	-	p	0	
	Potamocypris mastigophora	p		p	0	
	Potamocypris humilis	p		p	0	
	Potamocypris gibbula	p		p	0	
Hydracarina	sp.A	p		p	0	
	sp.B	p		235	0	0.0
	sp.C	76	97	264	0	0.1
	sp.E	p		p	0	
	sp.F	p		198	0	0.0
	spp.X	p		246	0	0.0
Diptera	Chironomidae	p		p	0	
Coleoptera	Dytiscidae	44	65	188	0	0.0
Trichoptera	Hydroptilidae	p		p	0	
Rotifera	*Brachionus calyciflorus*	340	1242	4821	0	0.3
	Brachionus rubens	p		857	0	0.1
Fish larvae	*Galaxias zebratus*	7	10	33	0	0.0
		97685		417016	1303	

Table 9.5 The mean numerical abundance (number.m^{-3}) and the mean percentage composition (by number) of the taxa of the limnetic community in Grootwitvlei. p = taxa present in low numbers (normally less than a total of three animals in four subsamples).

RONDEVLEI **Limnetic community**

Group	Species (or lowest taxon)	Avg.	sd.	Max.	Min.	%
Cyclopoida	*Thermocyclops oblongatus*	184879	109047	438296	53442	29.9
Harpacticoida	*Attheyella* sp.	857	2669	10242	0	0.1
Cladocera	*Ceriodaphnia cornuta*	89076	88283	315084	11751	14.4
	Ceriodaphnia reticulata	1647	6378	24700	0	0.3
	Daphnia pulex	23630	57794	191323	0	3.8
	Daphnia obtusa	348	1348	5220	0	0.1
	Moina micrura	39852	52061	148910	0	6.4
	Chydorus gr.sphaericus	8957	26707	103646	0	1.4
	Chydorus gr.brevilabris	p		p	0	
	Alona near *harpularia*	442	856	2812	0	0.1
	Alona near *guttata*	p		600	0	0.0
	Alona near *monacantha*	p		200	0	0.0
	Oxyurella cf.*tenuicaudis*	p		1230	0	0.0
	Pleuroxus gr.aduncus	498	576	1640	0	0.1
	Leydigia macrodonta	75	220	819	0	0.0
	Leydigia near *leydigia*	p		700	0	0.0
	Leydigia near *acanthocercoides*	p		p	0	
	Macrothrix spinosa	840	1174	3816	0	0.1
	Macrothrix hirsuticornis	p		p	0	
Ostracoda	*Gomphocythere obtusata*	277	471	1582	0	0.0
	Sarscypridopsis juveniles	389	607	1808	0	0.1
	Sarscypridopsis elizabethae	759	1276	4821	0	0.1
	Sarscypridopsis spinifera	271	652	1808	0	0.0
	Sarscypridopsis glabrata	p		1205	0	0.0
	Sarscypridopsis misc.	p		819	0	0.0
Notonectidae	*Anisops aglaia*	41	66	223	0	0.0
Corixidae	*Micronecta winifreda*	6	24	72	0	0.0
Pleidae	*Plea pullula*	1	4	14	0	0.0
Diptera	Chironomidae	168	397	1311	0	0.0
Diptera	Psychodidae	p		p	0	
Protura	Protura	p		p	0	
Rotifera	*Brachionus calyciflorus*	131308	124827	326002	0	21.2
	Brachionus rubens	134092	230080	507790	0	21.7
Platyhelminthes	Turbellaria	p		p	0	
Nematodes	Nematodes	p		p	0	
		618944		2098059	65193	

Table 9.6 The mean numerical abundance (number.m^{-3}) and the mean percentage composition (by number) of the taxa of the limnetic community in Rondevlei. p = taxa present in low numbers (normally less than a total of three animals in four subsamples).

the Grootvleis) and *G. obtusata* (Rondevlei) appear to be largely planktonic and consequently constituted a small, yet significant, percentage of the zooplankton numbers. The other ostracod species were less common and are most likely to have appeared in the limnetic community as a result of their littoral natatory habit.

Hydracarina were present in small numbers in Suurdam, Gillidam, Grootrondevlei and Grootwitvlei. Suurdam and Gillidam contained a similar assemblage of mite species and Grootwitvlei contained three species (A-C) in common with these two vleis.

The notonectid, *Anisops aglaia*, occurred in Suurdam, Gillidam, Sirkelsvlei and Rondevlei and, although not always numerically important, constituted a significant proportion of the biomass. In Rondevlei the corixid, *Micronecta winifreda*, and the pleid, *Plea pullala*, comprised the fast-moving planktonic hexapoda.

The Chironomidae, present normally in small numbers occurred in all six vleis. Other hexapod taxa are rare and only very young larvae of the Dystiscidae (Coleoptera), Libellulidae and Coenagrionidae (Odonata), Psychodidae (Diptera) and Hydroptilidae (Trichoptera) were found in the surface water. Proturans and collembolans, tardigrads and nematodes were present in small numbers on occasion and turbellarians constituted a small, but noticeable percentage of the total zooplankton numbers in Sirkelsvlei.

Mean numerical abundance of net zooplankton is greatest in Rondevlei; Sirkelsvlei and Grootwitvlei both had numbers about a sixth of those of Rondevlei. Much of the abundance in Rondevlei was contributed by the high numbers of rotifers but, even ignoring rotifers, zooplankton numbers were more than three times greater than in either Sirkelsvlei or Grootwitvlei. Grootrondevlei and Gillidam had mean numbers almost half those of Sirkelsvlei and Grootwitvlei, while those of Suurdam were less than a fiftieth of those of the latter two vleis.

SEASONAL VARIATION

Suurdam

Since the numerical abundance of zooplankton in Suurdam was very low, the error contributed by sampling and subsampling procedures may have been greater than in the other vleis (fig. 9.1~~5~~6). The vlei is small however, and thus variation due to horizontal patchiness was minimal. Seasonal variation was not great in any of the taxa. *Microcyclops crassipes,* the most abundant zooplankter, occurred in greatest numbers in late summer to autumn and in late winter to spring (fig. 9.2a). Sampling

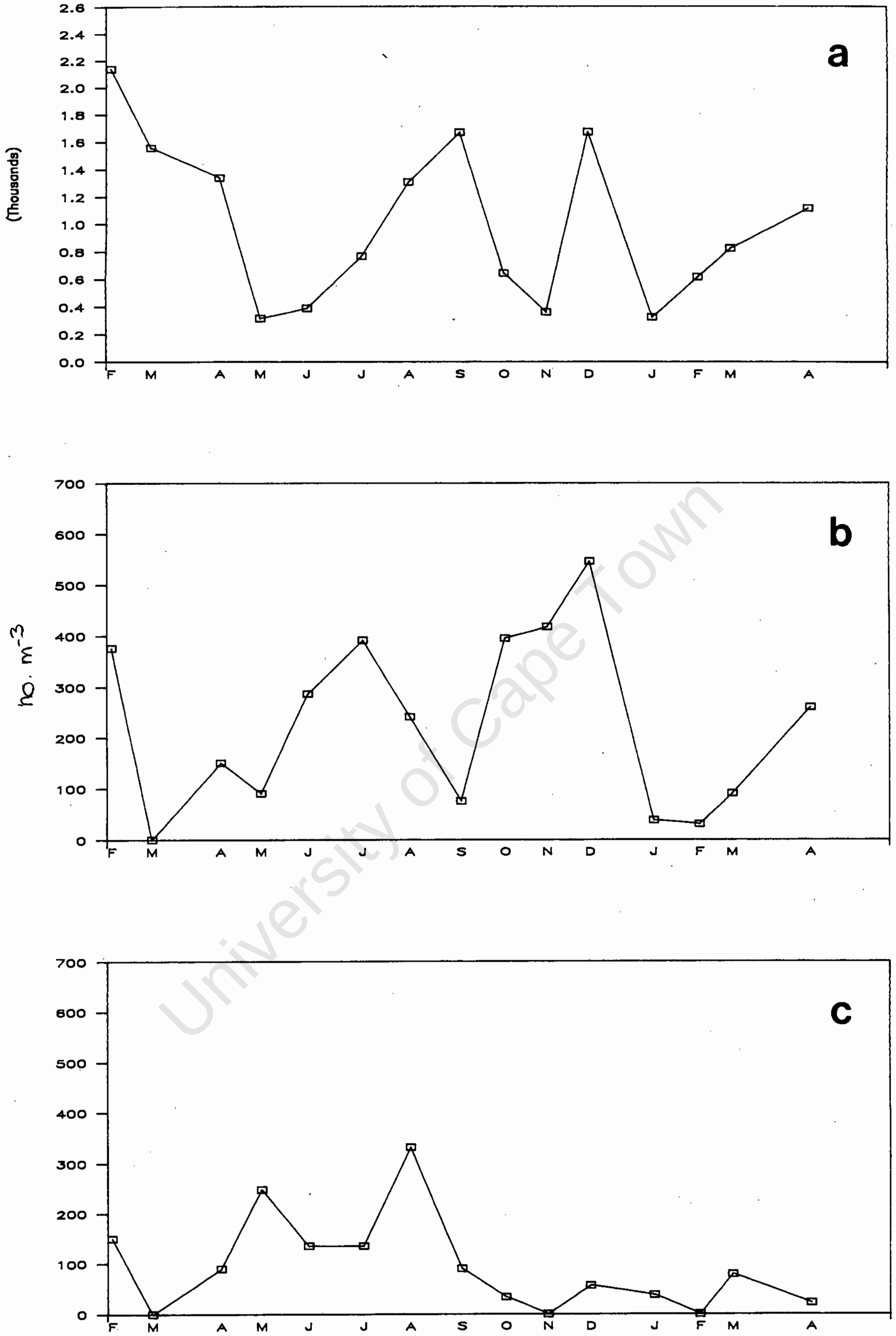
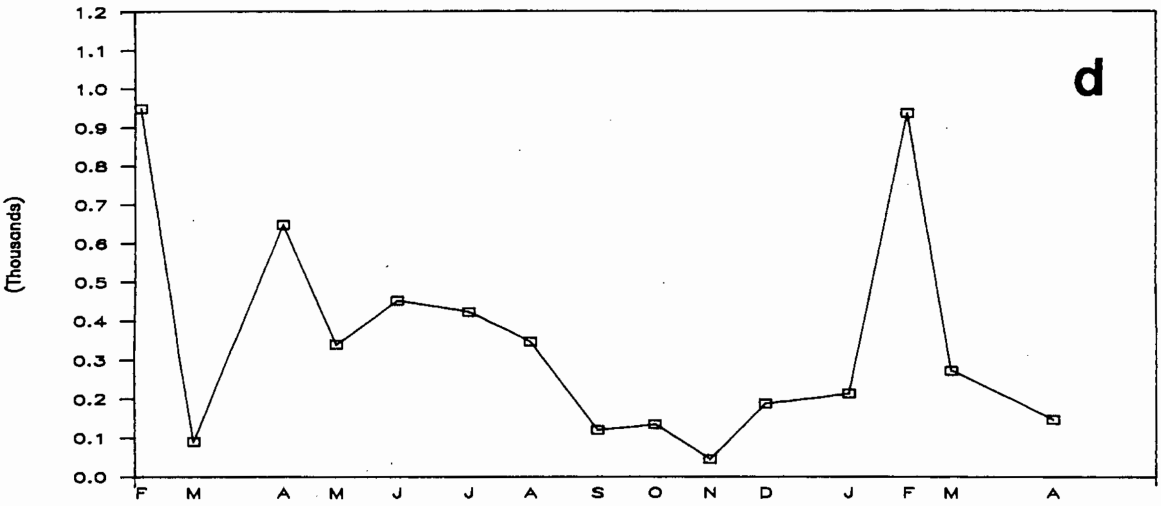


Figure 9.2 Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Suurdam. (a) *Microcyclops crassipes*, (b) *Rak* near *labrosus*, (c) *Physocypria* sp.n., (d) Hydracarina, (e) *Anisops aglaia*.



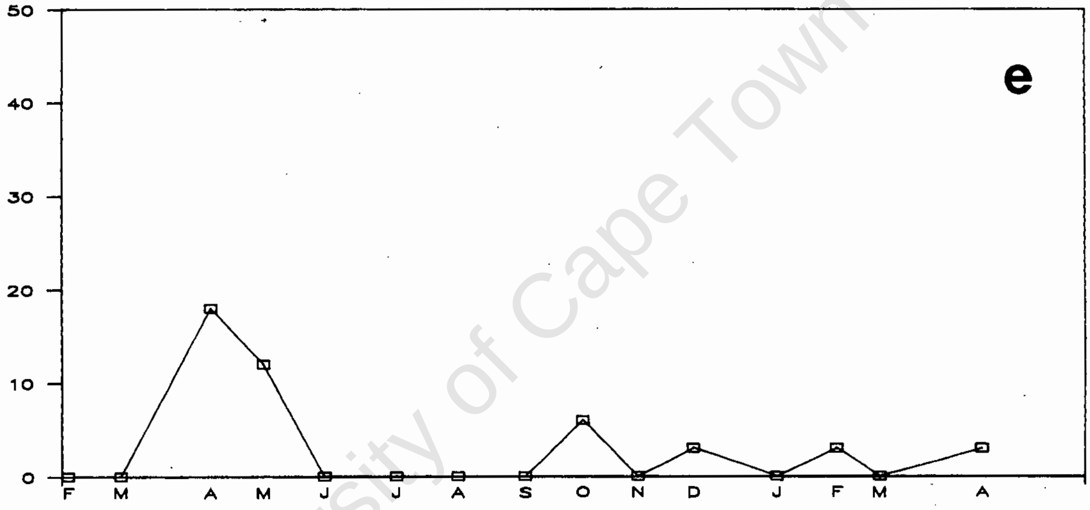


Figure 9.2 (cont.) Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Suurdam. (a) *Microcyclops crassipes*, (b) *Rak* near *labrosus*, (c) *Physocypria* sp.n., (d) Hydracarina, (e) *Anisops aglaia*.

interval was too great for a detailed analysis of the population dynamics, but seasonal changes in population structure are displayed in fig. 9.3. Ovigerous females and egg sacs were noted only in mid-summer, coinciding with one of the two periods of low numbers of copepodites (mid-summer and early winter). The proportion of adult females appears to have remained fairly constant (7 ± 3%) with adult males increasing in percentage during the periods of low copepodite numbers. The harpacticoid copepod *Nitocra* sp. was present in very low numbers, probably because of its largely benthic habit. The seasonal variation in numbers was small, but similar to that of *M. crassipes.* Ovigerous females were present in seven of the fifteen months.

The species most abundant after *M.crassipes* was the chydorid, *Rak* near *labrosus*. It was present throughout the year, occurring in lowest numbers in late summer to autumn (fig. 9.2b). The ostracod *Physocypria* sp.n. was present most months, but generally highest numbers occurred in autumn and winter (fig. 9.2c).

Water mites were present in Suurdam in greater numbers than in any of the other vleis. The two most common species (spp. A and B) were present in small numbers during most of the year. Mite numbers were lowest in spring and early summer (fig. 9.2d). *Anisops aglaia* was found in small numbers during the warmer months, but seems to have been absent during the winter and the beginning of spring. Nymphs were present only in summer (fig. 9.2.e). Of the immature insects that occurred in the water column, chironomids were present in small numbers in most months and dytiscids and libellulids in the summer months only. Tardigrads were encountered in one month and nematodes were found on a few occasions.

Gillidam

The greater zooplankton abundance in Gillidam than in Suurdam was almost entirely as a result of the higher numbers of *Metadiaptomus purcelli.* The species showed a marked variation in abundance, greatest numbers occurring in late winter and spring in the first year and in late summer in the second year (1982)(fig. 9.4a). The population structure (fig. 9.5) showed little variation in the proportion of ovigerous females through the year (0.3 ±0.4%), but two very distinct maxima in the proportion and numbers of nauplii occurred in winter and in mid-summer. The greatest proportions of adult males and females (9 and 17%) were present in the late summer preceding the winter maximum of nauplius numbers and in the spring and early summer preceding the mid-summer nauplius maximum. The seasonal variation thus indicates two broad reproductive periods during the year, although smaller pulses are probably masked by the sampling interval. Greatest numbers of

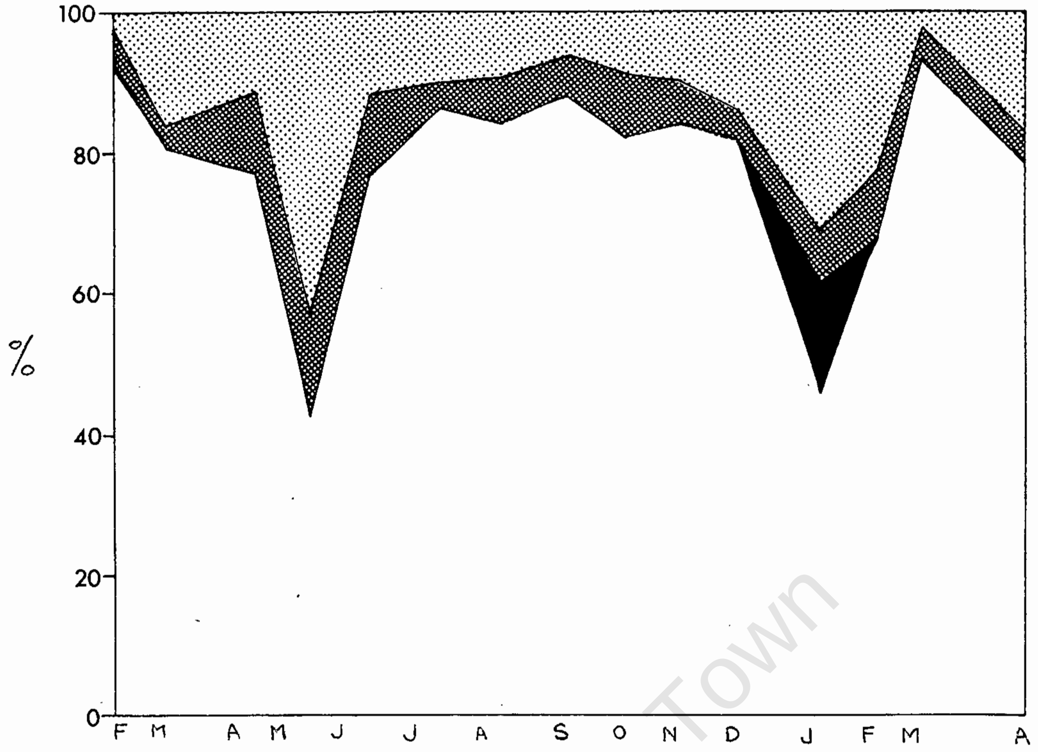


Figure 9.3 Seasonal variation in the population structure of *Microcyclops crassipes* in Suurdam. [░]- adult males, [▓]- adult non-gravid females, [■]- adult gravid females, [□]- copepodites, [▒]- nauplii.

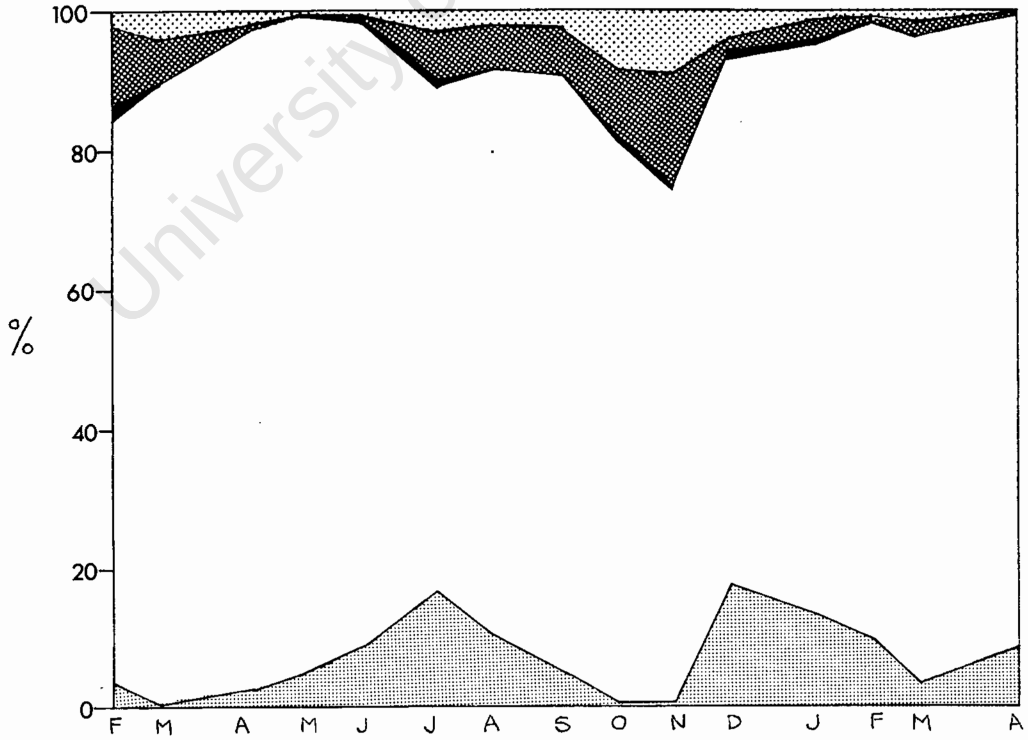


Figure 9.5 Seasonal variation in the population structure of *Metadiaptomus purcelli* in Gillidam. [░]- adult males, [▓]- adult non-gravid females, [■]- adult gravid females, [□]- copepodites, [▒]- nauplii.

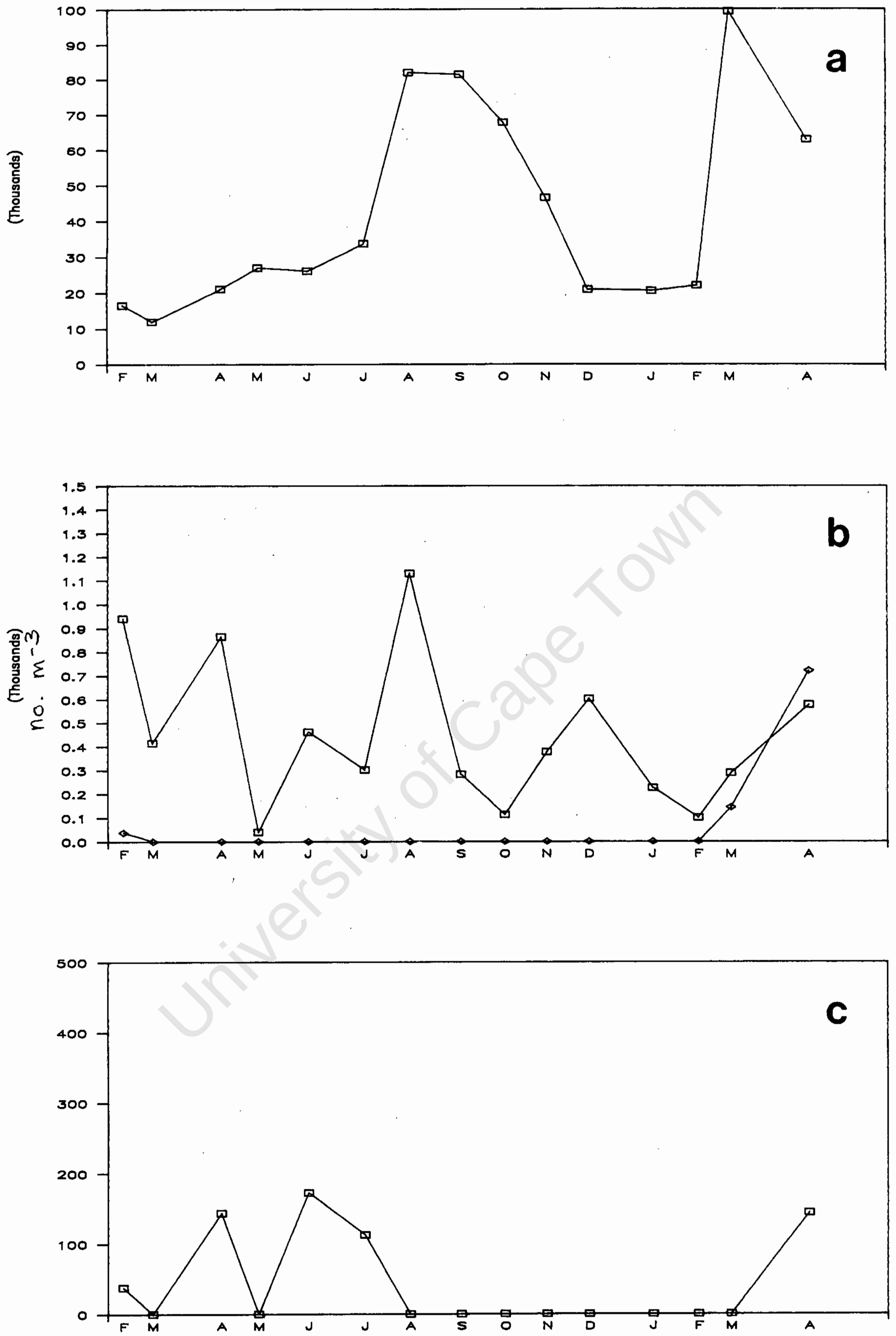


Figure 9.4 Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Gillidam. (a) *Metadiaptomus purcelli*, (b) *Alona* gr. *intermedia* (□) and *Ephemeroporus* gr. *barroisi* (◇), (c) *Physocypria* sp.n., (d) Hydracarina, (e) *Anisops aglaia*, (f) Chironomidae.

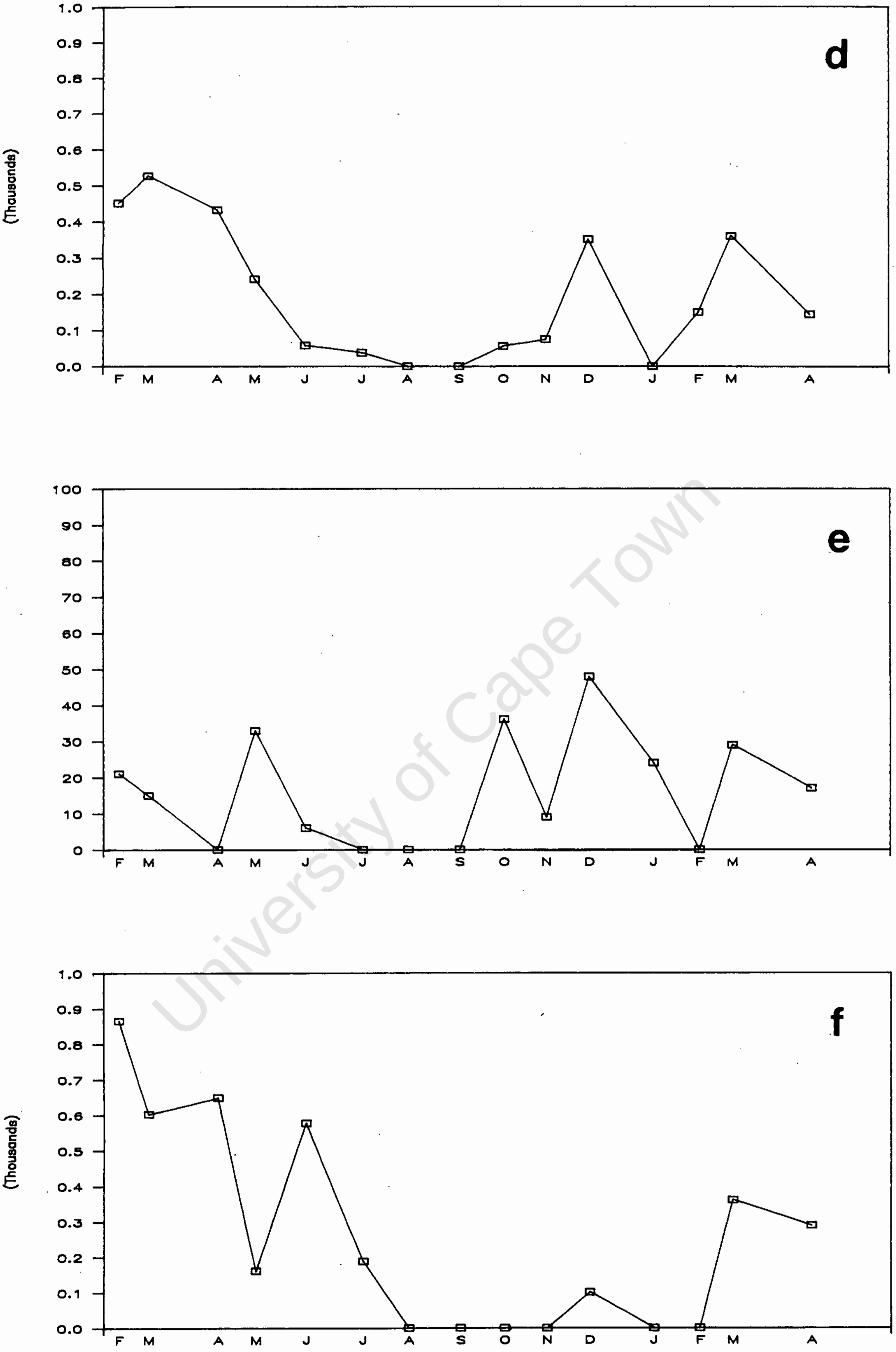


Figure 9.4 (cont.) Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Gillidam. (a) *Metadiaptomus purcelli*, (b) *Alona* gr. *intermedia* (□) and *Ephemeroporus* gr. *barroisi* (◇), (c) *Physocypria* sp.n., (d) Hydracarina, (e) *Anisops aglaia*, (f) Chironomidae.

Microcyclops crassipes occurred in autumn to mid-winter and in mid-summer, somewhat in contrast to the maxima of *M.purcelli.* A harpacticoid species was present in two of the months during the study period, but the specimens were not mature enough for specific identification.

The copepod *Tropocyclops prasinus* occurred as an incidental in July and may be more closely associated with beds of the sedge *Scirpus prolifer.*

The chydorid *Alona* gr. *intermedia* was the next most abundant species after *M.purcelli* and was present throughout the year with ~~little~~ no obvious pattern to the seasonal variation in numbers (fig. 9.4b). The other chydorid species, *Ephemeroporus* gr. *barroisi,* occurred only briefly at the end of each summer. The ostracod *Physocypria* sp. n. was present in similar numbers to those in Suurdam in the five months (autumn and early winter) in which it occurred (fig. 9.4c).

Water mites were present in greatest numbers from mid-summer to autumn and were hardly noted in the water column from mid-winter to early summer. Species B and C were the most common forms, although species A and D were generally present in small numbers (fig. 9.4d). Notonectids (*Anisops aglaia*) were again absent from mid-winter to early spring, but were present in much greater numbers than in Suurdam in the warmer months, presumably as a result of the high numbers of *Metadiaptomus purcelli,* a likely prey species. The populations consisted almost entirely of nymphs from early to mid summer and almost entirely of adults for the remaining warm months, until early winter (fig 9.4e). Of the immature insects, the chironomids were present in relatively high numbers from late summer through autumn to mid-winter (fig. 9.4f) and Dystiscidae, Coenagrionidae and Hydroptilidae were present in small numbers, mostly in summer. Nematodes were found in most samples through the year.

Sirkelsvlei

Total zooplankton numbers in Sirkelsvlei were more than double those in Gillidam as well as being greater than those in the Grootvleis (fig. 9.1~~5~~6). A large proportion of the mean total number was contributed by very high numbers of the rotifer *Brachionus plicatilis*, even though it was present in only three of the fifteen months. Excluding the rotifers, Sirkelsvlei zooplankton numbers were well below those of Grootwitvlei, although remaining well above those of Gillidam and Grootrondevlei.

The species occurring in greater numbers than even *B.plicatilis* was the calanoid copepod *Metadiaptonus capensis*, which is found only in Sirkelsvlei and in a

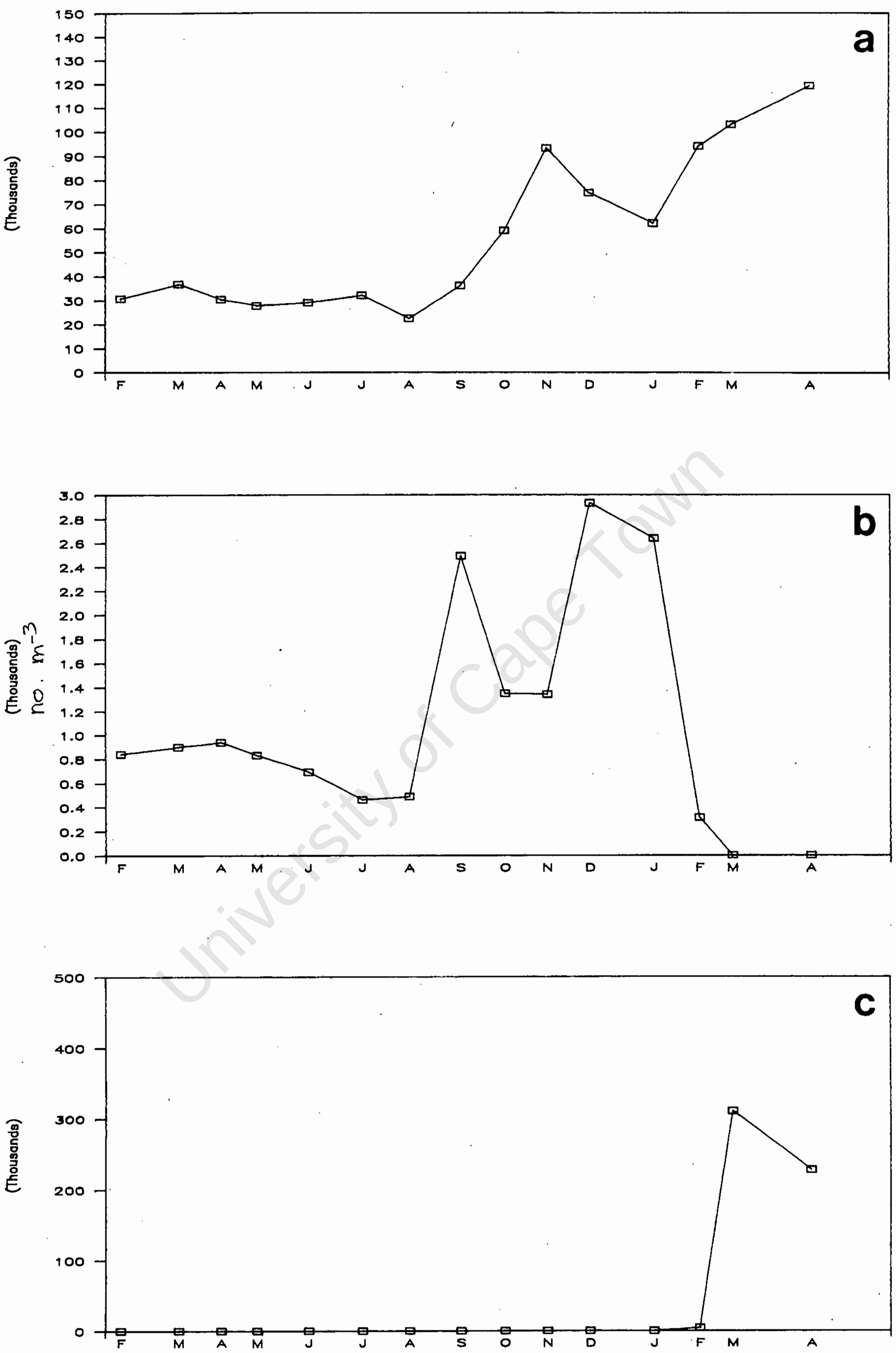


Figure 9.6 Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Sirkelsvlei. (a) *Metadiaptomus capensis*, (b) *Lovenula simplex*, (c) *Brachionus plicatilis*, (d) *Gomphocythere expansa* (□) and *Sarscypridopsis glabrata* (◇), (e) Turbellaria, (f) *Daphnia hodgsoni* (□) and *Ilyocryptus sordidus* (◇).

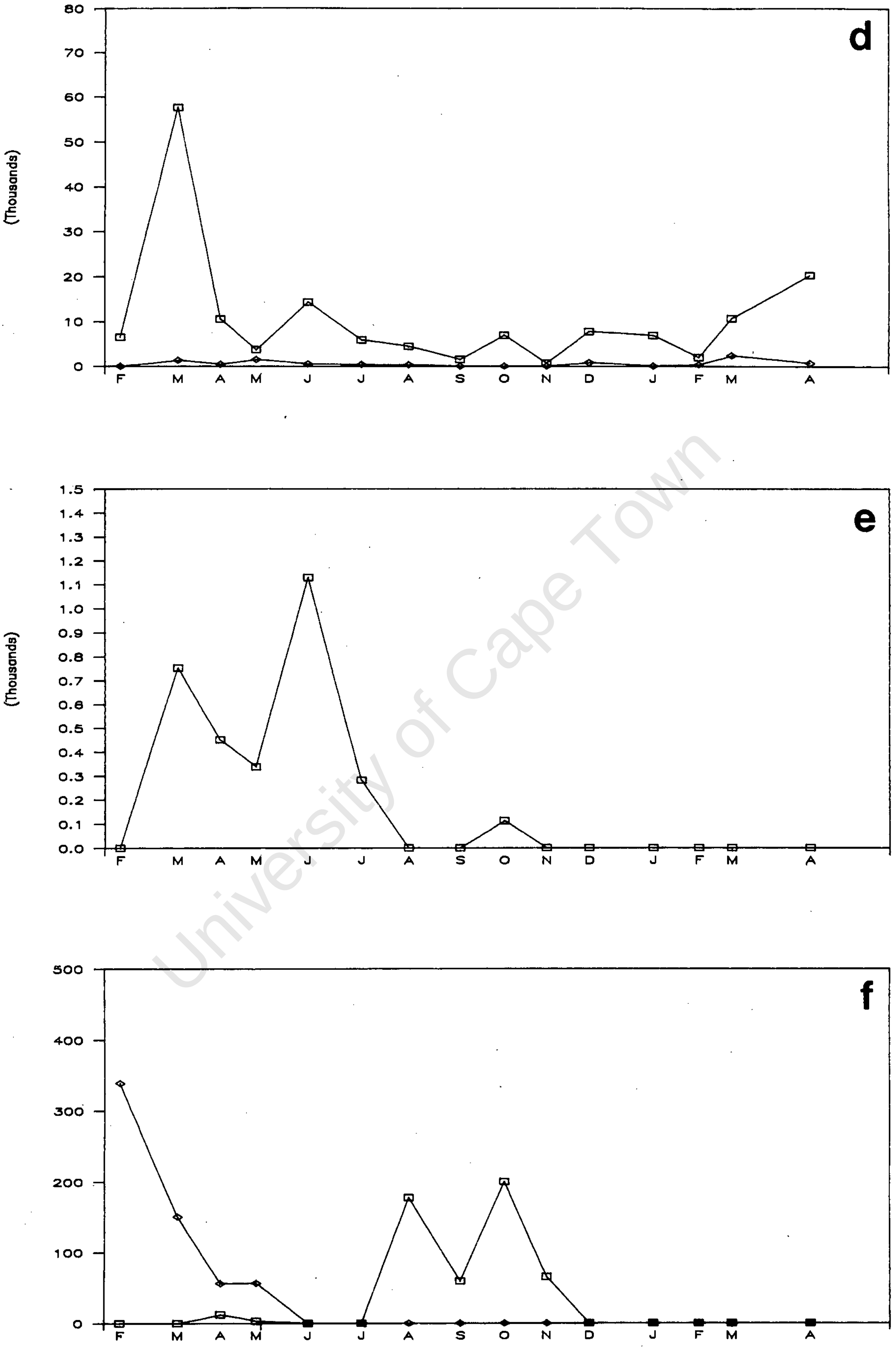


Figure 9.6 (cont.) Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Sirkelsvlei. (a) *Metadiaptomus capensis*, (b) *Lovenula simplex*, (c) *Brachionus plicatilis*, (d) *Gomphocythere expansa* (□) and *Sarscypridopsis glabrata* (◇), (e) Turbellaria, (f) *Daphnia hodgsoni* (□) and *Ilyocryptus sordidus* (◇).

few other vleis with waters of relatively high salinity. Numbers showed a small decrease in the winter months, an increase in early summer and even greater numbers in the late summer of the second year (fig. 9.6a). Changes in the population structure are difficult to interpret accurately (fig. 9.7), probably again as a result of sampling intervals being too widely spaced relative to turnover times. Ovigerous females were present as a relatively high percentage (5 ± 4%) throughout the year. Adult males (27 ± 7%) and adult non-gravid females (11 ± 7%) constituted a greater percentage of the population than they did of the *M. purcelli* populations.

Lovenula simplex occurred in relatively low numbers but, because it is large, it contributed significantly to zooplankton biomass. Seasonal variation is similar to that in *M.capensis* with a winter minimum in numbers and a spring to mid-summer maximum. In late summer there was a crash in numbers, with no *Lovenula* present in March and April of the second year (fig. 9.6b). The plot of population structure appears to show four marked pulses of reproduction (fig. 9.8). Higher proportions of ovigerous females precede four marked maxima in the proportion of copepodites in March, June, September and January with consequent decrease in the proportion of adult males and females. The average percentage of adult males (38 ± 20%) and non-gravid females (19 ± 12%) was even greater than for *M. capensis* populations.

The rotifer *Brachionus plicatilis* occurred in numbers two to three times greater than *M. capensis* in the two months of maximum numbers of the latter. It appeared in the mid to late summer of the second year corresponding to the crash in *Lovenula simplex* numbers (ie February, March and April) (fig. 9.6c).

The ostracod *Gomphocythere expansa* was found in relatively high numbers (greater than in the Grootvleis), throughout the year, with maximum numbers probably present in late summer (fig. 9.6d). Interestingly, it was not the smaller larval stages that madee up the numbers in the water column, but a generally greater or equal number of medium-sized to large individuals of this so-called benthic species. Greater numbers did however occur on or near the bottom sediments. *Sarscypridopsis glabrata*, was the only other ostracod to occur in any number. It appeared in the water column throughout most of the year, but was absent during spring and early summer and seemed most abundant during late summer and autumn (fig. 9.6d).

Turbellarians were present in similar numbers to *S.glabrata* from late summer to mid-winter, but apart from an odd occurrence in October, disappeared from the water column in later months (fig. 9.6e).

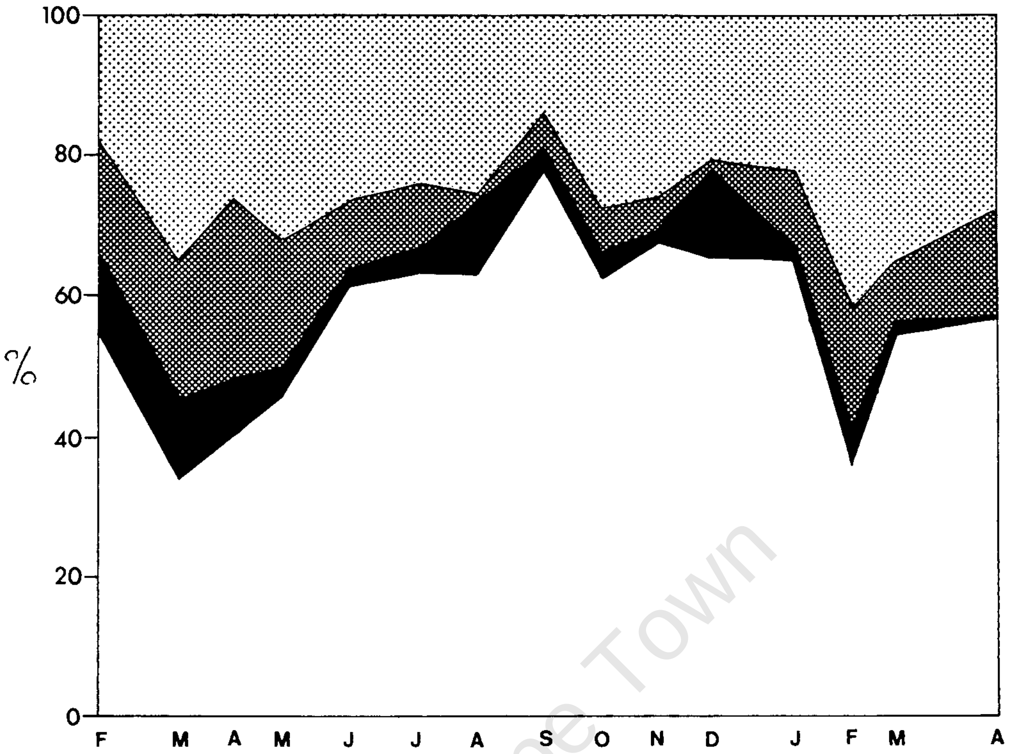


Figure 9.7 Seasonal variation in the population structure of *Metadiaptomus capensis* in Sirkelsvlei. [░]- adult males, [▓]- adult non-gravid females, [■]- adult gravid females, [□]- copepodites.

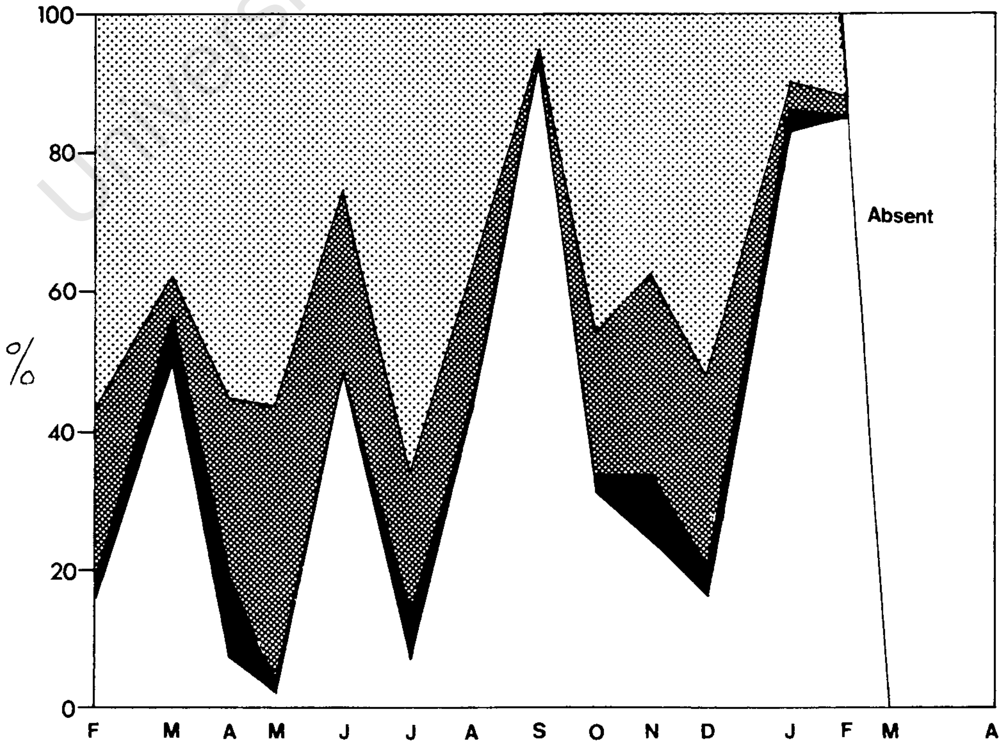


Figure 9.8 Seasonal variation in the population structure of *Lovenula simplex* in Sirkelsvlei. [░]- adult males, [▓]- adult non-gravid females, [■]- adult gravid females, [□]- copepodites.

The cladocerans were not well represented, with *Daphnia hodgsoni* present in small numbers from the end of winter to early summer and the benthic *Ilyocryptus sordidus* only found in late summer and autumn of the first year (fig. 9.6f). The absence of littoral vegetation may be part of the reason for the lack of Chydoridae.

Of the insects, *Anisops aglaia* was absent once again from mid-winter to early spring as well as occasionally during the warmer months. Numbers were lower than in Gillidam. The population from late spring to mid summer again consisted almost entirely of nymphs. Chironomids were present almost throughout the year ,but occurred in greatest numbers in the late summer of each year, as did the ostracods. Water mites were noticeably absent from the plankton.

Grootrondevlei

Total mean zooplankton abundance was similar to that of Gillidam (fig. 9.1~~5~~6). *Metadiaptomus purcelli* was the most abundant zooplankton species (over 80%) and occurred at a mean density similar to that in Gillidam. The range in abundance was far greater, though, with the maximum number almost twice as great and the minimum three times less. Numbers were lowest in winter, rising slowly to a peak in the late summer of each year (fig. 9.9a). Population structure (fig. 9.10) displays a series of maxima in the proportion of copepodites following increases in the percentage of ovigerous females. The very low proportions of copepodites in November and January correspond to a particularly low population abundance in both months. Adult males and non-gravid females were present as mean percentages of 12 ± 8% and 11 ± 7% respectively, constituting a greater proportion than in Gillidam.

Lovenula simplex was present in far lower numbers than in Sirkelsvlei. Abundance was lowest in winter and highest in autumn and spring/early summer. In the first year numbers were low in late summer and in the second year the population crashed at this time (fig. 9.9b). Population structure does not show the same distinctive pulses of reproduction as in Sirkelsvlei and is difficult to interpret accurately (fig. 9.11). The mean percentages of adult males and non-gravid females are 17 ± 12% and 9 ± 9% respectively, which are a lot lower than those in Sirkelsvlei.

Daphnid species were the most abundant zooplankters after *M.purcelli. Ceriodaphnia dubia* was present only in mid to late summer of the second year, but in March constituted almost 25% of the zooplankton numbers (fig. 9.9c). Three *Daphnia* species appeared at different times during the study period (fig. 9.6d).

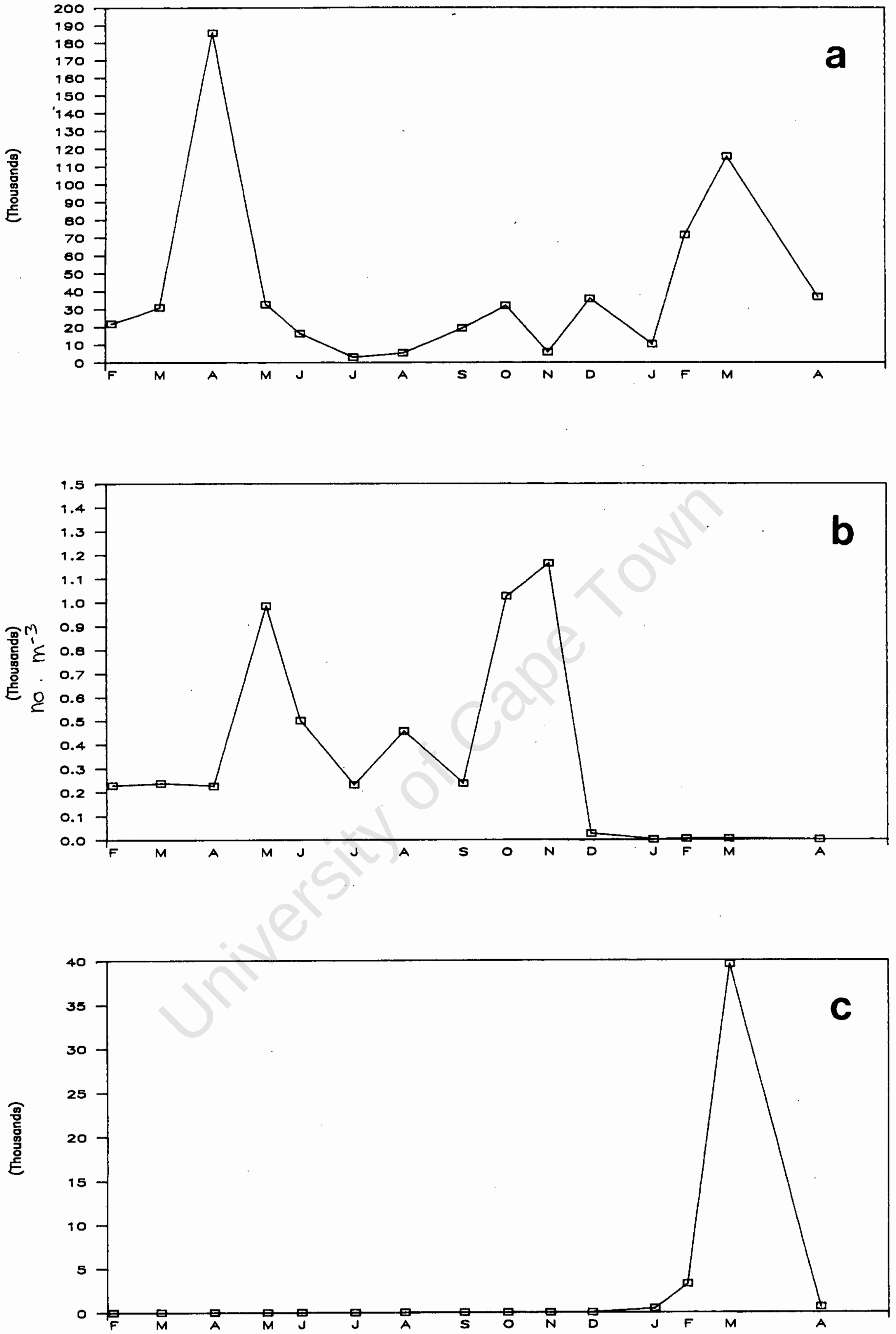


Figure 9.9 Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Grootrondevlei. (a) *Metadiaptomus purcelli*, (b) *Lovenula simplex*, (c) *Ceriodaphnia dubia*, (d) *Daphnia barbata* (□) *Daphnia laevis* (◇) and *Daphnia pulex* (△), (e) *Alona intermedia*, (f) *Gomphocythere expansa* (□).

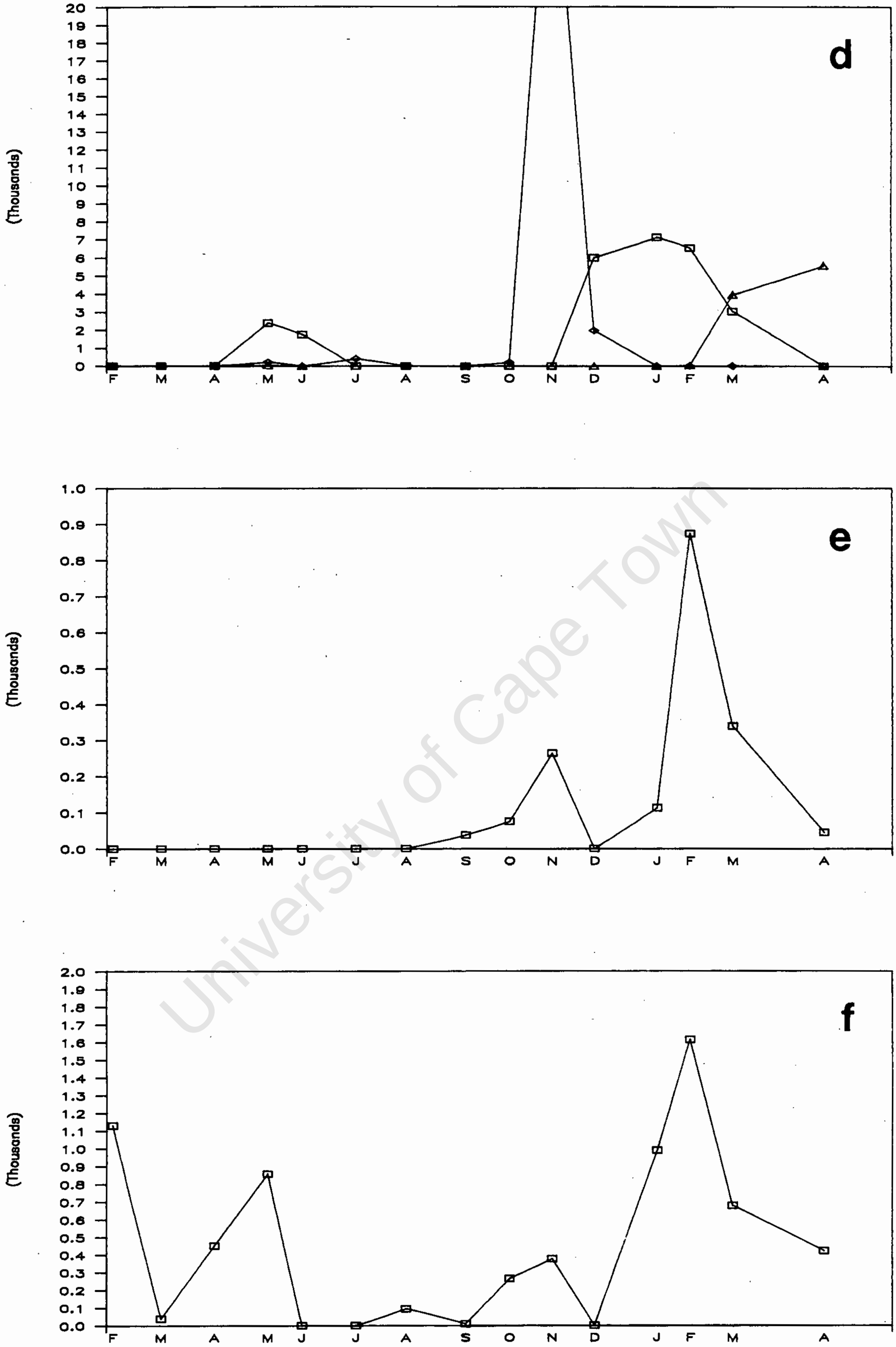


Figure 9.9 (cont.) Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Grootrondevlei. (a) *Metadiaptomus purcelli*, (b) *Lovenula simplex*, (c) *Ceriodaphnia dubia*, (d) *Daphnia barbata* (□) *Daphnia laevis* (◇) and *Daphnia pulex* (△), (e) *Alona intermedia*, (f) *Gomphocythere expansa* (□).

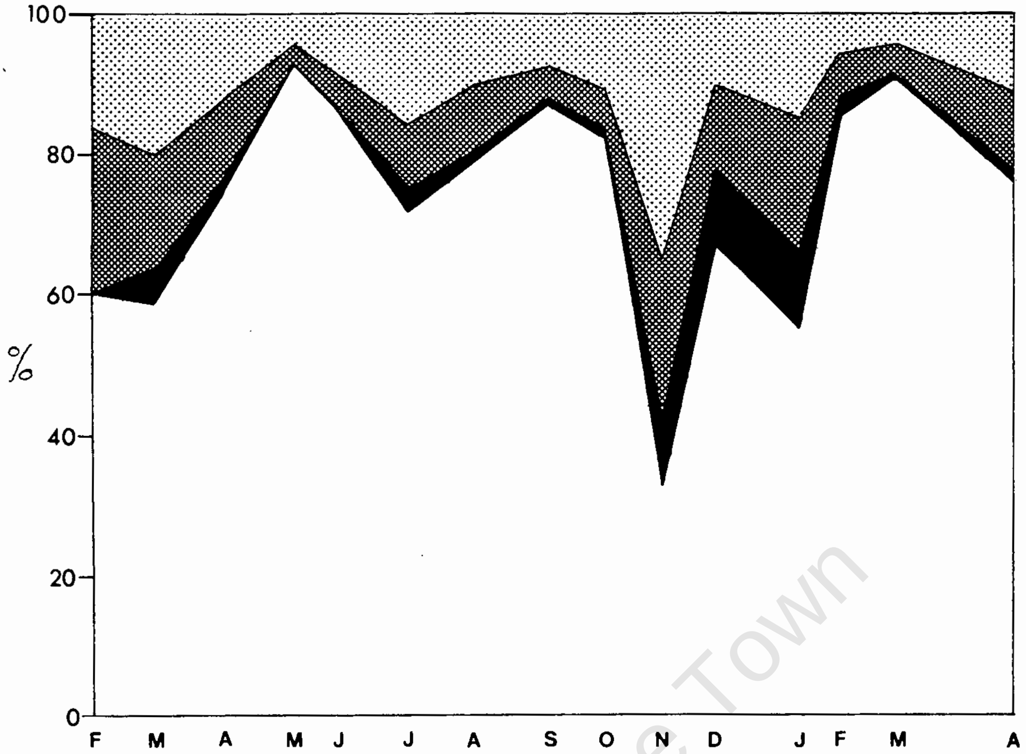


Figure 9.10 Seasonal variation in the population structure of *Metadiaptomus purcelli* in Grootrondevlei. [░]- adult males, [▓]- adult non-gravid females, [■]- adult gravid females, [□]- copepodites.

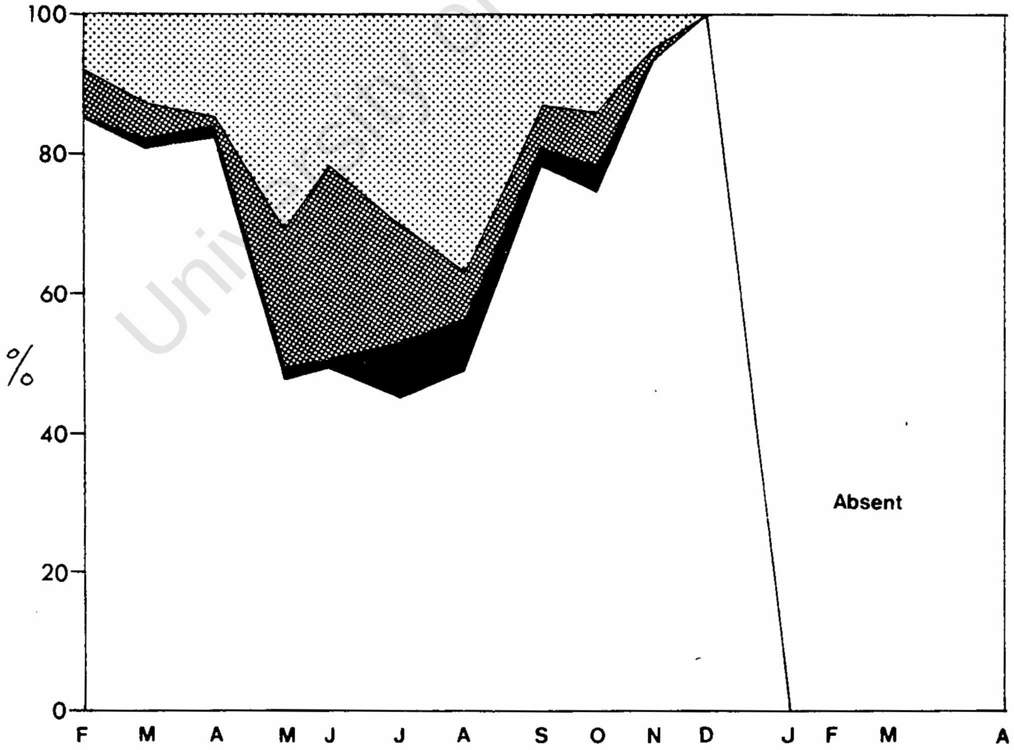


Figure 9.11 Seasonal variation in the population structure of *Lovenula simplex* in Grootrondevlei. [░]- adult males, [▓]- adult non-gravid females, [■]- adult gravid females, [□]- copepodites.

Daphnia barbata occurred from autumn to early winter of the first year, with a small number of *D.laevis* in two of the months and an odd occurrence of *D.pulex*. During mid winter and much of spring almost no *Daphnia* were present, but in late spring/early summer a short pulse of *D.laevis* appeared; in November it constituted over 80% of the total zooplankton abundance. *D.barbata* succeeded *D.laevis* lasting through most of summer and constituting at most 37% of the total zooplankton (January). *D.barbata* was in turn succeeded by *D.pulex* from late summer through to autumn.

An interesting feature of the *Daphnia* populations was the high percentage of helmeted individuals. Nobel and Schaefer (1967) note that the head of *D.barbata* may be rounded or pointed and Seaman and Kok (in press) state that the head is usually pointed antero-dorsally. The populations of *D.barbata* in Grootrondevlei all appear to have pointed heads and these individuals were in fact assumed to be cyclomorphs until the *Daphnia* were identified to species level. Young *D.laevis* were also found to possess pointed heads. The possession of helmets thus appears to be a species trait and not true cyclomorphosis, and the statement of Seaman and Kok (in press) that 'no true cyclomorphosis, where individuals of a population change form throughout a season, has been found in South Africa', appears in this case to hold true.

The chydorid *Alona* gr. *intermedia* was present only in Grootrondevlei from spring until autumn (fig. 9.9e), while the other two chydorids, *Chydorus* gr. *sphaericus* and *Alona* gr. *karua*, were each found in small numbers in a single month during the study period.

Gomphocythere expansa was once again present in significant numbers almost throughout the year. Greatest numbers occurred in mid to late summer of both years and lowest numbers during the winter months (fig. 9.9f). In contrast to Sirkelsvlei, the *Gomphocythere* were almost all small- to medium-sized larvae. Of the other ostracods, *Parastenocypris pardalis* was present in small numbers in the late summer of each year and a few individuals of *Sarscypridopsis glabrata* and *S.elizabethae* were encountered in mid summer.

Various water mites (spp. X) were occasionally present in the water column, but not the same forms as found in Suurdam and Gillidam. Of the insects, *Anisops aglaia* was absent from both the Grootvleis, chironomid larvae were present in small numbers throughout the year, and dytiscid larvae and proturans were occasionally present.

The cyclopoid *Microcyclops crassipes* was present through most of the year in even lower numbers than in Gillidam, occurring in reasonable numbers only in late summer and autumn of each year. *Paracyclops poppei* and *Tropocyclops prasinus* were found in small numbers in February of the second year, and the cladoceran *Diaphanosoma perarmatum* in small numbers in March of the second year. These three species are probably closely associated with the littoral.

Grootwitvlei

The total zooplankton abundance in Grootwitvlei was high relative to that of the other vleis (fig. 9.1~~5~~6). *Metadiaptomus purcelli* made up over 80% of the total zooplankton numbers, as in Gillidam and Grootrondevlei, but the average numbers of *M.purcelli* were almost double those in Gillidam and Grootrondevlei. The range in numbers was also much greater, from a low of 1288 m^{-3} to a high of 205 481. Seasonal variation was similar to that in Gillidam, with greatest numbers occurring in late winter to spring and high numbers also occurring in autumn (fig. 9.12a). Seasonality was not as distinct as in the other vleis, probably due to some influence of horizontal patchiness effects, resulting from the more pronounced heterogeneity of the vlei basin. Various samples analysed from other stations in the vlei agreed with the basic trends, but showed the "spring" peak present from mid-winter. The apparently contradictory trend shown in the variation of population structure (fig. 9.13), where a pulse of nauplii (in autumn/early winter) precedes a high proportion of ovigerous females and low proportion of copepodites, can be explained by the mid-winter population maximum in contrast to the delayed local maximum (spring) in fig. 9.12a. The population structure diagram confirms a major population maximum over the broad period of mid-winter to spring as well as indicating a number of smaller population pulses. The percentages of adult males and non-gravid females were 13 ± 10% and 5 ± 5% respectively, similar to those of Gillidam and Grootrondevlei. *Lovenula simplex* was absent, but *Microcyclops crassipes* was present in very low numbers with a slight peak from late summer to autumn (as in Grootrondevlei). The harpacticoid *Bryocamptus* sp. was found in the water column in low numbers from late autumn to early winter and in spring (fig. 9.12g).

The zooplankter with the highest average numbers after *M.purcelli* was the cladoceran, *Moina micrura* which although it was present in only four months of the study period reached a very high abundance (almost 50% of the total zooplankton number in April) (fig. 9.12b). *Chydorus* gr. *sphaericus* was present in low numbers through most of the summer months but increased in the autumn of each year, particularly in the second (fig.9.12c). *Macrothrix* near *goeldi* occurred from mid-

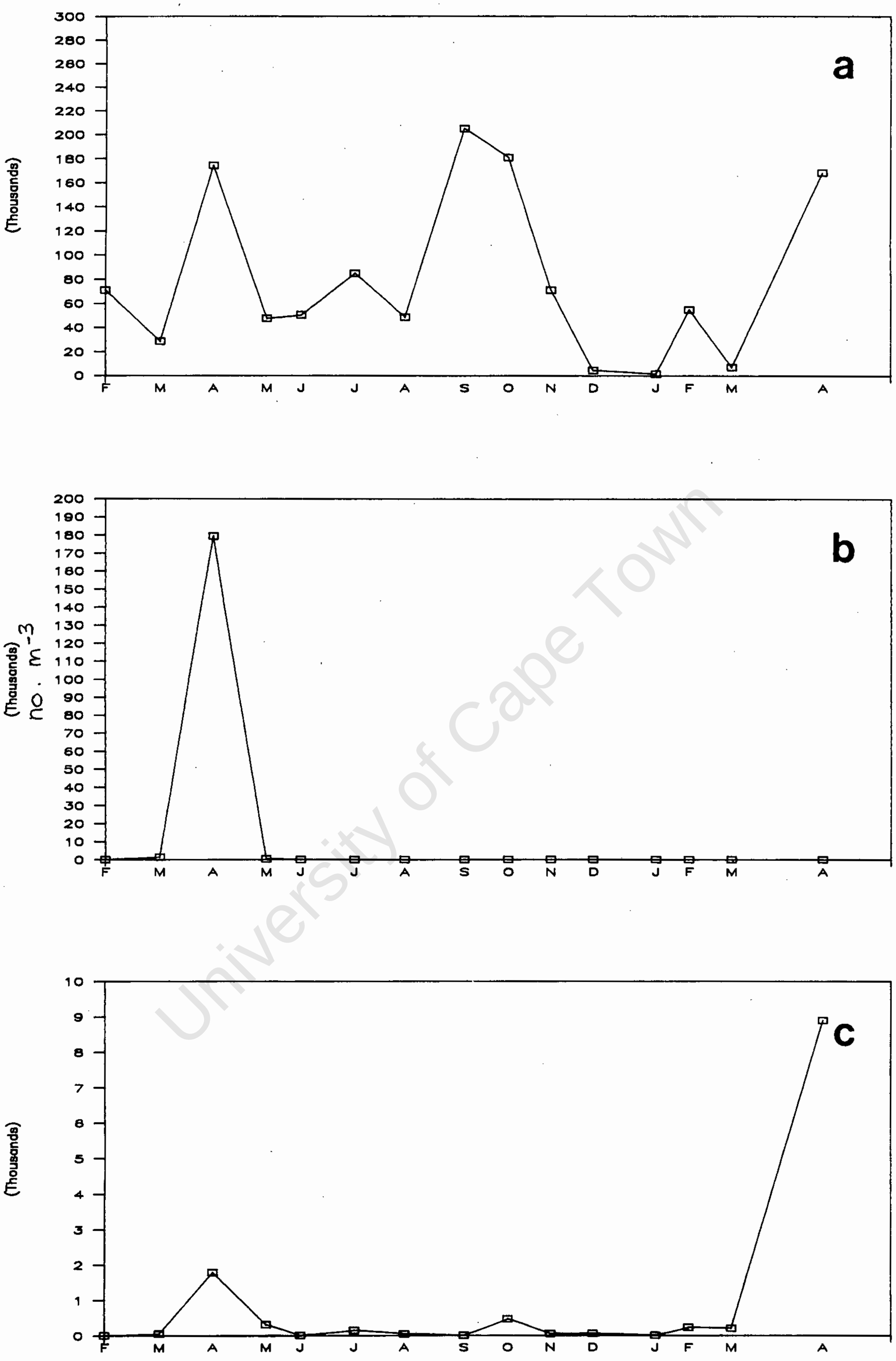


Figure 9.12 Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Grootwitvlei. (a) *Metadiaptomus purcelli*, (b) *Moina micrura*, (c) *Chydorus* gr. *sphaericus*, (d) *Macrothrix* near *goeldi*, (e) *Gomphocythere expansa*, (f) *Sarscypridopsis* and *Potamocypris* (□) and *Parastenocypris pardalis* (◇), (g) *Bryocamptus* sp., (h) *Ilyocryptus sordidus*, (i) Hydracarina, (j) *Brachionus calyciflorus* (□) and *B.rubens* (◇), (k) *Galaxias zebratus* juveniles.

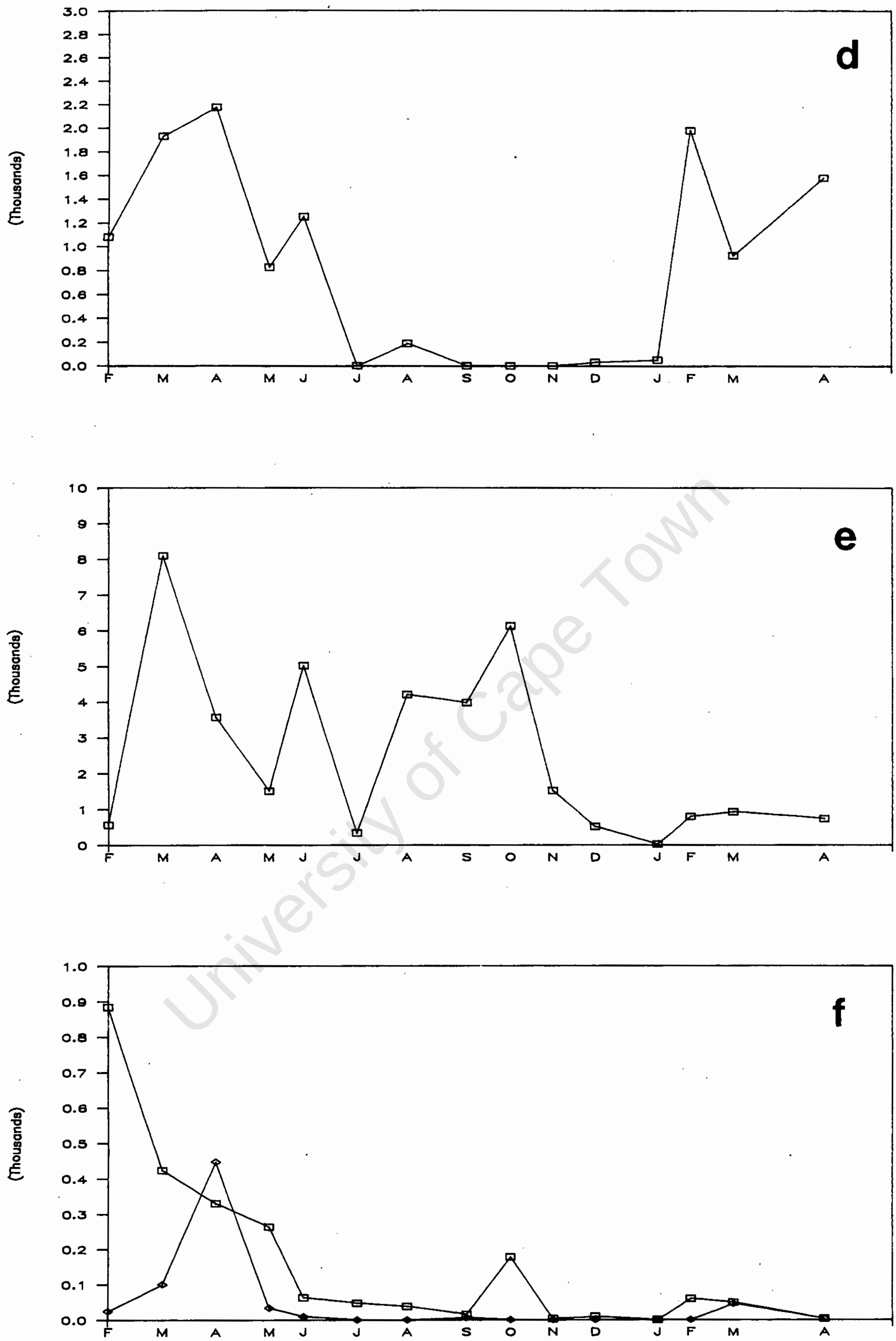


Figure 9.12 (cont.) Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Grootwitvlei. (a) *Metadiaptomus purcelli*, (b) *Moina micrura*, (c) *Chydorus* gr. *sphaericus*, (d) *Macrothrix* near *goeldi*, (e) *Gomphocythere expansa*, (f) *Sarscypridopsis* and *Potamocypris* (□) and *Parastenocypris pardalis* (◇), (g) *Bryocamptus* sp., (h) *Ilyocryptus sordidus*, (i) Hydracarina, (j) *Brachionus calyciflorus* (□) and *B.rubens* (◇), (k) *Galaxias zebratus* juveniles.

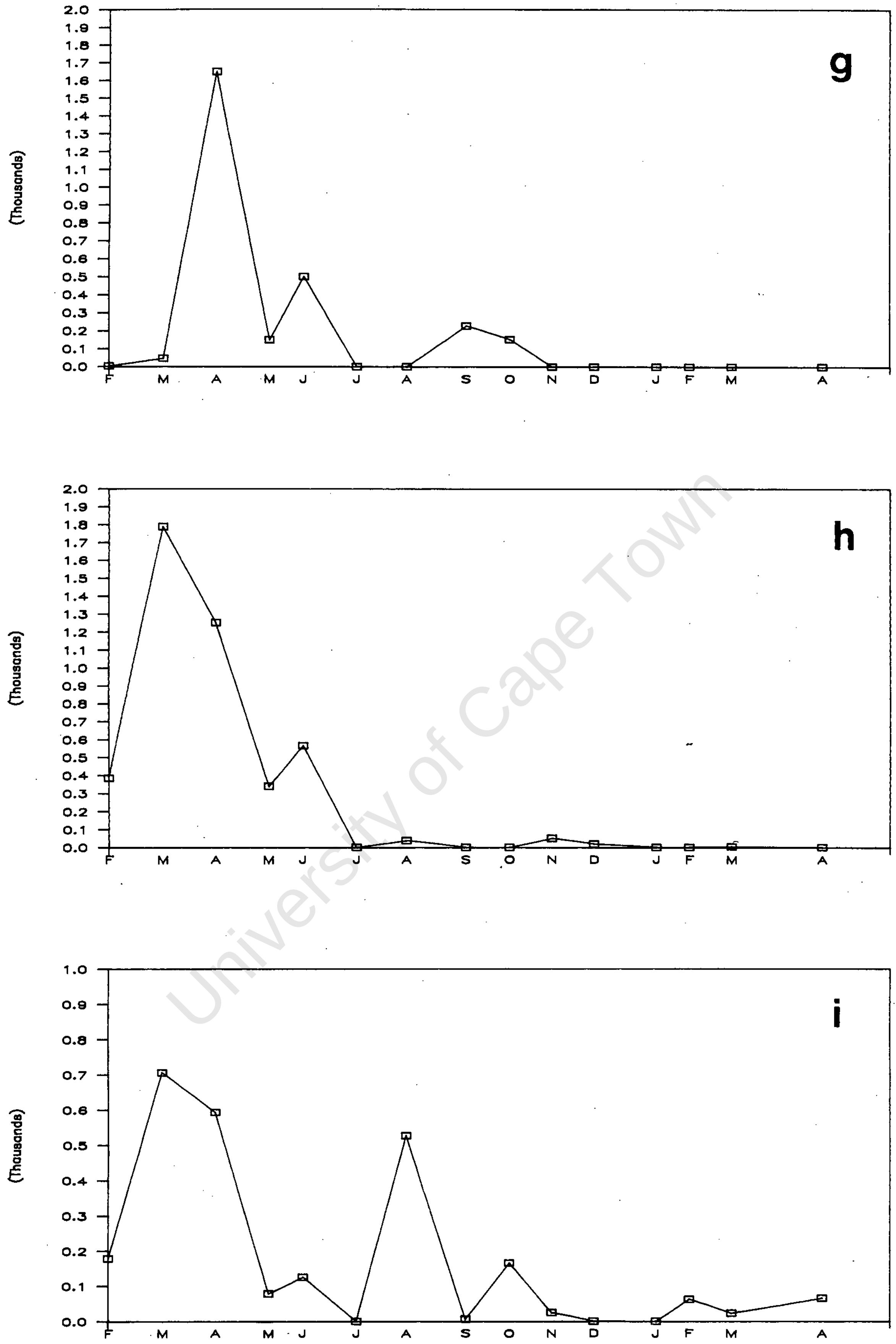


Figure 9.12 (cont.) Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Grootwitvlei. (a) *Metadiaptomus purcelli*, (b) *Moina micrura*, (c) *Chydorus* gr. *sphaericus*, (d) *Macrothrix* near *goeldi*, (e) *Gomphocythere expansa*, (f) *Sarscypridopsis* and *Potamocypris* (□) and *Parastenocypris pardalis* (◇), (g) *Bryocamptus* sp., (h) *Ilyocryptus sordidus*, (i) Hydracarina, (j) *Brachionus calyciflorus* (□) and *B.rubens* (◇), (k) *Galaxias zebratus* juveniles.

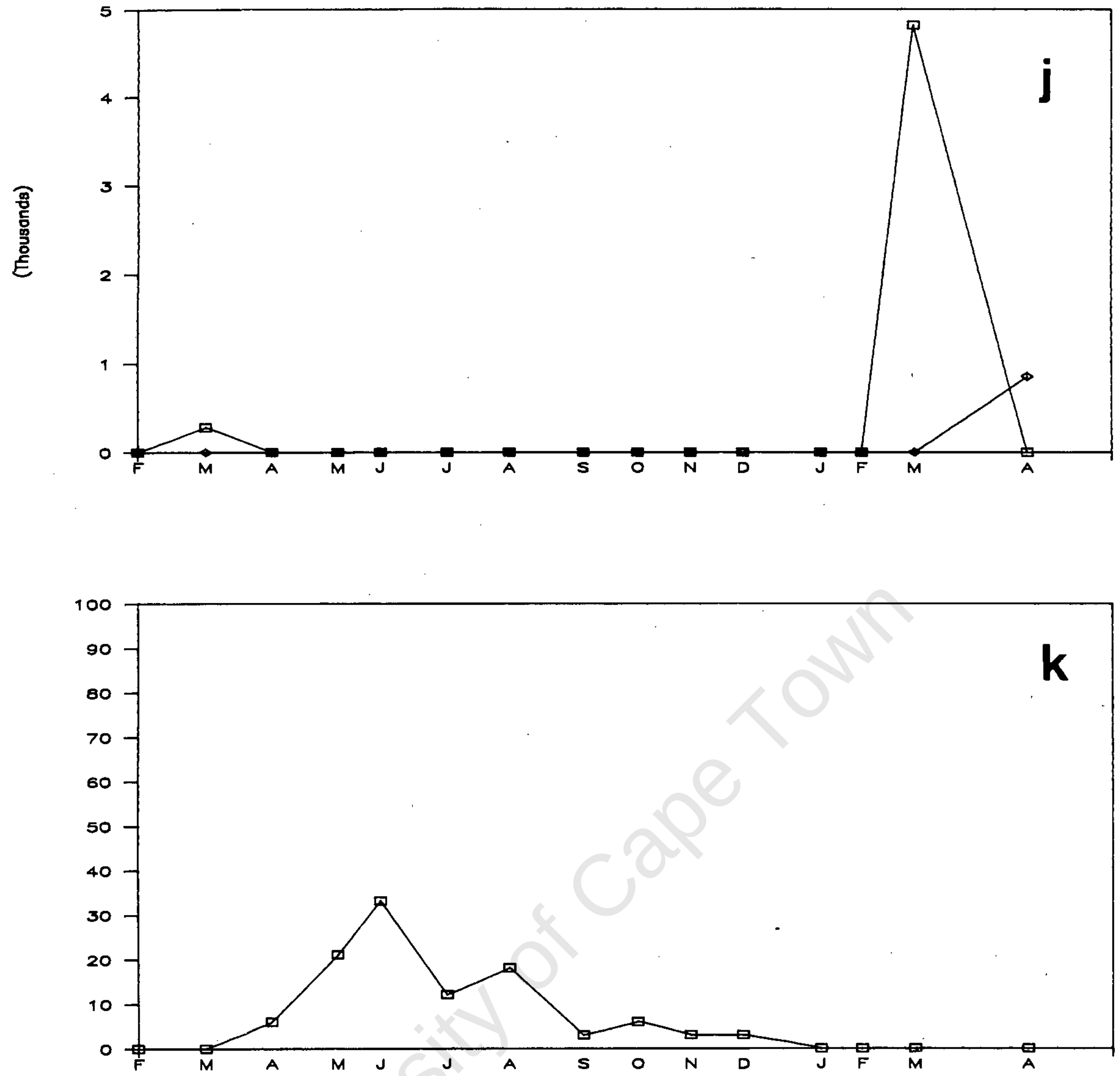


Figure 9.12 (cont.) Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Grootwitvlei. (a) *Metadiaptomus purcelli*, (b) *Moina micrura*, (c) *Chydorus* gr. *sphaericus*, (d) *Macrothrix* near *goeldi*, (e) *Gomphocythere expansa*, (f) *Sarscypridopsis* and *Potamocypris* (□) and *Parastenocypris pardalis* (◇), (g) *Bryocamptus* sp., (h) *Ilyocryptus sordidus*, (i) Hydracarina, (j) *Brachionus calyciflorus* (□) and *B.rubens* (◇), (k) *Galaxias zebratus* juveniles.

summer through to mid-winter of each year but was uncommon in the water column in spring and early summer (fig. 9.12d). The benthic macrothricid *Ilyocryptus sordidus* also appeared in the water column at the end of summer through to autumn of the first year, but never in the same numbers as the above.

Gomphocythere expansa was on average the third most numerous species in the zooplankton. It was present throughout the year, but was least abundant in the middle summer months (fig. 9.12e). Almost all the *Gomphocythere* were small- to medium-sized larvae but, in contrast to Grootrondevlei some adults were found. *Parastenocypris pardalis* occurred only in small numbers, but is a particularly large ostracod and therefore significant in biomass. It was found only in the open water in late summer to autumn of each year. Various other *Sarscypridopsis* and *Potamocypris* species occurred in small numbers at different times in the year (fig. 9.12f).

The rotifers *Brachionus calyciflorus* and *Brachionus rubens,* did not occur in the same very high numbers as rotifers found in Sirkelsvlei and Rondevlei. Seasonal variation was very marked, with populations appearing only briefly in the late summer of both years (fig. 9.12j). Water mites were present most months in similar magnitudes of abundance to Suurdam and Gillidam (fig. 9.12i). As noted in Grootrondevlei, *Anisops aglaia* was absent as were chironomid and dysticid larvae, while hydroptilid larvae were present occasionally in small numbers.

An interesting addition to the plankton were juveniles of the fish *Galaxias zebratus*. These were present in relatively small numbers but displayed a distinct seasonality, appearing in greatest abundance in autumn and early winter; they were absent from the plankton in summer (fig. 9.12k).

Rondevlei

Rondevlei had by far the greatest total mean zooplankton abundance of the six vleis (fig. 9.1~~5~~6). The dominant zooplankter was the cyclopoid *Thermocyclops oblongatus*, although the two rotifer species also occurred in high numbers. The numbers were considerably greater than those of the dominant copepod species of the other vleis, the mean abundance being more than twice as great as that of *M.purcelli* in Grootwitvlei. Numbers showed maxima in autumn to early winter and in spring/early summer (fig. 9.14a). The population shows a number of apparent pulses in reproduction (fig. 9.15). A high proportion of ovigerous females and an increasing proportion of nauplii precede the spring/early summer population maximum. Other changes, however, are less easy to interpret. An interesting

Figure 9.13 Seasonal variation in the population structure of *Metadiaptomus purcelli* in Grootwitvlei. [░]-adult males, [▓]- adult non-gravid females, [■]- adult gravid females, [☐]- copepodites, [░]- nauplii.

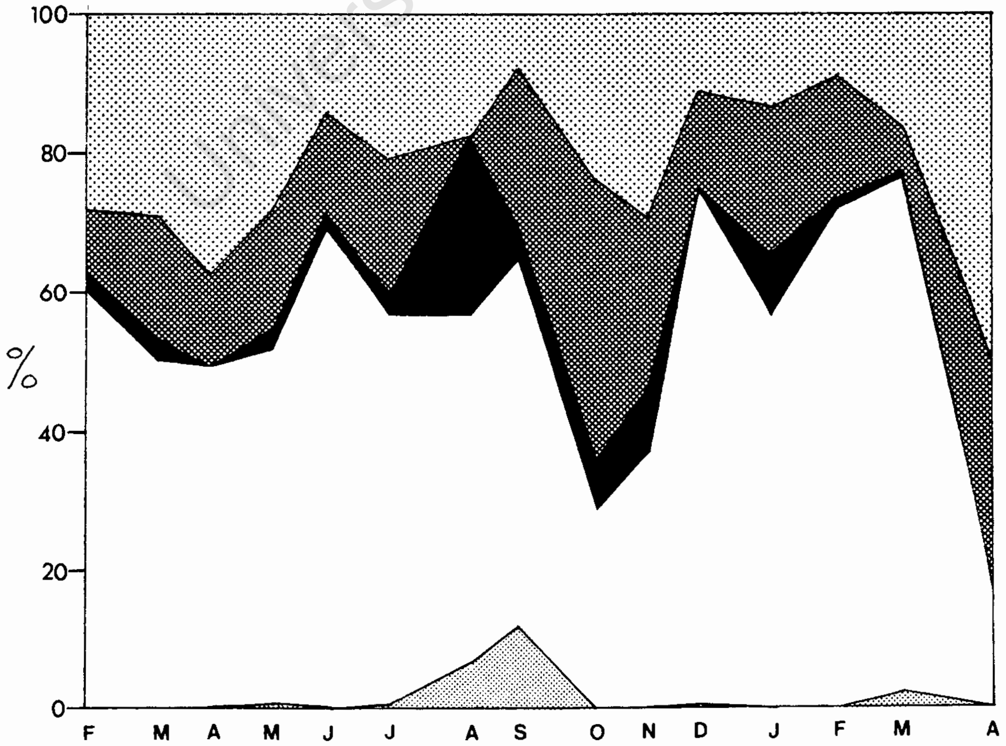


Figure 9.15 Seasonal variation in the population structure of *Thermocyclops oblongatus* in Rondevlei. [░]- adult males, [▓]- adult non-gravid females, [■]- adult gravid females, [☐]- copepodites, [░]- nauplii.

feature is the low percentage of copepodites during the population maxima, particularly in the spring/early summer maximum. The mean percentage of adult males (22 ± 12%) and non-gravid females (18 ± 10%) was also greater than in the other dominant copepod species. A harpacticoid species yet again contributed to zooplankton community numbers for a few months of the years (fig. 9.14b).

The rotifers *Brachionus calyciflorus* and *B. rubens* occurred in very high numbers through most of the study period. Greatest abundance appeared to be in very late summer, with high numbers also in late winter to spring. Lowest numbers occurred in early to mid summer (fig. 9.14c).

The next most abundant zooplankter was the cladoceran *Ceriodaphnia cornuta*. The species was always present in the zooplankton. Population maxima occurred in late summer to autumn of the first year and mid to late summer of the second year. Lowest numbers occurred during winter and spring. A different species of *Ceriodaphnia*, *C.reticulata*, appeared in similar numbers in September, but was absent the rest of the year (fig.9.14d). *Moina micrura* was present in slightly lower numbers than *C. cornuta*, but with a very similar seasonal variation in abundance ie. late summer maxima and a winter through spring minimum (fig.9.14d). *Daphnia pulex* occurred from late winter to early summer, while *D.obtusa* occurred only in September (fig. 9.14f). Numbers of both, when present, were similar to those of *C.cornuta* and *M.micrura*, yet appear to be separated in time from the latter two species. J Green (pers.comm.) comments on the co-occurrence of *D.pulex* and *D.obtusa* as being unusual. *Chydorus* gr. *sphaericus* also appeared in high numbers in the open water, in the months immediately preceding the maximum in *Daphnia* numbers (late winter-early spring)(fig.9.14g). The remaining cladoceran species did not occur in very large numbers in the open water. *Macrothrix spinosa* was found in reasonably high numbers from late summer to early winter of the first year (fig.9.14k) and *Alona* near *harpularia* and *Pleuroxus* gr. *aduncus* occurred somewhat more abundantly than the rest.

Amongst the Ostracoda, *Gomphocythere obtusata* replaces *G.expansa* of the other vleis, although in much lower numbers than in Sirkelsvlei or Grootwitvlei. Medium-sized larvae were the most common form and some adults were encountered; very few small larvae were found. The species was absent in the winter months (fig. 9.14h). A number of *Sarscypridopsis* species were present, making up in total a significant number of individuals (fig. 9.14i). None of the *Potamocypris* species encountered in Grootwitvlei were found in Rondevlei.

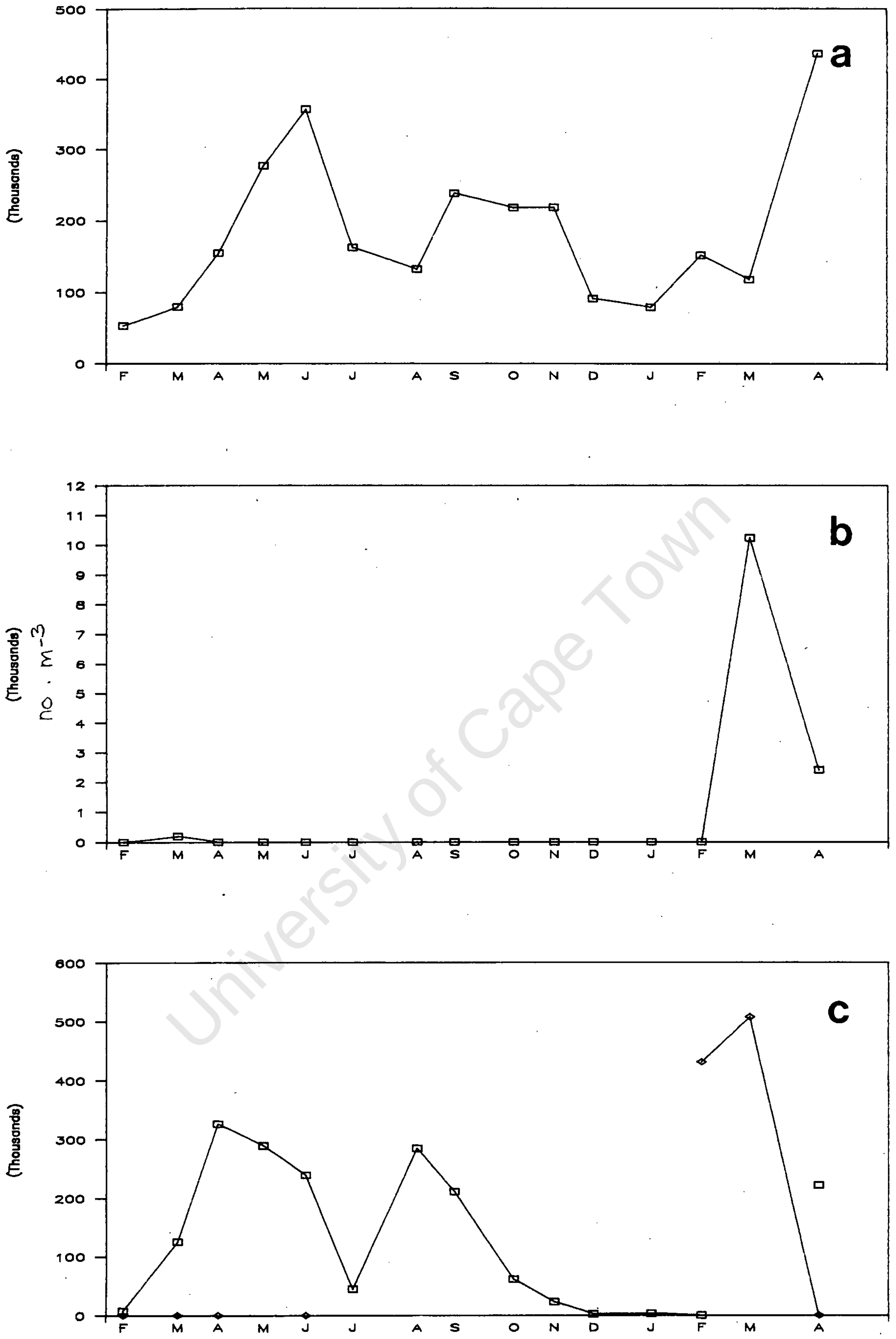


Figure 9.14 Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Rondevlei. (a) *Thermocyclops oblongatus*, (b) *Attheyella* sp., (c) *Brachionus calyciflorus* (□) and *B.rubens* (◇), (d) *Ceriodaphnia cornuta* (□) and *C. reticulata* (◇), (e) *Moina micrura*, (f) *Daphnia pulex* (□) and *D.obtusa* (◇), (g) *Chydorus* gr. *sphaericus*, (h) *Gomphocythere obtusata*, (i) *Sarscypridopsis* spp., (j) *Anisops aglaia* (□) and *Micronecta winifreda* (◇), (k) *Macrothrix spinosa* (□) and *M.hirsuticornis* (◇).

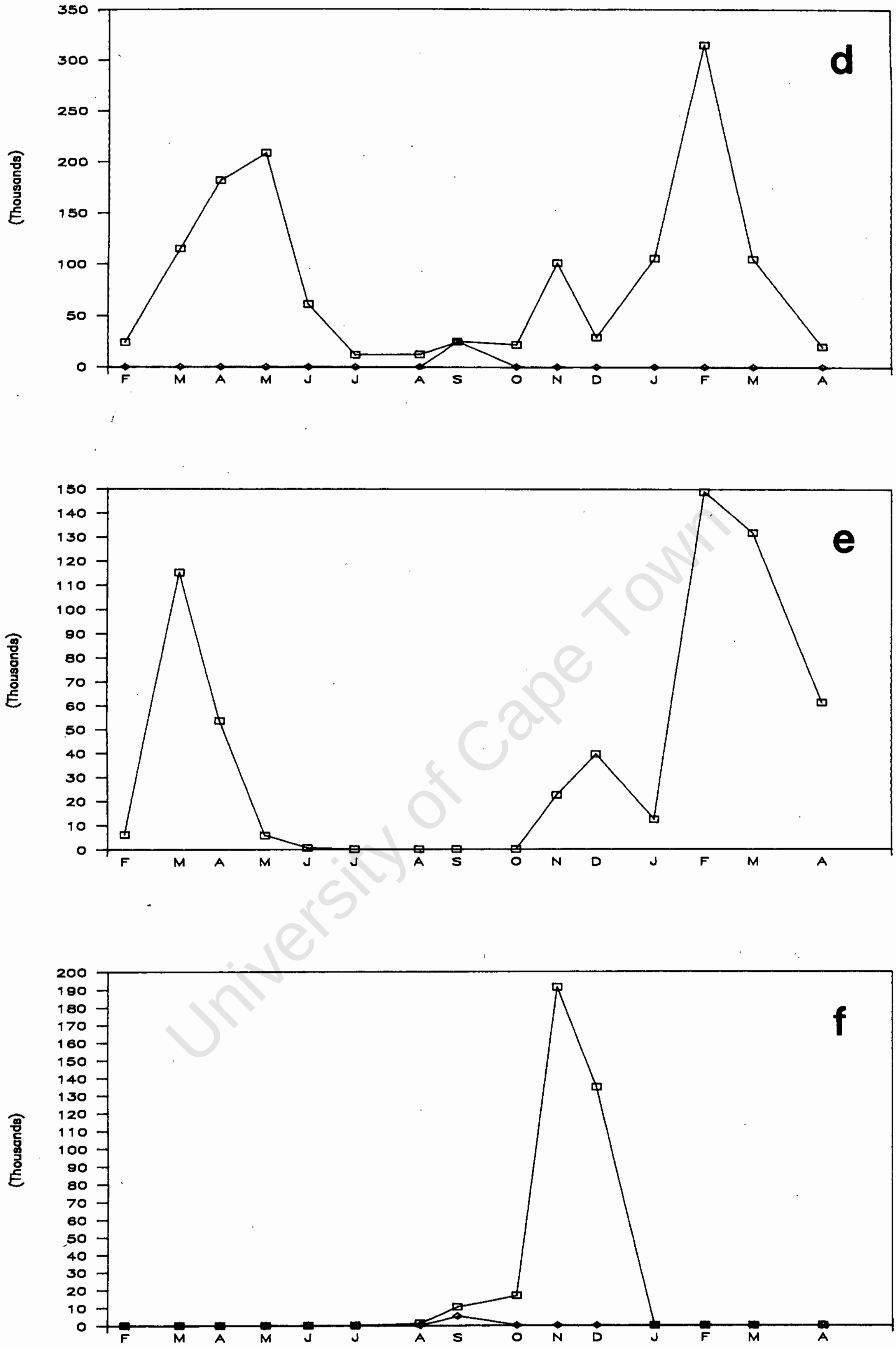


Figure 9.14 (cont.) Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Rondevlei. (a) *Thermocyclops oblongatus*, (b) *Attheyella* sp., (c) *Brachionus calyciflorus* (□) and *B.rubens* (◇), (d) *Ceriodaphnia cornuta* (□) and *C. reticulata* (◇), (e) *Moina micrura*, (f) *Daphnia pulex* (□) and *D.obtusa* (◇), (g) *Chydorus gr. sphaericus*, (h) *Gomphocythere obtusata*, (i) *Sarscypridopsis* spp., (j) *Anisops aglaia* (□) and *Micronecta winifreda* (◇), (k) *Macrothrix spinosa* (□) and *M.hirsuticornis* (◇).

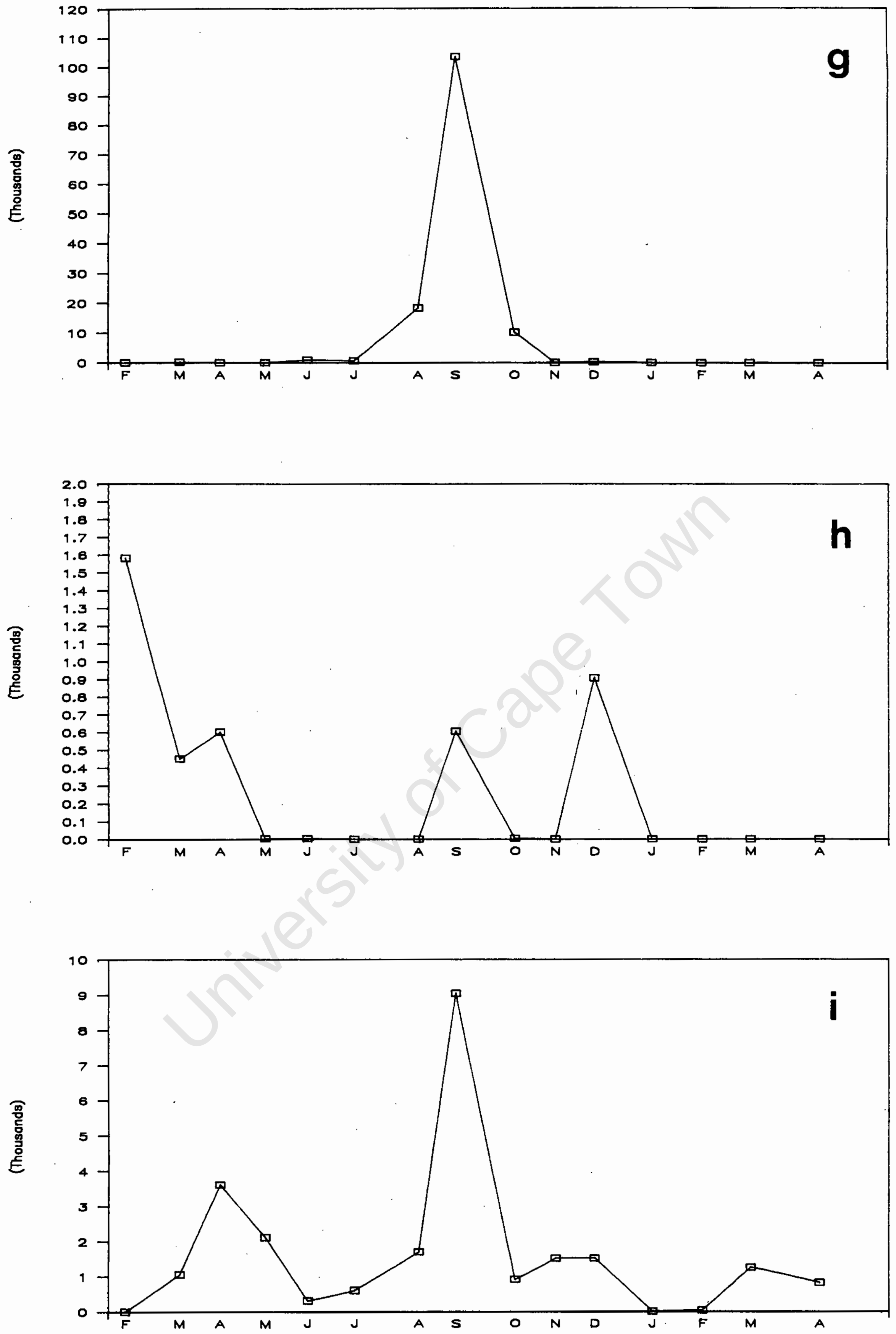


Figure 9.14 (cont.) Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Rondevlei. (a) *Thermocyclops oblongatus*, (b) *Attheyella* sp., (c) *Brachionus calyciflorus* (□) and *B.rubens* (◇), (d) *Ceriodaphnia cornuta* (□) and *C. reticulata* (◇), (e) *Moina micrura*, (f) *Daphnia pulex* (□) and *D.obtusa* (◇), (g) *Chydorus* gr. *sphaericus*, (h) *Gomphocythere obtusata*, (i) *Sarscypridopsis* spp., (j) *Anisops aglaia* (□) and *Micronecta winifreda* (◇), (k) *Macrothrix spinosa* (□) and *M.hirsuticornis* (◇).

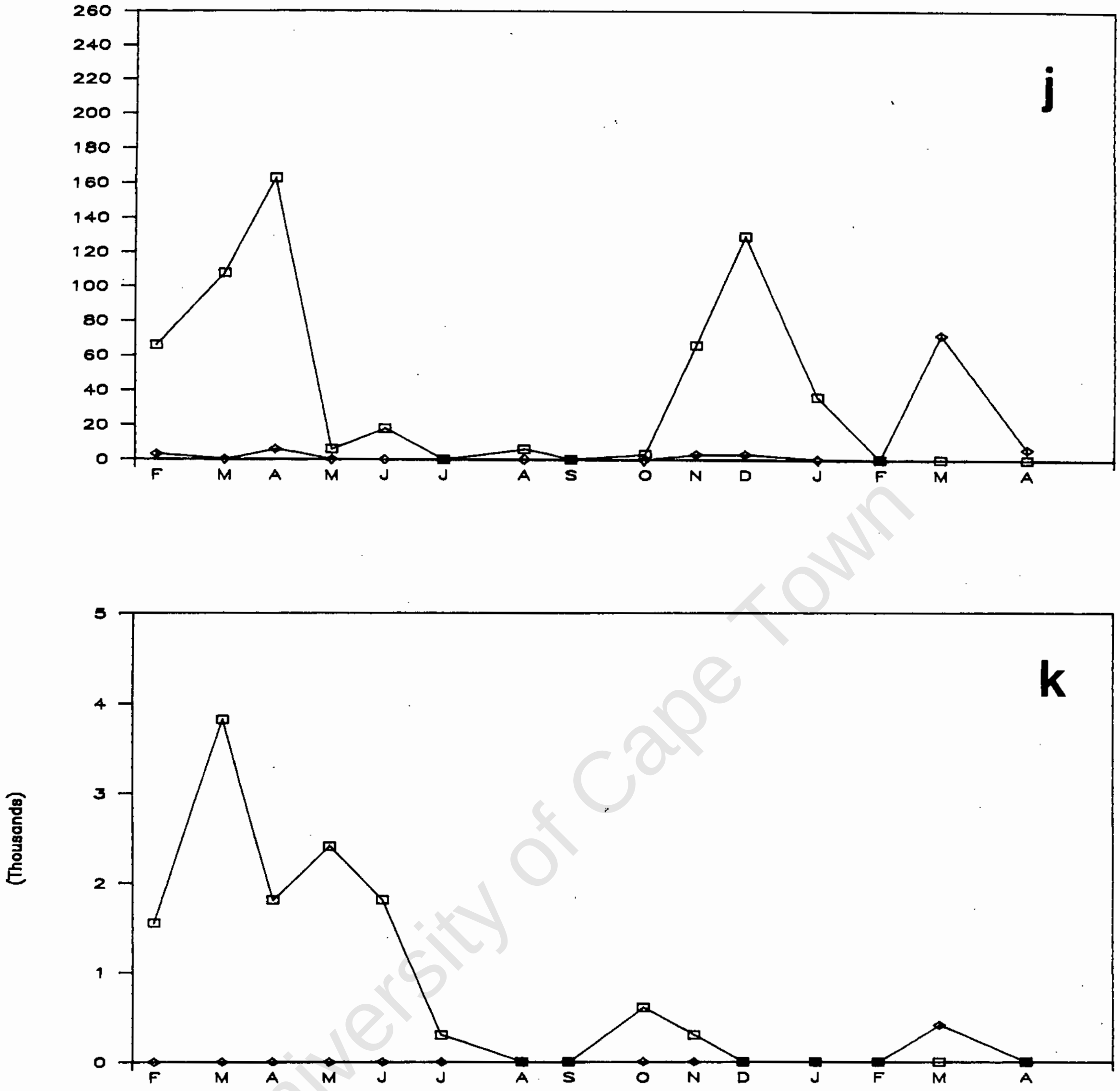


Figure 9.14 (cont.) Seasonal variation in the abundance (number.m^{-3}) of the major taxa constituting the zooplankton in Rondevlei. (a) *Thermocyclops oblongatus*, (b) *Attheyella* sp., (c) *Brachionus calyciflorus* (□) and *B.rubens* (◇), (d) *Ceriodaphnia cornuta* (□) and *C. reticulata* (◇), (e) *Moina micrura*, (f) *Daphnia pulex* (□) and *D.obtusa* (◇), (g) *Chydorus* gr. *sphaericus*, (h) *Gomphocythere obtusata*, (i) *Sarscypridopsis* spp., (j) *Anisops aglaia* (□) and *Micronecta winifreda* (◇), (k) *Macrothrix spinosa* (□) and *M.hirsuticornis* (◇).

The notonectid *Anisops aglaia* was present in Rondevlei in greater numbers than in the Cape Point vleis and was also all but absent in the winter and spring months, with nymphs first appearing in early summer and reaching maturity in the mid to late summer months. The corixid *Micronecta winifreda* was found in small numbers during the summer months (Fig 9.14j) and the pleid, *Plea pullala*, was encountered only in March of the second year, in small numbers ~~(fig. 9.14j)~~. Water mites were entirely absent. Chironomids and pschodids both occurred in only a few months of the year, while some collembolans, turbellarians and nematodes were occasionally present.

THE EFFECT OF PHYSICAL, CHEMICAL AND BIOLOGICAL VARIABLES

The zooplankton normally responds quickly to changes in the limnetic environment and thus the community composition at any moment in time is the net result of a complex of interactions with abiotic and biotic variables. Rates of turnover are fairly rapid and lag periods between the change in a variable and the population response are not expected to be much greater than one to a few weeks for most species (see Introduction). Amongst other things the period of lag should be a function of the rate of change of the variable, the absolute and relative magnitude (or concentration) of the variable and the state of the responding population. Underlying the effects of the less predictable variables driving change in community composition and abundance, is a seasonality marked by temperature change and linked to phytoplankton periodicity. The amplitude of this seasonality tends to increase, albeit inconsistently, with latitude (Hart 1985). A matrix of Pearson product-moment correlation coefficients was calculated between species present in significant numbers (generally those recorded in numbers greater than 'present', see tables 9.1-9.6) in more than one month of the study period and ten major physical, chemical and biological variables (table 9.7). With a sampling interval of one month, no account was taken of lag. Wind strength (resulting in mixing) is commented on as a separate variable. The use of correlation coefficients obviously only identifies master variables with overriding influences on population dynamics throughout the year. The short-term influences of variables, especially short term 'cues', may not be obvious, but an attempt is made here to identify most effects on the taxa. This section thus attempts to explain seasonal variation in relation to the changing limnetic environment (intra-lake variation) and the section that follows attempts to relate species diversity and community structure to inter-lake differences in the limnetic environment.

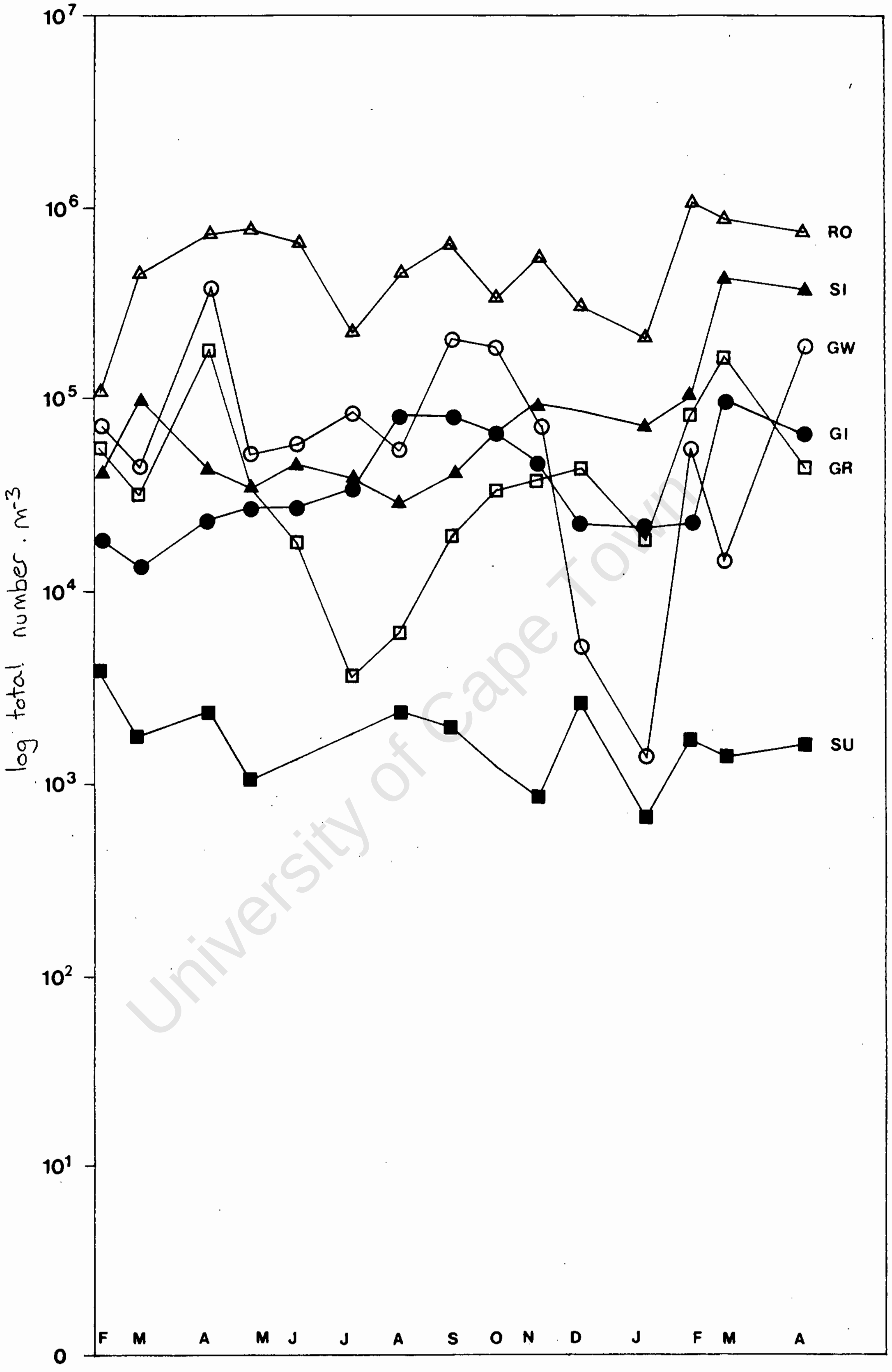


Figure 9.16 Seasonal variation in total zooplankton abundance in each of the studied vleis. Suurdam (■), Gillidam (●), Sirkelsvlei (▲), Grootrondevlei (□), Grootwitvlei (○) and Rondevlei (△). Abundance as log total number.m^{-3}.

SUURDAM		COND	PH	ACID	F-C	COL	A_{250}	E_2/E_3	DEP	TMP	CHL
Cyclopoida	*Microcyclops crassipes*	•	•	•	•	•	•	•	•	•	•
Harpacticoida	*Nitocra* sp.	•	•	•	•	•	(***)	•	•	•	•
Cladocera	*Rak* near *labrosus*	•	•	•	•	•	•	•	•	•	•
Ostracoda	*Physocypria* sp.n.	•	•	•	•	(***)	•	•	•	•	•
Hydracarina	spp.A - X	•	•	•	•	•	•	•	•	•	•
Notonectidae	*Anisops aglaia*	•	•	•	•	•	•	•	•	•	•
Diptera	Chironomidae	•	•	•	•	•	•	•	•	•	•

GILLIDAM		COND	PH	ACID	F-C	COL	A_{250}	E_2/E_3	DEP	TMP	CHL
Calanoida	*Metadiaptomus purcelli*	•	•	•	•	•	•	•	•	•	•
Cyclopoida	*Microcyclops crassipes*	•	•	•	•	•	•	•	•	•	•
Harpacticoida		•	•	•	•	•	(**)	•	•	•	•
Cladocera	*Alona* gr.*intermedia*	•	•	•	•	•	•	•	•	•	•
	Ephemeroporus gr.*barroisi*	•	•	•	•	•	•	•	•	•	***
Ostracoda	*Physocypria* sp.n.	(**)	(**)	•	•	•	•	•	•	•	•
Hydracarina	spp.A - X	•	•	•	•	•	•	(**)	•	•	•
Notonectidae	*Anisops aglaia*	•	•	•	•	•	•	•	•	**	•
Diptera	Chironomidae	•	•	•	•	•	•	(***)	•	•	•

SIRKELSVLEI		COND	PH	TALK	F-C	COL	A_{250}	E_2/E_3	DEP	TMP	CHL
Calanoida	*Lovenula simplex*	(**)	•	•	•	•	**	•	•	•	•
	Metadiaptomus capensis	•	•	•	•	•	•	**	(**)	•	•
Cladocera	*Daphnia hodgsoni*	(**)	(**)	(**)	•	•	**	•	***	•	•
	Ilyocryptus sordidus	•	•	•	•	•	•	•	•	•	•
Ostracoda	*Gomphocythere expansa*	•	**	•	•	•	•	•	•	•	•
	Sarscypridopsis glabrata	**	•	•	•	•	(**)	•	(**)	•	***
Notonectidae	*Anisops aglaia*	•	•	**	•	•	•	•	•	•	•
Diptera	Chironomidae	•	•	•	•	•	•	•	•	•	•
Rotifera	*Brachionus plicatilis*	•	•	•	(***)	•	(**)	****	(***)	•	****
Platyhelminths	Turbellaria	•	**	•	•	•	•	•	•	•	•

GROOTRONDEVLEI		COND	PH	TALK	F-C	COL	A_{250}	E_2/E_3	DEP	TMP	CHL
Calanoida	*Lovenula simplex*	•	•	(**)	**	•	•	(**)	•	•	•
	Metadiaptomus purcelli	•	•	•	•	•	•	**	•	•	•
Cyclopoida	*Microcyclops crassipes*	**	•	•	(***)	(**)	•	***	•	•	•
Cladocera	*Daphnia barbata*	•	•	•	•	•	(**)	**	(**)	**	(**)
	Daphnia laevis	•	•	•	•	•	•	•	•	•	•
	Daphnia pulex	***	**	***	(**)	(**)	•	**	(**)	•	•
	Ceriodaphnia dubia	**	•	**	•	•	(**)	**	(**)	•	•
	Alona gr.*intermedia*	***	•	•	•	•	•	•	(**)	•	•
Ostracoda	*Gomphocythere expansa*	**	•	•	•	•	•	**	•	•	•
Hydracarina	spp.X	•	•	•	•	•	•	•	•	•	•

GROOTWITVLEI		COND	PH	TALK	F-C	COL	A_{250}	E_2/E_3	DEP	TMP	CHL
Calanoida	*Metadiaptomus purcelli*	•	•	•	•	•	•	•	•	•	•
Cyclopoida	*Microcyclops crassipes*	•	•	•	•	•	•	•	•	•	•
Harpacticoida	*Bryocamptus* sp.	•	•	•	•	•	•	•	•	•	•
Cladocera	*Moina micrura*	•	•	•	•	•	•	•	•	•	•
	Chydorus gr.*sphaericus*	***	•	**	•	•	•	**	(**)	•	•
	Ilyocryptus sordidus	•	•	•	•	•	•	•	•	•	•
	Macrothrix near *goeldi*	•	•	**	•	•	•	•	•	•	•
Ostracoda	*Gomphocythere expansa*	**	•	•	•	•	•	•	•	•	•
	Parastenocypris pardalis	•	•	•	•	•	•	•	•	•	•
	Sarscypridopsis and *Potamocypris* spp.	•	•	•	•	•	•	•	•	•	•
Hydracarina	spp. A - X	•	•	•	•	•	•	•	•	•	•
Coleoptera	Dytiscidae	•	•	•	•	•	•	•	**	•	•
Rotifera	*Brachionus calyciflorus*	**	•	•	•	•	•	•	•	•	•
	Brachionus rubens	**	•	•	•	•	•	•	•	•	•
Fish larvae	*Galaxias zebratus*	•	•	•	•	•	•	•	•	(***)	•

RONDEVLEI		COND	PH	TALK	PALK	F-C	COL	A_{250}	E_2/E_3	DEP	TMP	CHL
Cyclopoida	*Thermocyclops oblongatus*	•	•		•	•	•	•	•	•	•	•
Harpacticoida	*Attheyella* sp.	**	•	•	**	•	**	•	•	(**)	•	•
Cladocera	*Ceriodaphnia cornuta*	•	•	•	•	•	•	•	•	•	•	•
	Daphnia pulex	•	•	•	•	•	•	•	•	•	•	(**)
	Moina micrura	**	•	•	**	•	•	•	**	(***)	•	•
	Chydorus gr.*sphaericus*	•	•	•	•	•	•	•	(***)	•	•	•
	Alona near *harpularia*	•	•	•	**	•	•	•	•	•	•	•
	Pleuroxus gr.*aduncus*	***	•	•	•	•	•	•	•	(***)	•	•
	Macrothrix spinosa	•	•	•	•	•	•	•	•	•	•	•
Ostracoda	*Gomphocythere obtusata*	•	•	•	•	(**)	•	•	•	•	•	•
	Sarscypridopsis spp.	•	•	•	•	•	•	•	•	•	•	•
Notonectidae	*Anisops aglaia*	•	•	•	•	•	•	•	•	•	•	•
Rotifera	*Brachionus calyciflorus*	•	•	•	•	•	•	•	•	•	•	***

Table 9.7 The levels of significance of the Pearson correlation coefficient (r) calculated as a measure of the intensity of association between zooplankton taxa and some of the major physical [colour (COL), depth (DEP), temperature (TMP)], chemical [conductivity (COND), pH, total and phenolphthalein alkalinity (TALK,PALK), polyphenols (F-C), humic substances (A_{250}, E_2/E_3)] and biological [phytoplankton (CHL)] variables. Where $P < 0.001$ = ****, $P < 0.01$ = ***, $P < 0.05$ = ** and ( ) indicates a negative correlation.

Wind is not considered to be an important factor influencing abundance of bottom species in these two vleis because of reduced mixing resulting from greater relative depths and shorter fetches than in the other vleis. Fish predation is also unlikely to be an important factor due to the intensity of colour (affecting visual predation). More importantly, no fish were found in either vlei, although *Galaxias zebratus* may be present, even if limited only to the *Scirpus* beds, as it has been captured in other vleis of similar pH in Cape Point. Adult Dystiscidae are captured only in the littoral *Scirpus* beds of both vleis.

Sirkelsvlei

The most significant correlations are found between the rotifer, *Brachionus plicatilis*, and the variables chlorophyll *a* (CHL), humic character (E_2/E_3), polyphenols (F-C) and depth (DEP). Of these, the relationship with chlorophyll *a* may well be causal - as a result of the levels of primary production and/or as a result of the food quality (possibly diatoms). Higher levels of primary production and increased grazing activity would result in increased production of autochthonous humic substances (high E_2/E_3) and hence a non-causal relationship. A further depth related variable which may also act to regulate the presence of *B.plicatilis* is total salinity (measured as conductivity). Although the correlation is not great the rotifer is a brackish water species and may well require salinities of $4^{\circ}/_{oo}$ or above. In contrast the calanoid *Lovenula simplex* disappears when salinities rise above approximately $8^{\circ}/_{oo}$. Thus between February and March, *Brachionus plicatilis* appears and *Lovenula simplex* disappears. Given the available data, it is not possible to determine whether the changes in numbers of the two species are related to each other or to changes in salinity. The disappearance of *L.simplex* with increasing salinity is also obvious in the data of Coetzee (1986). The species persisted to salinities of approximately $10^{\circ}/_{oo}$ in De Hoop vlei before disappearing. *Daphnia hodgsoni*, although only present in small numbers, was also significantly correlated with depth and negatively correlated with salinity. The species was possibly also responding to salinity levels, as primary production was at a minimum and there was no evidence of improving food quality (chlorophyll *b*:*a*, *c*:*a* and *a*:POC ratios). *Metadiaptomus capensis* does not appear to be controlled in the same way. The population experiences a similar mid-summer depression in abundance, probably also as a result of predation, in this case by *Anisops aglaia* and *Lovenula simplex*. With the disappearance of *L.simplex*, *M.capensis* numbers increase rapidly. The response may however also be related to primary production, resulting from a distinct drop in chlorophyll *a* in December before the late summer bloom. Abundances of a number of other taxa correlate with abiotic and biotic variables, although most appear to be non-causal. Abundance of *Sarscypridopsis glabrata* is low and correlates positively with chlorophyll *a* (CHL) and conductivity (COND), and negatively with depth (DEP) and HS concentration (A_{250}). The ostracod is a benthic species and all four correlations probably only reflect a greater incidence of capture at low water levels.

Grootrondevlei

Since seasonal variation in most variables is relatively lower in Grootrondevlei than in the other vleis, correlations between abiotic and biotic variables and the seasonal variation in abundance of the taxa are least likely to be causal in this vlei. Thus the apparent relationships presented in table 9.7 should be approached with caution. Much of the seasonal variation in abundance appears to be due to competitive or predator-prey interactions. The dominant calanoid, *Metadiaptomus purcelli*, undergoes a mid-summer depression of abundance similar to populations in Gillidam and *M.capensis* in Sirkelsvlei. Once again this is probably related to predation, in this case by *Lovenula simplex* (and to a much lesser extent by *Microcyclops crassipes* on the naupliar and early copepodite stages). The absence of *Anisops aglaia* from both the Grootvleis is interesting, but not easily explained. Total absence as a result of net avoidance is unlikely, as is extinction due to vertebrate predation, especially since the healthy population of the large *L.simplex* suggests that predation-pressure is not heavy. Also unexplained is the population crash of *L.simplex* in mid-summer. As noted above, physical and chemical conditions are relatively constant and thus should not be responsible. The most likely supposition is large-scale predation by a fish predator, but there is no evidence for this. *M.purcelli* numbers increase in the months following the November maximum of *L.simplex* and minimum of *M.purcelli* copepodites. An interesting succession of limnetic herbivorous cladoceran species occurs over the same summer period. A brief, but high, maximum of *Daphnia laevis* occurs at the same time as maximum *L.simplex* numbers. The population crashes with *L.simplex* and both are succeeded by the smaller *Daphnia barbata*. As *D.barbata* populations decline some three months later another brief, but high maximum of *Ceriodaphnia dubia* appears, to be followed by a population of *Daphnia laevis*. *Daphnia* and *Ceriodaphnia* species are known as co-exploiters with complex competitive interactions occurring between them (Lynch 1978, Smith and Cooper 1982). The succession of the above species very probably results from differences in food preference as a result of body size and thus follows resource alteration (as described by Lynch 1978, Makarewicz and Likens 1979 and Smith and Cooper 1982). Predation pressure, however may also be related to body size, and thus the appearance of the smaller *D.barbata* and *C.dubia* may be predation related. Chlorophyll *a* levels are very low throughout this period (<3ug l^{-1}) as are levels of phaeopigments, indicating an additional particulate food source, possibly bacterial. There are a number of statistically significant correlations (table 9.7) between abiotic and biotic variables and the limnetic cladocerans, but none appears directly to control, or can be shown to cue, the appearance of the different species. The chydorid *Alona* gr. *intermedia* is present in much lower numbers and shows correlations with depth and conductivity. It is a benthic species and as such, decreasing depth should increase the sample catch, while conductivity is a depth-related variable (concentration/ dilution). How much this masks changes in the total population size is not known. *Gomphocythere expansa* on the other hand, is also a bottom species, but sample abundance is probably regulated by the life-history as the result of a swimming larval stage. In Sirkelsvlei both adults and juveniles were present in the water column throughout the year, whereas in Grootrondevlei the numbers were almost entirely made up of juveniles.

Grootwitvlei

Far less apparent correlation exists between the abiotic and biotic variables and the taxa due to the more pronounced seasonal variation of the physico-chemical environment. Abundances of *Metadiaptomus purcelli* show some similarities in seasonal variation to those in Gillidam and Grootrondevlei, with low numbers in mid-winter and mid-summer. Whereas in these two vleis invertebrate predation might have caused the mid-summer depression in numbers of the copepod, these predators are absent from Grootwitvlei. The cause of this minimum may thus be related to some life-history or behavioural function. On the other hand, predation by fish was surmised as the cause of the extinction of the *Lovenula simplex* population in Grootrondevlei. In the same way fish predation may well be the pressure preventing the appearance of the *L.simplex* populations in the adjoining Grootwitvlei. In addition with increasing water temperatures, decreasing water levels and, most importantly, decreasing colour levels, visual predators may place an increasingly efficient predation pressure on *M.purcelli* during the summer months - size selective fish predation is well known to control zooplankton abundances (Hall *et al.* 1976, O'Brien 1979, Zaret 1980). Certainly a significant number of juvenile *Galaxias zebratus* were captured in the net plankton during the winter months. A general decrease in numbers and increase in size from July through to the summer reflected maturation during the year. As noted in chapter 2, *G.zebratus* is an incredibly hardy species (present in waters of pH 3.6) and its presence is expected in all the vleis. The absence of *Daphnia* spp. may also be related to predation (see

Gophen 1985), since the physical and chemical environment is unlikely to limit those species present in Grootrondevlei and food quality and abundance is unlikely to be limiting (see Richman and Dodson 1983). The appearance of *Moina micrura* in a shortlived, but very numerous, population coincided with a distinct chlorophyll maximum, but little else. *Chydorus* gr. *sphaericus*, present in low numbers as a littoral invader, is commonly associated in the open water with blue-green blooms, where it is inclined to feed on bacterial aggregates (Hutchinson 1967, Bern 1987). Its presence in Grootwitvlei coincides with the initial chlorophyll maximum and the tail of the second chlorophyll maximum and thus it may well be a similar response. The rotifer *Brachionus calyciflorus* was present in unusually low numbers, yet displayed a response to the chlorophyll maxima similar to *C.sphaericus.* Taxa such as *Macrothrix* near *goeldi, Ilyocryptus sordidus, Gomphocythere expansa, Sarscypridopsis* and *Potamocypris* spp. are all bottom species and showed little obvious relation to any of the abiotic or biotic variables.

Rondevlei

Correlations between the abiotic and biotic variables and the abundance of taxa suggest a greater number of causal relationships than in the other five vleis. While some of the more abundant taxa, such as *Thermocyclops oblongatus* and *Ceriodaphnia cornuta*, appear to be controlled more by predator-prey and competitive interactions, chlorophyll levels and nutrient enrichment come close to acting as 'master variables' for others. Depth is also an important variable regulating the incidence of capture of benthic species. Abundance of *Thermocyclops oblongatus* displays two minima. The mid-summer depression is yet again most likely to be related to predation by *Anisops aglaia*, present in high numbers over these three to four months, and the mid-winter depression may be influenced by stormwater inflow as well as temperature. A large volume of urban runoff enters the vlei between July and September, resulting in extensive mixing and nitrogen enrichment (see chapter 5). In the previous section an unusual depression in copepodite abundance was noted following the spring pulse of nauplii. Cyclopoid copepods during their juvenile stages are often herbivorous and show a high survival rate in highly productive environments (Neill and Pocock 1980, Soto 1985). In addition, adult *T.oblongatus* may be primarily herbivorous raptors (see above). The crash in phytoplankton standing crop from October to December may thus have contributed to the mid-summer depression of abundance by reducing the survival rate of juvenile (particularly larval) copepods - an effect that checked a spring maximum in numbers and become apparent as a lag-effect some months later. A very high proportion of the phytoplankton biomass through most the year is thought to be contributed by blue-green algae (see chapter 8). Copepods in general show a much greater capability of selecting food than daphnids and can probably avoid the toxic, indigestable or unmanageable blue-green species. This algal food source should however not suit the presence of *Daphnia* species, both as a result of the low food quality and the excessive food quantity (Richman and Dodson 1986). It is thus interesting to note a negative correlation between numbers of *Daphnia pulex* and chlorophyll *a* levels ($P < 0.05$). The appearance of *D.pulex* coincides with the crash in phytoplankton standing stock and most probably the replacement of blue-green dominance by chlorophyte dominance, certainly at the beginning of the low chlorophyll period (see chapter 8). The more palatable chlorophyte species and/or the bacteria associated with the algal decomposition would then act as suitable food source for *Daphnia* spp. (Lampert and Taylor 1985, Bern 1987, Kankaala 1988). *Daphnia obtusa* co-occurs briefly at the beginning of the same period. *Ceriodaphnia cornuta* and *Moina micrura* are both present in high numbers, generally during warm months of low water levels and the periods of greatest phytoplankton abundance. The interaction of these factors probably combined with predation pressure, particularly in the first part of summer, prevents a significant correlation with any one variable, except for *M.micrura* with depth ($P < 0.01$). *Ceriodaphnia* ingest small-sized particles (Smith and Cooper 1982) and some species have been found to be facultative bacterial feeders (Gophen *et al.* 1974, Smyly and Collins 1975), although preferences for a small blue-green algal species have been demonstrated (Lampert and Taylor 1985). They tend to live close to the bottom sediments, if oxygen levels are adequate (Nauwerck 1963, Connel 1978). *M.micrura* is larger and thus tends to feed on larger-sized particles (Smith and Cooper 1982). It may well also favour living close to the sediments where high bacterial biomasses are associated with the thick layer of organic particulate matter and where there may be reduced predation pressure from visual and tactile limnetic predators. High levels of autotrophic and heterotrophic production, higher temperatures allowing rapid development of essentially opportunistic species in an environment of high sustained predation pressure, and lower water levels causing increased numbers in the surface community, should thus explain the variation in abundance of the two species. *Chydorus* gr. *sphaericus* appears briefly in the limnetic community as a very numerous population during the winter inflow of stormwater (high in dissolved nitrogen levels) - possibly as a result of succession within the blue-green community. Abundance of *Brachionus calyciflorus* is highly positively correlated with chlorophyll *a* levels ($P < 0.01$). Thus seasonal changes in food quality appear to be less important than changes in total primary production. *Brachionus rubens* appeared after the crash in phytoplankton standing crop and the total rotifer abundance is even more closely correlated to chlorophyll *a* levels. The chydorid

Pleuroxus gr. *aduncus,* is a bottom species less inclined to wander like *C.sphaericus* and consequently displays a strong negative correlation between abundance and water level. *Macrothrix spinosa* and the ostracods *Gomphocythere obtusata* and *Sarscypridopsis* spp. are also all bottom species, but less restricted, appearing in the water column variously at times of mixing, as larval stages etc.

Much of the above discussion of seasonal variation in abundance may be termed 'subjective deduction' based on the data collected and the findings presented in the literature, but with no experimental proof to back up the causal relationships suggested. I have attempted to be cautious, but at the same time thorough in discussing the likely causes of change in species abundance, but obviously the distinction between the two is difficult to define. The use of the correlation matrix in attempting to identify so-called "master variables" is probably simplistic, but does appear to have some merit in Rondevlei at least. The complex interactions within the abiotic environment, as well as biological interactions, should mask most correlations, yet useful pointers have still become apparent in some cases, particularly with the variables controlling rotifer abundance.

DIVERSITY AND COMMUNITY STRUCTURE

Number of taxa

If the total (or cumulative) numbers of taxa constituting each limnetic community (tables 9.1 - 9.6) are considered large differences between the vleis are apparent - from Sirkelsvlei with only 15 taxa to Rondevlei with 35. However if the mean monthly number of taxa is considered, the differences are far smaller ranging from 6.7 in Sirkelsvlei to 12.1 in Rondevlei (table 9.8). The number of taxa viewed as a mean (over 15 months) is a figure that is more comparable with spot sampling (from other studies) and is thus introduced in this section. The total number, although intrinsically more accurate, is more prone to additions from the littoral and benthic regions, particularly in these small and shallow waterbodies. The difference between the two sets of figures reflects the seasonal succession occurring in each vlei, thus Rondevlei, Grootwitvlei and Grootrondevlei experience a greater degree of intra-annual succession than do the Cape Point vleis. The latter vleis are populated by more perennial species and in particular lack the limnetic cladoceran and the more numerous ostracod taxa of Rondevlei, Grootwitvlei and Grootrondevlei. Suurdam, in spite of its depauperate zooplankton numbers, has a comparable number of taxa present in the limnetic community and Sirkelsvlei, with relatively rich zooplankton abundance, has a depauperate number of taxa. Suurdam and Gillidam both have a strong component of water mites contributing to the number of taxa, whereas Sirkelsvlei and to some extent Grootrondevlei both lack the water mites, but instead support a number of ostracod species. The rotifers contribute little to the total number of taxa in any of the vleis.

	SU	GI	SI	GR	GW	RO
TOTAL NUMBER	15	16	12	21	31	35
MEAN NUMBER	9.2 ±1.6	7.9 ±2.5	6.7 ±1.1	7.7 ±2.5	11.7 ±4.1	12.1 ±3.3
H' DIVERSITY	1.94 ±0.54	0.32 ±0.28	0.86 ±0.31	0.67 ±0.40	0.67 ±0.55	1.69 ±0.31
J' EVENNESS	2.03 ±0.55	0.34 ±0.27	1.05 ±0.40	0.79 ±0.52	0.60 ±0.43	1.58 ±0.23
CRUSTACEAN SPECIES	3.8 ±0.4	3.5 ±1.0	4.5 ±1.0	6.2 ±1.7	8.3 ±3.0	9.1 ±2.9
LIMNETIC SPECIES	1.0 ±0.0	1.9 ±0.4	2.3 ±0.7	4.2 ±1.3	2.1 ±1.1	3.2 ±0.7

Table 9.8 The total number of taxa (as listed in tables 9.1-9.6) constituting the zooplankton in each vlei over 15 months (cumulative number), the mean monthly number of taxa, the Shannon index of diversity (H'), the index of evenness (J'), the mean number of crustacean species and the mean number of limnetic crustacean species. All figures (except the total number) are monthly means (± sd).

Crustacean species

If the numbers of species of Crustacea only are considered (thus omitting the rotifers, water mites, insects, nematodes and turbellarians, most of which were not identified to species level) a very different distribution of numbers is noted (table 9.8). Suurdam, Gillidam and Sirkelsvlei all contain low mean numbers, in contrast to Grootwitvlei and Rondevlei. Comparison of the means with the multiple range test of Newman and Keuls (Zar 1974) shows a significant difference ($P < 0.05$) between the Cape Point vleis and Grootrondevlei, and between Grootrondevlei and the waters of Grootwitvlei and Rondevlei (ie. $GI = SU = SI \neq GR \neq GW = RO$).

Fryer (1980, 1985) has related the number of crustacean species to both pH and the size of the water body. Examining a large number of lakes of similar size in Britain, he found a correlation between pH (from 3 to 7) and species number, as did Okland and Okland (1980) in Norwegian ponds and lakes. The relationship was strongest between pH 3 and 5, indicating a general intolerance of acid conditions. The same relationship appears to hold true in the studied vleis. However, if plotted on the same axes (as the data of Fryer), these data yield a regression of smaller slope (where Y axis = species number) as a result of the lower-than-expected diversities in Sirkelsvlei and Grootrondevlei, thus indicating additional limiting factors. In Sirkelsvlei one of the factors is likely to be the fluctuations in salinity. The size of the water body, however, also appears to play a role in determining the species number, with more crustacean species occurring in large water bodies. Fryer (1985) divides waterbodies into three size categories viz. $<5000\text{m}^2$, $5000 - 12000\text{m}^2$ and $>12000\text{m}^2$. He finds an almost seven-fold difference in the number of chydorid species in small and large water bodies. The studied vleis certainly do differ in size, and fall into the small (Suurdam and Gillidam) and large categories. The low species numbers of Suurdam and Gillidam may result from effects of both pH and water body size, although the variation in species number between the remaining vleis cannot be accounted for by size effect. Fryer (1985) further notes that difference in habitat diversity between large and small waterbodies are insufficient to explain the large difference in species number. Between the large vleis it may account for some variation however, particularly since littoral vegetation is completely absent in Sirkelsvlei.

Limnetic crustacean species

If the chydorids, as well as the other littoral-benthic crustacean species are excluded, leaving only the truly limnetic species, further changes in the distribution of species numbers are apparent (table 9.8). Comparing the mean numbers of limnetic species (using the Newman Keuls multiple range test, $P < 0.05$) a significant difference is found between Suurdam and the means of Gillidam, Sirkelsvlei and Grootwitvlei and between Rondevlei and Grootrondevlei (ie $\mathrm{SU} \neq \mathrm{GI} = \mathrm{GW} = \mathrm{SI} \neq \mathrm{RO} \neq \mathrm{GR}$). The reason for the relatively higher number of limnetic forms in Grootrondevlei than in Grootwitvlei is not apparent, but may well be related to predation pressure from visually feeding planktivorous fish common in the more productive, alkaline and, for much of the year, less coloured environment of Grootwitvlei. The species absent from Grootwitvlei are all the larger limnetic forms (*Lovenula, Daphnia* spp.), thus reflecting the predicted and well documented effect of visual predation (Hall *et al.* 1976, O'Brien 1979, Zaret 1980, Post and McQueen 1987) on larger individuals. The large limnetic species of Rondevlei survive extinction *via* predation as a result of the high turbidity of the system (secchi disc 18-45 cm, H Langley pers.comm.), but may be limited by the densities and palatability of the phytoplankton (as noted in the previous section).

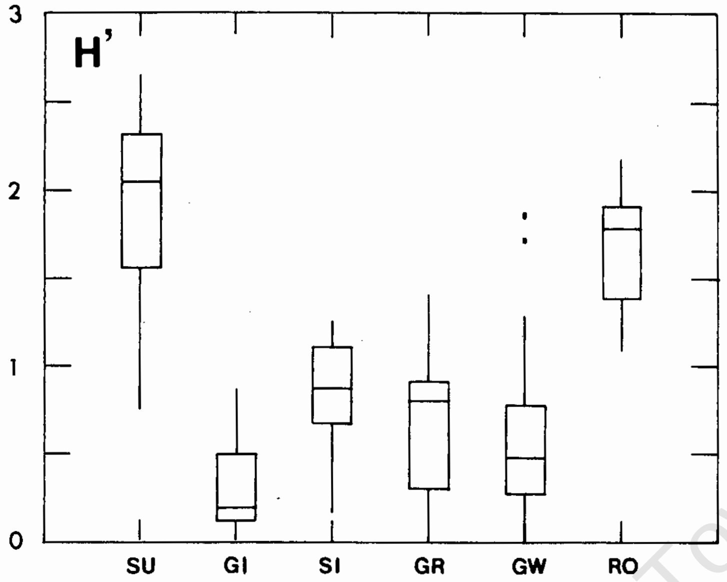
Species numbers in the other black- or brownwater systems around the world are variable, but generally low. Very little information exists of most of the systems and thus it is difficult to draw any broad generalizations about either the diversity or the zooplankton abundance of brownwater faunas. Dark brown waters are often very acid and very shallow. As a result of low light penetration, the lack of stable stratification and the complexation of micronutrients, they appear to be low in primary productivity. Levels of heterotrophic activity are generally coupled to primary productivity and may thus also be significantly reduced. The pH and colour affect fish, both in their presence or absence and in their effectiveness as predators, often resulting in a depauperate fish fauna or even the absence of fish. In dark brown waters there are therefore a number of integrated, indirect factors acting on zooplankton community structure. Other waters described as brown waters vary from only slightly stained to moderately stained, however, and in addition many are alkaline. In these waters the indirect effects noted above may be insignificant or even reversed. The term "brownwater" thus covers a wide range of colour levels (see chapter 1) and any attempted generalization of the community structure is further confounded by the lack of information on comparable systems. Table 9.9 attempts to summarize some of the available literature describing brownwater limnetic communities - the lack of comparable systems is obvious, as well as the variable number of taxa. However in comparison to the temperate forest pond, Päärjärvi and Tjeukemeer, all of which are neutral/alkaline and only slightly coloured, the presence of a single dominant calanoid copepod species and very few cyclopoid species (also of low abundance) are features common to a number of the brownwater lakes and vleis (the obvious exception of course being Suurdam).

Shannon index of diversity (H')

The index (from Shannon and Weaver 1949) was calculated for each of the six vleis. It measures the diversity per individual in a many-species population and can be regarded as a measure of the 'uncertainty' of encountering any one of the taxa (Pielou 1969). It thus takes into account the relative abundances of the different taxa, in contrast to using species number as a measure of diversity. Diversity (H') is lowest in Gillidam, Grootrondevlei and Grootwitvlei (table 9.8) and high in Suurdam and Rondevlei. The low values reflect the extreme dominance of a single species, *Metadiaptomus purcelli*, in these three vleis whereas other taxa contribute a greater relative abundance in the other three vleis (fig. 9.15a-f). This is confirmed by a **measure of evenness (J')** (Pielou 1969) which shows a similar pattern of values (table 9.8). Comparison of these diversity values with those obtained in two studies of comparable systems, shows all except Suurdam and Rondevlei to be particularly

Lake	colour	pH	total taxa	rotifers	cyc.	cal.	lim. clad	litt. benth. clad	comment	ref.
AUSTRALIA Dune lakes NE, N S Wales	0.17-0.38 Abs. 385 (SD 07-1.7)	3.5 6.0	1-6	0	(2)	1	-	0-3	*Calamoeicia tasmanica* dominant. Water mites present.	Timms 1982
Dune lakes Fraser Island Queensland	- (SD 2.3-3.4)	4.8-5.3	2		(1)	1			Described as humic. Water mites present.	Arthington *et al.* 1986
NORTH AMERICA Florida Lake Mize				1(+)	1				Dominated by rotifers.	Nordlie 1976
Lake Newman		neutral		(p)	1	1	1		Dominated by copepods and cladocerans.	
Virginia Brownwater swamps		acid		2(+)	2		p	2	Dominated by rotifers.	Anderson *et al.* 1977
B.Carolina Robinson impoundment	- (SD 1.1-3.0)	3.4-5.9	54	4(+29)	2(+5)	1	1	2(+10)		Mallin 1984
Georgia Lake Whitney	176 H (SD 0.5m)	3.5-5.9	30	2	4	1	1		Dominated by calanoids, *Daphnia* and rotifers.	Stoneburner and Smock 1980
EUROPE Finland Karhujärvi	200-400H	4.2-4.5	19	3(+6)	1	1	1	3(4)	Dominated by cladocera.	Rask *et al.* 1986
Pääjärvi	40H	7.0		23	6			9		Ilmavirta 1978 Sarvala *et al.* 1981
Netherlands Tjeukemeer	<20H	7.5-9.5		p	4(4)	1(+)	1(+2)	3(2)		Vijverberg 1977 De Haan 1984 De Haan 1972
Belgium 'temperate forest pond'	10-20H	7-8	35	2(+17)	1(+6)			8	Slightly humic. Rotifers most abundant.	Deronde *et al.* 1984
JAPAN	'reddish brown -coffee black'	4.4-5	5-8	2	1	1	(1-5)			Ueno 1934

Table 9.9 Summary of some of the available literature describing the zooplankton community composition of brown- or blackwater systems. x indicates apparent dominance in abundance, (x) indicates rare or not common.



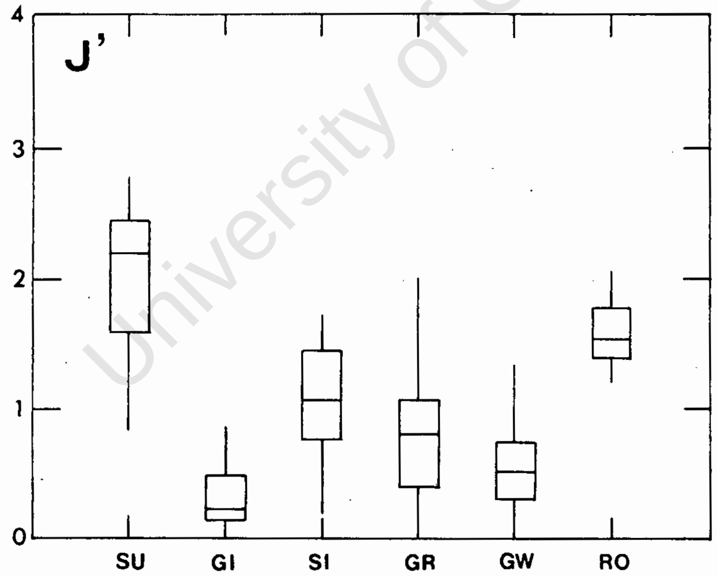


Figure 9.17 Box and whisker plot of the Shannon index of diversity (H') and the index of evenness (J'). Suurdam (SU), Gillidam (GI), Sirkelsvlei (SI), Grootrondevlei (GR), Grootwitvlei (GW), Rondevlei (RO).

low. Ryan (1984) reports H' values of 1.07-1.28 and 1.30-1.49 for only the crustacean zooplankton of small, shallow, acid, brownwater lakes in Newfoundland, and Coetzer (1987) reports H' values generally >1.0 for the zooplankton of Rocher pan, a shallow vlei of salinity comparable to that of Sirkelsvlei. In complete contrast to these sytems, the large eutrophic and highly alkaline Lake Valencia (Venezuela) has diversity values ranging from 1.35 to 2.09 in the open waters, with a total number of 40 zooplankton taxa (of which 27 are Rotifera). Finally Timms (1981), in lake Bullenmerri (Eastern Australia) with a salinity of $8^{\circ}/_{\infty}$ and abundant *Brachionus plicatilis* (thus similar in some respects to Sirkelsvlei), found a diversity (H') of 0.78 for the limnetic zooplankton (8 species). In none of the studies however did the Ostracoda contribute fully to the diversity - in the first and third apparently because none were encountered, and in the second because they were lumped as a single group, as were cyclopoid and harpacticoid copepods.

Community structure

In a number of recent studies Sprules (1979, 1980, 1984 and Sprules and Knoechel 1984) has promoted the importance of the size structure of zooplankton communities as the variable best correlated with the productivity and physico-chemical characteristics of lakes and best reflecting the relations with lake trophy and planktivorous fish distribution expected from the literature . He also notes that if taxonomic groupings are to be used, a few simple groupings rather than a full taxonomic breakdown is all that is necessary. Thus using seven simple taxonomic groupings plotted against relative abundance and an approximate size classification plotted against log abundance an attempt was made to define the community structure of each of the vleis in relation to obvious biological and physico-chemical characteristics using both of the above alternative forms of classification.

Taxonomic groupings are used in fig. 9.1$\overset{8}{5}$ (a-f), the seven groupings being (i) rotifers, (ii) cyclopoid copepods, (iii) calanoid copepods, (iv) limnetic cladocera (*Daphnia* spp., *Ceriodaphnia* spp. and *Moina* spp.), (v) littoral/benthic cladocera (Chydoridae, Macrothricidae, *Ilyocryptus* spp. etc.), (vi) ostracoda and (vii) others (water mites, insects, etc.). The features of the community structure apparent from the figures are the extreme dominance in abundance (and presumably in biomass) of the calanoid copepods in all but Suurdam and Rondevlei, the increasing abundance of rotifers with increasing productivity and alkalinity, the complete absence of calanoids in eutrophic Rondevlei and the reduced abundance and diversity of Crustacea in the highly acid waters of Suurdam. In addition the almost complete absence of Cladocera in Sirkelsvlei is a feature almost certainly related to salinity. Timms (1981) in his comparison of lakes Purrumbete ($0.4^{\circ}/_{\infty}$) and

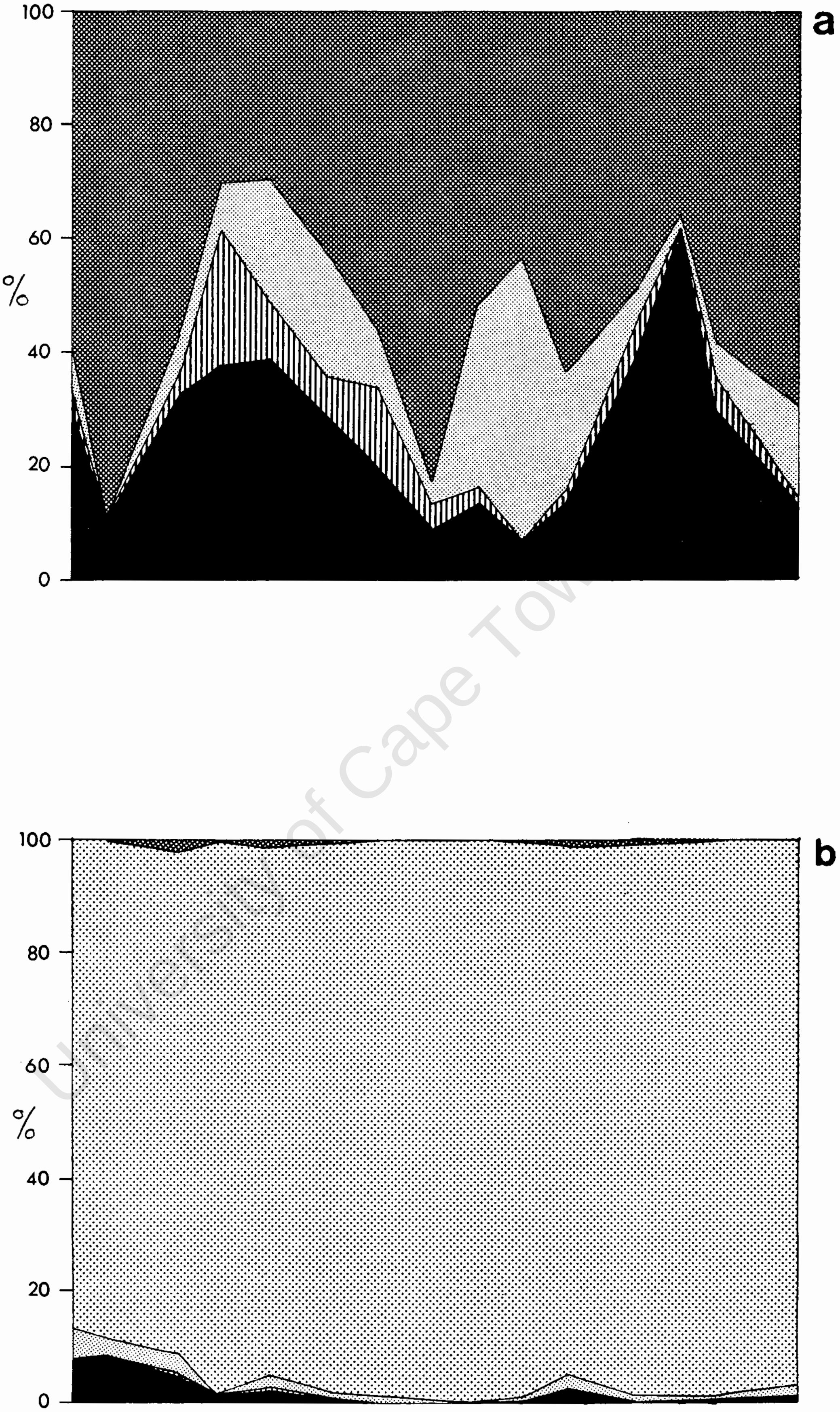


Figure 9.18(a-f) Zooplankton community structure according to seven simple taxonomic groupings, expressed as percentage composition (by number) - (i) rotifers [□], (ii) cyclopoid copepods [▓], (iii) calanoid copepods [░], (iv) limnetic cladocera [⁙], (v) littoral/benthic cladocera [░], (vi) ostracoda [|||||], (vii) others [■].
(a) Suurdam, (b) Gillidam, (c) Sirkelsvlei, (d) Grootrondevlei, (e) Grootwitvlei and (f) Rondevlei.

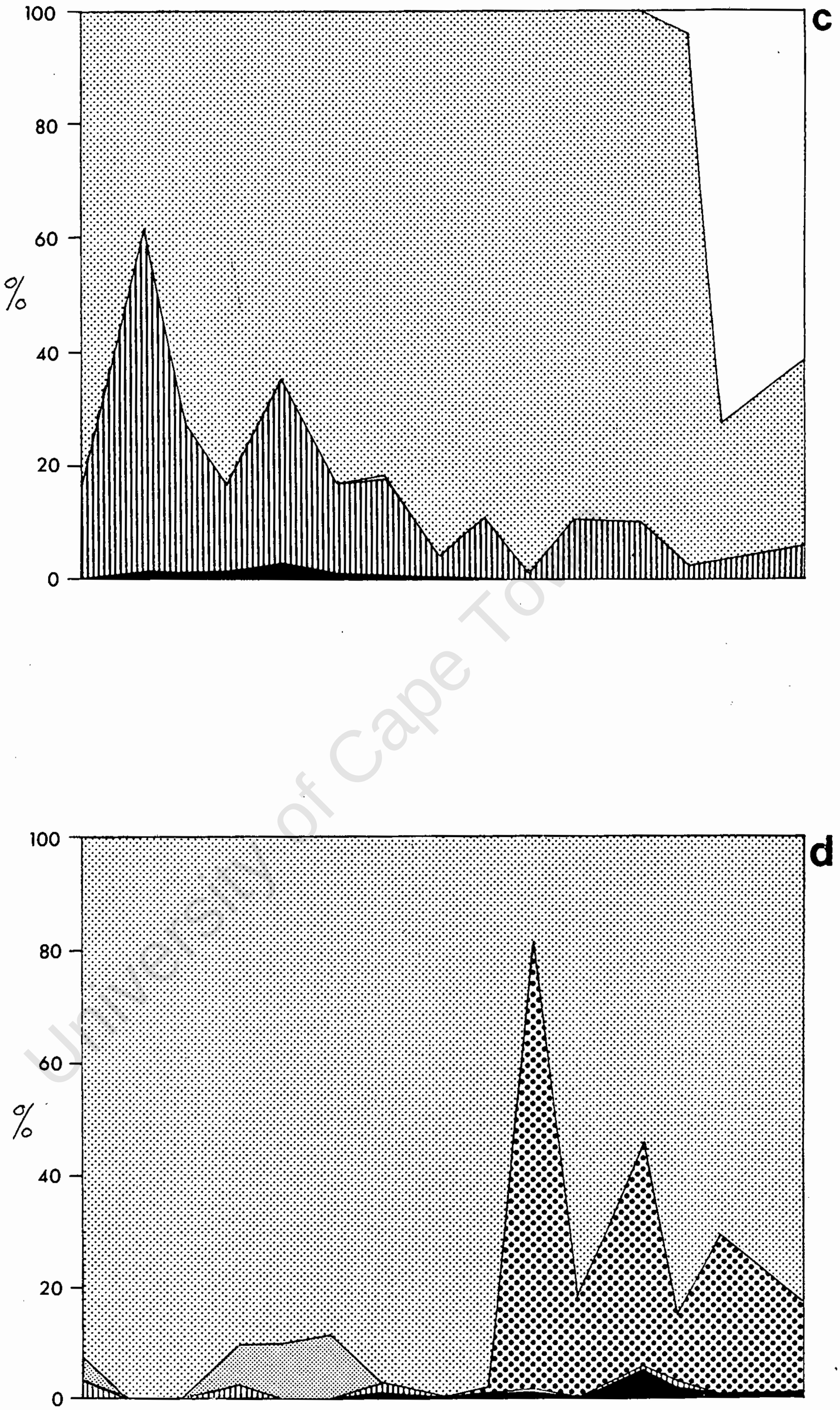


Figure 9.18(a-f) (cont.) Zooplankton community structure according to seven simple taxonomic groupings, expressed as percentage composition (by number) - (i) rotifers [☐], (ii) cyclopoid copepods [▓], (iii) calanoid copepods [░], (iv) limnetic cladocera [⁙], (v) littoral/benthic cladocera [▒], (vi) ostracoda [|||||], (vii) others [■]. (a) Suurdam, (b) Gillidam, (c) Sirkelsvlei, (d) Grootrondevlei. (e) Grootwitvlei and (f) Rondevlei.

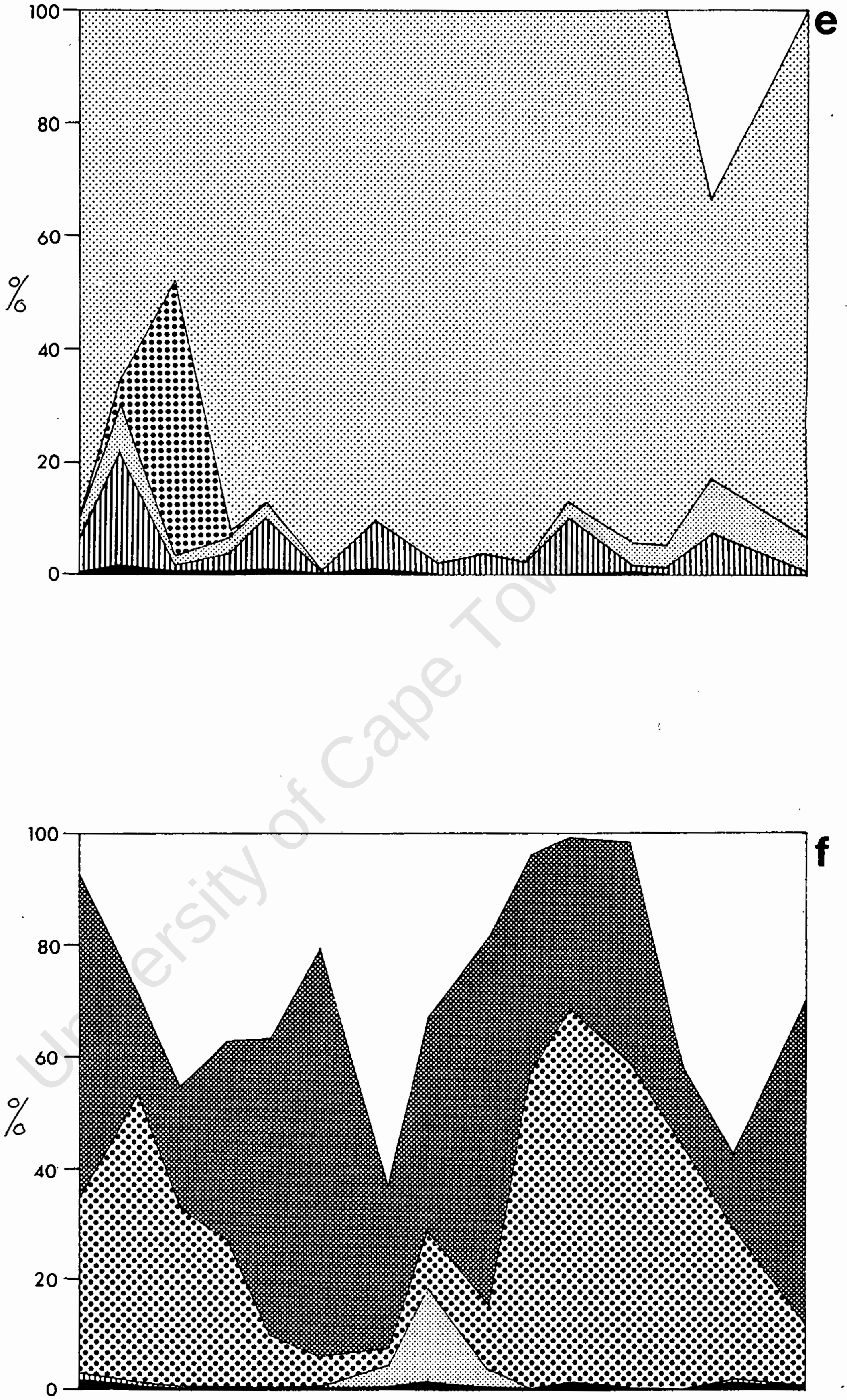


Figure 9.18(a-f) (cont.) Zooplankton community structure according to seven simple taxonomic groupings, expressed as percentage composition (by number) - (i) rotifers [□], (ii) cyclopoid copepods [▩], (iii) calanoid copepods [░], (iv) limnetic cladocera [⁘], (v) littoral/benthic cladocera [▒], (vi) ostracoda [|||||], (vii) others [■]. (a) Suurdam, (b) Gillidam, (c) Sirkelsvlei, (d) Grootrondevlei, (e) Grootwitvlei and (f) Rondevlei.

Bullenberri ($8^{\circ}/_{oo} \approx$ Sirkelsvlei) found 3 and 0 cladoceran species respectively and Geddes *et al.* (1981) found only one (halophilic) cladoceran species in salinities greater than $5^{\circ}/_{oo}$ (they found only two additional species, *Daphnia* sp. and *Moina* sp., in salinities between 3 and $5^{\circ}/_{oo}$). In Rocher Pan, over a similar salinity range, however, Coetzer (1987) found relatively low abundances of a total of 5 limnetic cladoceran species and 5 littoral/benthic cladoceran species. He made no mention of fish or insect predators. The relatively high abundance of ostracods may also be a salinity related feature; certainly the data of both Geddes *et al.* (1981) and Coetzer (1987) support it.

The **size classification** is approximate in that only adult lengths were used, even though large proportions of some faunal groups were in the juvenile or larval stages. In addition not all the faunal groups were included - water mites, chironomids and other insect larvae, turbellarians and nematodes were either present in small numbers or were of variable size and were thus excluded. Only the crustacean zooplankton, rotifers and the predator *Anisops* were included. The lengths used were measurements taken from the sample animals and checked against measurements from the literature where available. Size categories were designated in 0.2 mm increments from 0 to 7 mm, thus forming 35 categories. Within the size categories predators and primary consumers are distinguished, as are ostracods, a group believed to suffer relatively minor predation pressure (Pennak 1978). A number of differences in the size distributions of the zooplankton of the six vleis are apparent in fig. $9.1\overset{9}{7}$ (a-f). Both Suurdam and Gillidam are dominated by very small individuals. Grootrondevlei contains relatively large-bodied grazers, in contrast to the size-restricted fauna of Grootwitvlei. Rondevlei also displays some size restriction, as well as containing large-bodied grazers. Discussion of the factors limiting abundance in many cases relates closely to the regulation of community size structure. This has been covered in the previous section and thus only a synopsis of the most important variables will be mentioned here.

Sprules and Knoechel (1984) suggest that small zooplankters may be more tolerant of high acidity than large zooplankters. Acidity may thus well be a factor limiting the size of the zooplankters in Suurdam and Gillidam. The relative effects of predation by either *Anisops* or *Galaxias* are not known, but probably affect abundance more than size structure of the community. The community in Grootrondevlei, judging from the size structure, does not experience heavy, size-selective visual predation pressure, although seasonal predation pressure has been proposed above to account for the disappearance of *Lovenula*. Food levels should

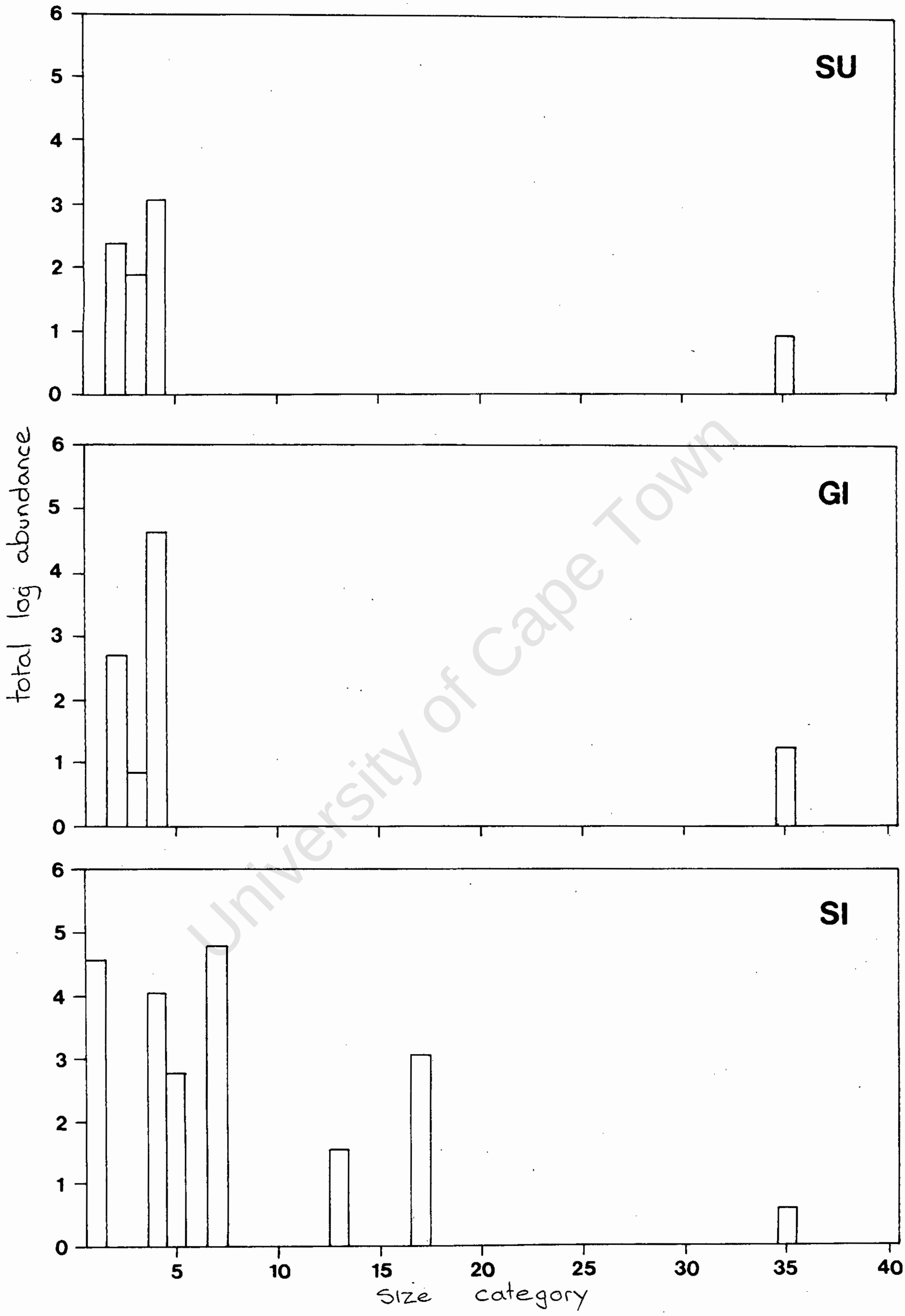


Figure 9.19(a-f) Zooplankton community structure according to size categories (0.2mm increments from 0-7mm) expressed as the total log abundance of each size category.
(a) Suurdam (SU), (b) Gillidam (GI), (c) Sirkelsvlei (SI), (d) Grootrondevlei (GR), (e) Grootwitvlei (GW) and (f) Rondevlei (RO).

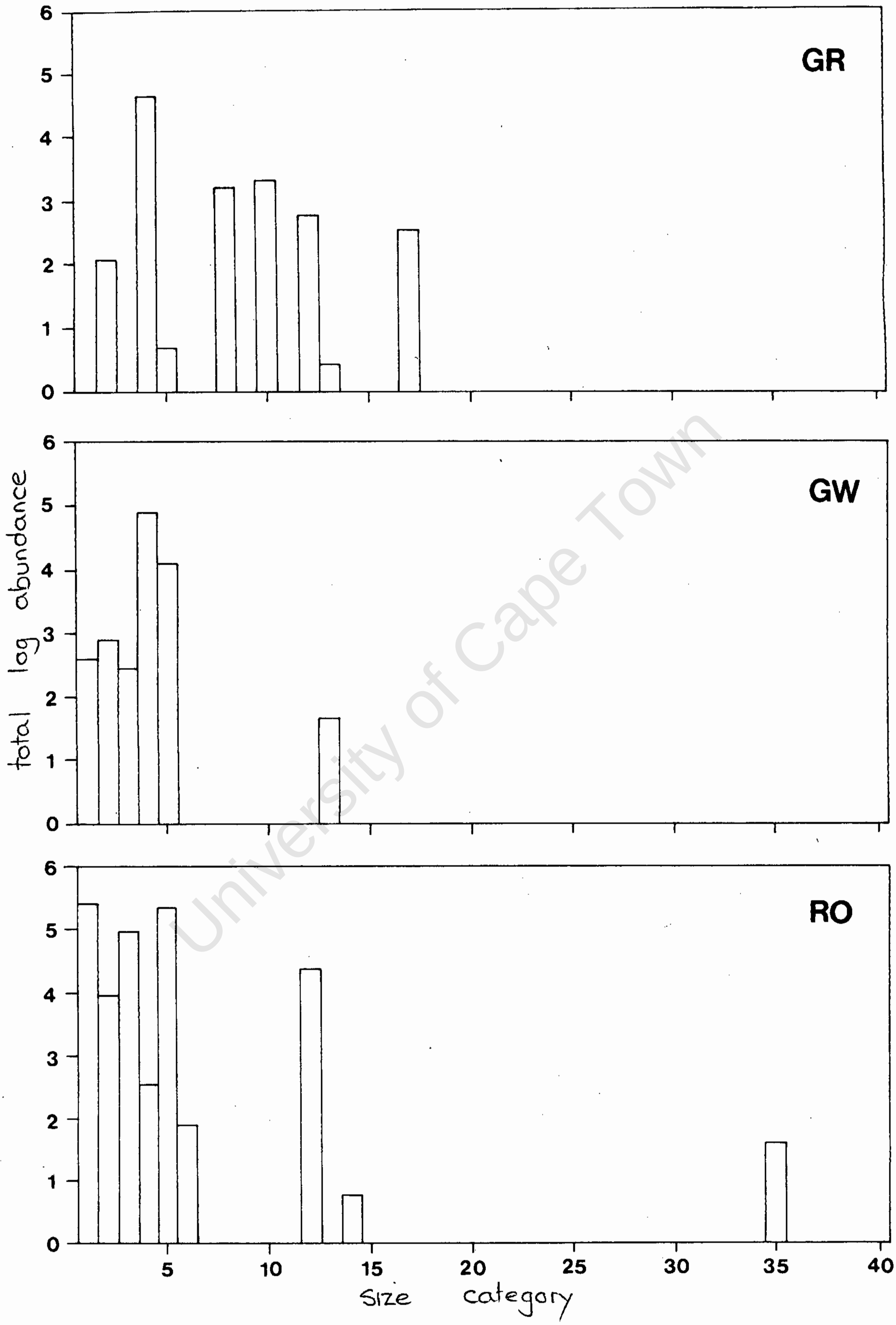


Figure 9.19(a-f) (cont.) Zooplankton community structure according to size categories (0.2mm increments from 0-7mm) expressed as the total log abundance of each size category. (a) Suurdam (SU), (b) Gillidam (GI), (c) Sirkelsvlei (SI), (d) Grootrondevlei (GR), (e) Grootwitvlei (GW) and (f) Rondevlei (RO).

be low and thus predation, if present, would be an important regulatory factor (Smith and Cooper 1982). The size-restricted community in Grootwitvlei, on the other hand is most probably regulated by a heavy predation pressure by large numbers of visual predators such as *Galaxias.* In Rondevlei predation pressure is also likely to be high (high fish densities - chapter 2), but the high turbidity as a result of eutrophication and the high food abundances allow cladoceran densities to outstrip predator control at times (cf. Smith and Cooper 1982). The salinity range in Sirkelsvlei, in excluding cladoceran species, limits the distribution of crustaceans in the upper size range and the effects of predation other than the seasonal depression of copepod abundance are not obvious.

The possible limiting effects of water colour on visual predation, in short, are complicated by the effects of lake productivity, acidity and salinity and it is difficult to make predictions based on the intensity of colour without taking these (and other) factors into account.

GENERAL DISCUSSION

Some comment must be made on the presence or absence of certain taxa under the physical, chemical and biological regimes of the vleis. The distribution of individual taxa, both geographically and in relation to physico-chemical and biological variables, in particular the more restricted or abundant forms, has been covered in the section 'Taxonomy, ecology and distribution of the taxa' above. Comment has also been made on the variables controlling seasonal succession and those controlling the species number, diversity and community size structure. What is left to do is briefly discuss the species assemblages in relation to the characteristics of each vlei. The Suurdam community, as mentioned before, appears to be composed of both acidophilous and acid-indifferent species. *Microcyclops crassipes* is found over a pH range of at least 3.7-9.4, but is most successful at low pH, and at very low pH replaces *Metadiaptomus purcelli* both in Suurdam and in the Nuweberg dam (Palmiet river, SW Cape -samples from B.Byren). The chydorid *Rak* and the ostracod *Physocypria* both appear limited to very acid dark waters, although vlei size may also be a factor determining their distribution. The Gillidam community is similar to that of Suurdam, but includes a few additional species. *Metadiaptomus purcelli* is unlikely to be excluded from Suurdam by low food levels, and pH and/or humic levels are probably the limiting factor. *Alona* gr. *intermedia* and *Ephemeroporus* gr. *barroisi* may both be limited by extreme acidity, but otherwise show a preference for acid rather than alkaline waters. The absence of ostracods in general, apart from *Physocypria* and *Paracypretta* in the *Scirpus* beds of Suurdam is also likely to be an effect of pH. Low pH can have a direct physiological effect on crustaceans (Fryer and Forshaw 1979) and in addition, by increasing calcium solubility, limits its incorporation into the ostracod shell. The absence of *Chydorus* gr. *sphaericus* from the very acid waters is interesting, as Fryer and Forshaw (1979) record its presence over a pH range of 4.36-7.05, Fryer (1980) records it as common below a pH of 5.0 and Krause-Dellin and Steinberg (1986) record it as pH-indifferent. Either the pH of Gillidam is close to the limit or other interfering effects, such as humic levels, may be compounding the pH effect. In Grootrondevlei the water is acid, but not extremely so, and humic levels are much reduced. Even though primary productivity is low, the food quality (as shown by the chl.*a* : POC ratio - chapter 8) is improved and the appearance of efficient filter-feeding limnetic cladocerans is the result. The succession of a number of species suggests that competitive exploitation of limited food resources, rather than predation, controls their presence, although when present, *Lovenula* may be effective in controlling their numbers. An interesting feature of all the vleis, in particular the acid ones, is the absence of bosminids. *Bosmina* spp. have been reported in high abundances in several studies of brown and acid waters (Anderson *et al.* 1977, Brandorff 1979, Janicki and De Costa 1979 and Mallin 1984) and *Bosmina longirostris* has recently been reported as widespread in southern Africa (Seaman and Kok, in press). It has been found in two acid brown water impoundments on the Palmiet river, in the south-western Cape (B Byren pers.comm.). Its absence in all six vleis is thus peculiar and not easily explained. Another common species absent from the vleis, but present in the two impoundments, is *Chaoborus* sp. and again there is no obvious explanation.

The community in Sirkelsvlei appears to be primarily defined by the relatively high and variable salinity. Species such as *Metadiaptomus capensis, Gomphocythere expansa, Sarscypridopsis glabrata, Sarscypridopsis tonsa* and *Brachionus plicatilis* are all known to be tolerant of raised salinities and species such as *Lovenula simplex* and *Daphnia hodgsoni* appear to form resting stages before salinities rise. The presence or absence of *Lovenula simplex* in south-western Cape vleis is not easily predicted. It may be controlled by predation (the most probable control in Grootwitvlei) and by rising salinities, yet it is present in most of the brackish water systems (Rocher Pan, De Hoopvlei, Sirkelsvlei, Zandvlei), the exception being Grootrondevlei with particularly low salinities. Coetzer (1987) notes a negative correlation betweeen *L.simplex* and conductivity in Rocher Pan. *L.simplex* certainly is generally absent from the alkaline, productive vleis, yet is also absent from the Table Mountain reservoirs with acid brown waters of similar character to

Grootrondevlei. The community of Grootwitvlei has many elements in common with Grootrondevlei, but increased predation, increased development of the submerged littoral vegetation and increased productivity in the limnion results in some differences - in particular the presence of a greater variety of littoral-associated ostracod species. Rondevlei, on the other hand, with its very high levels of productivity, supports a much greater number of cosmopolitan and common pan-Ethiopian species. Species such as *Gomphocythere obtusata, Thermocyclops oblongatus, Ceriodaphnia cornuta* and *C.reticulata, Moina micrura* and *Brachionus calyciflorus* are all common in highly productive South African systems. The switch from *Metadiaptomus purcelli* to *Thermocyclops oblongatus* as the dominant copepod follows the recognized trend of cyclopoid dominance in highly productive environments (Neill and Peacock 1980, Soto 1985). *Metadiaptomus purcelli* is widespread in the south-western Cape as the dominant copepod and generally dominant zooplankter in almost all non-eutrophic, non-saline ($<3^{\circ}/_{oo}$ salinity) waterbodies, above a pH of approximately 4.5. It is not limited entirely to brown waters, although it is in these waters that the species commonly dominates.

Much of the community structure and species abundance, and the variation in both, can thus be explained by the major physical, chemical and biological variables. The most important variables have been relatively well studied and documented and can be used to explain most trends in the different systems. In using these variables to explain community structure the more obvious indirect effects of high concentrations of humic substances (such as reducing light penetration, maintaining a low pH, possibly reducing nutrient availability, etc) have been taken into consideration. No attempt has been made, however, to examine the possible direct effects of the high levels of humic substances on the limnetic fauna. The reason for this is very simply that very few studies have been conducted to establish the direct effects of aquatic humic substances on the zooplankton. Some of the direct effects on the biota that are known have been listed in chapter 1. The known direct effects, both positive and negative, that might affect the zooplankters include the complexation of metals and organic pollutants (reducing toxicity), the inhibition of the activity of various enzymes, effects on cellular ion transport, mitochondrial respiration and oxidative phosphorylation, and specific toxic effects resulting from phenolic constituents. Aquatic humic substances in addition occur in colloidal and detrital as well as dissolved forms and have the ability to precipitate alone or together with other organic molecules such as proteins and acidic polysaccharides (Prakash *et al.* 1972). They could therefore form a potential 'particulate' food source for filter feeding herbivorous/detritivorous species in the less acid brown waters, depending on the character and toxicity of the humic compounds. The presence of this particulate fraction is discussed in chapter 7. A study by Petersen and Persson (1987) investigated the acute and chronic toxicity effects of three different humic substances (HS) at different concentration and three different pH's on *Daphnia magna*. They found no biological effect at pH 7, a slight effect at pH 6 and lowest survival at pH 5. In addition, at pH 5 the greatest biological effect was either in the absence of HS or at concentrations exceeding 10 mg C l^{-1} (300 Hazen units). They suggest that the biological behaviour of the aquatic HS conforms to second-order rate phenomena controlled at low concentrations by high levels of free metal ions, and at low pH by direct toxic action of the HS due to increased lipophilicity. The study shows that, regardless of the type of HS, at low concentrations it tends to be beneficial to aquatic invertebrates (probably as a result of metal complexation), but at high concentrations it becomes toxic when pH is reduced. This is not unexpected, as many organic compounds demonstrate a pH-dependent biological activity, with toxicity increasing with decreasing pH (Saarikoski and Viluksela 1981, Petersen *et al.* 1986). The mechanism suggested for this toxicity is increased lipid solubility and membrane permeability. A further interesting result of the study was that the humic acid with the greatest phenolic hydroxyl content also displayed the greatest biological activity (toxicity), at both pH 5 and 6, and was able to complex more trace metals per unit carbon. Both the carboxyl and phenolic hydroxyl functional groups are known to be involved in metal complexation (see chapter 6). The relative aromatic content of the HS is thus an important determinant of the toxicity, and the character of the humic mixture (allochthonous/autochthonous) as well as the concentration and pH of the water should determine the final biological activity.

The direct effects of the humic substances in the studied vleis may therefore contribute significantly to the effects on the biota already discussed. Suurdam and Gillidam, with low pH and high relative phenolic content, may well be species-limited as a result of pH-dependent humic toxicity effects. The high phenolic content of HS in Grootrondevlei and the high levels in Sirkelsvlei, although limited by pH, may also contribute to limiting the presence of some species. Certainly the relationship between pH and crustacean species numbers noted earlier yields a smaller slope than that calculated by Fryer (1980) and may well be related to the higher concentrations of HS. Seasonal humic toxicity effects (as a result of concentration and/or pH) are probably important, but are not generally obvious from the correlation matrix of table 9.7. The study of Petersen and Persson (1987) has thus allowed significantly greater insight into the possible consequences on the biota of the high humic levels in the vleis, but further laboratory studies should be conducted to confirm the effects on the natural fauna of brownwater systems, in contrast to the effects on laboratory cultures of *Daphnia magna*.

SUMMARY

Suurdam had particularly low zooplankton abundances. The community was dominated by the cyclopoid copepod *Microcyclops crassipes*. Limnetic cladoceran species were absent and the next most abundant zooplankter was the chydorid *Rak* near *labrosus*. Juveniles of the ostracod *Physocypria* sp.n., water mites and some insect larvae made up most of the rest of the community. The total number of taxa was thus low, with few crustracean species. Diversity (H') and evenness (J') were relatively high, both as a result of the presence of a number of water mite species and because of a limited dominance in the numbers of *Microcyclops crassipes*. The zooplankters were mostly small in size. The community appears to be composed of both acidophilous and acid-indifferent species and the factors limiting species richness are probably both pH and the character and quantity of humic substances, resulting in pH-dependent humic toxicity effects. *Anisops aglaia* may affect seasonal abundance in the community by predation, and there may be low levels of heterotrophic activity resulting in a limited bacterial food source for some species, but no data is available for the latter supposition.

Gillidam had markedly higher zooplankton abundances than Suurdam, almost entirely as a result of the high numbers of the calanoid copepod *Metadiaptomus purcelli*. *Microcyclops crassipes* was present, but in lower numbers and limnetic species of Cladocera were again absent. Two chydorid species, *Alona* gr. *intermedia* and *Ephemeroporus* gr. *barroisi*, and the ostracod *Physocypria* sp.n, together with water mites and some insect larvae, made up most of the rest of the community. Again the total number of taxa was low, with few species of Crustacea, however, species diversity (H') and evenness (J') were also low as a result of the dominance of *Metadiaptomus purcelli*. The species composition was similar to that of Suurdam apart from the appearance of some additional taxa, which may be a consequence of the higher pH and lower levels of humic substances. Zooplankters were again mostly small. Predation by *Anisops aglaia* may affect the seasonal abundance of *Metadiaptomus purcelli*, but other factors influencing seasonal variation and abundance are not obvious.

Zooplankton abundance in Sirkelsvlei was high, largely as a result of high numbers of the calanoid copepod *Metadiaptomus capensis* and the rotifer *Brachionus plicatilis*. A second calanoid species, the large predatory *Lovenula* *simplex* occurred, as well as a number of ostracod species and small numbers of the limnetic *Daphnia hodgsoni*. Water mites were absent. The total number of taxa was low, and the mean number of species of Crustacea and of limnetic Crustacea, was not significantly greater than in Gillidam. High seasonal total salinities appear to strongly influence the community composition, although a relatively high primary production may also be important. Greater pH and a marked difference in the character of the humic compounds should reduce some of the effect of the pH-dependent humic toxicity. Predation by *Anisops aglaia* and *Lovenula simplex* appears to have some effect on the seasonal variation in abundance of some species.

Grootrondevlei displayed a mean abundance of zooplankton similar to Gillidam, but a far greater range. *Metadiaptomus purcelli* dominated the zooplankton with the limnetic cladocerans *Ceriodaphnia dubia*, *Daphnia barbata*, *Daphnia laevis* and *Daphnia pulex* appearing at some stage in the community. *Lovenula simplex* and *Microcyclops crassipes* were present, as well as a number of ostracod and chydorid species. Various water mites were occasionally present and some insect larvae, however *Anisops aglaia* was not found in either of the Grootvleis. The total number of taxa was relatively high. The number of crustacean species was greater than the Cape Point vleis and the number of limnetic crustacean species was the highest of all the vleis. Species diversity was low, once again as a result of the dominance of *Metadiaptomus purcelli*. Due to the presence of relatively large-bodied grazers, the average size of the zooplankton was noticeably greater. Predation pressure, certainly visual, appears to be low and a reduced pH-dependent humic toxicity, resulting from both increased pH and lower levels of humic substances, and not complicated by high salinities, may allow the presence of additional species. The quality and quantity of the food source in Grootrondevlei may also be a factor important to the limnetic Cladocera.

Grootwitvlei had higher mean zooplankton abundances than the first four vleis. Similarly to Grootrondevlei, *Metadiaptomus purcelli* dominated the zooplankton, but apart from *Moina micrura*, the limnetic Cladocera were absent. *Microcyclops crassipes* was present in small numbers, but *Lovenula simplex* was absent, and water mites were present in greater numbers. As a result of more littoral/benthic ostracod and chydorid species, the total number of taxa and the number of crustacean species was second only to Rondevlei. However, the number of limnetic crustacean species was similar to those of the Cape Point vleis. Diversity (H') and evenness (J') were low, as in Grootrondevlei. The community appears to be size-restricted, probably as a result of visual predation by fish, which may thus be the cause of the absence of *Lovenula simplex* and the large-bodied grazers.

Rondevlei had by far the greatest total zooplankton numbers. The most abundant species were the cyclopoid *Thermocyclops oblongatus* and the rotifers *Brachionus calyciflorus* and *Brachionus rubens.* Limnetic cladocera were represented by *Ceriodaphnia cornuta* and *Ceriodaphnia reticulata, Moina micrura*, and *Daphnia pulex* and *Daphnia obtusa*. A large number of chydorid, as well as ostracod species, were present, water mites were absent and *Anisops aglaia* was again present. The community consisted of a greater number of cosmopolitan and common Pan-Ethiopian species, in contrast to the restricted south temperate Gondwanian species, present in the more humic waters. The total number of taxa, and the number of species of Crustacea and of limnetic Crustacea, were all highest in Rondevlei. Diversity (H') and evenness (J') were high, but less than Suurdam. Some size-restriction seems to occur, again as a result of predation, although large-bodied grazers such as *Daphnia* did occur over a short period. Some species of limnetic Cladocera may be limited by the palatability of the blue-green algal species present.

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CONCLUDING REMARKS.

Having examined the community composition and structure, and its variation in each vlei, it was necessary to find a measure of overall similarity between the communities. This was achieved by grouping the communities in time and space using the complementary classification and multi-dimensional scaling (MDS) ordination techniques described by Field *et al.* (1982). Classifications were performed using a Bray-Curtis measure of similarity and group average sorting, and ordination analysis was by non-metric MDS scaling of the Bray-Curtis similarity matrix. MDS ordination displays the data as a two-dimensional plot, with least interpoint distances between stations (in this case between the samples for each month) of greatest similarity.

In fig 10.1, four distinct groups are displayed, reflecting the differences in community composition discussed in chapter 9. Suurdam, Sirkelsvlei and Rondevlei each clearly contain species assemblages distinct from those in any of the other vleis and are separated, using classification techniques, at a percentage similarity of <1.5%. Gillidam, Grootrondevlei and Grootwitvlei form a mixed group, since they contain similar communities (similarity >15.0% between all stations) and are separated from the first three vleis at the 1.5% level. Within this group, Gillidam shows a closer grouping than the Grootvleis. The overall distribution is dictated by the dominant copepod species in each, and so the common presence of *Metadiaptomus purcelli* explains the close grouping of Gillidam, Grootrondevlei and Grootwitvlei.

Within each group, analysis by classification gives a percentage similarity of >51.7% in Suurdam, >24.0% in Sirkelsvlei and >28.1% in Rondevlei. No attempt has been made to use these results to explain differences in community structure in terms of the environmental variables. This has been done by using the correlation matrix in chapter 9 and, further, this type of analysis using MDS and similar programmes often results in arbitrary variables being apparent determinants of community structure, even when there is little causal relationship (King *et al.* in press).

In conclusion, the six vleis do reflect the concentrations and character of the humic substances in their waters. The toxicity of HS and pH are closely linked and it is difficult to separate the effects of each. In Sirkelsvlei, relatively high salinity had an interfering and probably overriding effect in determining community composition.

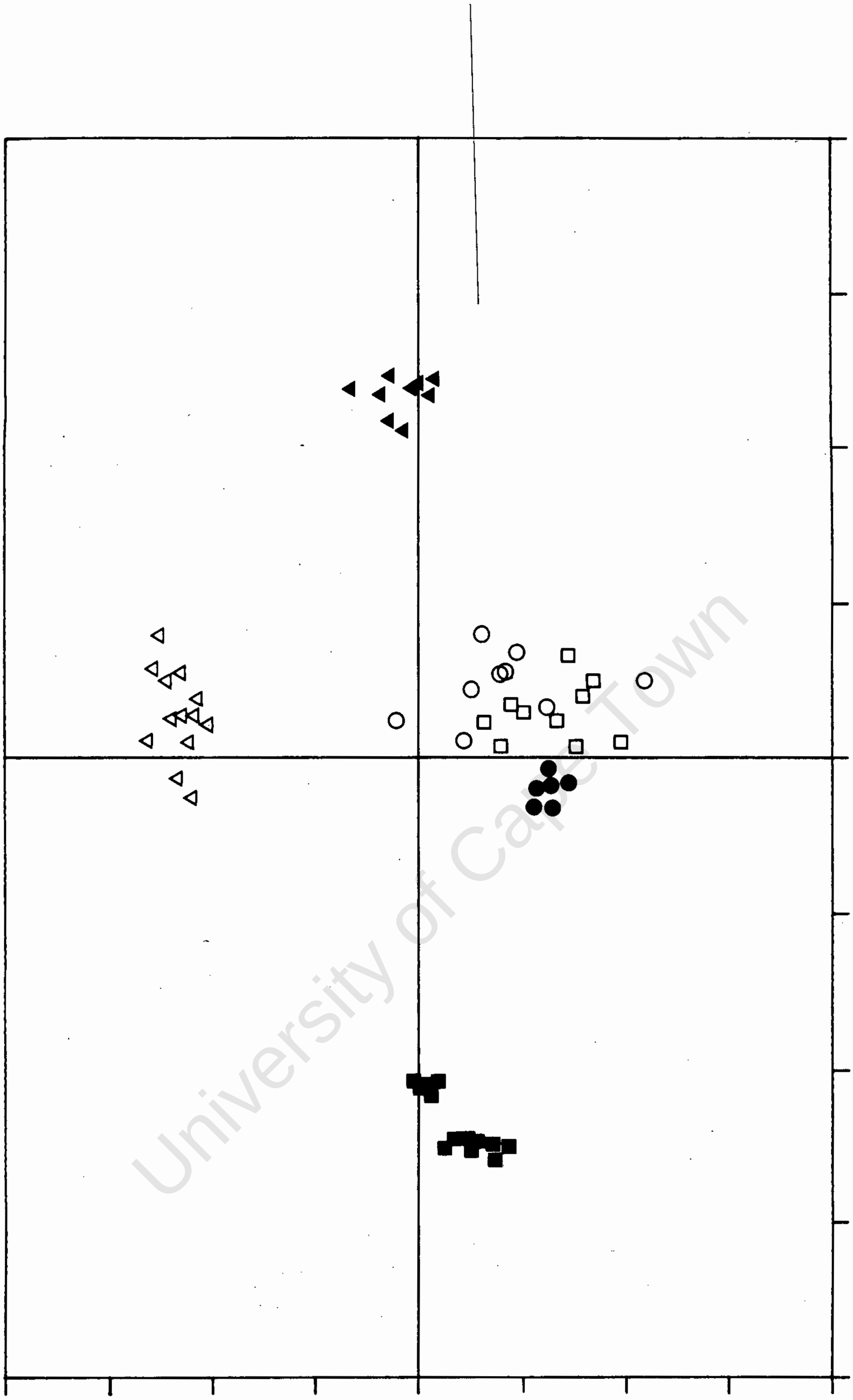

Figure 10.1. Multi-dimensional scaling (MDS) ordination of the zooplankton communities of the six vleis, where each point represents a monthly station at a single vlei. Suurdam (■), Gillidam (●), Sirkelsvlei (▲), Grootrondevlei (□), Grootwitvlei (○) and Rondevlei (△).

From the data presented in this thesis, the hypotheses presented in chapter 1 appear to hold true.

Water colour does reflect HS levels, although HS character also has an effect on colour. The character of the HS can be related to catchment geology and vegetation. In further studies it would be of interest to investigate the differences in character more thoroughly by the use of fractionation procedures.

The effects of HS on the inorganic chemical environment are complex, but are apparent even in a study as broad as this one. Again, further studies to investigate the complexation of HS and various chemical species would be of interest

The biota does differ distinctly between the six vleis and levels of primary and secondary production certainly appear to be affected by the concentration and character of HS. Other chemical variables also exert a strong influence, however, and this is not always linked to the presence of HS. Thus high concentrations and highly humified material both appear to exert a strong effect, whereas intermediate levels are probably not important determinants of community structure and composition.

Two further lines of research would repay investigation. Further information on the distribution of the copepod and limnetic cladoceran species in relation to environmental variables would provide a particularly interesting database because of the extremely restricted distributions of these species. Laboratory investigations into a) the population isolating mechanisms of the copepod species, in particular of the metadiaptomids, by looking at feeding regimes and environmental tolerances, especially to pH-dependent humic toxicity, and b) an investigation into the predator-prey interactions of Lovenula simplex (and other predators) in relation to water colour and pH, would both be fascinating studies yielding information important in developing the conclusions reached in the present study.

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