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SOME ASPECTS OF THE ECOLOGICAL STRUCTURE
OF A SEGMENTED BARRIER LAGOON SYSTEM
WITH PARTICULAR REFERENCE TO THE
DISTRIBUTION OF FISHES

by

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THESIS SUBMITTED TO RHODES UNIVERSITY
IN PARTIAL FULFILMENT FOR THE REQUIREMENTS OF THE
DEGREE OF MASTER OF SCIENCE

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January, 1985.



Frontispiece: The Wilderness lakes system.

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ACKNOWLEDGEMENTS

I gratefully acknowledge:

Professor B.R. Allanson and Dr A.K. Whitfield for their constant advice and encouragement throughout this study.

Messrs G.L. Christmas and D. Forsyth for their help and advice concerning the construction and maintenance of field equipment.

Mr. K. Wagner for his regular assistance in the field and laboratory.

Professor E. van der Merwe and Mr P Thompson for help and advice on statistical procedure.

Mr C. Beuthin for his help with computer programming.

Miss D.J. Snook for her friendship and encouragement whilst writing up and for her assistance with typing.

Dr R.D. Walmsley for some final editorial comments.

The staff of Rondevlei Research Station, Cape Department for Nature and Environmental Conservation for allowing me to work on Rondevlei and to use their wet laboratory facilities.

The Lakes Area Development Board and the National Parks Board of Trustees for allowing me to work in areas under their managerial jurisdiction.

The South African Council for Scientific and Industrial Research for financing this work.

ABSTRACT

The Wilderness lakes system represents a segmented barrier lagoon and comprises three interconnected lakes; Rondevlei, Langvlei and Eilandvlei. The latter is further linked by the Serpentine channel to the Touw river and Wilderness lagoon. The role of these channels, as well as a sluice in the Serpentine, in structuring certain aspects of the ecology of the system was investigated.

An analysis of the salt budget of the lakes suggests that the Serpentine dampens tidal processes to such an extent that they play only a minor role in the overall budget. Furthermore, the channel between Eilandvlei and Langvlei prevents any tidal salt input to the upper lakes. Their estuarine environments are however maintained by salt inputs which occur when the mouth is closed. This unusual phenomenon means that the sluice may have a minimal effect on the salt budget of the system because it is only closed when the mouth of the lagoon is open.

Environmental conditions in each of the lakes, the Touw river and Wilderness lagoon were compared in terms of their physico-chemical characteristics and submerged macrophyte communities. A principal components analysis suggests that the physico-chemical environment of each lake is similar. The Touw river however has a very different environment, whilst that of Wilderness lagoon has some similarities to both the lakes and the river.

During the study macrophyte communities recovered from a major recession which occurred between 1979 and 1981. Biomasses in excess of 1000g m^{-2} were recorded in both Langvlei and Eilandvlei. In the latter however, macrophyte growth was less prolific than in the former, as some areas of the littoral supported no growth at all. Macrophyte encroachment in the channels is a major factor inhibiting water flow between the lakes. This encroachment is most severe in the Eilandvlei/Langvlei channel where macrophytes covered 80% of the channel's area.

The dominant fish fauna throughout the system is composed of a marine/estuarine migratory component. In the lakes the Mugilidae and Sparidae are the most common families, whilst in the lagoon and Touw river predators such as Lichia amia and Argyrosomus hololepidotus also commonly occur. Eilandvlei serves as the initial nursery area for most migratory species. An estimated 52000 fish migrated up the Serpentine towards Eilandvlei during February 1984. Most fish do not penetrate as far as Langvlei, and this can be related to macrophyte encroachment in the Eilandvlei/Langvlei channel. However, it is argued that should this channel be dredged and the macrophytes removed, the nursery potential of the system would not be greatly enhanced. This is because environmental heterogeneity, in association with an abundance of food in Eilandvlei, make this lake the most attractive nursery area to juvenile marine/estuarine fish.

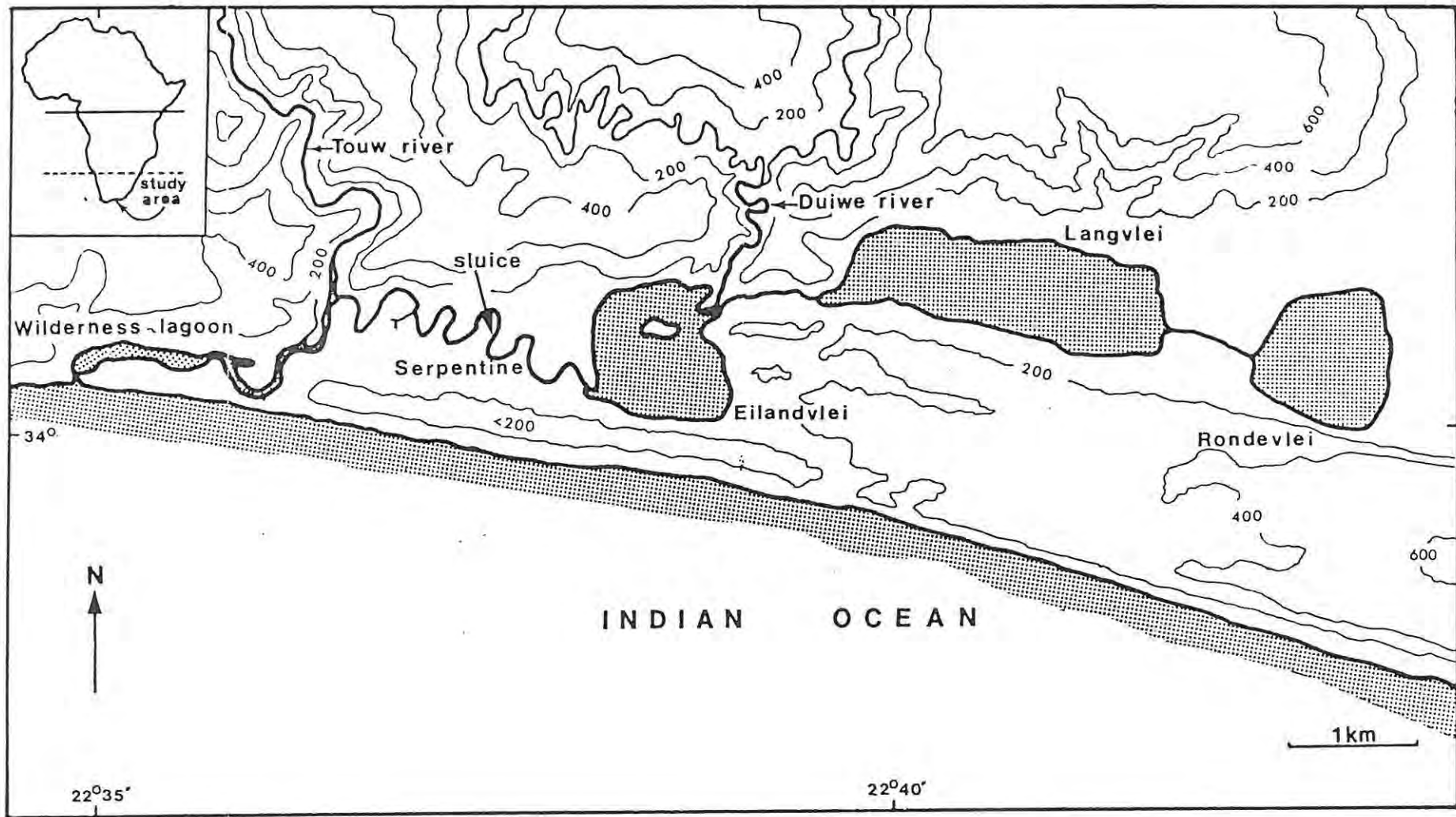


Figure 1: Map of the Wilderness lakes system (contours in feet above sea level).

PART 1

GENERAL INTRODUCTION

1 Introduction

The coastal lakes of southern Africa form an important component of the subcontinent's aquatic ecosystems (Allanson, 1981a) and fall into two geographically distinct groups. The northern series lies on the coastal plain of Zululand between Natal and southern Mozambique and comprises several large and smaller lakes. The southern series is located between Wilderness and Knysna in the southern Cape. All these lakes are small, the largest being Swartvlei with an area of about 11km^2 (Hill, 1975). Lake St Lucia in Natal is the largest coastal lake in southern Africa covering an area of 310km^2 (Day *et al.*, 1953) and constituting over 75% of South Africa's total estuarine area (Noble and Hemens, 1978).

This study concerns only the western lakes of the Wilderness series which are collectively referred to as the Wilderness lakes system (Figure 1). They represent the segmentation of an initially larger barrier lagoon and comprise Rondevlei, Langvlei and Eilandvlei together with Wilderness lagoon. All are estuarine in nature and are interconnected by a series of channels through which water flows for at least part of the year. Together with the estuary mouth and a sluice gate which was constructed in 1981, these channels form a series of constrictions within the system. These may play an important role in determining the ecological structure of the Wilderness lakes system.

Recently several aspects of the ecology of the Wilderness lakes have been studied. Allanson and Whitfield (1983) have examined physico-chemical characteristics. Gorgens (1979, 1980), Hughes and Gorgens (1981) and Gorgens and Hughes (1980, 1982) have investigated the hydrology and the CSIR (1981, 1982) the hydraulics. Howard-Williams (1980), Jacot-Guillarmod (1981) and Weisser and Howard-Williams (1982) have focused their attention on the macrophyte communities. Coetzee (1978, 1983) has examined the zooplankton of the system whilst Davies (1981, 1985) has surveyed the benthic invertebrates.

Data concerning the fish fauna are lacking. Van Wyk (1977) has listed the species present in Rondevlei, whilst Coetzee (1981) has analysed the gut contents of Hyporhamphus capensis from this lake. Information regarding other vertebrates associated with the Wilderness lakes has been mostly limited to unpublished reports. Greig (1979) and Palmer (1979) have documented the occurrence of amphibians and mammals found along the Serpentine. Boshoff (1979), Underhill et al (1980) and Boshoff and Palmer (1981) have reported on the waterfowl of the system.

Most of the research in the work cited above was carried out between 1976 and 1981. According to the predictions of Tyson (1978), who has modelled rainfall patterns in South Africa, there is a ten year rainfall cycle in the southern Cape and these years represent a period of above average precipitation. This period ended at the end of 1981 following a year of exceptionally heavy rainfalls which elevated water levels throughout the Wilderness lakes.

The cumulative effect of high freshwater inflows to the southern Cape coastal lakes may have been the cause of the observed senescence of previously extensive macrophyte beds (Allanson and Howard-Williams, 1984). It is certain that the six floods which occurred between October 1980 and September 1981 resulted in the salinity of the lakes falling to previously unrecorded levels: The salinity of Rondevlei dropped from 16 to 9⁰/oo between September 1980 and June 1981 whilst over the same period in Langvlei and Eilandvlei, salinities decreased from 10 to 5⁰/oo and 9 to 4⁰/oo respectively. These lower salinities remained constant throughout the present study.

Environmental conditions throughout my study were therefore characterized by drought, low water levels and low salinity. It also included the period during which the macrophyte communities were recovering. In addition, the sluice had been constructed in the Serpentine and constituted an element of human interference which was not previously present. I therefore investigated the impact of the sluice upon the tidal recharge of salt following the floods of 1980/81. I also examined the salt budget of the lakes when the mouth is closed. Whilst similar investigations have been common in other parts of the

world, notably the United States (Nixon, 1981), our understanding of such processes in southern African estuaries is at an elementary stage.

I have focused my attention upon physico-chemical characteristics, aquatic macrophytes and the fish fauna. Methods used in the physico-chemical programme were the same as those used by Allanson and Whitfield (1983) so these data sets are directly comparable. The objectives of the macrophyte programme were largely to document changes in distribution and biomass over the post-recession period. In addition, quantitative data concerning macrophyte encroachment within the constrictions between the lakes were collected. I hope that these data will increase our understanding of the role of these channels in structuring the Wilderness lakes ecosystem. The fish programme marked the first serious attempt to determine species composition and diversity throughout the system. In order to assess the impact of the sluice upon fish migrations, the movement of fish around it under several hydraulic conditions was investigated. In addition I attempted to determine the magnitude of migration under a normal hydraulic regime. A literature review suggests that this is the first attempt to quantitatively assess fish migration in a southern African estuary.

The broad spectrum of this thesis is designed to complement the work of previous studies. This has involved a comparison of data collected over a five year period of above average rainfall with data collected during conditions of drought and hydraulic manipulation. In addition to investigations directly related to those of previous authors, the thesis includes research into the migration, distribution and diversity of the fish fauna as well as an analysis of the salt budget of the Wilderness lakes. It is hoped that these investigations will further our understanding of the ecological structure and function of the Wilderness Lakes system.

The Wilderness lakes system lies parallel to the coast ($25^{\circ}59'S$ $22^{\circ}34.5'E$) between Wilderness and Knysna and comprises Rondevlei, Langvlei, Eilandvlei and Wilderness lagoon. All three lakes are interconnected and are linked by a narrow, winding channel known as the Serpentine to the Touw river which flows into the lagoon at Wilderness (Figure 1). The estuarine area covers about 9.11km^2 and most of it falls below the 5m above mean sea level (msl) contour (Jacot Guillarmod, 1981).

The whole system is situated on a series of Quarternary sands (Tyson, 1971) which is known as the Wilderness-Knysna coastal embayment. Just inland of this embayment is a 200m high Tertiary platform comprising the foothills of the Outeniqua mountains which consist of intensely folded Table Mountain Sandstone. These mountains give rise to the streams and rivers that feed the lakes and Wilderness lagoon. The system is estuarine in nature but is only periodically open to the sea.

2.1. Geological history

Although the precise geological processes involved in the formation of the system are still under dispute, it is known that it was formed during the Pleistocene glaciations and Martin (1962) and Birch et al (1978) state that glacio-eustasis was responsible. They theorize that during the peak of the Eemian transgression, when the sea level was not less than seven metres above its present level, the area was inundated with sea water and formed a gently shelving shoreline. The sea level then fell and extended the rivers falling over the Tertiary cliffs onto the exposed littoral.

Over the series of transgressive pulses which followed, aeolian processes created a number of parallel barrier dunes along an east-west axis. The existing barrier dunes were probably formed at the same time as the Rondevlei basin was eroded as a deflation hollow. Finally, at the end of the Flandrian transgression, the sea rose to about 2.5m above its present level, filling the area that now constitutes the lakes, Serpentine and Wilderness lagoon.

Table 1: Morphometric characteristics of the lake basins (calculated by the author).

MORPHOMETRIC PARAMETER	EILANDVLEI	LANGVLEI	RONDEVLEI
Length (km)	1.67	2.97	1.44
Surface area (km ²)	1.50	2.16	1.43
Mean breadth (km)	0.90	0.73	0.99
Volume + 1.5mamsl (m ³ x 10 ³)	4808	6487	3763
Maximum depth (m)	6.5	4.0	6.0
Mean depth (m)	3.2	3.0	2.6
Length of shoreline (km)	5.16	7.75	4.26
Development of shoreline	1.21	1.53	1.05
Volume development	1.48	2.24	1.31

Whilst Rondevlei is definitely a flooded deflation basin, it is quite possible that the rest of the system represents a segmented barrier lagoon. Orme (1973) has suggested that segmentation has occurred to some extent in all the major Zululand lagoons. An obvious example is the Kosi system which has evolved into 5 separate lakes linked by a series of channels. Environmental factors in the Wilderness area may have been predisposed to initiate the segmentation of an initially larger barrier lagoon extending from the present mouth of the Touw river to the eastern extremity of Langvlei. These are discussed below.

The long axis of the system lies approximately parallel to prevailing south-westerly winds. Nearshore circulation may thus have been capable of transporting sediments along the shores of the original lagoon. Furthermore, the system receives most of its water from the Touw river at its western end and therefore probably experienced little disturbance to shore-building processes further along the original lagoon.

The barrier dunes in the area between Eilandvlei and Langvlei extend inland (Figure 1). This extension may have formed an initial constriction upon which deposited sediments commenced the process of segmentation. The marshy area between Eilandvlei and Langvlei may thus have been formed with a similar process occurring in the area of the Serpentine.

Van Heerden (1983) reports that similar aeolian and eustatic processes caused the formation of the dunes and deflation basins of the unsegmented Bot river estuary. Evolution of coastal lakes in such a manner is by no means confined to southern Africa and both Hutchinson (1957) and Barnes (1980) refer to similar processes in Europe, Australia and North America.

2.2. Morphology and hydrology

Morphometric parameters describing the lake basins were calculated according to the methods described by (Hutchinson, 1957) and are shown in Table.1. They will be discussed in relation to several aspects of the ecology of the system in later sections. The bathymetry of the

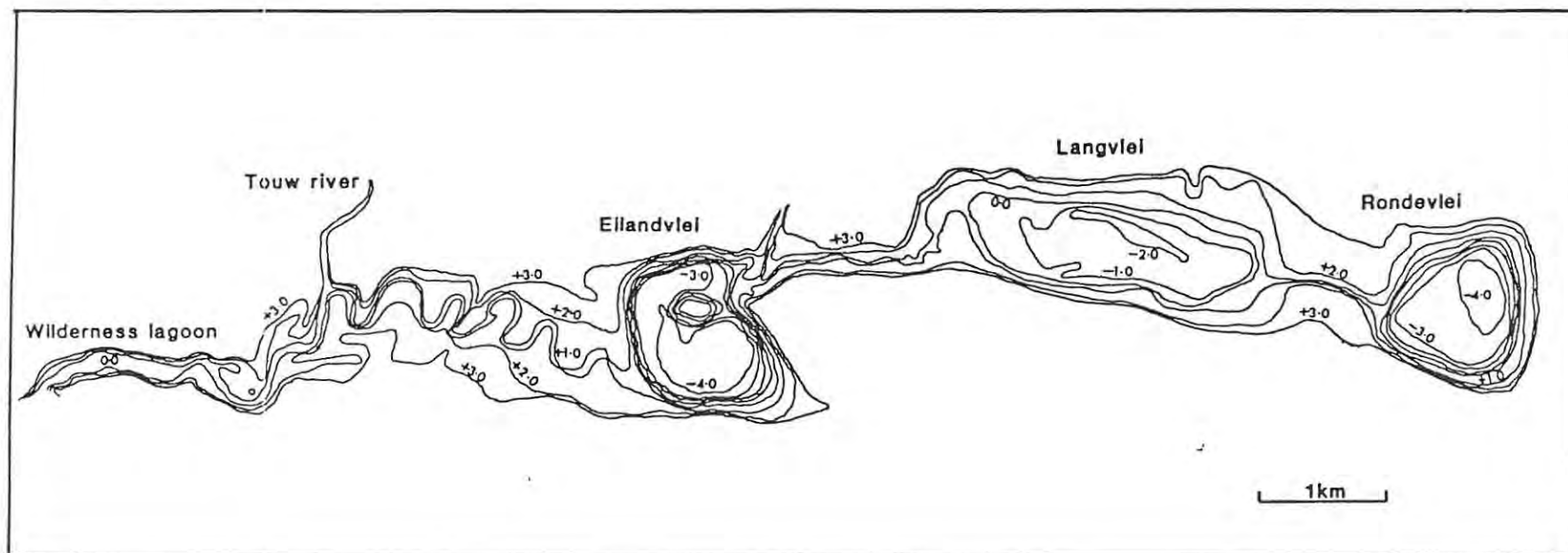


Figure 2: Bathymetric map of the Wilderness lakes system (contours in metres relative to msl). Adapted from CSIR, (1981).



Figure 3: Aerial view of Langvlei (foreground) and Rondevlei.



Figure 4: Aerial view of Eilandvlei.



Figure 5: The Langvlei/Rondevlei channel over a period of low water levels.



Figure 6: The Langvlei/Rondevlei channel during flood conditions.



Figure 7: The Eilandvlei/Langvlei channel over a period of low water levels.



Figure 8: The Eilandvlei/Langvlei channel during flood conditions. Note severe macrophyte encroachment in comparison with the Langvlei/Rondevlei channel.

system is shown in Figure 2. Rondevlei is the lake with the smallest surface area (1.43km^2 ; Martin, 1962) and volume. Its maximum depth is approximately 6.0m and as might be expected of a deflation hollow, its shoreline development approaches unity. Langvlei is the shallowest lake, its maximum depth is 4.0m. In spite of this however, it has the largest surface area (2.16km^2 ; Martin, 1962) and the greatest volume (CSIR, 1981). Figure 3 shows an aerial view of both these lakes.

Eilandvlei (Figure 4) is the lake most characteristic of a segmented system. According to Orme (1973) the more rounded a lake, the more advanced its stage of segmentation. The shoreline development of this lake was calculated to be 1.21 (Table 1) indicating that it is approaching circularity. With a maximum depth of 6.5m it is the deepest in the system. Its surface area is 1.5km^2 (Martin, 1962) and it is broken by "Drommedaris eiland" after which the lake is named.

All three lakes are surrounded by littoral vegetation. Scirpus littoralis forms the inner zone and Phragmites australis and Juncus kraussii dominate the more landward zones. A marsh composed mainly of the latter surrounds much of the southern and western areas of Langvlei and extends to form a 15ha area around the Eilandvlei-Langvlei channel.

The channel connecting Langvlei and Rondevlei (Figures 5 and 6) was dredged over the site of an artificial cut in 1975. Its straight edges are determined by levees from the resulting spoil. In November 1982 I examined its bathymetry by taking depth measurements at 0.5m intervals across 22 transects along its length. Its depth relative to mean sea level could then be calculated from water levels recorded in both Langvlei and Rondevlei. At this time its mean breadth was 9.2m and its bottom was calculated to lie about 0.4m above msl. However, a sandbar at its western extremity is exposed when the level of Langvlei drops below 1.1m above msl. Free water exchange between the lakes is then prevented.

The Eilandvlei-Langvlei channel (Figures 7 and 8) is 1.6km long and when surveyed, had a mean width of 8.4km. It is shallower than the Langvlei-Rondevlei channel and most of it lies 0.7m above msl. It was



Figure 9: Aerial view of the Serpentine. The position of the sluice is marked by an arrow.



Figure 10: The sluice in operation.



Figure 11: The head of water maintained by the sluice can be determined by lowering or lifting a series of wooden slats.

calculated that when water levels in the lakes drop to 1.0m above msl, areas within the channel become exposed and free water exchange between the lakes is prevented. Unlike the Langvlei/Rondevlei channel, it has many inlets and backwaters penetrating the surrounding swamp. Aquatic macrophytes also grow prolifically in it. Figures 5-8 show that even at high water levels, this channel is severely choked by macrophytes in comparison with the Langvlei-Rondevlei channel. This important point will be discussed further in each of the remaining chapters.

The Serpentine (Figure 9) meanders through a 54ha reed swamp between Eilandvlei and the Touw river and is approximately 5.6km in length. Most of its bottom lies at mean sea level (CSIR, 1981) and its maximum depth is about 2.0m. It joins the Touw river approximately 2.5km upstream from its mouth in the upper region of Wilderness lagoon.

Approximately two-thirds up the length of the Serpentine towards Eilandvlei is the sluice gate (Figures 9 and 10). This was constructed between November 1981 and May 1982. One of its functions is to prevent a drawdown of water in Langvlei following the dredging of the Eilandvlei/Langvlei channel. However, during the present study this channel was not deepened. Another function is to increase the water depth in the lagoon for the maximum length of time in order to enhance its recreational potential. When the mouth is closed the sluice is left open while river discharge steadily increases water levels throughout the system. Once the mouth opens the sluice is shut, retaining water in the lakes, while the area below it drains out to sea. With no water draining from the lakes, the scouring action of the water passing through the mouth is less, so the mouth closes sooner than without hydraulic manipulation. Water is then gradually released from above the sluice, thereby increasing lagoon depth sooner than if the natural hydraulic regime had been maintained.

The concrete superstructure of the sluice channels the water in the Serpentine through a 420cm cross-section which can be blocked by a series of horizontal wooden slats. These slats are slotted between two guide rails either side of the superstructure and placed on top of each other (Figure 11). The head of water maintained by the sluice can therefore be regulated by altering the number of slats in position. A



Figure 12: The upper reaches of Wilderness lagoon.



Figure 13: The lower reaches of Wilderness lagoon

potential effect of the sluice is to artificially increase the ecological consequences of segmentation.

The Serpentine flows into the upper region of the lagoon which is surrounded by Phragmites australis (Figure 12). Some of this area lies as deep as 3.5m below msl (CSIR, 1981). Most of the lower lagoon is less than 1.0m deep when the mouth is open and it is wider than the upper lagoon (Figure 13). In places it is 100m across and surrounded by private property developments which have caused the destruction of local emergent vegetation.

The major source of freshwater to the system is the Touw river which has cut a steep valley through the Tertiary platform to reach the sea at Wilderness (Figure 14). Hughes and Gorgens (1981) have reported that the catchment area of this river is 80km², whilst the CSIR (1981) state that it covers 103km². Its maximum water course is 33km. Only 0.2% of the catchment is used for agricultural purposes, 15% is managed plantation and 85% natural veld and forest. Most of the veld is fynbos (southern Cape heathland; Moll and Jarman, 1984). It is thus quite pristine.

As a typical acid Cape river the waters of the Touw river are brown in colour, acidic, and rich in humic substances (Figure 15). These are mostly derived from the microbial degradation of plant material (Cole, 1979) and are therefore rich in carbon. The humates have chelating properties and so tend to combine with inorganic substances such as phosphates, iron and calcium. They are also resistant to further biological degradation and chemical oxidation (Wetzel, 1975). This generally renders substances bound up in them unavailable for recycling within the water column. As less leaf litter falls from fynbos than from deciduous trees (King and Day, 1979), these waters have low quantities of non-colloidal or dissolved material. What is present, is not readily broken down because of low numbers of bacteria in the water. It can therefore be concluded that the Touw river is a poor source of readily degradable allochthonous detritus. The light climate of the nearby Karatara river was investigated by Allanson and Howard-Williams (1984) who concluded that because of the humates and high specific attenuation of blue light, the river was unproductive.

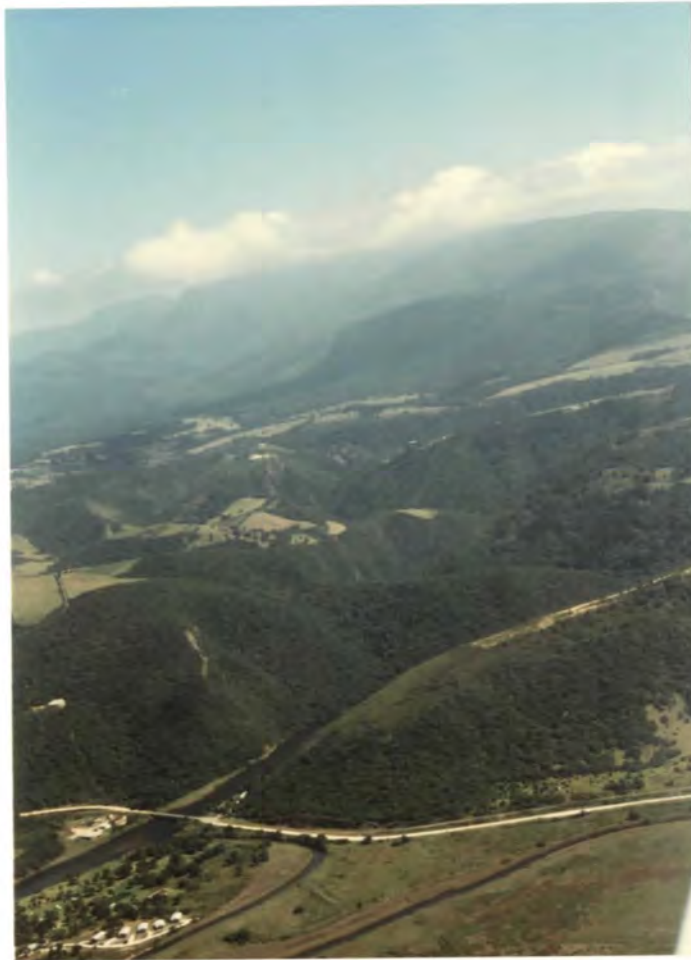


Figure 14: The Touw river cuts a deep valley through the foothills of the Outeniqua mountains.



Figure 15: A gauging station on the Touw river. Note heavily stained humic water

The CSIR (1981) have calculated that the Touw river is the source of 80% of freshwater entering the lakes. Most of the remaining water enters via the Duiwe river which, because of agricultural malpractice, has a highly degraded catchment. Analysis of water from this river over the present study showed that, following high rainfalls, it carried concentrations of nitrate (N) and total phosphate up to $170\mu\text{g l}^{-1}$ and $280\mu\text{g l}^{-1}$ respectively, as well as sediment loads of up to 476mg l^{-1} .

As the Touw river basin's lag time is only 12 hours (Hughes and Gorgens, 1981), heavy rain can cause it to swell rapidly. When this occurs, flood water in its lower reaches is directed along the Serpentine. A back flow towards Rondevlei results, causing water levels in all three lakes to rise. The lakes therefore buffer water level changes in the lagoon.

In common with many other estuaries in southern Africa, western Australia and other arid areas (Day, 1981a), the mouth of the Touw river is not permanently open to the sea. On the sandy shores of high energy coasts such as the Wilderness-Knysna embayment, marine processes tend to form bars across the mouths of estuaries. Depending on the magnitude of fluvial discharge, these bars may be scoured or strengthened until the mouth closes. Once closed, the water level in the estuary rises due to freshwater inputs and eventually the sandbar is topped, and the mouth breached. Such estuaries have been termed blind estuaries (Day, 1951) and bar-built estuaries (Jennings and Bird, 1967).

During periods of exceptionally heavy rain, the buffering capacity of the lakes is not high enough to prevent a significant rise in the water level of the lagoon. This causes the sandbar at the mouth to be breached, hence causing the system to drain. In practice the mouth is opened by dredging when low lying property at Wilderness is likely to be flooded. It is predicted that by maintaining the height of the sill at the mouth of the lagoon between 2.1 and 2.4m above msl, all floods except those with a return period of one hundred years will be prevented from inundating the Wilderness area (CSIR, 1982).

2.3. Climate

The Outeniqua mountains exert a considerable influence upon the weather in the George-Knysna area. Their effect on shallow weather systems frequently produces orographic mists and rain and in addition, complicate air movements producing anabatic and katabatic winds (Tyson, 1971).

South-westerly winds predominate throughout the year, although in summer there are often south-easterly anabatic winds. During the winter north-easterly (berg) winds are common. Howard-Williams and Allanson (1978) have reported that about 80% of the winds are below 20km h^{-1} and speeds above 30km h^{-1} seldom occur.

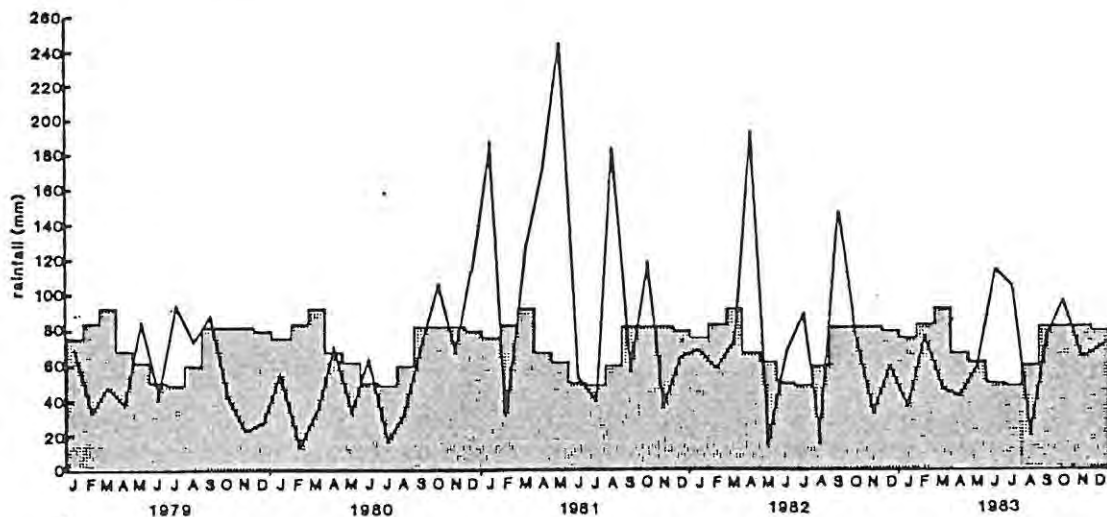


Figure 16: Monthly rainfall recorded at Swartvlei from January 1979 to December 1983. The shaded histogram represents average monthly rainfall recorded at George (Tyson, 1971).

The Wilderness lakes lie between the western Cape winter rainfall region and the eastern Cape summer rainfall area so precipitation tends to be aseasonal. There is however, a slight minimum in June and July and a maximum during February and March (Figure 16). Whilst the mean annual rainfall at Swartvlei between 1975 and 1983 was 733mm, Midgley and Pitman (1969) state that higher rainfalls occur in elevated catchments, especially to the east. Gorgens and Hughes (1980) report that the catchments of the Touw river, Duiwe river and Langvlei stream each receive just over 900mm per annum. Evaporation in these catchments

increases towards the north and in the headwaters of the Touw river is about 1600mm per annum (Pitman et al. 1981). In the coastal region however, evaporation is lower and at Swartvlei a mean of 1127mm has been recorded (Howard-Williams and Allanson, 1978). This is higher than the mean annual rainfall. During the present study rainfall was below the monthly average for 71% of the time.

The mean daily maximum temperature range recorded at the Rhodes University Swartvlei field laboratory is from 19°C in winter to 26°C in summer, whilst the mean daily minimum range is from 6°C in winter to 16°C in summer (Howard-Williams and Allanson, 1978). The absolute minimum and maximum temperatures recorded at Swartvlei field laboratory are 2°C and 34°C respectively.

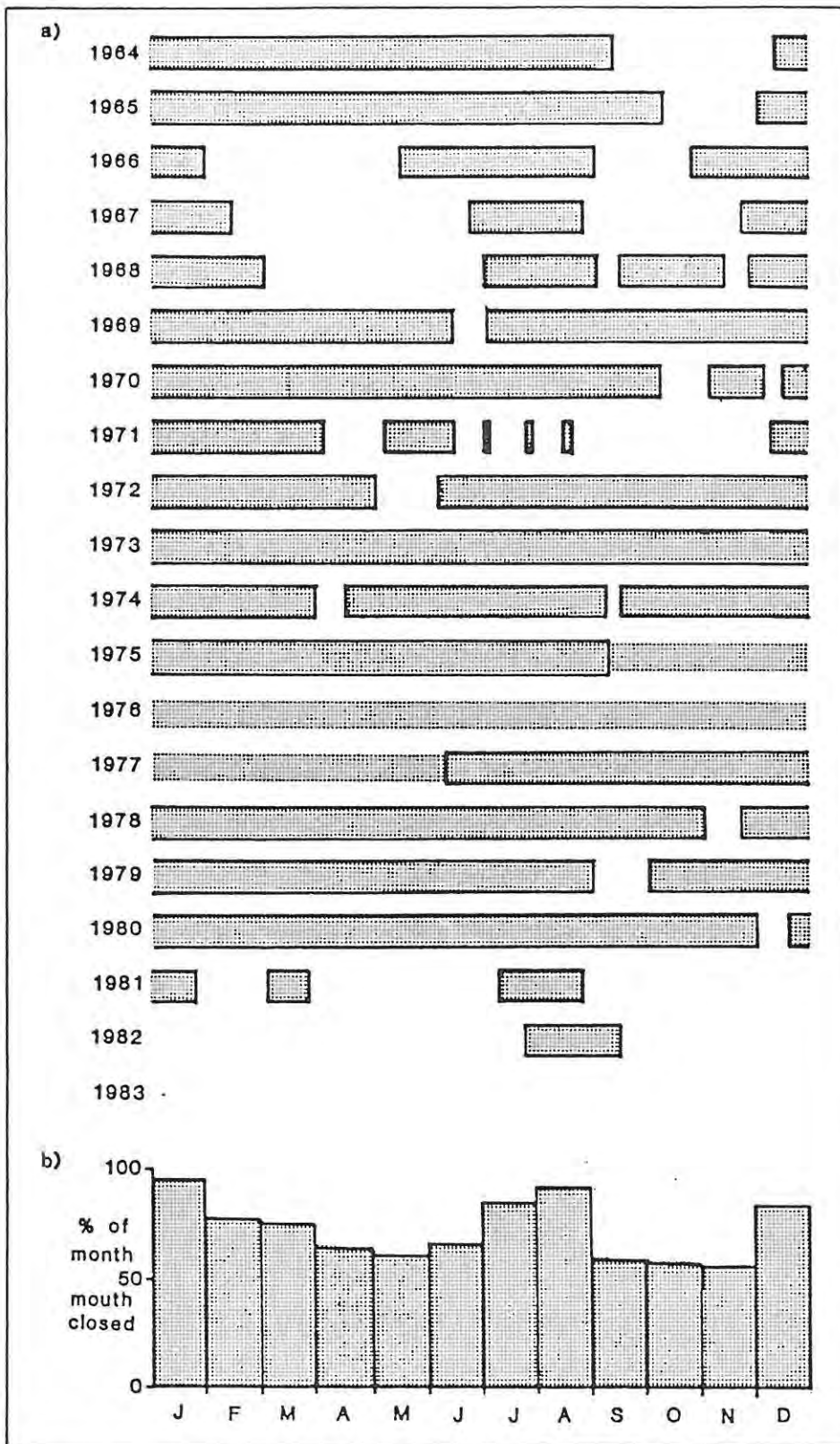


Figure 17: Sandbar status at the mouth of the Touw river between January 1964 and December 1983; a) historical record of mouth closure,  = mouth closed, unshaded areas = mouth open,  = period of missing records. b) mean percentage of each month that the mouth was closed over the above period.

PART II

1

CONDITIONS PRIOR TO THE STUDY

1.1. Hydraulics and sandbar status

Both the hydraulics and hydrology of the system have been discussed in detail by Gorgens (1979, 1980), Hughes and Gorgens (1981), Gorgens and Hughes (1980, 1982) and the CSIR (1981, 1982). As with all periodically closed estuaries, the degree of constriction imposed upon water flow by the mouth is dependent on the relationship between sandbar status and fluvial discharge.

A recent history concerning the status of the sandbar at the mouth of Wilderness lagoon is shown in Figure 17a. Figure 17b shows that the mouth is most commonly open during the spring months of September, October and November. Over the 15 year period between September 1964 and September 1979, the mouth was open for 970 days, which is equivalent to 27% of the time (Figure 17b). However, between January 1979 (when regular physico-chemical data from the system first became available) and January 1983 (when the collection of these data ceased) the mouth was open for 45% of the time. Furthermore, during the present study the mouth was closed for only 52 days, i.e. it was open for 90% of the time. From the data available for the last twenty years, it therefore seems that this work may have been completed over a period when the mouth was open for an unusually long time. It is possible that the complex interaction of factors responsible for mouth closure such as longshore sand movement, wave patterns and wind direction were not conducive to bar formation. However, the reasons why the mouth remained open for so long were more probably:

(1) In 1981 persistent heavy rains caused high discharges from the Toub river which kept the mouth of the Wilderness lagoon open. In addition, on 3 March 1981 the lagoon was artificially closed by a bulldozer moving sand from the adjacent beach and dunes into the mouth. Three major floods occurred in the following three months which may have scoured the mouth very efficiently.

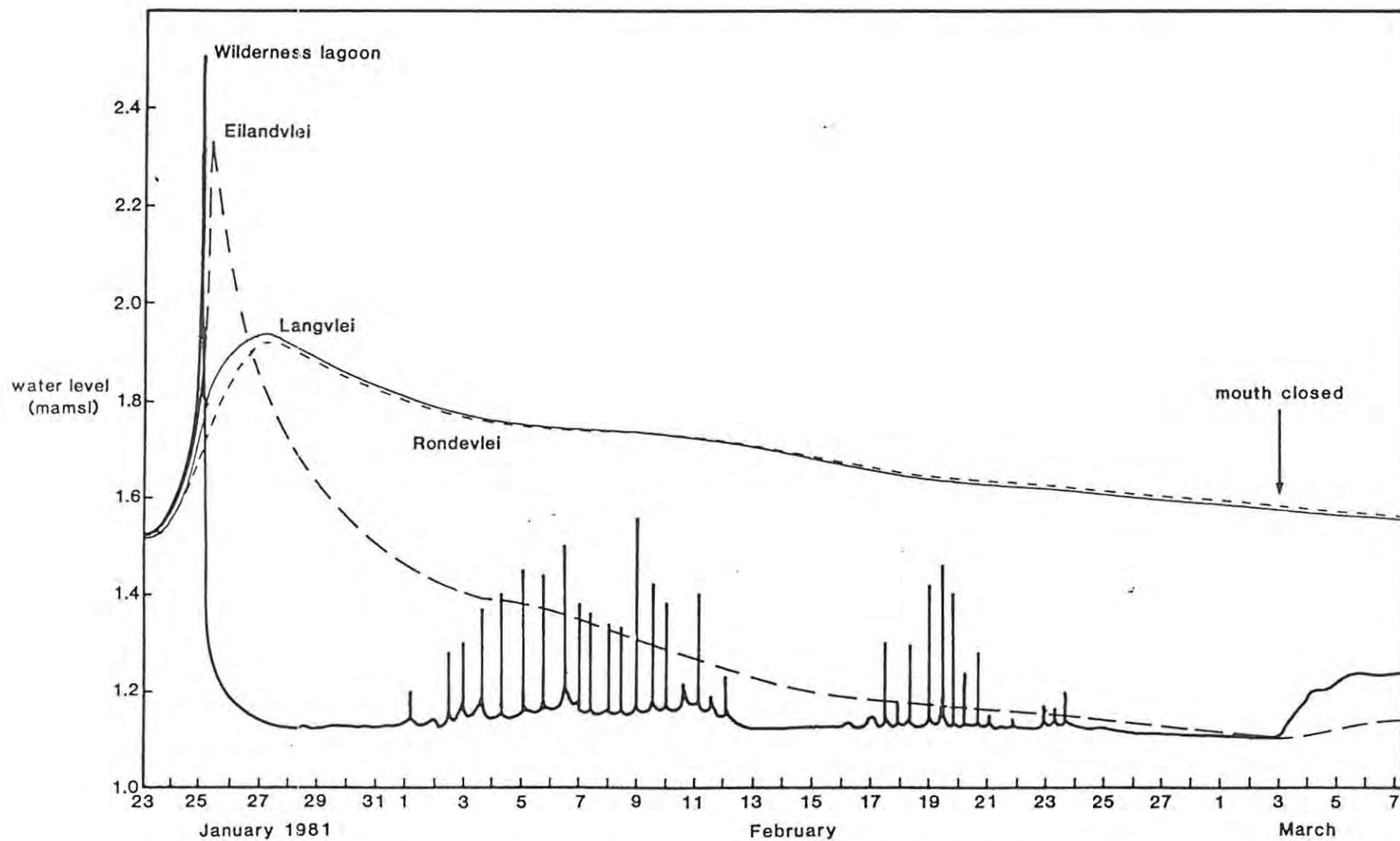


Figure 18: Water level fluctuations throughout the Wilderness lakes system following a flood on 25 January 1981.
(Raw data supplied by the Department of Water Affairs, Pretoria.)

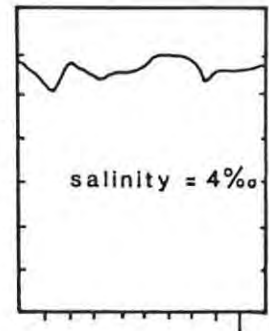
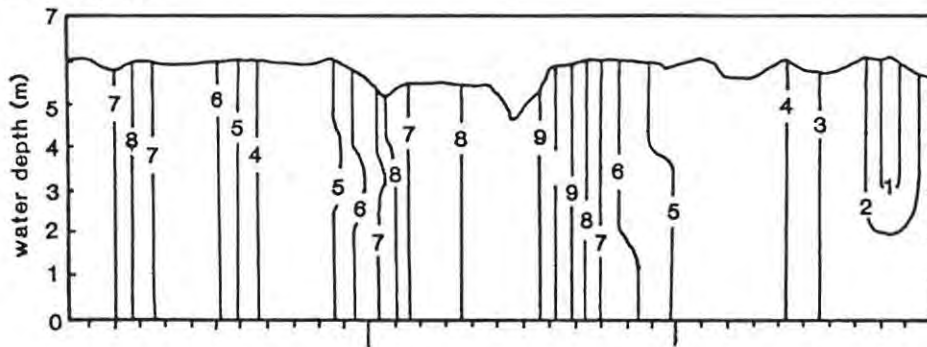
(2) Under normal circumstances bar formation is due to longshore drift and aeolian transport building up sand in the mouth area during periods of low discharge (Heydorn and Tinley, 1980). After the floods, and following the artificial closure, it seems that an unusually large portion of sand was washed out to sea. Without these sand reserves bar formation may have been retarded. During 1982 and 1983 it is probable that natural erosional and depositional processes along the coastline were restoring these lost "deposits".

The consequences of these floods upon some physico-chemical properties of the system will be discussed in section 1.2. of this chapter. However, an examination of water levels throughout the system following a flood on 24 and 25 January 1981 illustrates the effect of the constrictions upon the hydraulics of the system. Figure 18 shows that immediately prior to the flood which opened the mouth, the levels of the lakes and lagoon were approximately in equilibrium. Increased fluvial discharge then caused levels to rise. As the Touw river directly feeds the lagoon, these increases were most marked in this area. On 25 January, when a water level of 2.51m above msl was attained, the mouth breached, causing levels to drop 1.2m within 12 hours. One week after this drop in water level a marked tidal prism in the lagoon became apparent. This must have been absorbed by the Serpentine as it was not observed in Eilandvlei.

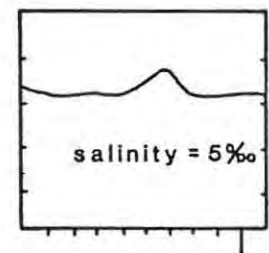
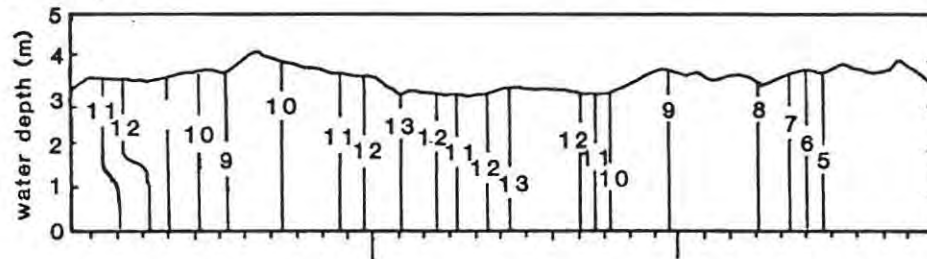
Levels in Eilandvlei also rose sharply, reaching a height of 2.33m above msl at midnight on 25 January. The fact that this peak was reached after water levels in the lagoon had subsided might be explained by a surge of water caused by the initial discharge velocity travelling up the Serpentine. A simple analogy can be made to upstream tidal delay as discussed by Dyer (1973) and Day (1981b). The fact that this surge occurred, and the rise in Eilandvlei's water level mirrored that of the lagoon, illustrates that the constriction imposed by the Serpentine does not severely inhibit flow.

Similarly, water levels in Langvlei and Rondevlei were in approximate equilibrium throughout the whole of this period, thus illustrating that flow between these lakes is also unrestricted. This does not appear to be the case in the Eilandvlei-Langvlei channel. Water levels in

a) Eilandvlei



b) Langvlei



c) Rondevlei

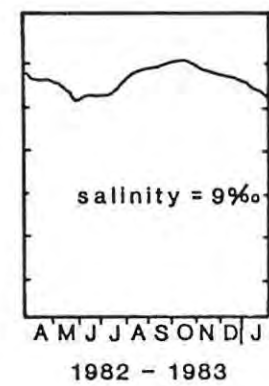
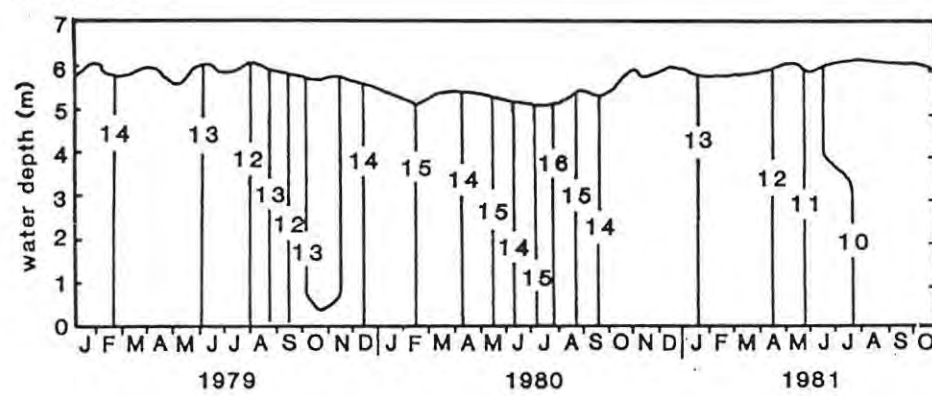
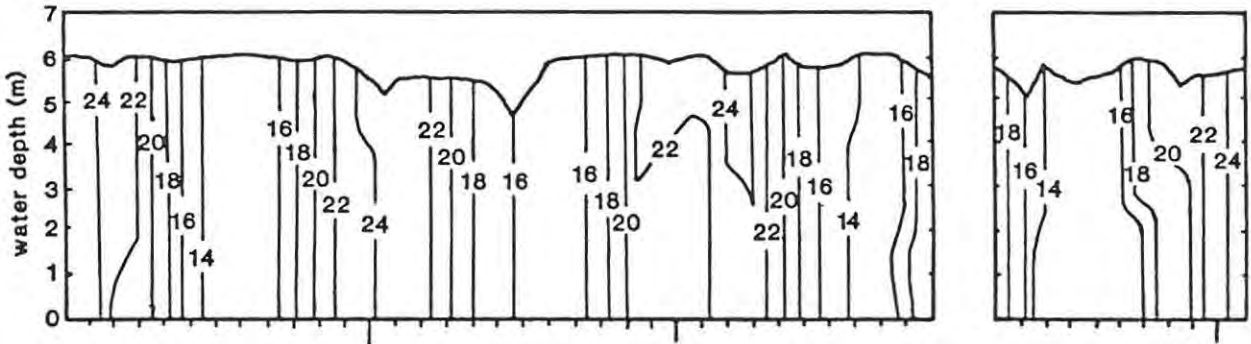
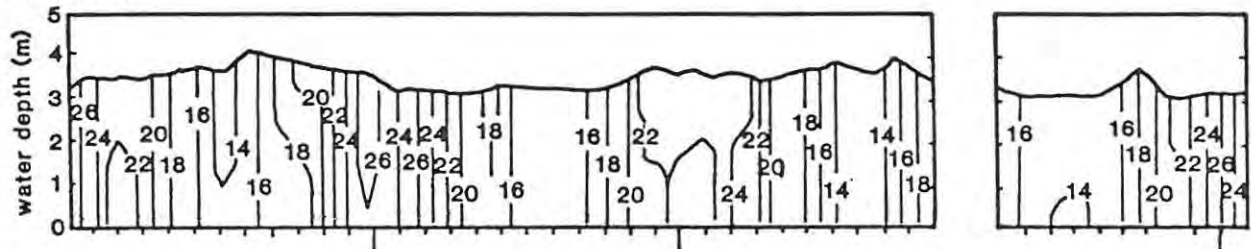


Figure 19: Depth-time distribution of salinity ($^{\circ}/_{\infty}$) in each of the Wilderness lakes between January 1979 and January 1983.

a) Ellandvlei



b) Langvlei



c) Rondevlei

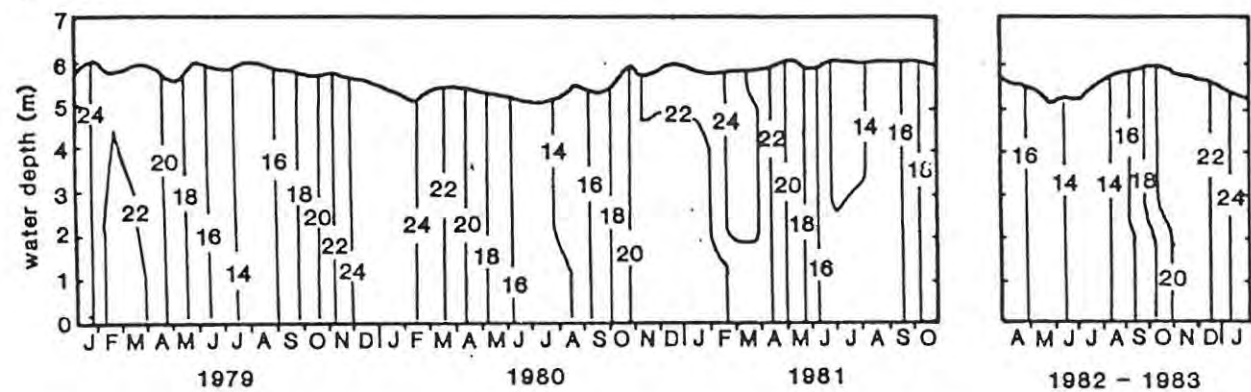
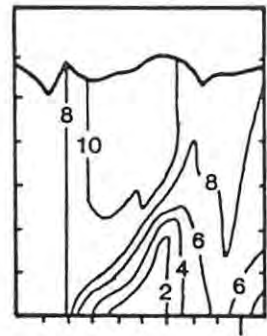
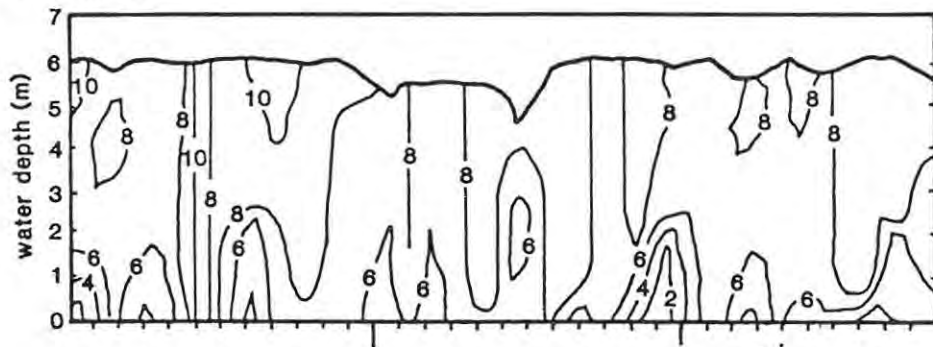
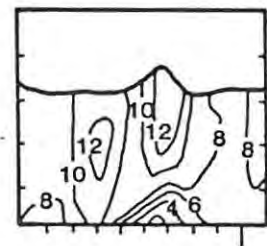
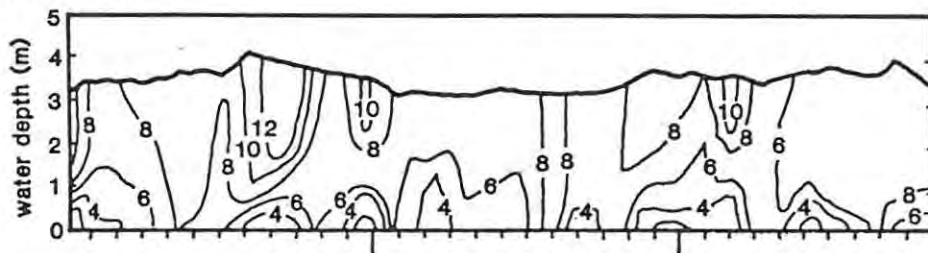


Figure 20: Depth-time distribution of temperature ($^{\circ}\text{C}$) in each of the Wilderness lakes between January 1979 and January 1983.

a) Eilandvlei



b) Langvlei



c) Rondevlei

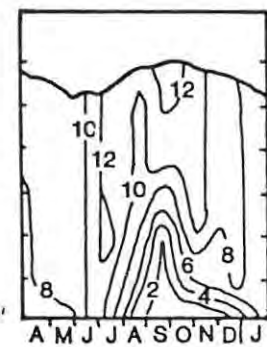
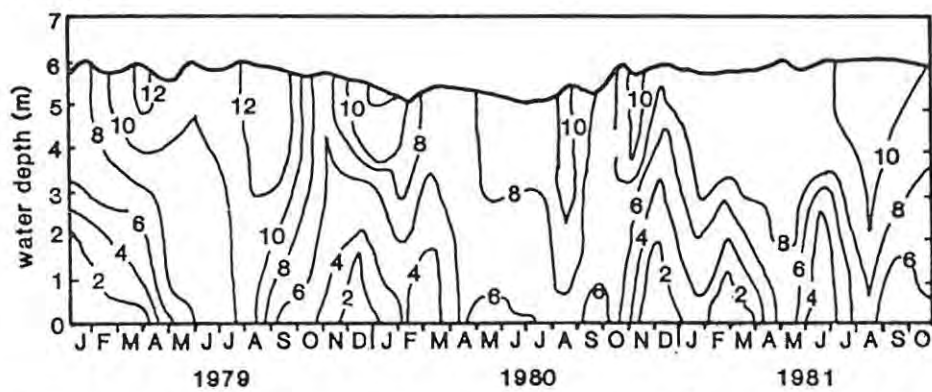


Figure 21: Depth-time distribution of oxygen (mg l^{-1}) in each of the Wilderness lakes between January 1979 and January 1983.

Langvlei and Rondevlei, whilst in equilibrium with each other, did not closely mirror those of Eilandvlei. Flow in the latter channel must therefore have been considerably restricted.

The open phase ended on 3 March 1981 when a bulldozer moved sand into the mouth. The tidal prism noticeable in the lagoon during the brief open phase rapidly disappeared as inputs from the sea were terminated. Similarly, freshwater could not flow out to sea so water levels in the lagoon quickly rose. The concomitant rise in Eilandvlei did not occur until the following day, as water level changes were slightly absorbed by the Serpentine.

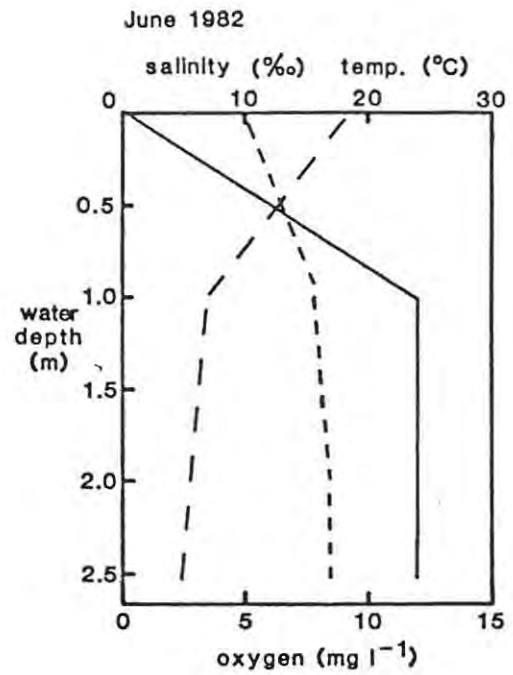
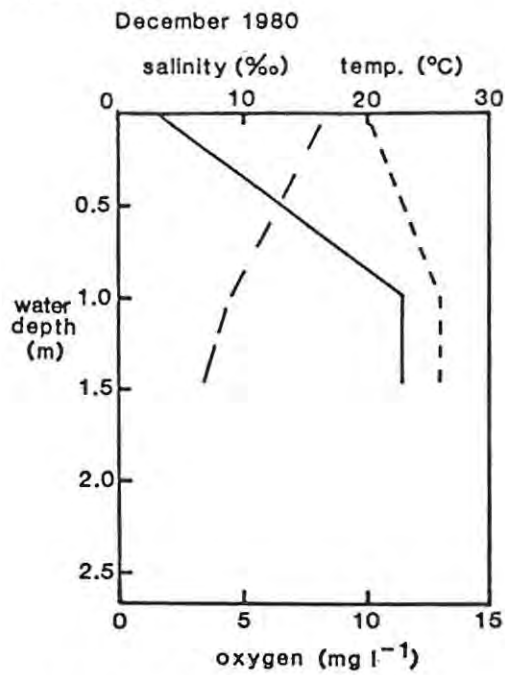
The events described above occurred before the construction of the sluice. However, by the very nature of this constriction it is apparent that the degree to which it restricts water flow is dependent upon its height relative to that of the water around it.

To summarize, it can be seen that the Serpentine and Langvlei-Rondevlei channel allow a relatively free passage of water through them in comparison with the Eilandvlei-Langvlei channel. One reason for this is that the mean depth of the latter is less than those of the other channels (Chapter 2.2. Part I). Another contributory factor is macrophyte encroachment. This will be discussed in more detail in Chapter 4, Part III. In conclusion, it is apparent that the Eilandvlei/Langvlei channel imposes the major permanent constriction in terms of water flow.

1.2. Physico-chemical characteristics

Since January 1979 physico-chemical data from the system have been collected monthly by the Institute for Freshwater Studies, Rhodes University. I analysed some of these unpublished data and showed that, except for brief periods under flood conditions, the limnetic portions of the system are holomictic with respect to salinity and temperature. Depth time distributions of these variables are given in Figures 19 and 20. For comparative purposes these figures have been extended to include data from my study. These data show that for most of the time the shallow nature of the lake basins allows the wind to mix the water

a) mouth open



b) mouth closed

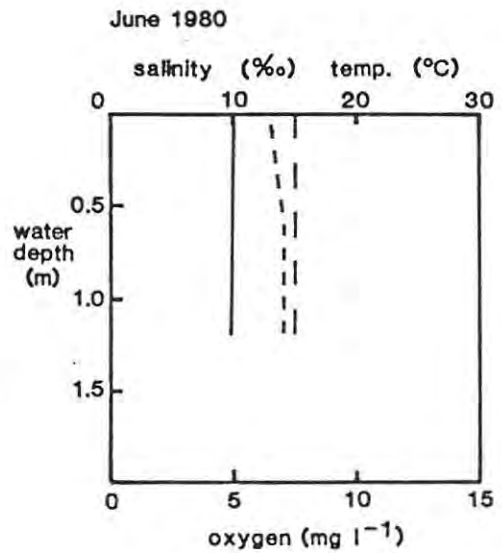
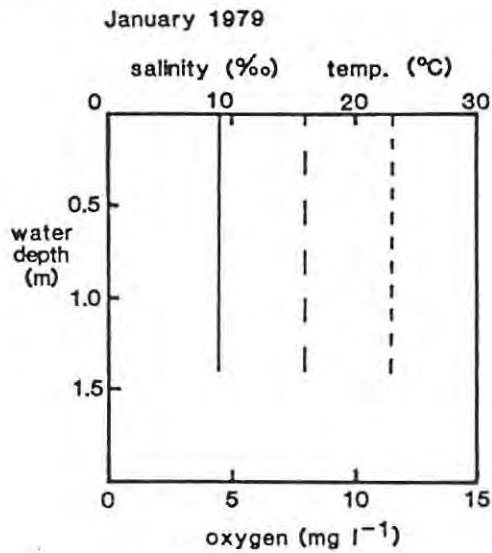


Figure 22: Depth profiles of salinity (—), temperature (---) and oxygen concentration (— —) in the Touw river during summer and winter when the mouth is a) open and b) closed.

column. An unusual characteristic of the system is its reverse salinity gradient. Rondevlei, the lake furthest from the sea, always has the highest salinity, whilst Eilandvlei has the lowest. This can be attributed to the fact that the former is also furthest away from the Touw river and only receives freshwater through precipitation.

The effect of the 1980/81 floods upon the salinity of all three lakes was quite considerable, resulting in the dilution of salt present in each lake. In Rondevlei the salinity dropped from 16 to 10⁰/oo between September 1980 and June 1981, whilst over the same period in Langvlei and Eilandvlei salinities decreased from 10 to 5⁰/oo and 9 to 4⁰/oo respectively (Figure 19). The possible consequences of this dilution upon the ecology of the system are discussed relative to the salinity regime over the present study in Chapter 2, Part III).

The deeper waters of all three lakes, especially Rondevlei, are subject to periods of low oxygen concentration, particularly in the summer months (Figure 21). In Figure 22 salinity, temperature and oxygen profiles recorded from the Touw river during open and closed phases in the winter and summer are shown. When the mouth is open an ectogenic meromixis occurs in both the lagoon and Touw river but, when closed this stratification tends to break down.

The results of data collected prior to the present study have been published by Allanson and Whitfield (1983). They summarize that there are not only chemical differences between the waters of each lake, the lower reaches of the Touw river and Wilderness lagoon, but there are also differences between flood and non-flood conditions within each lake.

Over periods of drought, salinities tend to increase due to increased evaporation and decreased inflows. If lake levels are low and the mouth is open, phosphorus incursion from the sea occurs. Allanson and Whitfield (1983) report that the range of total phosphorus recorded in Wilderness lagoon over drought conditions was 1 - 17 µg l⁻¹, although in flood conditions 39 µg l⁻¹ was recorded. The major source of phosphorus and nitrogen during times of flood is however, the Duiwe river which enters Eilandvlei. The maximum concentration of total phosphorus,

nitrate (N) and sediment load recorded from this river during my study were given in Chapter 2, Part I. During the floods of 1980/81 suspended sediment carried by this river was largely responsible for reducing secchi disc transparency in Eilandvlei to 20cm, whilst total phosphorus and nitrate (N) concentrations rose to $85\mu\text{g l}^{-1}$ and $174\mu\text{g l}^{-1}$ respectively.

Allanson and Whitfield (1983) also reported that changes in the concentration of chlorophyll tended to follow those of phosphorus, but eutrophic conditions arising from floods were short-lived. This is because phosphorus inputs are quickly locked into the sediments of the system, as high oxygen concentrations in its waters keep redox values above +300mv. These results indicate that whilst some of the catchment is mismanaged, the lakes are in a sound ecological condition and are currently capable of absorbing high nutrient inputs via the Duiwe river.

1.3. Aquatic macrophytes

Several authors (e.g. Howard-Williams 1980; Jacot Guillarmod, 1981 and Weisser and Howard-Williams, 1982) have previously investigated macrophyte communities in the Wilderness lakes. Their works show that since 1975 the structure of these communities has been changing constantly. During 1979 and 1980 a major recession occurred in which most of the submerged growth in the lakes disappeared. This has been summarized by Davies (1981). The recession was such that in Rondevlei, which has never supported prolific macrophyte beds, no submerged plants were located in May 1979. By November 1979, the littoral Potamogeton pectinatus beds and extensive charophyte meadows covering the bottom of Langvlei had also disappeared. Following this disappearance, a sudden decline in P. pectinatus in Eilandvlei resulted in the senescence of these previously extensive beds by January 1980. Over the same period a minor recession in other parts of the system was recorded. There was some reduction of P. pectinatus in the Serpentine, whilst in the lagoon a few isolated patches of Ruppia cirrhosa and P. pectinatus disappeared.

Although it is known that water transparency in all three lakes

decreased between 1977 and 1979 (Weisser, 1979), the reasons for this are not clear. Weisser suggested that agricultural malpractice in the catchment areas of the system resulted in increased fertilizer run-off into the lakes, culminating in a dinoflagellate bloom. A more likely explanation for the decline in Langvlei was proposed by Howard-Williams (1980). This is that a fungal disease attacked the charophyte meadows and a long windy spell circulated the nutrients released following decomposition. These nutrients may have been in circulation long enough for an algal bloom to develop, which may have prevented further macrophyte growth. This is a similar hypothesis to that proposed by Phillips et al (1978) concerning a mechanism for macrophyte decline in the progressively eutrophicated waters of the Norfolk Broads. They believe that senescence can often be due to an increased growth and shading by epiphytes and filamentous algae, and that phytoplankton development is a subsequent rather than causative effect.

More recently Allanson and Howard-Williams (1984) have suggested that a simultaneous recession in Swartvlei may have been caused by the cumulative properties of influent water. These brown humic stained waters increase the specific attenuation of blue light in the water column. This attenuation may have been accentuated by successive floods, with a secondary decrease in transparency due to the accumulation of suspensoids, thus further reducing photosynthetic production. Work cited by the above authors suggests that P. pectinatus has a critical dependency on the concentration of calcium and the calcium : magnesium ratio. Persistent flooding may have severely reduced this ratio in the waters of Swartvlei. A similar process may have occurred in the Wilderness lakes system.

Although the definite cause of the macrophyte senescence is unknown, these apparently disastrous fluctuations in macrophyte stocks may be part of long-term natural cycles (Allanson and Whitfield, 1983).

1.4. Fauna

Coetzee (1983) investigated the zooplankton of the Wilderness lakes in 1976. The most important species were the copepods Acartia natalensis and Pseudodiaptomus hessei as well as the larvae of Musculus virgiliae.

The mean daytime standing crops of zooplankton in Eilandvlei, Langvlei and Rondevlei were 6, 17 and 15 mg m^{-3} respectively. At night, numbers in the surface layers increased considerably owing to a general upward migration of zooplankton and benthic organisms. The lowest numbers, but the greatest variety, were encountered in the lagoon where species composition depended on whether the mouth was open or closed.

The distribution and biomass of macroinvertebrates in the system were investigated between 1979 and 1981 by Davies (1981). The fauna is typically estuarine, and includes chironomid larvae, amphipods such as Corophium triaenonyx and Grandidierella lignorum, isopods such as Exosphaeroma hylecoetes and Cyathura estuaria as well as the bivalve Musculus virgiliae, crabs, prawns and polychaetes. Davies' study was carried out during the macrophyte senescent phase discussed in the previous section. At no time were there any macrophytes in Rondevlei. In Langvlei they were scarce and in Eilandvlei they declined throughout the study period. However, he showed that most of the zoobenthos was associated with aquatic macrophytes. It was therefore not surprising that the macrophyte senescence resulted in a major decline in the epifauna of the lake from 297 g m^{-2} dry mass in May 1979 to 23 g m^{-2} dry mass in May 1980.

Prior to the current study, data concerning the fish fauna of the system were lacking. Kok (1981) recorded 23 species in the system which is less than the neighboring Knysna and Swartvlei systems where he recorded 74 and 45 species respectively. He determined that peak recruitment of marine/estuarine species into these estuaries occurs during November, December and January (Kok, pers. comm.). In the Wilderness and Swartvlei systems, this recruitment is dependent on the mouth being open.

A small amount of data from Rondevlei was collected by van Wyk (1977). He showed that between 1972 and 1975 the mean length of marine/estuarine species such as Mugil cephalus, Liza richardsoni and Rhabdosargus holubi increased. This was because the Langvlei/Rondevlei channel had dried up and juvenile fish could not recruit into this lake. Throughout this period there was no evidence that any of these species could breed under such conditions. In 1975 this channel was

dredged, allowing the recruitment of smaller fish into the lake.

PART III

CONDITIONS DURING THE STUDY

1

PHYSICO-CHEMICAL CHARACTERISTICS

1.1. Materials and methods

Both the position of sampling stations and the variables measured in this programme were based on those of Allanson and Whitfield (1983). For the purpose of this analysis data from stations in Rondevlei, Langvlei, Eilandvlei, the Serpentine, Wilderness lagoon and the tidal area of the Touw river were used (Figure 23). At each of these stations salinity, dissolved oxygen and temperature were measured at 1.0m intervals throughout the water column, or at intervals of 0.5m at shallow (2.0m deep) stations. Salinity was measured using a Goldberg optical salinometer (American Optical Corporation) checked with distilled water. Oxygen and temperature were measured with a YSI 15A dissolved oxygen meter calibrated against the Winkler titration. A 140mm diameter secchi disc with black and white quadrats was used to determine water transparency to the nearest 0.1m from the surface.

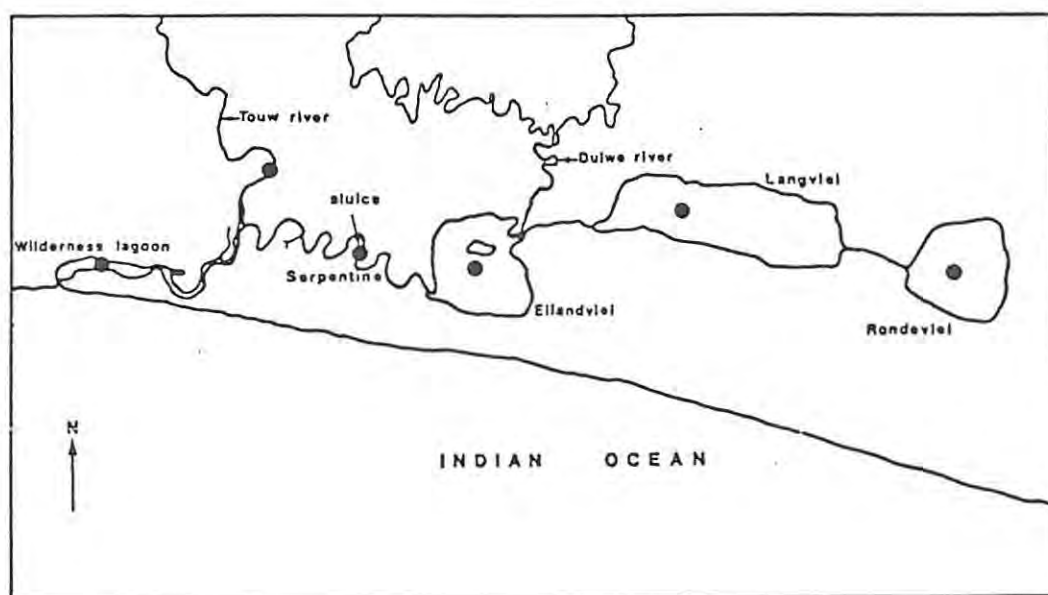


Figure 23: Location of physico-chemical sampling stations mentioned in the text.

Samples for the analysis of pH, alkalinity, phosphorus and nitrate (N) were collected at mid-depth in a Friedinger-Nansen reversing bottle. An integrated sample for chlorophyll a determination was taken using a 5cm diameter hosepipe lowered through the top 1.5m of the water column. All samples were kept in plastic bottles previously cleaned in acid and rinsed with distilled water and, except for chlorophyll analysis, stored in a refrigerator overnight before being analyzed the following day.

Chlorophyll a analysis commenced immediately on return to the laboratory using the method of Golterman, (1969) slightly modified to correct for phaeophytin. Soluble reactive phosphate (SRP) and total phosphate (TP), were determined using the molybdate reduction method of Mackereth, Heron and Talling (1978) modified by Allanson (1981b). Samples for analysis of total phosphate were first digested in a pressure cooker for half an hour with perchloric acid.

Nitrate (N) was determined using the cadmium reduction method described by Strickland and Parsons (1968). A Beckman Electromate (model 1009) pH meter was used to determine pH and alkalinity, the latter being expressed as total alkalinity (Strickland and Parsons, 1968).

In order to simplify the description of variables measured in each of the lakes, Wilderness lagoon and the tidal area of the Touw river, (Afifi and Clark, 1984), a principal components analysis was performed on the combined data using the method of Hull and Nie (1981).

In essence, principal components analysis involves the construction of a correlation matrix between the original variables. From the eigenvectors (correlation coefficients) of this matrix, the analysis computes the linear function of all the variables which will account for as much of the variation in all the samples as is possible. This function is termed the first principal component (C_1). The analysis then goes on to identify a second linear function of the original variables which is independent of the first, and which accounts for as much as possible of the residual variability. This function is defined as the second principal component (C_2). Further components are thus

Table 2: Details of some physico-chemical variables measured in the Wilderness lakes system between April 1982 and January 1983.

	TOUW RIVER	WILDERNESS LAGOON	EILANDVLEI	LANGVLEI	RONDEVLEI
pH $\bar{x} \pm \text{SE}$ (range)	7.60 $\pm$ 0.12 (7.15 - 8.42)	7.89 $\pm$ 0.16 (7.32 - 8.85)	8.12 $\pm$ 1.97 (7.73 - 9.85)	8.36 $\pm$ 0.29 (7.82 - 9.82)	8.45 $\pm$ 1.67 (7.98 - 9.85)
alkalinity (meq l ⁻¹) $\bar{x} \pm \text{SE}$ (range)	2.00 $\pm$ 0.09 (1.71 - 2.45)	1.83 $\pm$ 0.16 (0.58 - 2.45)	1.82 $\pm$ 0.83 (1.37 - 2.27)	1.98 $\pm$ 0.09 (1.60 - 2.51)	1.87 $\pm$ 1.07 (1.35 - 2.33)
chlorophyll a ($\mu\text{g l}^{-1}$) $\bar{x} \pm \text{SE}$ (range)	---	1.60 $\pm$ 0.44 (0.30 - 4.60)	10.40 $\pm$ 3.00 (3.20 - 30.90)	17.30 $\pm$ 4.90 (1.40 - 47.5)	12.50 $\pm$ 1.97 (4.40 - 25.70)
soluble reactive phosphorus ($\mu\text{g l}^{-1}$) $\bar{x} \pm \text{SE}$ (range)	3.00 $\pm$ 0.63 (0.50 - 6.00)	3.60 $\pm$ 0.73 (1.00 - 7.70)	5.00 $\pm$ 1.28 (0.50 - 13.80)	4.90 $\pm$ 1.37 (1.10 - 11.70)	5.10 $\pm$ 0.75 (2.40 - 10.10)
total phosphorus ($\mu\text{g l}^{-1}$) $\bar{x} \pm \text{SE}$ (range)	20.20 $\pm$ 4.60 (1.20 - 51.00)	32.80 $\pm$ 7.05 (7.40 - 78.00)	28.10 $\pm$ 6.07 (6.00 - 72.00)	26.70 $\pm$ 5.59 (7.20 - 51.60)	36.00 $\pm$ 5.67 (8.80 - 57.67)
nitrate N ($\mu\text{g l}^{-1}$) $\bar{x} \pm \text{SE}$ (range)	18.00 $\pm$ 5.60 (3.00 - 62.00)	14.90 $\pm$ 4.12 (1.00 - 43.00)	8.70 $\pm$ 3.03 (0.50 - 34.00)	8.60 $\pm$ 2.16 (1.00 - 21.00)	8.20 $\pm$ 4.62 (1.00 - 49.00)
secchi disc transparency (m) $\bar{x} \pm \text{SE}$ (range)	---	---	1.20 $\pm$ 0.44 (0.40 - 1.70)	1.70 $\pm$ 0.16 (0.80 - 2.30)	1.50 $\pm$ 0.40 (1.10 - 1.70)
bottom oxygen (mg l ⁻¹) $\bar{x} \pm \text{SE}$ (range)	5.60 $\pm$ 0.28 (0.90 - 6.00)	6.80 $\pm$ 0.27 (0.20 - 9.50)	5.10 $\pm$ 0.28 (0.20 - 8.70)	5.20 $\pm$ 0.29 (0.60 - 10.40)	6.30 $\pm$ 0.31 (0.40 - 10.60)
mean oxygen (mg l ⁻¹) $\bar{x} \pm \text{SE}$ (range)	6.60 $\pm$ 0.21 (3.70 - 7.40)	7.90 $\pm$ 0.21 (4.30 - 10.20)	7.90 $\pm$ 0.17 (7.40 - 10.10)	8.10 $\pm$ 0.24 (7.80 - 14.20)	7.90 $\pm$ 0.23 (7.40 - 11.60)

computed until all the variability has been accounted for. The eigenvector of each variable is its correlation coefficient with the principal component. The higher the eigenvector (be it positive or negative) the greater the weighting of its variable in the component. The eigenvalue of a component is the sum of its squared eigenvectors. The proportion of any component's eigenvalue relative to the sum of all the eigenvalues for all the components represents the proportion of variability in the data matrix that is accounted for by that component. Each set of variables from each station (i.e. each row of the data matrix) is then given a score relative to its relationship with each component. The scores for any one component can then be plotted against those for another to represent the relationship between the two components graphically.

1.2. Results and discussion

Over the study period the mouth was closed for only 54 days. It closed on 23 July 1982 and following a minor flood, the only one to occur that year, it breached on 15 September (Figure 17a). Throughout the sampling period water levels were high enough to afford a free exchange between the lakes. A summary of some physico-chemical characteristics recorded from the lakes, Wilderness lagoon and tidal areas of the Touw river over the study period is given in Table 2.

Before examining these results, some physico-chemical variables measured 10m from either side of the sluice before and after its construction merit discussion (Table 3). In April 1982 water exchange between the upper and lower reaches of the Serpentine had been prevented for five months by coffer dams built around the sluice whilst it was under construction. Below the sluice there was an algal scum on the water surface, whilst in the water Potamogeton pectinatus was rotting. Reduced oxygen levels and elevated phosphorus and nitrate levels indicated that the water was stagnant. By May 1982 the coffer dams had been removed and water quality below the sluice was the same as above it.

Table 3: Details of some physico-chemical variables measured above and below the sluice during and after its construction.

DEPTH (m)	BELOW SLUICE						ABOVE SLUICE					
	SALINITY (°/‰)	TEMPERATURE (°C)	OXYGEN (mg l ⁻¹)	SRP (µg l ⁻¹)	TP (µg l ⁻¹)	NO3-N (µg l ⁻¹)	SALINITY (°/‰)	TEMPERATURE (°C)	OXYGEN (mg l ⁻¹)	SRP (µg l ⁻¹)	TP µg l ⁻¹	NO3-N µg l ⁻¹
	<u>April 1982 - during sluice construction</u>											
0.0	12	20.0	5.2	-	-	-	3	19.0	8.3	-	-	-
0.5	18	20.0	0.8	92.0	322.0	9.5	3	19.0	7.1	6.7	27.6	1.0
1.0	19	19.5	0.2	-	-	-	3	17.0	7.0	-	-	-
	<u>May 1982 - after sluice construction</u>											
0.0	3	13.5	8.4	-	-	-	3	12.5	8.6	-	-	-
0.5	3	13.5	8.4	8.6	37.8	9.0	3	12.5	9.2	1.0	33.6	17.0
1.0	3	13.5	8.4	-	-	-	3	12.5	8.6	-	-	-

The cause of this ephemeral eutrophication was that the coffer dams prevented a head of low salinity water from Eilandvlei countering a tidal push of high salinity water from the lagoon. This resulted in saline water from the lagoon accumulating below the sluice and, because of evaporation, its salinity increased (Table 3). These high salinities killed the *P. pectinatus*, which then decomposed. This caused a decrease in the dissolved oxygen concentration in the water and resulted in nutrient release from both the sediments and rotting plant material. The consequences of this localised occurrence shall be discussed with reference to the subsequent distribution of macrophytes in Chapter 3, Part III. However, this situation must be regarded as an isolated event, for in the absence of coffer dams, with the sluice closed there is a constant trickle of water through its slats.

Throughout the study period conditions in the lakes remained constant with respect to salinity. In Eilandvlei the salinity was 4⁰/oo, in Langvlei it was 5⁰/oo and in Rondevlei 9⁰/oo (Figure 19). In the lagoon and Touw river, salinities were generally higher and depended on the state of the tide and stability of meromixis. The lakes were generally holomictic with respect to temperature (Figure 20). The lowest recorded temperature was 13⁰C in Rondevlei during July and August 1982, whilst the highest was 26⁰C recorded in Langvlei during January 1983. The system was well oxygenated but in September and October 1982 concentrations on the bottom of all three lakes dropped to 2mg l⁻¹ (Figure 21). Although this corresponded to a 25% level of saturation, it had no serious consequences as the phenomenon was short lived.

The lowest pH readings were obtained from the Touw river where a mean of 7.6 was recorded. Howard-Williams and Allanson (1978) report that the mean pH of three rivers feeding the Swartvlei catchment is 4.3. A pH of 7.6 might therefore seem a high value for an acid Cape river if it were not for the fact that this station was usually meromictic and samples were taken from mid-way through the water column. This depth often corresponded with the region of the halocline so the low pH values characteristic of the catchment waters were increased through partial mixing with sea water. In general terms, pH increased away from the Touw river to a maximum of 8.5 in Rondevlei. Alkalinity showed

little variation throughout the system with an average value of about 1.9mEq l^{-1} .

Chlorophyll *a* levels in the Touw river were undetectable and in the lagoon never exceeded $4.6\mu\text{g l}^{-1}$. In view of the high light attenuation (Allanson and Howard-Williams, 1984) and low nutrient levels (Howard-Williams, 1977) of such rivers, low phytoplankton stocks in the Touw river are to be expected. The low levels in the lagoon might be attributed to the short residence time of water which is characteristic of the open phase of most estuaries.

In the lakes chlorophyll *a* levels were higher. They ranged from 3.2 to $30.9\mu\text{g l}^{-1}$ in Eilandvlei with a mean of $10.4\mu\text{g l}^{-1}$, whilst in Rondevlei levels ranged from 4.4 to $25.7\mu\text{g l}^{-1}$ with a mean of $12.5\mu\text{g l}^{-1}$. Langvlei had a mean concentration of $17.3\mu\text{g l}^{-1}$ with a range of 4 to $47.5\mu\text{g l}^{-1}$. The latter also had the highest water transparency with a mean secchi disc reading of 1.7m followed by 1.5m in Rondevlei and 1.2m in Eilandvlei. Higher phytoplankton stocks therefore occurred in the lakes with the clearest water. The low transparency in Eilandvlei was probably due to the suspended sediment brought into the lake by the Duiwe river (Chapter 2, Part I). Water levels in Wilderness lagoon and the Touw river were too low to obtain secchi readings.

In comparison with other South African estuaries (Day, 1981d), the system was characterized by low nutrient concentrations. The mean concentrations of SRP $\pm$ SE in Eilandvlei, Langvlei and Rondevlei were $1.82 \pm 0.83\mu\text{g l}^{-1}$, $1.98 \pm 0.89\mu\text{g l}^{-1}$ and $1.87 \pm 1.07\mu\text{g l}^{-1}$. In the lagoon and Touw river there was little variation in the levels of SRP, with means of $3.0\mu\text{g l}^{-1}$ and $3.6\mu\text{g l}^{-1}$ respectively. The concentration of TP in all areas varied between 20 and $47\mu\text{g l}^{-1}$. Phosphorus levels in the Touw river were the lowest from the system but this might be expected considering the low levels of this nutrient in acid Cape rivers (Howard-Williams, 1977; Branch and Day, 1984). Mean nitrate (N) levels in Eilandvlei, Langvlei and Rondevlei were $8.7\mu\text{g l}^{-1}$, $8.6\mu\text{g l}^{-1}$ and $8.2\mu\text{g l}^{-1}$ respectively. In the Touw river and lagoon they were $18.0\mu\text{g l}^{-1}$ and $14.9\mu\text{g l}^{-1}$ respectively. This suggests a riverine origin for allochthonous nitrate and is in agreement with the findings of

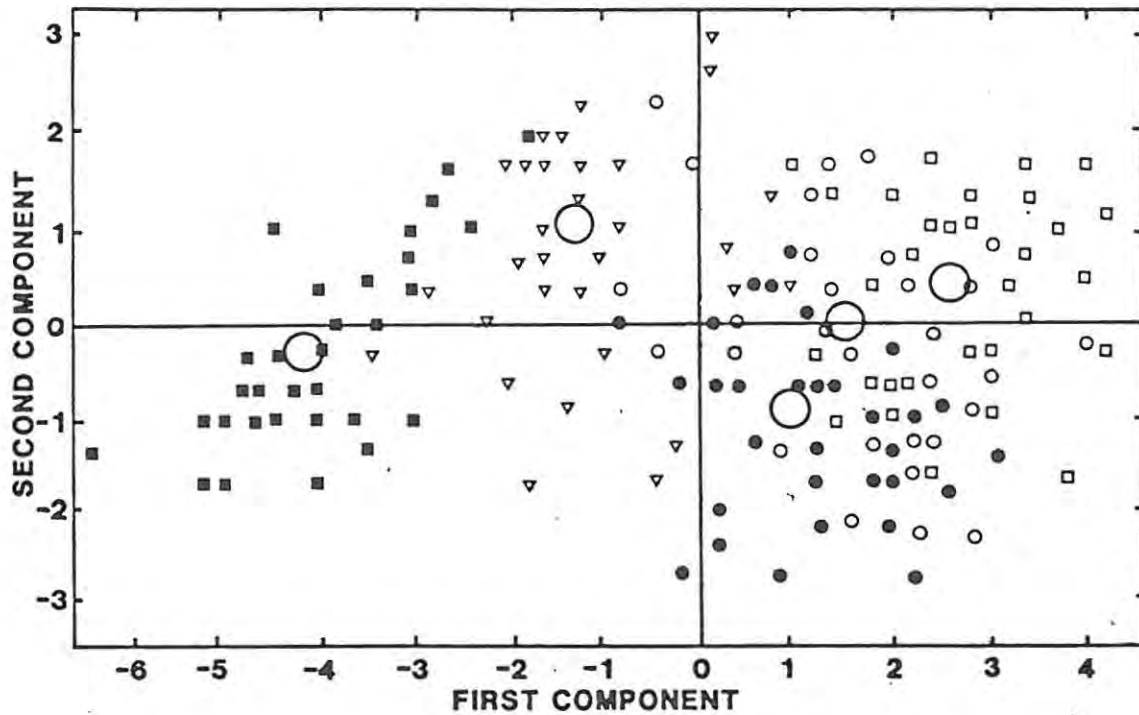


Figure 24: Relationship between physico-chemical entities and the first two principal components extracted from the Wilderness lakes data matrix. Plots for individual stations are shown ($\square$ = Rondvlei, $\circ$ = Langvlei, $\bullet$ = Eilandvlei, $\blacksquare$ = Touw river, ∇ = Wilderness lagoon) as are the station centroids ($\bigcirc$). For further explanation see text.

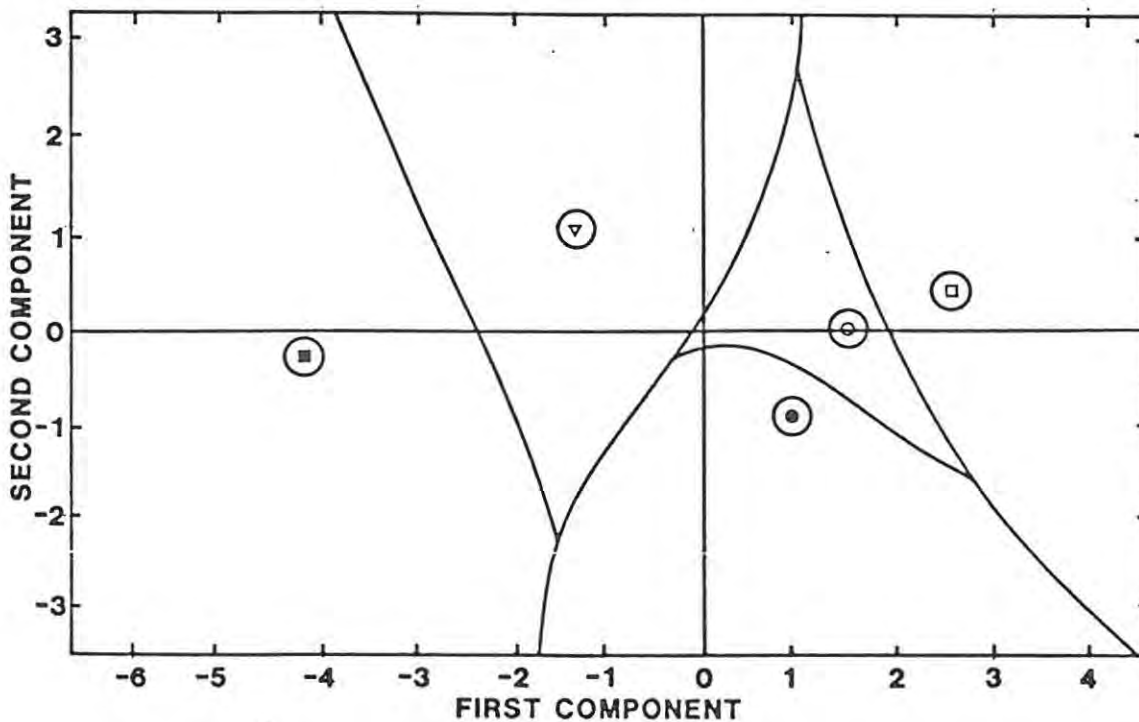


Figure 25: "Territorial map" drawn around the centroid of each station. For further explanation see text.

Branch and Day (1984) for the Palmiet estuary which is also fed by an acid Cape river.

The data presented above compare with those of Allanson and Whitfield (1983) for drought conditions. Their data were combined with those collected during the present study so that a more representative data set could be used for the principal components analysis. This type of analysis is more commonly used for taxonomic purposes (eg Moss *et al*, 1977; van de Venter *et al*, 1984) where it is used to simplify the interpretation of complex interrelationships between morphological measurements. However, it has also been used successfully to describe species associations (Field *et al*, 1980) and habitat differences (Johnson, 1981). More recently Culver and Beattie (1983) have used it to describe differences in the soil chemistry of a Colorado meadow.

In the analysis of the Wilderness lakes system data, the following variables were used; pH, alkalinity, chlorophyll *a*, SRP, TP, nitrate (N), mean water temperature, bottom and mean oxygen concentrations and bottom and surface salinities. Thirty-one measurements of all these variables in each lake were compiled to give a data matrix of 155 readings of 11 variables. Four components were found to account for all the variance in the data matrix (Table 4). As the first 2 components accounted for 97% of the variance in the data matrix, these were the only ones used in this analysis.

Table 5 shows the 4 major eigenvectors of these two components and from these, the weighting of each variable in both components has been calculated. Approximately 50% of the variance of C_1 is accounted for by chlorophyll *a* concentration. This suggests that one of the major discriminant factors between the stations is phytoplankton stocks. Similarly, 58% of the variance of C_2 is accounted for by salinity which suggests that this variable is also of major importance in discriminating between the environments of each station. As chlorophyll *a* concentration and salinity are heavily weighted in both components, it might be suggested that fluctuations in other variables play only a minor role in discriminating between stations.

Table 4: Eigen values of each principal component extracted from the Wilderness lakes data matrix.

COMPONENT	EIGENVALUE	PERCENT OF VARIANCE	CUMULATIVE PERCENT
1	5.48	90.13	90.13
2	0.40	6.60	96.73
3	0.15	2.58	99.31
4	0.42	0.69	100.00

Table 5: Eigenvectors of the first two principal components extracted from the Wilderness lakes data matrix.

FIRST COMPONENT			SECOND COMPONENT		
VARIABLE	EIGENVECTOR	% VARIANCE	VARIABLE	EIGENVECTOR	% VARIANCE
chlorophyll <u>a</u>	-0.67	50	surface salinity	-0.72	38
pH	-0.38	17	bottom salinity	-0.53	20
surface salinity	-0.35	14	chlorophyll <u>a</u>	0.50	19
total phosphorus	-0.26	8	nitrate	-0.32	17
		= 89			= 94

In Figure 24 the scores of each data set are plotted relative to their relationship with C_1 and C_2 . The larger points indicate the location of station centroids (means). As chlorophyll a and pH are heavily weighted in C_1 , the position of each station relative to this component is what might be expected. The Touw river has the lowest score relative to C_1 and examination of the raw data shows that pH and chlorophyll a levels from this station were the lowest in the system. Similarly, Langvlei and Rondevlei which have high scores had high pH values and chlorophyll a concentrations.

The position of the centroid of each station relative to C_2 might also be expected. Eilandvlei, the station with the lowest salinity, has the lowest score and the lagoon has the highest. The proximity of the centroids of Eilandvlei, Langvlei and Rondevlei suggest that their physico-chemical properties are similar. The Touw river is located furthest away from the lakes, whilst the lagoon occupies an intermediate position.

The next step in the analysis was to draw a "territorial map" around the centroids of each station. This represents a hypothetical "ideal solution" to the analysis. Ideally all the scores for each station should lie within the territory around its centroid. This "map" is drawn in Figure 25. A comparison between the observed plots and ideal territories shows that only 66% of the observed plots fell where they were expected (Table 6). This confirms that there was a considerable

Table 6. Territorial overlap between each station (see Figure 25). The percentage of plots from each station in the left hand column that fall within the territory of another station are shown.

STATION	NO. OF CASES	OBSERVED STATION MEMBERSHIP				
		EILANDVLEI	LANGVLEI	RONDEVLEI	TOUW RIVER	LAGOON
EILANDVLEI	31	68	23	3	0	6
LANGVLEI	31	29	32	26	0	13
RONDEVLEI	31	0	29	71	0	0
TOUW RIVER	31	0	0	0	84	16
LAGOON	31	7	10	0	7	75

degree of overlap between some of the stations. In general terms it can be seen that environmental overlap between the lakes was quite extensive. Although there were some similarities between the environments of the lagoon and Eilandvlei and Langvlei, there was no similarity between the Touw river and any of the lakes.

The strongest overlaps were between Langvlei and Eilandvlei and Langvlei and Rondevlei: 29% of Langvlei's plots fell into Eilandvlei's territory and 26% into Rondevlei's. Similarly 23% of Eilandvlei's plots fell into Langvlei's territory. This suggests that according to the variables used in the analysis, the environments in the lakes and especially Langvlei and Eilandvlei are similar. The significance of these results in terms of the distribution of fish will be discussed in Part IV.

2.1. Introduction

In the previous chapter it was suggested that the successive floods during 1981 and 1982 were responsible for flushing much of the salt in the lakes out to sea. Prior to these floods the salinities in all three lakes fluctuated (Figure 19). At the end of 1981 the salinities in each lake were the lowest ever recorded. Throughout 1982 until measurements ceased, salinities remained constantly low at 4⁰/oo in Eilandvlei, 5⁰/oo in Langvlei and 9⁰/oo in Rondevlei.

From November 1981 until the end of the above period, water exchange along the Serpentine was prevented by the construction and operation of the sluice. The hypothesis therefore arose that the sluice was preventing a tidal flux of salt in the Serpentine from replenishing that lost during the floods, thereby potentially resulting in the lakes becoming fresh. This would have disastrous consequences upon the system's flora and fauna which are predominantly estuarine. The early work on estuaries by Remane (1934) has often been cited to show that marine fauna becomes rapidly impoverished as the salinity of the water decreases. More specifically, Whitfield *et al* (1981) have reported that most South African marine/estuarine fish do not occur where there are salinities below 3⁰/oo. The inhibitory effect of the Serpentine and its sluice upon salt flux, and thus the maintenance of an estuarine environment, is therefore of paramount importance in the Wilderness lakes system. Salt flux in the Serpentine under conditions when the mouth was both open and closed was therefore investigated.

2.2 Open phase

To examine tidal flux of salt in the Serpentine the net flux computations discussed by Kjerfve (1979) were used. These are as follows:

Eqn. 1: to calculate the net flux per unit width at time t_1 within one tidal cycle (Xt_1)

$$Xt_1 = \frac{p}{3} \left[0.5 c(d_1 t_1) v(d_1 t_1) + c(d_2 t_1) v(d_2 t_1) + c(d_3 t_1) v(d_3 t_1) \right]$$

(kg cm⁻¹ s⁻¹)

where c = concentration of salt (kg l⁻¹)

v = velocity of water (cm s⁻¹)

d = three depths from surface to bottom

p = density of water (g cm⁻³)

Eqn. 2: to compute the net flux per unit width over one tidal cycle (F)

$$F = \frac{1}{n} \left[0.5 X(t_1) D(t_1) + \sum_{k=1}^{n-1} X(t_k) D(t_k) + 0.5 X(t_n) D(t_n) \right]$$

(kg cm⁻¹ s⁻¹)

where d = absolute depth of water (m)

n = no. of sampling intervals in one tidal cycle

$X(t_k)$ = net flux at time k (kg cm⁻¹ s⁻¹)

This investigation commenced in January 1984, 50 days after all slats in the sluice had been removed. Lake levels had equilibrated and there was a free flow of water along the Serpentine. Salt concentration was determined with a Goldberg optical salinometer (American Optical Corporation), water velocity was measured with a Savonius type rotary current meter manufactured and calibrated at Rhodes University and water depth was measured with a metre stick.

Boon (1977, cited by Kjerfve, 1979) showed that the calculated discharge error for the cross-section of a channel decreases with an increasing number of stations in that section. However, Kjerfve (1978) and Kjerfve et al (1981) state that providing the instantaneous lateral velocity is known, a single sampling location in a cross-section is sufficient to determine flow discharge. Flux was measured through the superstructure of the sluice as this has a rectangular cross-section

and precise volumes of water flowing through it could be calculated. In addition, preliminary investigations established that lateral current velocities through the sluice were uniform across its width. All readings were therefore measured at a point half way across the channel. Readings were taken every 20 minutes per tidal cycle.

Daily tidal fluxes between the spring tides of 18 January and 2 February 1984 are plotted in Figure 26. This shows that the flux of salt along

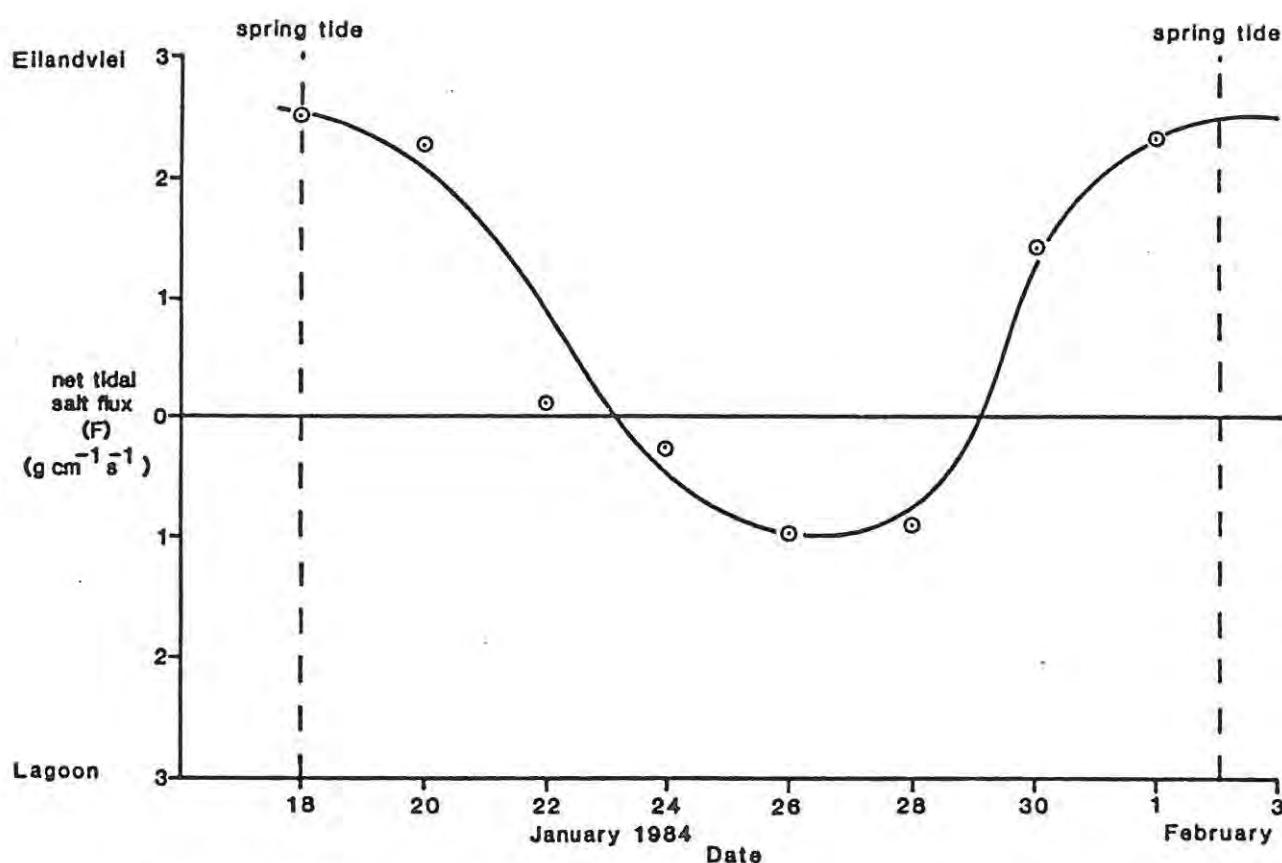
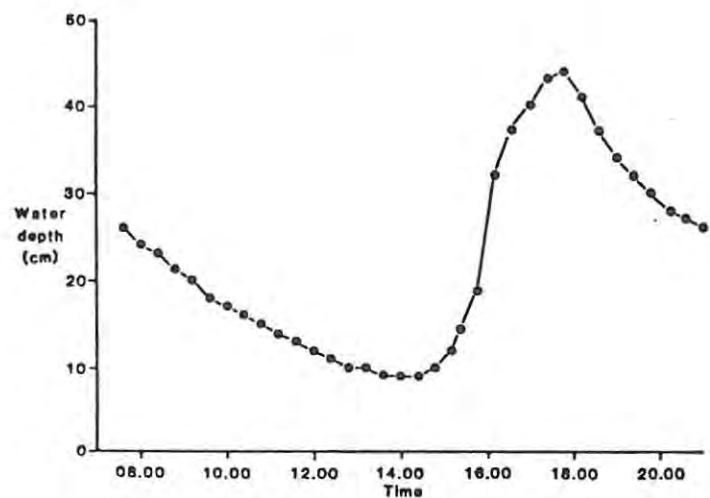


Figure 26: Net tidal salt flux in the Serpentine over a period between two spring tides.

the Serpentine corresponded well with the lunar tidal cycle. During the spring phase the tidal prism was at its greatest, as were water velocities flowing up towards Eilandvlei (Figure 27). This resulted in a net movement of salt up the Serpentine. During the neap phase the amplitude of the prism and water velocities were at their lowest. Over the sampling period water flow at neap tide

a) Water depths



b) Water Velocities

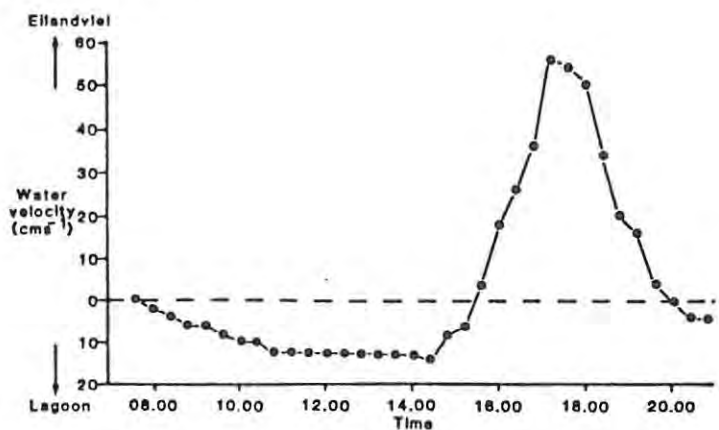
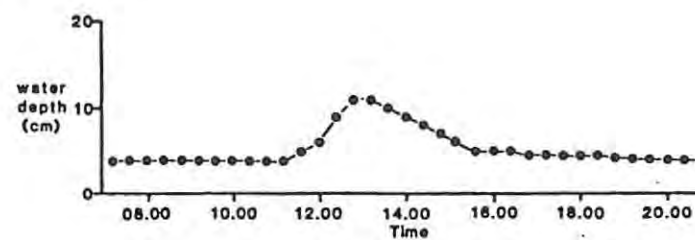


Figure 27: Water depths (a) and velocities (b) recorded at the sluice over a spring tide on 18 January 1984. For further explanation see text.

a) Water depths



b) Water velocities

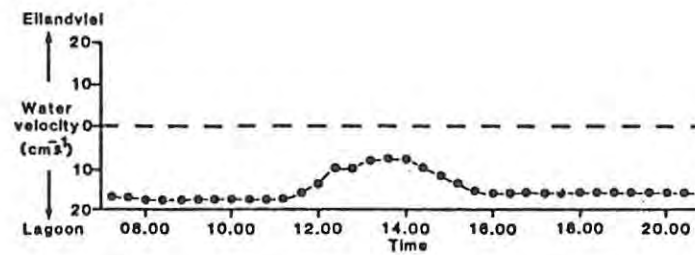


Figure 28: Water depths (a) and velocities (b) recorded at the sluice over a neap tide on 26 January 1984. For further explanation see text.

was always towards the lagoon (Figure 28), resulting in a transfer of salt from the upper to the lower reaches of the Serpentine. Table 7 shows the daily rates of salt flux per centimetre cross-section of the sluice per second over the sampling period which were taken from the curve in Figure 26. To estimate the amount of salt transferred in one tidal cycle these were multiplied by 420 (the width of the sluice in cm) and by 45000 (the number of seconds in a cycle). Finally, because there are approximately two tides per day, these figures were doubled to give a net daily transfer and added together to estimate the absolute gain in salt for the waters above the sluice. These calculations showed that over the examined lunar tidal cycle, 386 tonnes of salt were transported up the Serpentine.

Table 7: Tidal flux of salt in the Serpentine between 12 January 1980 and 1 February 1984. For further explanation see text.

DATE	NET TIDAL SALT FLUX* (g cm ⁻¹ s ⁻¹)	MASS PER TIDAL CYCLE (kg)	DAILY TRANSFER (kg)
18 Jan	+ 2.60	+ 49140	+ 98280
19 Jan	+ 2.40	+ 45360	+ 90720
20 Jan	+ 2.00	+ 37800	+ 75600
21 Jan	+ 1.40	+ 26460	+ 52920
22 Jan	+ 0.70	+ 13230	+ 26460
23 Jan	- 0.10	- 1890	- 3780
24 Jan	- 0.55	- 10395	- 20790
25 Jan	- 0.80	- 30240	- 60480
26 Jan	- 1.00	- 18900	- 37800
27 Jan	- 1.00	- 18900	- 37800
28 Jan	- 0.90	- 17910	- 17010
29 Jan	+ 0.10	+ 1890	+ 3780
30 Jan	+ 1.30	+ 24570	+ 49140
31 Jan	+ 2.00	+ 37800	+ 75600
1 Feb	+ 2.40	+ 45360	+ 90720
Net gain of salt in Eilandvlei =			385560
* + denotes flux toward Eilandvlei			
- denotes flux toward the lagoon			

Most of this salt probably entered Eilandvlei and evidence for this was observed at high water on the spring tide of 2 February 1984. A survey of the upper reaches of the Serpentine and the south-west corner of Eilandvlei showed that salinity intrusion had taken place (Figure 29).

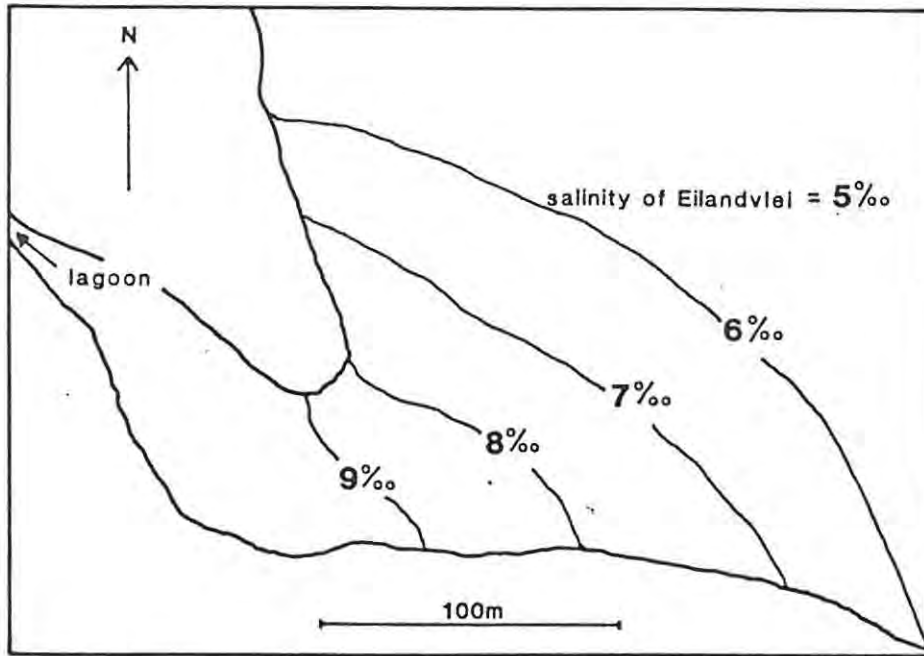


Figure 29: Approximate positions of isohalines protruding into Eilandvlei from the Serpentine during the peak of a spring tide on 2 February 1984. For further explanation see text.

Over the period of the above investigation it was fortunate that environmental conditions were relatively uniform. The underlying rhythm of tidal flux was therefore expressed without meteorological constraints acting upon it. Bowden (1953) noted the effect of wind drift upon tides in the English channel and several authors (e.g. Glen, 1979 and Congdon and McCoomb, 1980) have discussed the effects of weather on estuarine currents. Although the latter state that barometric pressure may affect tidal amplitude in the estuaries of south-western Australia, Dyer (1979) concludes that it is wind that has a major effect upon tides. Farmer and Osborne (1976) and Farmer (1976) have observed the effect of katabatic winds, such as are present around Wilderness, on estuarine stratification and tidal prism in Canadian Pacific estuaries. Whitfield (pers. comm.) has observed that in Swartvlei lake, which is connected to the sea by a 7.2km convoluted channel, strong onshore winds in May 1984 associated with low barometric pressures and spring tides increased the level of the lake by 0.4m over a five day period between a neap and spring tide. Calculations based on data from Liptrot and Allanson (1978) show that to gain an increase of this magnitude, approximately $4080\text{m}^3 \times 10^3$ of

water must have entered the lake. On a normal spring tide only $2040\text{m}^3 \times 10^3$ enters.

Although wind strength in the George-Knysna area is highly unpredictable (Allanson and Howard-Williams, 1984), it seems possible that it can play a major role in determining tidal prism, and thus flux, within the Swartvlei system. The proximity of the Wilderness lakes system to Swartvlei suggests that in the former, wind can also augment tidal flux. Another meteorological factor affecting tidal flux is rainfall which increases river discharge and dampens the tidal prism in estuaries. This has been discussed by Branch and Day (1984) in the Palmiet river estuary and by Barnes (1974) for estuaries in general. Sandbar status at the mouth, (Chapter 1.1. Part II) is also related to discharge and wind, and influences tidal flux even when the mouth is open.

In conclusion, it can be stated that whilst tidal flux in the Serpentine does occur, the interaction of meteorological factors ultimately determine the magnitude of tidal flux in the Touw river system. Interpretation of the data beyond this conclusion is not justified. In a review of twenty years of research into flux measurements in tidal marshes, Nixon (1981) states that because of the unpredictability of flux, no one has yet learned how to attain an acceptable set of long term net flux measurements within estuaries. However, because it has been established that tidal flux of salt occurs in the Serpentine, it can be concluded that if the sluice is closed when the mouth is open, this flux will be inhibited.

The implications of this work are that tidal flux in the Eilandvlei-Langvlei channel is unlikely to ever occur. Over the examination period lake levels were the lowest in five years so in terms of this variable, conditions for flux were ideal. The dampening effect of the Eilandvlei-Langvlei channel on major floods in the system was discussed in Chapter 1.1. Part II. These observations can be extended further to postulate that even when tidal fluctuations in Eilandvlei are observed (e.g. Coetzee, 1978), it seems improbable that a flux could penetrate into Langvlei.

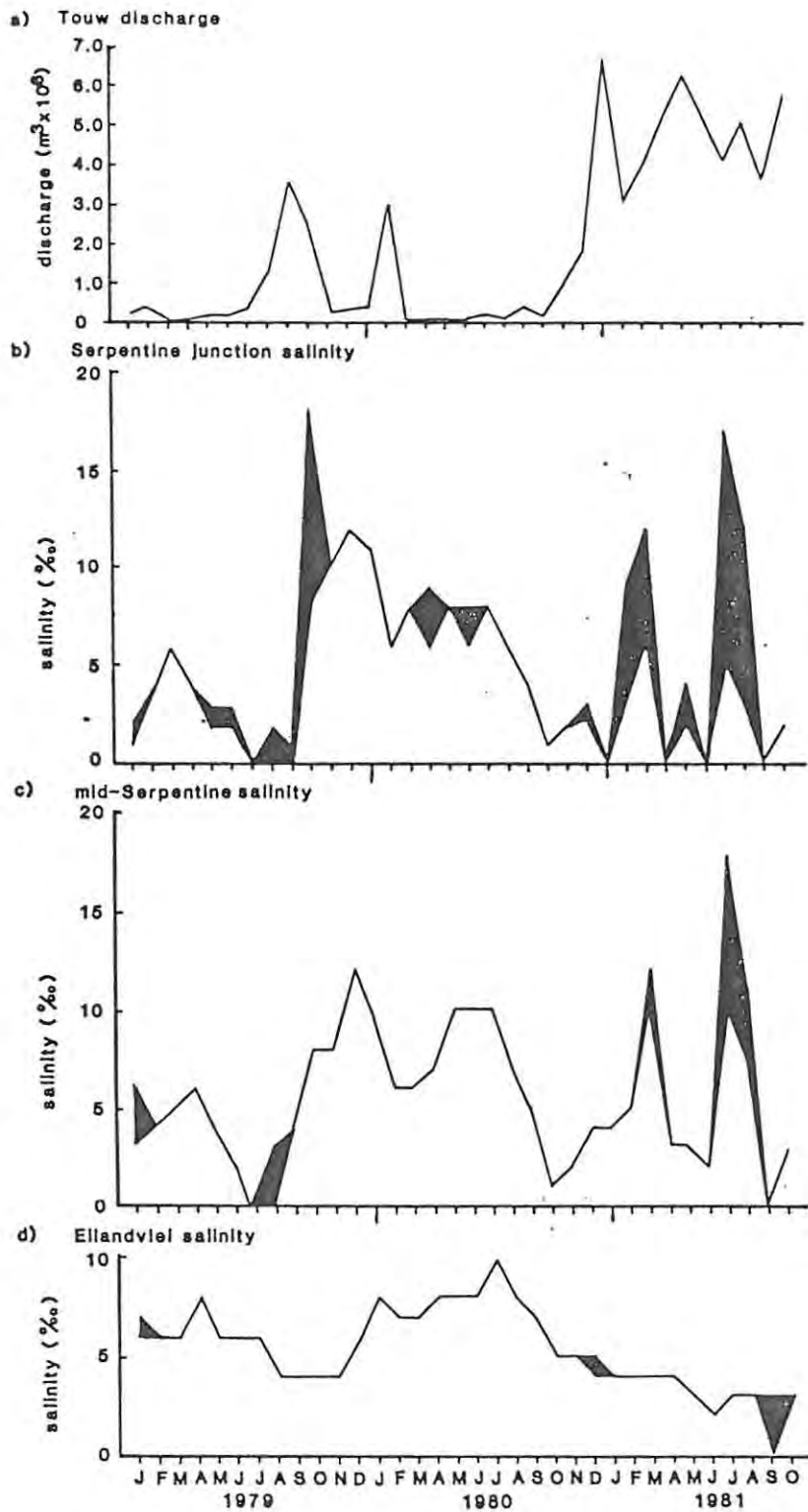


Figure 30: Following high discharges from the Touw river (a) during September 1979, the lagoon mouth opened for one month so that by October 1979 salinities at the Touw/Serpentine junction (b) rose markedly. This salinity peak was then observed to travel up the Serpentine (c) in December 1979 and by January 1980 the salinity of Eilandvlei (d) was observed to rise. Shaded areas represent periods of meromixis. For further explanation see text.

2.3. Closed phase

Once it had been established that tidal flux possibly plays a role in the salt budget of Eilandvlei, fluctuations in salinity during the closed phase were scrutinized more closely. The period between November 1979 and July 1980 was chosen for examination as during this time, the system remained closed to the sea, yet the salinity of Eilandvlei increased from 4 to 10⁰/oo. Similarly, increases from 10 to 13⁰/oo and 12 to 16⁰/oo were observed in Langvlei and Rondevlei respectively. These increases could not be explained by evaporation alone. For example, while the increase in Eilandvlei would have required a loss of 60% of the original water, the volume of this lake only decreased by 13%. Furthermore, it was calculated that over this period the mass of salt in Eilandvlei, Langvlei and Rondevlei increased by 22100, 1386 and 1020 tonnes respectively, i.e. there was a net gain of 24506 tonnes which is equivalent to an 18% increase. The question therefore arose as to where this salt originated?

Analysis of data from other areas of the system gave rise to a second hypothesis that at the Touw-Serpentine junction, discharge from the Touw river mixes with saline water from the lagoon and then carries salt up the Serpentine as it flows towards the lakes. (Figures 30,a-d). A flood in September 1979 (Figure 30a) breached the mouth (indicated by a break in the shading at the top of the Figure) and diluted the water at the Serpentine junction (Figure 30b). Owing to tidal action the salinity at the junction increased to 18⁰/oo in the bottom waters before the mouth closed the following month. During December this peak was observed at a station mid-way along the Serpentine (Figure 30c) and by January 1980 there was a concomitant peak in the salinity of Eilandvlei (Figure 30d). A similar progression can be seen following a flood in February 1980, which resulted in a peak in salinity at the Serpentine junction in April, in the mid-Serpentine in May and in Eilandvlei in June.

In order to test this hypothesis it was necessary to calculate the mass of salt carried into Eilandvlei via the Serpentine and correlate it with the observed increase in salt in all three lakes. This was determined via 4 steps:

(1) Calculation of water volume reaching the Touw-Serpentine junction from an upstream gauging station

$$\text{Water reaching junction} = T_d - (T_a \times e)$$

where T_d = discharge at gauging station ($\text{m}^3 \times 10^3$)

T_a = surface area of river between junction and gauging station (m^2)

e = evaporation (mm)

(2) Calculation of the volume of water entering the Serpentine

$$\text{water entering Serpentine} = \frac{T_d - (T_a \times e) \times 5.09}{5.53}$$

where 5.09:5.53 is the ratio of the surface area of the Serpentine and lakes to the whole system

(3) Calculation of the water entering Eilandvlei

$$\text{water entering Eilandvlei} = \frac{T_d - (T_a \times e) \times 5.09}{5.53} - (S_a \times e) - (R_a \times e \times 0.6)$$

where S_a = surface area of Serpentine (m^2)

R_a = surface area of reedswamp (m^2)

0.6 = a constant giving evapo-transpiration from a reedswamp relative to that of an open lake (see page 59)

(4) Calculation of the mass of salt carried up the Serpentine and deposited in Eilandvlei

$$\text{mass} = S_s \left[\frac{T_d - (T_a \times e) \times 5.09}{5.53} - (S_a \times e) - (R_a \times e \times 0.6) \right]$$

where S_s = concentration of salt in the Serpentine (kg l^{-1})

In this manner the movement of salt up the Serpentine each month from November 1979 to July 1980 was computed. These calculations are summarized in Table 8 which records that over the whole of this period

Table 8: Calculated flux of salt up the Serpentine towards Eilandvlei between November 1979 and July 1980. For further explanation see text.

PERIOD BETWEEN SAMPLING DATES	TOUW DISCHARGE ($\text{m}^3 \times 10^6$)	VOLUME OF DISCHARGE IN SERPENTINE ($\text{m}^3 \times 10^3$)	SALINITY OF SERPENTINE (kg l^{-1})	NET FLUX (tonnes)
Nov - Dec	0.247	161.4	0.014	2260
Dec - Jan	0.364	256.9	0.012	3082
Jan - Feb	2.954	2642.0	0.003	15852
Feb - Mar	0.125	58.9	0.006	353
Mar - Apr	0.123	56.1	0.007	393
Apr - May	0.112	62.7	0.010	627
May - Jun	0.151	79.7	0.010	794
Jun - Jul	0.190	127.5	0.010	1278
Net flux of salt up the Serpentine =				24639

24639 tonnes of salt were transported up the Serpentine and deposited in Eilandvlei by the process discussed above. In comparison with the observed increase of 24506 tonnes this estimate is highly acceptable and represents a discrepancy of less than 1%. However, several assumptions have been made in the above model and the close agreement of observed increases with those calculated may be regarded as fortuitous. Errors inherent to these assumptions and to the model are as follows:

- 1) The surface areas of the lakes and Wilderness lagoon are taken from data published by the CSIR (1981) whereas those of the Serpentine and

Touw river have been estimated from maps. It is not known how accurate these estimations are.

2) Evaporation data from the Wilderness area are not available so mean monthly data from George airport were used.

3) Estimation of the rate of evapo-transpiration was based on a value given by Linacre et al (1970) in Australia and Rijks (1969) (both cited by Smid, 1975). Howard-Williams (1983) also used the same figure. However, there is disagreement between various authors as to the influence of wetland vegetation on water loss from the soil. This is discussed by Priban and Ondok (1980) and highlighted by Bernatowicz et al (1976) who cite two Russian workers (Uryvajev, 1963 and Novikova, 1963) who believe that evapo-transpiration can be three times greater than evaporation from an open water surface or only half as much respectively. Bernatowicz et al (1976) discussed in detail the effect of microclimate upon evapo-transpiration and conclude that the interaction of air temperature, reedbed humidity and wind penetration (affected by reed height) determine water losses. In addition, as evapo-transpiration increases with the density of reeds, it will not only vary between swamps but also within swamps. Variability in the micro-climate of the swamps around Lake Chilwa has been observed by Howard-Williams and Lenton (1975). The factor of 0.6 that of an open water surface should therefore be treated with caution.

4) No attempt has been made to account for losses through ground seepage. However, Pitman (1980) has suggested that only small amounts of water may be lost through seepage in Lake Sibaya, which was formed by similar processes in the Pleistocene glaciation (Hill, 1975).

5) It is difficult to calculate the amount of salt that was initially present in the lagoon. Data available from two stations positioned in shallow water in the lagoon suggest that 18000 tonnes were present. The hypothesis states that the 24000 tonnes of salt observed to enter the lakes must have originally been present in the lagoon when the mouth closed. It is possible that because of salinity stratification present in the lagoon, most of the salt lay in the deeper waters, whilst it was

only the shallower areas that were sampled. This would account for the disparity between these two masses.

6) A possible phenomenon arising from the point above is that of cyclical introduction of salt from the sea via breeze and spray. Yoshimura (1936, 1937) has reported this phenomenon in Japan and cites Delebecque (1894) and Clarke (1924) who have described it occurring in Bordeaux and Florida respectively. However, Allanson and Van Wyk (1969) concluded that salt breeze, which tends to increase the ratio of chloride to sodium, is unlikely to significantly affect the salinity of coastal lakes in Zululand. Unfortunately, data concerning the concentration of these two ions in the Wilderness lakes is unavailable. In view of Allanson and Van Wyk's work, it has been assumed that cyclical introduction does not play a major role in the salt budget of the Wilderness lakes system.

In its current form the model does not therefore represent an empirical solution to salt flux during the closed phase. However, it does suggest a mechanism by which salt can enter the lakes during the closed phase. Furthermore, it suggests that this redistribution may play an active role in the salt budget of the lakes.

2.4. Discussion

In this chapter it was shown that tidal flux in the Serpentine occurs, and over the spring tidal cycle examined, 385 tonnes of salt were deposited in Eilandvlei. The question arises as to whether there is ever a tidal flux in the Eilandvlei/Langvlei channel? Calculations based on the tidal flux data show that on the spring tide of 18 January 1984, there was a net influx of $583\text{m}^3 \times 10^3$ of water into Eilandvlei. Assuming the surface area of the lake to be approximately 1.5km^2 (Table 1), this would increase the level of Eilandvlei by 0.0023m. It is clear therefore, that even if there had been a free connection between Eilandvlei and Langvlei at this time, the rise in the water level of Eilandvlei could not have been sufficient to instigate a flux in the Eilandvlei/Langvlei channel.

According to the observations of Whitfield (pers. comm.) and data from Liptrot and Allanson (1978), strong onshore winds associated with low barometric pressure increased the tidal flux of water into Swartvlei two-fold. A similar increase in the Wilderness lakes system would only result in a water level rise in Eilandvlei of 0.0002m. In view of the observations regarding flow restriction in the Eilandvlei/Langvlei channel (Figure 18), it seems unlikely that tidal flux into Langvlei ever occurs.

During the 15 year period from September 1964 to September 1979 the mouth was open on 26 distinct occasions (Figure 17). On average it remained open for 42 days after initial breaching. Similarly the average time that the mouth was closed between open phases was 169 days. From the tidal flux work it was shown that over a period between two spring tides, 386 tonnes of salt were deposited in Eilandvlei. As the average period over which the mouth is open is 42 days, approximately three spring tidal cycles could occur before mouth closure. The average gain over an open period can therefore be estimated to be 1155 tonnes. (This is possibly an overestimation as tidal flux cannot be initiated until the level of the lakes has drawn down). According to these data the ratio of the mass of salt deposited in Eilandvlei during open and closed phases could be said to be 1155:15623 ie 1:14.

The limitations of assuming the above data as representative have already been discussed and conclusions arising from them must be treated with caution. However, the data presented suggests that more salt enters the limnetic portions of the system when the mouth is closed than when it is open. As policy regarding the use of the sluice is such that it is only closed when the mouth is open, its impact on the salt budget of the system may be minimal.

3.1. Materials and methods

Six littoral transects were positioned at approximately equidistant intervals around both Langvlei and Eilandvlei. The limits of each transect were defined as the edge of the emergent zone and the deepest point at which macrophyte growth was recorded. A macrophyte sampler designed by Howard-Williams and Longman (1976) was used to sample a 0.0625m^2 area at intervals along the length of each transect.

Samples were labelled and returned to the laboratory where each was sorted into species and sun dried before being weighed. To calculate a conversion factor for absolute dry weight, sub-samples of each species were weighed and dried in an oven at 55°C until no further weight loss was observed. Results were expressed as g m^{-2} dry weight. The total biomass along each transect was established by multiplying the mean biomass for each species within each transect by the total transect length.

This process was repeated in May 1982, August 1982, November 1982, February 1983 and May 1983 and supplemented by observations throughout the year. The growth of submerged macrophytes in both Rondevlei and the lagoon was never sufficient to sample effectively. However, notes on the distribution of plants at both localities were made.

3.2. Results and discussion

The results of the macrophyte surveys in Eilandvlei and Langvlei are summarized in Figures 31 and 32 respectively. The pie charts (Figure 31a and 32a) represent the gravimetric contribution of each species to the total biomass of submerged macrophytes recorded in all transects in each season. Figures 31b and 32b show the mean biomass of submerged vegetation per square metre recorded from all stations within each lake. Figures 31c and 32c show the average biomass per transect and the average transect length recorded each season.

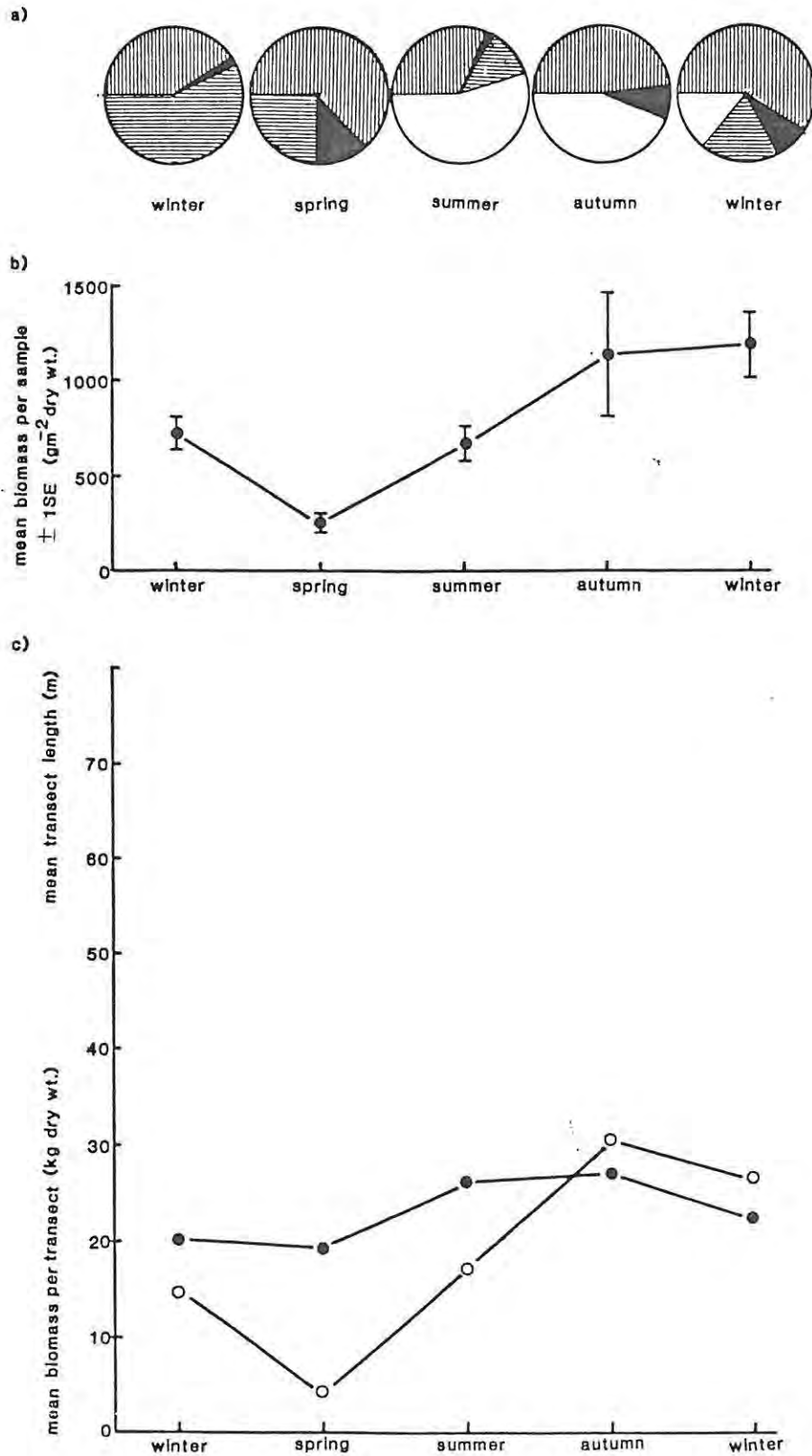


Figure 31: Macrophyte data from Eilandvlei between winter 1982 and winter 1983: (a) seasonal changes in the composition of the macrophyte community throughout the lake (= *P. pectinatus*, = Characeae, = *N. marina*, = *Enteromorpha*). (b) seasonal changes in standing crops of all macrophyte species throughout the lake. (c) seasonal changes in mean biomass per transect () and in mean transect length ().

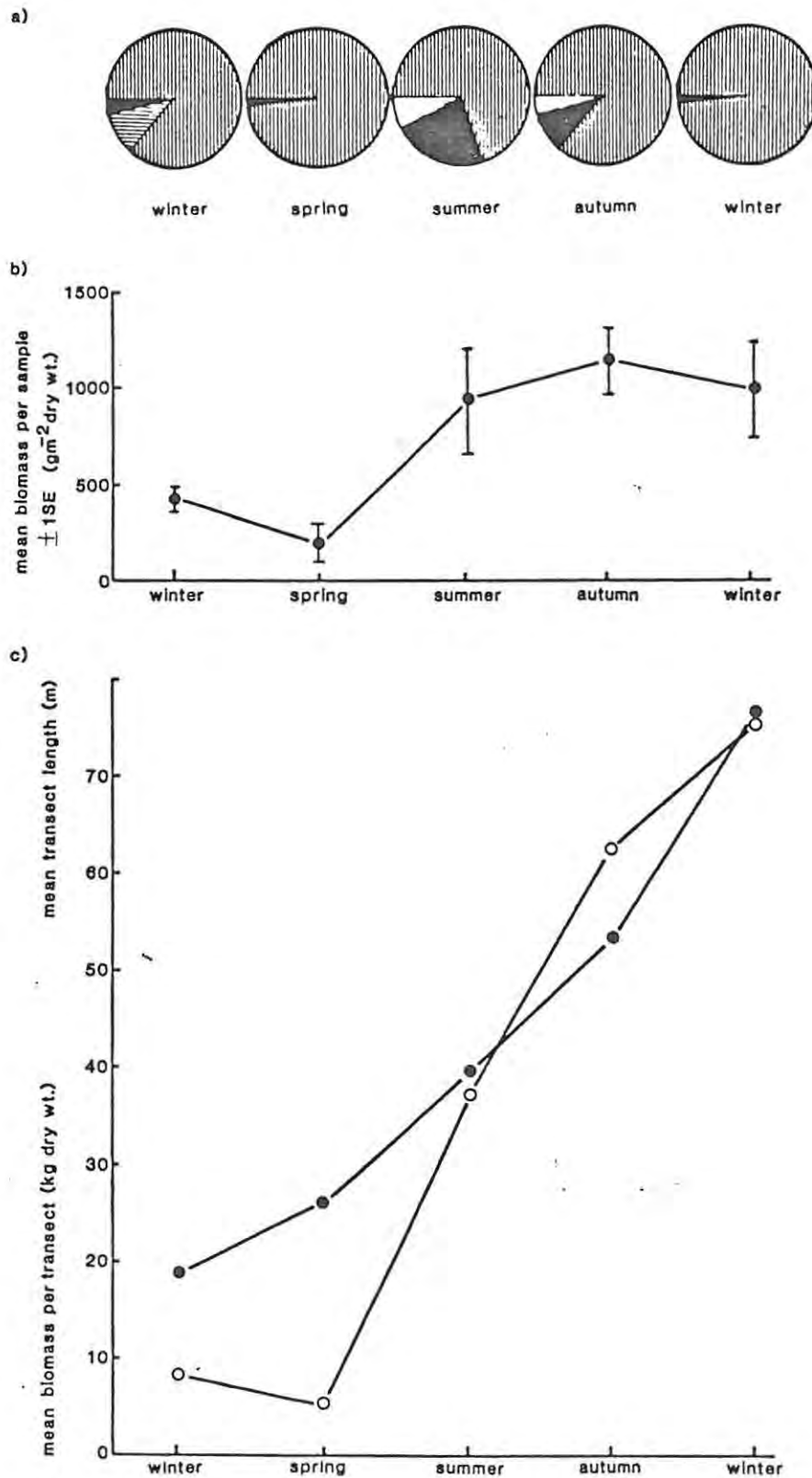


Figure 32: Macrophyte data from Langvlei between winter 1982 and winter 1983: (a) seasonal changes in the composition of the macrophyte community throughout the lake (key as in Figure 31). (b) seasonal changes in standing crops of all macrophyte species throughout the lake. (c) seasonal changes in mean biomass per transect (○) and in mean transect length (●).

Notwithstanding quite large standard errors, seasonal changes in mean standing crop in both lakes followed the same pattern and were within the same order of magnitude. In both lakes the mean biomass per square metre approximately doubled from winter 1982 to winter 1983. In Eilandvlei the biomass increased from around 700g m^{-2} dry mass to 1200g m^{-2} . In Langvlei the biomass increased from 400g m^{-2} dry mass to 1000g m^{-2} . Another characteristic of both lakes was that community structure was constantly changing, especially in Eilandvlei.

In Eilandvlei, beds of Najas marina along the northern shore and around the northern side of the island contributed 60% of the total biomass of submerged vegetation in the winter of 1982. Over the spring however, these beds started to recede and were replaced by Potamogeton pectinatus. Isolated patches of charophytes were also present. By the summer of 1982-83 large amounts of filamentous alga (identified as Enteromorpha by Dr A. Jacot Guillarmod) started to grow both epiphytically and epipsammically. Its shading effect on other submerged vegetation resulted in their reduced growth and disappearance from several areas of the lake. Although this alga gradually diminished over the rest of the study period, it never entirely disappeared. A characteristic of Eilandvlei was that there were several beaches and areas within the littoral that did not support macrophyte growth. This was not the case in Langvlei.

In Langvlei, a band of N.marina present along the northern shore during the winter of 1982 was replaced by P.pectinatus in the spring. Throughout all seasons the latter species contributed over 70% of the total biomass of submerged vegetation recorded in this lake. Although some Enteromorpha was recorded over the spring and summer, it was never as prolific as in Eilandvlei. Charophyte meadows covering the bottom of the lake prior to the recent recession did not recover. However, P.pectinatus grew prolifically and by the winter of 1983 the canopy was present right across the lake in some areas.

The presence of N. marina along the northern littoral of both lakes in the winter of 1982 and summer of 1982/83 suggests that this species may be a pioneer. In the autumn it might have been present as a primary colonizer after the recession, and in the summer it was the first



Figure 33: Submerged macrophyte beds along the littoral of Eilandvlei.



Figure 34: Submerged macrophyte beds along the littoral of Langvlei.

species to colonize areas that had been shaded out by Enteromorpha. It seems possible that the summer biomass of N.marina in Langvlei was lower than in Eilandvlei because the shading effect of Enteromorpha in the spring was less. The biomass of Enteromorpha in Eilandvlei was similar to that of the P.pectinatus it had replaced (Figure 31a,b), since even when the growth of Enteromorpha was at its greatest in Eilandvlei, the mean biomass of vegetation per square metre in both lakes was of the same order of magnitude. Liptrot and Allanson (1978) noted a similar phenomenon in Swartvlei estuary where the biomass of epiphytic Enteromorpha occasionally exceeded that of its supporting Zostera.

The reason why Enteromorpha should have grown more prolifically in Eilandvlei than in Langvlei is not known. One factor might be the nutrient status of the water in both lakes. Although levels of phosphorus and nitrogen in Eilandvlei were higher over the study period than in Langvlei, a Mann-Whitney U test showed that this was not significant. Whatever the causes of the growth it appears that the greater changes in plant community structure in Eilandvlei may largely have been a consequence of the epiphytic Enteromorpha.

The average transect length in Eilandvlei between May 1982 and May 1983 varied from 19m in September 1982 to 27m in March 1983 (Figure 31c). In Langvlei however, it increased from 29m in May 1982 to 76m in May 1983 (Figure 32c). It follows that whilst initial biomasses per transect in both lakes were similar, they were approximately three times as great in Langvlei as in Eilandvlei by May 1983. At the end of the study the mean biomass per transect in Langvlei was 75kg dry mass, whilst in Eilandvlei it was 26kg dry mass. Figures 33 and 34 show a typical band of submerged vegetation along the littoral of Eilandvlei and Langvlei respectively.

In these two lakes macrophyte colonization can be partly related to the bathymetry of the lake basins. Howard-Williams and Liptrot (1980) showed that in Swartvlei P. pectinatus beds, which had one of the highest biomass for any submerged aquatic (Howard-Williams, 1978), extended only to a depth of about 2.3m. This can be attributed to

critical light attenuation corresponding with a littoral shelf at this depth. Langvlei and Eilandvlei do not have a clearly defined littoral shelf, but both the mean and maximum depth in Langvlei are less than in Eilandvlei (Table 1). More extensive beds were recorded in the former where the maximum depth is only 4.0m, and over the study period was approximately 3.0m. Light attenuation in Eilandvlei and Langvlei was not determined, but the mean secchi disc reading over this period was 1.7m in Langvlei and 1.2m in Eilandvlei.

Using the expression formulated by Walmsley et al (1980);

$$E = \frac{n(100)}{(1.3/SD + 0.54)}$$

where E = depth of euphotic zone (m)

SD = secchi disc visibility (m)

it can be shown with reservation that the euphotic zone, taken as that depth at which 99% of incident radiation is extinguished, extended to the bottom of Langvlei throughout most of the study period.

Although this expression was formulated from secchi readings similar to those recorded in the Wilderness lakes system, it was based on readings obtained from a turbid impoundment. In addition, the compensation point of macrophytes is probably higher than for planktonic algae (Moss, 1980) for which the 1% level of radiation is generally accepted as the limit of the euphotic zone (Cole, 1979). Nevertheless, it illustrates that secchi disc readings in Langvlei are in agreement with the observed distribution of macrophytes over the study period.

Although no quantitative assessments of standing crops were made in Rondevlei and Wilderness lagoon, qualitative data are available. In Rondevlei during May 1982 very sparse patches of short (< 5cm) Ruppia cirrhosa covered approximately 30% of the littoral to a depth of about 1.0m. By May 1983 these patches had expanded to cover approximately 90% of the littoral.

Changes in the macrophyte community of the lagoon were less noticeable than in Rondevlei. Isolated stands of P.pectinatus were seen growing among the emergent vegetation, and in deeper areas Enteromorpha was present throughout the year. However between the end of July and early September, when the mouth was closed, mats of epispammic Enteromorpha proliferated in several areas. These eventually broke away from the sand and started to float, covering approximately 60% of the water area. Once the mouth opened these mats quickly disappeared as they were flushed out to sea. As the lagoon is temporarily endorheic when the mouth is closed, Enteromorpha can proliferate without being washed out to sea. Liptrot and Allanson (1978) recorded a similar phenomenon in Swartvlei where this alga grew mainly in association with beds of Zostera capensis.

The absence of Zostera from Wilderness lagoon is surprising as this species is ubiquitous throughout southern African estuaries (Day, 1951) and is present in both the nearby lagoons at Knysna (Day et al 1952) and Swartvlei (Liptrot and Allanson, 1978). The presence of intertidal flats and high water velocities near the mouth when it is open as well as unstable sediments when it is both open and closed, may account for this paucity. Day (1981c) reports that in areas where Zostera is present, growth is dependent on water velocity, the nature of the substratum and the transparency of the water. In the upper reaches of the lagoon these factors appear to be suited for growth so it may be the quality of water which is limiting this plant. Branch and Day (1984) noticed a similar paucity of attached macrophytes in the Palmiet estuary which is also fed by an acid Cape river. Day (1981c) reports that the minimum salt tolerance of Z.capensis is around 10⁰/oo. This is higher than the average salinity recorded during both open and closed phases.

The distribution of submerged macrophytes in the Wilderness system is such that in the past, Eilandvlei and Langvlei have supported prolific beds, whilst no such growth in Rondevlei and the lagoon has been observed. Weisser and Howard-Williams (cited in Weisser, 1979) attributed the paucity in Rondevlei to high salinities prior to the Langvlei-Rondevlei channel being dredged. However, after 1975 increased water exchange between these two lakes caused the salinity of Rondevlei

to drop from 26⁰/oo in 1975 to 15⁰/oo in 1978 (Coetzee and Palmer, 1978). Although P.pectinatus can survive at 15⁰/oo (Day 1981c) the simultaneous macrophyte recession in Swartvlei, Langvlei and Eilandvlei suggests that environmental conditions in the southern Cape coastal lakes were unsuitable for macrophyte growth at this time.

Howard-Williams (1980) and Day (1981c) have stated that species distribution is more closely related to the nature of the substratum than to changes in salinity. However, Verhoeven and Van Viersen (1978) concluded that vegetational changes in two brackish lagoons on Corsica were due to decreases in salinity. In Rondevlei post-recession growth suggests that the substratum in this lake is suitable for macrophytes, and prior to the recession salinity was a limiting factor. The reason why growth was not as prolific as in the other lakes might be related to the absence of root stock left by growth in previous years.

This study has shown that by February 1983, the macrophyte communities in Eilandvlei and Langvlei had recovered from an earlier senescence. Furthermore, evidence suggests that as a result of the 1980/81 floods, the lowered salinities in Rondevlei permitted P. pectinatus beds to become established for the first time. In comparison with the 1978 data for Eilandvlei (Howard-Williams, 1980), the biomass of this lake had increased by 45%. This recolonization under a completely different salinity regime illustrates how the macrophyte communities of the Wilderness lakes system can recover from an apparently cataclysmic collapse.

A brief account of the effect of constrictions upon local hydrology was given in Part II where it was proposed that not only channel bathymetry restricted water flow, but also macrophyte encroachment. Chapter 2 of Part III dealt with the flux of salt in the Serpentine and further reference was made to the role of macrophyte growth, particularly in the Eilandvlei/Langvlei channel, in inhibiting water exchange between the lakes. This chapter deals directly with macrophyte growth in these channels.

4.1. Materials and methods

The Howard-Williams/Longman cutter used in the lakes was used to sample macrophyte growth in the Eilandvlei/Langvlei and Langvlei/Rondevlei channels. In December 1982, 22 transects were positioned across the length of the former channel and 17 across the latter. In the Serpentine 10 samples were taken from the upper reaches in December 1982. This process was not repeated as these beds were mown by the Lakes area Development Board (under whose jurisdiction the lakes were managed at the time) in February 1983. Samples were treated in the same manner as those taken from the lakes.

4.2. Results and discussion

The spatial encroachment of macrophytes in the Eilandvlei/Langvlei and Langvlei/Rondevlei channels during the summer of 1982/83 are summarized in Table 9. Macrophyte growth covered 80% of the former channel's area with Potamogeton pectinatus comprising 65% of the area (80% of which formed a canopy). Only 30% of the Langvlei/Rondevlei channel supported macrophyte growth. P.pectinatus covered 20% of the area and only 40% of it formed a canopy. Most of the Serpentine above the sluice supported a uniform bed of P.pectinatus. Below the sluice only 5% of the Serpentine supported macrophyte growth. This might be attributed to the progressively eutrophic conditions observed below the sluice over the period of its construction (Chapter 1, Part III). This eutrophication corresponded with the critical period over which macrophyte recolonization throughout the rest of the system commenced.

Table 9: Percentage of water area in the Eilandvlei/Langvlei and Langvlei/Rondevlei channels choked by macrophytes.

	% OF CHANNEL COVERED	
	EILANDVLEI/LANGVLEI	LANGVLEI/RONDEVLEI
no growth	20	70
<u>P. pectinatus</u> and	65	20
emergents	4	10
<u>P. pectinatus</u> and	11	0
emergents		

Table 10: Mean biomass $\pm$ standard error and the range of P. pectinatus recorded from the Serpentine, Eilandvlei/Langvlei and Langvlei/Rondevlei channels.

	gm ⁻² dry wt. + SE (range)	gm ⁻³ dry wt. + SE (range)
Serpentine	279 $\pm$ 70 (10 - 720)	399 $\pm$ 87 (25 - 825)
Eilandvlei/ Langvlei	755 $\pm$ 149 (17 - 2389)	1468 $\pm$ 250 (62 - 4090)
langvlei/ Rondevlei	429 $\pm$ 50 (80 - 870)	662 $\pm$ 104 (95 - 1666)

Growth in this area may thus have been prevented. The dominant emergent species in the Serpentine and Eilandvlei/Langvlei channel was Phragmites australis and in the Langvlei/Rondevlei channel were Scirpus littoralis and P.australis.

Where P.pectinatus occurred, its mean biomass in the Eilandvlei/Langvlei and Langvlei/Rondevlei channels was 755 and 429g m⁻² dry mass respectively. In the Serpentine, the mean biomass was 279g m⁻² dry mass (Table 10). However, these values mean little in terms of encroachment and the restricting effect of macrophytes on water flow. Plant biomass was therefore related to water depth and expressed in terms of biomass per cubic metre of water (Table 10). Biomasses expressed in terms of volume show the same trend as those expressed in terms of area. When expressed in terms of gm⁻³, the mean biomass of macrophytes in the Eilandvlei/Langvlei channel was 1468g m⁻³ dry mass and the maximum 4090g m⁻³. Howard-Williams (1978) reports that the maximum biomass of 1952g m⁻² dry mass of P.pectinatus recorded in Swartvlei was one of the highest he found in the literature. As the P.pectinatus biomass of 2389g m⁻² dry mass recorded in this study was taken from only 0.74m of water, its density was 3732g m⁻³. This must have a significant inhibitory effect on water flow.

Unlike the Langvlei/Rondevlei channel which has steep sides, the Serpentine and Eilandvlei/Langvlei channel gently slope towards their deepest point. Marginal colonization by emergents, which according to Howard-Williams and Liptrot (1980) can grow in water 0.3 - 0.5m deep, has thus occurred. Such encroachment in the Serpentine is not too severe but in areas of the Eilandvlei/Langvlei channel, which is on average only 9.0m wide, emergents grow right across its width (Figures 7 and 8). Water flow is thus restricted in a similar manner to that discussed by Pegram (1983).

In Chapter 1.1. Part II it was suggested that the Eilandvlei-Langvlei channel constituted the major permanent constriction to water flow in the system. From the macrophyte surveys described in this chapter, it is also apparent that of all the constrictions, this channel supports the most luxuriant growth. It is therefore probable that macrophyte

growth in the channels is a major factor inhibiting water flow. Unfortunately, most authors (eg Haslam, 1980 and Peltier and Welch, 1969) have focussed most of their attention on the effects of water flow in determining the distribution of aquatic plants and not on the modifying effects of macrophytes upon local hydraulics.

Ogrosky and Mockus (1964) have shown that water velocities decrease with increasing vegetation height and cover. Similarly, Haslam (1980) states that large submerged plants tend to impede water flow and Howard-Williams (1983) suggested that they have a dampening effect on flood peaks. The role of P.pectinatus in the hydraulics of the constrictions is therefore of interest.

Of the authors who have investigated the effects of macrophytes on current velocities (eg Zieman, 1974 and Fonesca et al, 1983), Madsen and Warncke (1983) examined the effect of Caltriche stagnalis on the velocity of a slow flowing stream in Denmark. Their observations covered velocities between $0.038 - 0.080 \text{ m s}^{-1}$ and showed that 5cm inside a weed bed, current speeds were reduced by 58 - 92%. These results are in agreement with the conclusions of Fonesca et al (1983) who report similar findings. Furthermore, the latter have shown that the greater the density of growth, the greater the effect on current velocity. These observations reinforce the statement made earlier. This is that macrophyte encroachment in the channels is a major contributory factor in inhibiting water exchange between the lakes.

It follows that because current velocity is decreased, the sediment carrying capacity of the water is diminished, and siltation could occur. Several authors quoted by Fonesca et al (1983) such as Wood et al (1969) and Marshall and Lucas (1970) have shown an increase in fine particles within macrophyte meadows. It is therefore possible that P.pectinatus in the channels causes current velocities to decrease, resulting in a faster rate of sedimentation. The resulting decrease in depth then restricts water flow to an even greater extent.

The overall conclusion to be drawn is that the shallow and convoluted morphometry of the Eilandvlei-Langvlei channel inhibits water flow. Related to this shallowness is the fact that this channel

is heavily colonized by emergent species which further constrict the channel, and which may continue to reduce its shallowness through sedimentation. However, the major factor contributing to this constriction is the high density of P.pectinatus. Whilst all three variables combine to varying degrees to restrict water flow in the Serpentine, Langvlei/Rondevlei and Eilandvlei/Langvlei channels, it is in the latter channel that they constitute a major permanent constriction. Thus the normal process of plant succession in the channels enhances the ecological consequences of segmentation. The influence of this upon the structure of the fish communities of the Wilderness lakes system will be discussed in the following chapter.

5.1. Materials and methods

The system was sampled for one year using four types of fishing gear. The year was divided into four seasons; June - August represented the winter, September - November the spring, December - February the summer and March - May the autumn. Each season a set of five multifilament gill nets each measuring 25m x 2.75m and with stretch meshes of 35, 45, 57, 73 and 93mm were set for three nights in different positions in each of the lakes. However in the lagoon, Touw river, lower Serpentine and upper Serpentine they were only set once each season. The position of these stations is shown in Figure 35.

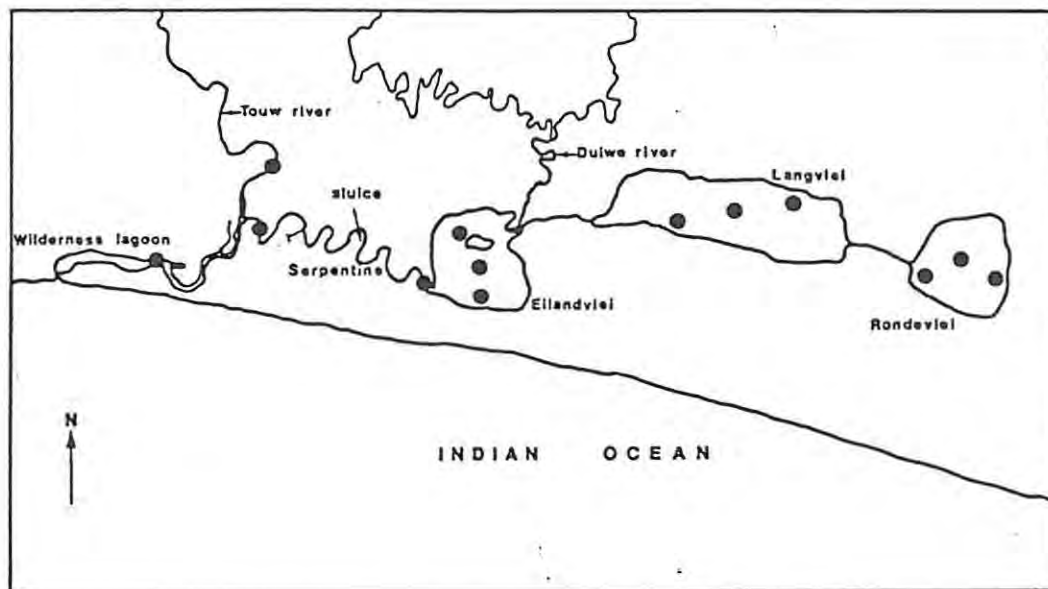


Figure 35: Location of gill net stations mentioned in the text.

Three beach seines were also used on a seasonal basis. The smallest measured 10m x 2m deep and was constructed from 28mm stretch mesh anchovy netting in the wings and 10mm stretch mesh for the bag. This was laid by hand and pulled onto beaches from water not more than 1.0m deep. It was used ten times in each of the lakes and the lagoon per season. A larger multifilament net (30m x 3m x 28mm stretch mesh) was laid from a boat 30m offshore and employed ten times in Rondevlei, Ellandvlei and the lagoon during the winter and spring. Filamentous

algae which grew over the littoral of the lakes in the summer of 1982/83 clogged the large multifilament seine so it was replaced with a monofilament net with a 25mm bar mesh. This net was laid in a similar way to the larger multifilament seine and was used ten times in each of the lakes and the lagoon during the summer and autumn. It was not possible to use seine nets in the Touw river because there were no suitable beaches on which to haul the net.

All fish caught in the gill nets were transported to the laboratory where they were identified, weighed and measured. From this information length/weight curves for each species were calculated based on the expression recommended by Tesch (1968) where

$$\text{weight} = a \times \text{length}^b$$

where a and b are constants.

Fish captured in the seine nets were identified and measured before being released into the water. Those greater than 50mm standard length (SL) were also fin clipped as part of a mark-recapture programme. When large numbers of individuals (>100) of the same species were caught in one haul, e.g. Hepsetia breviceps, a 10% sub-sample was taken for measurement purposes. Smaller fish, of the size ranges not selected for by the gill nets, were also transported to the laboratory in order that their length/weight relationships could be determined. Most fish were identified in the field according to the classification of Smith (1949) and Smith (1975). Fish that could not be readily identified, i.e. some of the juvenile Mugilidae, were preserved in 10% formalin and identified in the laboratory using the van der Elst and Wallace (1975) key.

In order to define the fish community mathematically, diversity indices were used. These express the ratio between species and individuals in a biotic community (Odum, 1959). Such indices are derived from information theory (Margalef, 1968), and equate diversity with the amount of uncertainty which exists regarding the species of an individual selected at random from a population (Pielou, 1966). They have been used to compare fish communities by several workers including

Kushlan (1976a), Shenker and Dean (1979) and Whitfield (1982; 1985). Each of these workers have used the Shannon-Weaver function (Shannon and Weaver, 1963):

$$H = - \sum P_i \log P_i$$

where P_i = proportion of i^{th} species.

As this index will always increase with the number of species present (Lloyd and Ghelardi, 1964; Hill, 1973), Heip's evenness index (Heip, 1975) was therefore also used:

$$E = (e^H - 1)/(S - 1)$$

where e = base of natural logs

H = Shannon-Weaver function

S = no. of species.

Like the evenness indices of Pielou (Pielou, 1966) and Sheldon (Sheldon, 1969), this is less dependent on species count and more a measure of their equitability or heterogeneity. Heip (1975) has shown this index to be statistically superior to both Pielou's and Sheldon's indices in that it is more sensitive to small changes in heterogeneity.

5.2. Results and discussion

Most fishing gears are selective to some extent and this depends upon many factors. Extrinsic factors include mesh size, mode of operation and meteorological events. Intrinsic factors are associated with the biology of the fish such as their size and behaviour (Lagler, 1968). Catches may not therefore be representative of the population as a whole, and it is thus necessary to estimate the efficiency of the fishing gear used.

Seventy-four percent of the fish captured were recorded in the 45, 57 and 73mm stretch meshes and only 26% from the 35 and 93mm nets. The cumulative number of species captured in all gears in each section of the system is shown in Figure 36. It can be seen

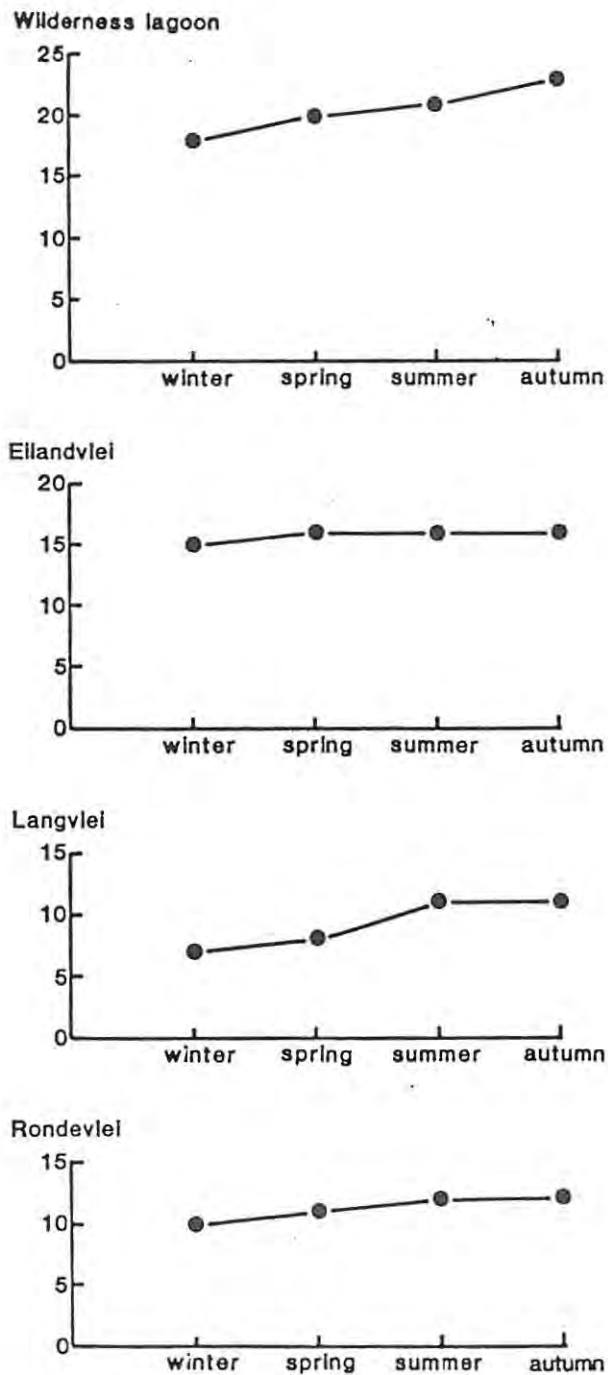


Figure 36: Cumulative numbers of fish species captured in all fishing gears used in each portion of the Wilderness lakes system.

36. It can be seen that by the second season of sampling 87, 100, 72 and 91% of the eventual number of species captured in Wilderness Lagoon, Eilandvlei, Langvlei and Rondevlei had already been recorded. The shape of these curves suggests that by the end of the investigation, all of the major species, and most of the unimportant ones, had been recorded. The interpretation of the results will therefore be made on the assumption that they are representative of the fish communities in the Wilderness lakes system.

Unfortunately the mark-recapture programme proved unsuccessful. Only one Liza dumerili and five Liza richardsoni were recaptured in the lagoon and one Lithognathus lithognathus and one Rhabdosargus holubi in Eilandvlei. Each of these fish were found in the area where they were originally caught.

In common with most estuaries (Blaber, 1980a; Day et al 1981), the dominant fish fauna of the Wilderness lakes system forms a marine/estuarine migratory component. A total of 32 fish species were recorded in the system and the catch composition of all gears used in Wilderness lagoon, Eilandvlei, Langvlei and Rondevlei are shown in Tables 11, 12, 13 and 14 respectively. These tables show that 23 species were recorded in the lagoon, 16 in Eilandvlei, 11 in Langvlei and 12 in Rondevlei. Table 15 shows the catch composition from stations where only gill nets were used, i.e. the Touw river and Serpentine stations. For comparative purposes, gill net data from all the stations have been included. This table shows that the number of species captured in gill nets decreased from the lagoon towards Rondevlei.

The system is dominated by iliophagous species from the families Mugilidae and Cichlidae. The Mugilidae comprised over 40% of the total biomass of fish captured in each area of the system and in Rondevlei and Langvlei contributed 50 and 58% respectively. L. richardsoni was the numerically dominant mullet species in all areas and was also gravimetrically dominant except in Eilandvlei where L. dumerili contributed the greatest biomass.

The dominance of the Mugilidae has commonly been recorded in other South African estuaries e.g. the Gamtoos (Marais, 1982), Mhlanga

Table 11: Summary of fish catches from Wilderness lagoon

	JUVENILE SEINE		MULTIFILAMENT SEINE		MONOFILAMENT SEINE		GILL NETS		TOTAL	
	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)
<u>Lichia amia</u>	14	990	4	617	3	412	95	23259	116	25278
<u>Trachurus capensis</u>	-	-	-	-	-	-	2	111	2	111
<u>Psammagobius knysnaensis</u>	25	27	39	33	-	-	-	-	64	60
<u>Gobius multifasciatus</u>	101	52	31	19	-	-	-	-	132	71
<u>Amblyrhynchotes honckenii</u>	-	-	-	-	1	40	-	-	1	40
<u>Monodactylus falciformis</u>	-	-	3	41	-	-	37	1008	40	1049
<u>Mugil cephalus</u>	172	715	94	486	1	313	11	4312	278	5826
<u>Liza dumerilii</u>	48	1320	91	5578	49	4551	153	14613	341	26062
<u>Liza richardsoni</u>	1318	5179	61	3917	55	12207	147	26497	1581	47800
<u>Liza tricuspidens</u>	2	66	-	-	1	91	14	3617	17	3774
<u>Myxus capensis</u>	-	-	4	408	-	-	16	3541	20	3949
<u>Tachysurus feliceps</u>	-	-	-	-	-	-	35	1091	35	1091
<u>Argyrosomus hololepidotus</u>	-	-	-	-	-	-	61	38001	61	38001
<u>Heteromycteris capensis</u>	16	20	1	3	-	-	1	110	18	133
<u>Solea bleekeri</u>	10	10	10	12	-	-	1	110	21	132
<u>Diplodus sargus</u>	-	-	-	-	7	804	-	-	7	804
<u>Lithognathus lithognathus</u>	19	514	66	11338	57	14807	20	2882	162	29541
<u>Pomadasys comersoni</u>	-	-	-	-	-	-	4	474	4	474
<u>Rhabdosargus holubi</u>	95	288	216	2248	159	6413	120	5847	590	14796
<u>Sarpa salpa</u>	1	2	150	100	-	-	-	-	151	102
<u>Hepsetia breviceps</u>	4	9	2	1	-	-	-	-	6	10
<u>Gilchristella aestivalis</u>	11	13	325	297	-	-	-	-	336	310
<u>Oreochromis mossambicus</u>	-	-	2	143	-	-	63	-	65	7161
	1836	9205	1099	25241	333	39638	780	132634	4048	206718

Table 12 : summary of fish catches from Eilandvlei.

	JUVENILE SEINE		MULTIFILAMENT SEINE		MONOFILAMENT SEINE		GILL NETS		TOTAL	
	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)
<u>Psammagobius knysnaensis</u>	8	9	1	1	-	-	-	-	9	10
<u>Gobius multifasciatus</u>	1	1	1	1	-	-	7	353	9	355
<u>Hyporhamphus capensis</u>	26	29	-	-	-	-	-	-	26	29
<u>Monodactylus falciformis</u>	4	2	31	453	4	262	161	7841	200	8558
<u>Mugil cephalus</u>	47	173	408	969	2	168	18	3226	475	4536
<u>Liza dumerili</u>	112	1732	273	8544	127	13758	205	19093	717	43127
<u>Liza richardsoni</u>	118	710	1760	1827	-	-	228	30360	2106	32897
<u>Myxus capensis</u>	-	-	2	210	-	-	32	6527	34	6737
<u>Hyporhamphus capensis</u>	-	-	40	111	-	-	-	-	40	111
<u>Lithognathus lithognathus</u>	25	943	55	495	58	12179	66	10443	204	24060
<u>Rhabdosargus holubi</u>	166	2752	140	1700	328	13835	67	3070	701	21357
<u>Rhabdosargus sarba</u>	1	27	-	-	-	-	-	-	1	27
<u>Hepsetia breviceps</u>	7461	3547	653	723	-	-	-	-	8114	4270
<u>Gilchristella aestuarius</u>	1391	1824	710	623	-	-	-	-	2101	2447
<u>Micropterus salmoides</u>	3	2101	-	-	2	308	1	145	6	2554
<u>Oreochromis mossambicus</u>	3818	25401	3	162	31	5116	206	29302	4058	59981
	13182	39251	4077	15819	552	45626	991	110360	18801	211056

Table 13: Summary of fish catches from Langylei.

	JUVENILE SEINE		MONOFILAMENT SEINE		GILL NETS		TOTAL	
	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)
<u>Mugil cephalus</u>	2	1	12	800	58	7948	72	87892
<u>Liza dumerili</u>	-	-	1	77	16	1524	17	1601
<u>Liza richardsoni</u>	-	-	5	1546	342	47056	347	43602
<u>Myxus capensis</u>	-	-	-	-	6	711	6	711
<u>Solea bleekeri</u>	-	-	-	-	1	26	1	26
<u>Rhabdosargus holubi</u>	-	-	-	-	1	135	1	135
<u>Hepsetia breviceps</u>	30893	2075	-	-	-	-	30893	2075
<u>Gilchristella aestuarius</u>	964	637	-	-	-	-	964	637
<u>Micropterus salmoides</u>	5	4	-	-	-	-	5	4
<u>Oreochromis mossambicus</u>	391	707	3	330	362	36855	756	37892
<u>Hyporhamphus capensis</u>	14	19	-	-	-	-	14	19
	32269	3443	21	2753	786	94255	33076	100451

Table 14: Summary of fish catches from Rondevlei.

	JUVENILE SEINE		MULTIFILAMENT SEINE		MONOFILAMENT SEINE		GILL NETS		TOTAL	
	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)
<u>Clinus superciliosus</u>	1	2	-	-	-	-	-	-	1	2
<u>Heteromycteris capensis</u>	399	973	285	889	-	-	-	-	684	1862
<u>Monodactylus falciformis</u>	-	-	-	-	-	-	1	8	1	8
<u>Mugil cephalus</u>	10	508	14	275	3	1455	41	20321	73	22559
<u>Liza dumerili</u>	14	713	4	391	38	4006	70	11277	126	16387
<u>Liza richardsoni</u>	162	23082	22	507	24	4374	364	51798	572	79735
<u>Myxus capensis</u>	-	-	1	12	1	62	10	1754	12	4828
<u>Rhabdosargus holubi</u>	-	-	-	-	1	92	32	4672	33	4764
<u>Hepsetia breviceps</u>	42073	30289	1458	977	-	-	-	-	43531	31266
<u>Gilchristella aestuarius</u>	1835	627	1084	784	-	-	-	-	2919	1411
<u>Syngnathus acus</u>	3	4	-	-	-	-	-	-	3	4
<u>Oreochromis mossambicus</u>	703	5179	6	7	841	78598	-	-	1550	83784
	45200	62357	2879	3836	908	88587	518	89830	49505	243610

Table 15: Summary of fish catches from gill nets only.

	WILDERNESS LAGOON		TOUW RIVER		LOWER SERPENTINE		UPPER SERPENTINE		EILANDVLEI		LANGVLEI		RONDEVLEI		TOTAL	
	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)	numbers	biomass (g)
<u>Lichia amia</u>	34	11342	51	8774	12	3901	-	-	-	-	-	-	-	-	97	24017
<u>Trachurus capensis</u>	2	111	-	-	-	-	-	-	-	-	-	-	-	-	2	111
<u>Gobius multifasciatus</u>	-	-	-	-	-	-	1	43	7	353	-	-	-	-	8	396
<u>Monodactylus falciformis</u>	8	408	7	78	22	522	37	1803	161	7841	1	135	32	4672	268	15459
<u>Mugil cephalus</u>	-	-	6	2940	5	21372	9	1653	18	3226	58	8008	41	23321	137	60520
<u>Liza dumerili</u>	94	8302	20	2341	44	3972	8	627	195	19093	16	1524	70	11277	447	47136
<u>Liza richardsoni</u>	147	26497	15	2799	74	13973	115	13740	227	30367	342	47053	314	45798	1234	180227
<u>Liza tricuspidens</u>	9	2834	2	617	3	168	-	-	-	-	-	-	-	-	14	3619
<u>Myxus capensis</u>	6	1734	4	758	8	1455	22	5113	32	6557	6	711	10	1754	88	18082
<u>Tachysurus feliceps</u>	13	455	8	214	16	421	-	-	-	-	-	-	-	-	37	1090
<u>Argyrosomus hololepidotus</u>	16	12654	15	8774	12	3901	-	-	-	-	-	-	-	-	43	25329
<u>Lithognathus lithognathus</u>	6	437	1	465	13	1940	9	1276	60	10443	-	-	-	-	89	14561
<u>Pomadasys commersoni</u>	1	137	-	-	3	437	-	-	-	-	-	-	-	-	4	574
<u>Rhabdosargus holubi</u>	7	3604	6	222	41	1327	7	277	67	3070	1	135	32	4672	161	13307
<u>Oreochromis mossambicus</u>	-	-	63	7161	-	-	116	19815	206	29302	362	36855	117	5043	864	98176
	343	68515	198	35143	253	53389	324	44347	973	110252	786	94421	616	96537	3493	502604

(Whitfield, 1980a) and Swartvlei (Whitfield, pers. comm.). According to Blaber and Whitfield (1977) estuaries provide an ideal habitat for mullet juveniles to change their feeding habits from planktonic macrophagous carnivores to benthic microphagous omnivores. This is difficult to accomplish in the rough coastal conditions off southern Africa. In addition, South African estuaries act as detritus traps (Whitfield, 1983), thus providing an abundant food supply for the various mullet species. According to Blaber (1976) and Whitfield and Blaber (1978c), these fishes avoid inter-specific competition through particle size selection and feeding periodicity.

In the Wilderness lakes, the size of mullet increased from Eilandvlei, where individuals less than 5cm SL were the dominant size group, to Rondevlei, where individuals greater than 30cm were commonly recorded. An indication of this trend can be seen by dividing the total mass of mullet in each lake by the number of individuals caught. The mean individual weight in Eilandvlei was 26g, in Langvlei 135g and in Rondevlei 154g. This suggests that Eilandvlei serves as the system's initial nursery area for mullet. The fact that larger individuals are found in Rondevlei may in part be a function of the Wilderness lakes system reverse salinity gradient (Chapter 1.2. Part II). Whitfield and Blaber (1978b) have suggested that seasonal migration of adult M. cephalus might be a negative response to freshwater organic cues. As the Serpentine introduces both fresh and saline water into the lakes, this may confuse some fish and if water levels are high enough they may migrate up towards Rondevlei where salinities are higher but no sea link exists.

The exotic cichlid Oreochromis mossambicus contributed 28, 38 and 34% to the total biomass of fish captured in Eilandvlei, Langvlei and Rondevlei respectively. However, 88% of these fish were captured during summer and 11% during autumn. The few captured over the winter and spring were mostly caught in gill nets indicating they were in deep water. In spite of the relative absence of this species during winter and spring, it must be considered an important component of these communities. Over the summer months, this species accounted for 46, 60 and 65% of the total biomass recorded in Eilandvlei, Langvlei and Rondevlei respectively. A similar disappearance of this fish from seine

net catches in Lake Sibaya over the winter has been recorded by Bruton and Boltt (1975). Since O. mossambicus is not a migrant, and was rarely captured in even gill nets over the winter, this species may be relatively inactive over this period.

Two other species exhibiting seasonal trends were the zooplanktivores Hepsetia breviceps and Gilchristella aestuarius. The former was the most common individual species in all the lakes. Together, both species comprised 96, 94 and 54% of the total catch in Eilandvlei, Langvlei and Rondevlei respectively. Between winter and summer there was an 18-fold increase in the numbers of individuals captured and this trend corresponds closely with data from Swartvlei (Whitfield, 1982). Whitfield calculated a 20-fold increase in the density of G. aestuarius between these two seasons and suggested that a winter offshore and summer onshore movement may have accounted for this increase. H. breviceps was the most common species in each of the lakes. In Wilderness lagoon however, it accounted for less than 1% of the total catch. One reason for this may be that stocks of zooplankton, its main food resource (Coetzee, 1982) are low in the lagoon (Coetzee, 1983).

The only other major contributors to the fish fauna of the lakes were the sparids Rhabdosargus holubi and Lithognathus lithognathus. Whilst only one R. holubi was captured in Langvlei, 701 were caught in Eilandvlei and 33 in Rondevlei. Together with the 204 L. lithognathus caught in Eilandvlei, they constituted 21% of the biomass of fish captured in this lake. Data suggest that like the Mugilidae, the Sparidae also utilize Eilandvlei as their initial nursery area. Individual R. holubi captured in Eilandvlei were smaller than those in Rondevlei, their mean weights being 30g and 144g respectively.

Of the 23 species recorded in the lagoon, nine were not found in other areas of the system. The majority of these fish were predators, the most important being Lichia amia and Argyrosomus hololepidotus. This greater species richness is typical of a lower estuarine environment and is partly a function of its proximity to the sea. The distribution of species in the lagoon is reflected in the catch composition of each gear. The dominance of juvenile mullet in the small seine net may be explained by their tendency to shoal over estuarine

mud and sand flats (Thomson, 1954, De Silva and Silva, 1979; Whitfield and Blaber, 1978b).

In the large multifilament and monofilament seine nets which were pulled through deeper water, larger fish and notably sparids were more common in the catches. Of this family the most commonly captured species was R. holubi. In view of the lack of submerged aquatic macrophytes this is perhaps surprising for Blaber (1974) reports that they feed mainly on submerged macrophyte vegetation, digesting the associated periphyton. However, Whitfield (1984: 1985) noted that during the macrophyte senescent phase in Swartvlei, R. holubi utilized epispammic filamentous algal mats as a food resource. Filamentous algae were present in the deeper areas of the lagoon throughout this study (Chapter 3) and were probably an important component of the diet of R. holubi in this area. In fact individuals of both this species and of the Mugilidae were often seen to regurgitate filamentous algae following capture in gill nets.

The mid-water predators A. hololepidotus and L. amia together constituted 34% of the biomass of fish captured in the gill nets set in the lagoon. None of the former and only a few L. amia were captured in the seine nets. Similarly, Whitfield and Blaber (1978a) working at Lake St Lucia observed that large piscivorous species were poorly represented in seine net catches. The numbers of these predators and the zoobenthic forager Tachysurus feliceps, which was also only captured in gill nets, are low in comparison with the Sundays and Gamtoos estuaries (Marais, 1981; Marais, 1982). Like A. hololepidotus which uses its olfactory line system to hunt (van der Elst, 1982) the tactile scavenger T. feliceps is abundant in turbid water estuaries (Marais, 1981; Marais, 1982; Marais and Baird, 1979). The clear water conditions typical of Wilderness lagoon (Chapter 1, Part III) may therefore render the environment unsuitable for large numbers of these two species.

Although no dietary analysis was conducted, it seems possible that the low biomass of A. hololepidotus and L. amia in comparison with other estuaries may also be due to the low biomass of the fodder fishes H. breviceps and G. estuarius. This may in turn have been a consequence

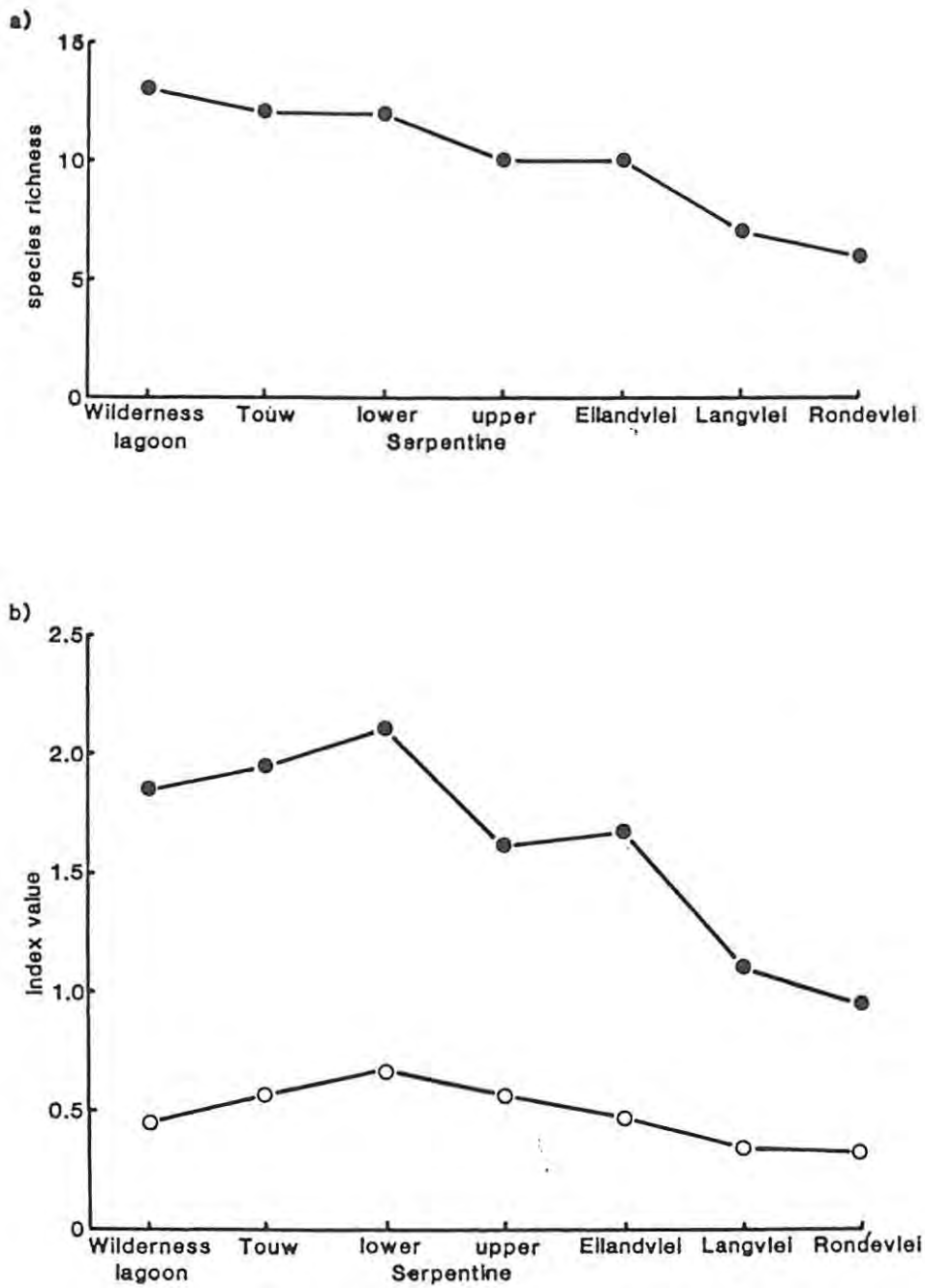


Figure 37: Numbers of fish captured in gill nets throughout the Wilderness lakes system represented as a) species richness and b) diversity according to the Shannon-Weaver diversity index (●) and Heip's evenness index (○).

of low zooplankton stocks. As more L. amia were captured than A. hololepidotus, the former's ability to swim at higher speeds than the latter may put it at an advantage as faster swimming prey, such as mullet, are more readily available to it. The only other mid-water predator captured in the lagoon was Trachurus capensis.

O. mossambicus was not recorded in the lagoon but a shoal of 63 was captured in gill nets in the Touw river during autumn 1983 when the mouth was closed. This observation is in agreement with those of Whitfield and Blaber (1979) for south-east African estuarine systems. Although Blaber (1978) suggested that this species avoided the lower estuary of the Kosi system because of the presence of highly mobile predators, Whitfield and Blaber (1978a) have shown that it does not feature in the diet of these fish to any significant extent. Whitfield and Blaber (1979) have shown that it avoids areas where current speeds are in excess of 0.1 m s^{-1} . Accordingly, this species may avoid the lagoon when the mouth is open because there are strong water currents.

As O. mossambicus is an exotic species, the question arises as to whether it poses a threat to the mullet species in the Wilderness lakes system? The natural range of O. mossambicus extends down the east coast of South Africa only as far as the Bushmans river between East London and Port Elizabeth in the Eastern Cape (Bruton and Boltt, 1975). However, within the limits of its natural distribution, it is often found in estuaries in association with mullet (Day *et al.*, 1953; Whitfield, 1980b). According to Whitfield and Blaber (1978c), competition with the mullet is reduced through different feeding mechanisms. In the Wilderness lakes system such resource segregation in association with an abundance of food (as evidenced by prolific macrophyte beds), most probably reduces interspecific competition to a minimum.

Having discussed the observed distribution of fish within the Wilderness lakes, it would be useful to describe these differences in terms of diversity. Figure 37a shows that according to the gill net catches, species richness of the system decreases up the estuary. The system can be divided into three areas of approximately equal species richness: Wilderness lagoon, the Touw river and lower Serpentine each

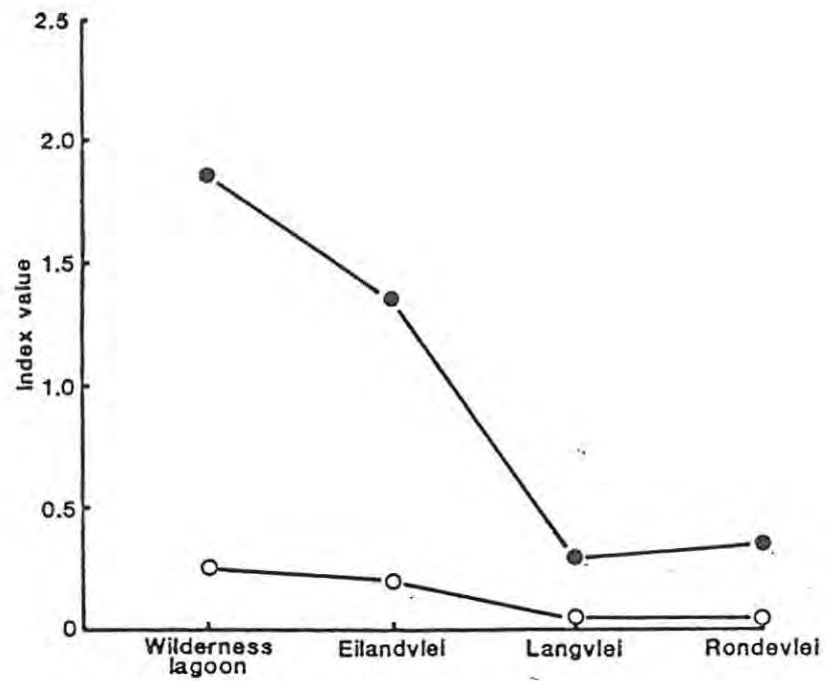


Figure 38: Numerical fish species diversity values from the Wilderness lakes system calculated from the Shannon-Weaver diversity index (●) and Heip's evenness index (○).

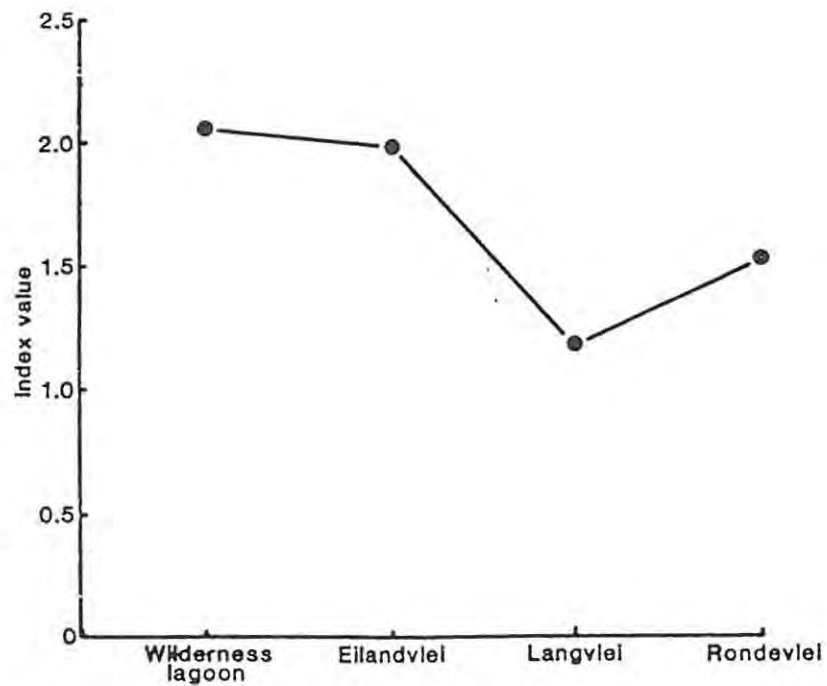


Figure 39: Gravimetric fish species diversity values from the Wilderness lakes system calculated from the Shannon-Weaver diversity index.

supported between 12 and 13 species; Eilandvlei and the upper Serpentine supported 10; whilst Langvlei and Rondevlei supported 7 and 6 species respectively.

Analysis of these data in terms of the Shannon-Weaver function (H) shows that the stations can be split into the same groups with $H = 2.0$, 1.6 and 1.0 (Figure 37b). However, indices from the Touw river, Wilderness lagoon and Serpentine stations are not directly comparable with those from the lakes as the sampling efforts were not equal (Lloyd and Ghelardi, 1964). The sampling effort in each of the lakes was three times higher than at these stations. Since H is similar for the Wilderness lagoon, Touw river and lower Serpentine stations, data from these were summed to represent fish captured in that area of the estuary where a tidal prism is noticeable. This gives a value of $H = 2.19$. If the same procedure is applied to Heip's evenness index (E), it appears that in the tidal area and Eilandvlei, E approximates 0.5 whilst in Langvlei and Rondevlei it approximates 0.33.

If the gill netting station in Wilderness lagoon is grouped with those in the Touw river and lower Serpentine, the total efforts applied to the lagoon and each of the lakes using gill nets, small multifilament and monofilament seines were equal. Community diversity and structure could therefore be compared using data from all three stations (Figure 38). When these data are examined together, fish communities can again be divided into Wilderness lagoon ($H = 1.87$), Eilandvlei ($H = 1.35$) and Langvlei and Rondevlei ($H = 0.33$). Heip's evenness index suggests that the community diversity is similar in Wilderness lagoon and Eilandvlei where $E = 0.22$ and in Langvlei and Rondevlei where $E = 0.04$.

The reason for H and E being highest in the lagoon is likely to be a function of the greater number of species. Support for this view comes from several workers in different fields who have suggested that species diversity can be related to the presence of predators. Kushlan (1976a) has shown that in the Florida Everglades, annual changes in species diversity increased with the number of predators. Addicot (1974), working on the protozoan communities of Pitcher plants, also documented a decrease in evenness when predators were removed. Similar observations were made by Paine (1971) when he removed carnivorous

starfish from rocky inter-tidal pools in New-Zealand. Dodson (1974) and Addicot (1974) have both suggested that by removing predation pressure, diversity can quickly decrease through an increase in competition between prey species. It is possible therefore, that species such as L. amia and A. hololepidotus play a role in maintaining a higher species diversity in the lagoon. The much lower diversities in Langvlei and Rondevlei are not just a function of the lower number of species present. They are also related to the strong numerical dominance of H. breviceps which constituted 95% of the catch in Langvlei and 88% in Rondevlei.

As this analysis gives no consideration to the variation in weight amongst species, the Shannon-Weaver index was re-worked using gravimetric data (Figure 39). This analysis caused H to increase markedly in each area of the system. In the Lagoon and Eilandvlei, H increased to 2.06 and 1.96 respectively, indicating the distribution of biomass amongst the species in these two areas was similar. Once again Langvlei had the lowest diversity ($H = 1.16$), but it was much higher than when numerical data were used. This is because species such as L. richardsoni which comprised 0.1% of the catch numerically, contributed 33% gravimetrically, whilst the numerically dominant H. breviceps only contributed 13% to the total biomass in this lake.

The use of biomass in the Shannon-Weaver function has more relevance in ecological terms than numerical data for it is more closely related to energy distribution between the species (Wilhm, 1968). In the Wilderness lakes system it does not appear that gravimetric diversity is grossly imbalanced through a strong domination of one species in any of the areas examined.

The Shannon-Weaver and Heip indices have helped to describe the fish communities of the system in terms of diversity. The results correspond well with field observations and suggest that the fish fauna of Langvlei and Rondevlei have a similar structure with a low diversity. The fish in these two lakes can be divided into two broad trophic categories; the gravimetrically dominant iliophagous species, i.e. the Mugilidae and O. mossambicus and the numerically abundant zooplanktivores dominated by H. breviceps.

In Eilandvlei, which is the major nursery area in the system, the species richness and diversity were higher and fish could be placed in three trophic categories. Once again the detritivorous Mugilidae were gravimetrically dominant and the zooplanktivorous H. breviceps was the most numerically abundant species. However, the zoobenthic feeders R. holubi and L. lithognathus also constituted 20% of the total biomass of fish in this lake.

In the lagoon, species richness and diversity were the highest in the system and the major components of the fish fauna could be divided into four trophic categories. The zooplanktivorous feeders were the least important and again the Mugilidae contributed the greatest biomass to the community. Zoobenthic feeders were more common than in Eilandvlei and also contributed a greater biomass. However, it was the piscivorous fishes such as L. amia and A. hololepidotus which were not present in other parts of the system, that contributed to the relatively high diversity in this area.

In the last chapter it was determined that Eilandvlei functions as the system's major nursery area for marine/estuarine fish. These fish enter and leave the lakes via the Serpentine. In this chapter factors associated with migration in the Serpentine, including the effect of the sluice, are investigated.

6.1. Materials and methods

In February 1984, two specifically designed traps were built to catch all fish moving across a section of the Serpentine. The traps were based on a fyke net design, their steel frames measuring 1m x 1m x 2m. They were covered in 50% monofilament shade cloth with a rectangular mesh size of about 1 x 2mm. The front of each trap supported a funnel, also made of shade cloth, which extended 0.5m into the trap to a mouth which measured 10 x 15mm (Figure 40). The back of each trap was covered from the bottom up by a sheet of netting measuring 1.0m x 0.6m. The 1.0m x 0.4m gap above this sheet allowed access to the trap so that it could be emptied with a dip net.

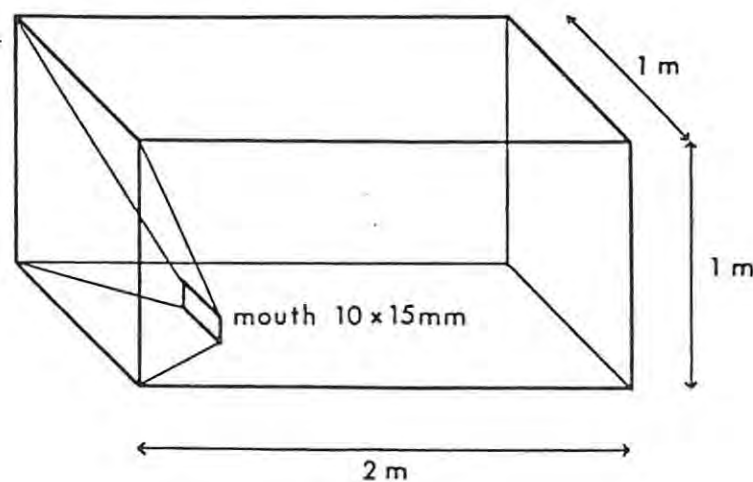


Figure 40: Structure of the fish traps used in the Serpentine.

The traps were placed back to back approximately 30m upstream of the open sluice in the Serpentine (Figure 41). Wings made of 50% shade

cloth were sewn onto the traps and extended across the width of the Serpentine. They were angled in such a manner as to funnel any fish encountering them into the mouth of the trap. The bottom of the wings were anchored and each was long enough to span the width of the Serpentine under all tidal conditions.



Figure 41: Position of the fish traps used in the Serpentine.

Problems were encountered when quantities of detritus and filamentous algae started to clog the mesh, thereby causing turbulence and a damming effect. This was partially alleviated by Potamogeton pectinatus beds above the traps which tended to stop detritus coming from Eilandvlei on the ebb tide. On the flood tide however this did not occur because the P. pectinatus beds below the nets were not as dense. This detritus drift problem was solved by placing a series of three floating nets across the Serpentine approximately 50, 35 and 5m below the traps. Observations around these nets showed that whilst floating detritus was trapped, fish movement was not affected.

Traps were set both during the day and at night and were emptied hourly. The water depth and current direction were recorded for each sampling hour. At the end of each sampling day the traps were removed and any fish remaining in them counted. It was found that never more than 5% of the fish entering the traps were missed by the dip net.

To investigate the effect of the sluice on fish migration in the Serpentine, a dip net measuring 50 x 40cm and constructed from monofilament shade cloth, was randomly swept within 3m of either side of the sluice for 5 minute periods. Captured fish from above and below the sluice were identified, counted and analyzed on a catch per unit effort (CPUE) basis.

6.2. Results and discussion

Like the fishing gears used in the lakes, the traps in the Serpentine may have been selective. However, observations of migrating fish shoals compared to trap catches suggested that this gear effectively sampled juvenile fishes. The majority of fish captured were in the 10-20mm SL size class which corresponded to the dominant size group of migratory shoals. The traps were found to be selective for fish above 10mm SL and 98% of individuals captured measured less than 60mm SL. Only two fish greater than 100mm SL were caught. These were both Liza richardsoni (160mm and 195mm SL) and were captured moving towards the lagoon. Altogether 14 species were captured. These were; Mugil cephalus, Liza richardsoni, Liza dumerili, Myxus capensis, Rhabdosargus holubi, Lithognathus lithognathus, Monodactylus falciformis, Gilchristella aestuarius, Hepsetia breviceps, Oreochromis mossambicus, Psammagobius knysnaensis, Gobius multifaciatus, Rhadogobius dewaali and Sandelia capensis. Only the first seven species listed form the marine/estuarine migratory component.

More fish were always captured in the net facing Wilderness lagoon, i.e. up estuary migration towards Eilandvlei was greater than seaward migration towards Wilderness lagoon. Migration also increased as water levels approached high tide and decreased towards low tide. The net migration per hour, i.e. the number of fish moving upstream minus those

moving downstream is plotted relative to depth in Figure 42. Curves for both daytime and night migration are plotted. Migration during the day was found to follow the expression $y = 1.74x^{1.417}$ ($r = 0.854$, $n = 36$) where y = the net number of fish moving upstream per hour and x = the mean water depth over that hour. At night, migration followed the expression $y = 2.567x - 8.893$ ($r = 0.861$, $n = 20$). Over the range of depths examined, day time migration was approximately three times greater than night time migration.

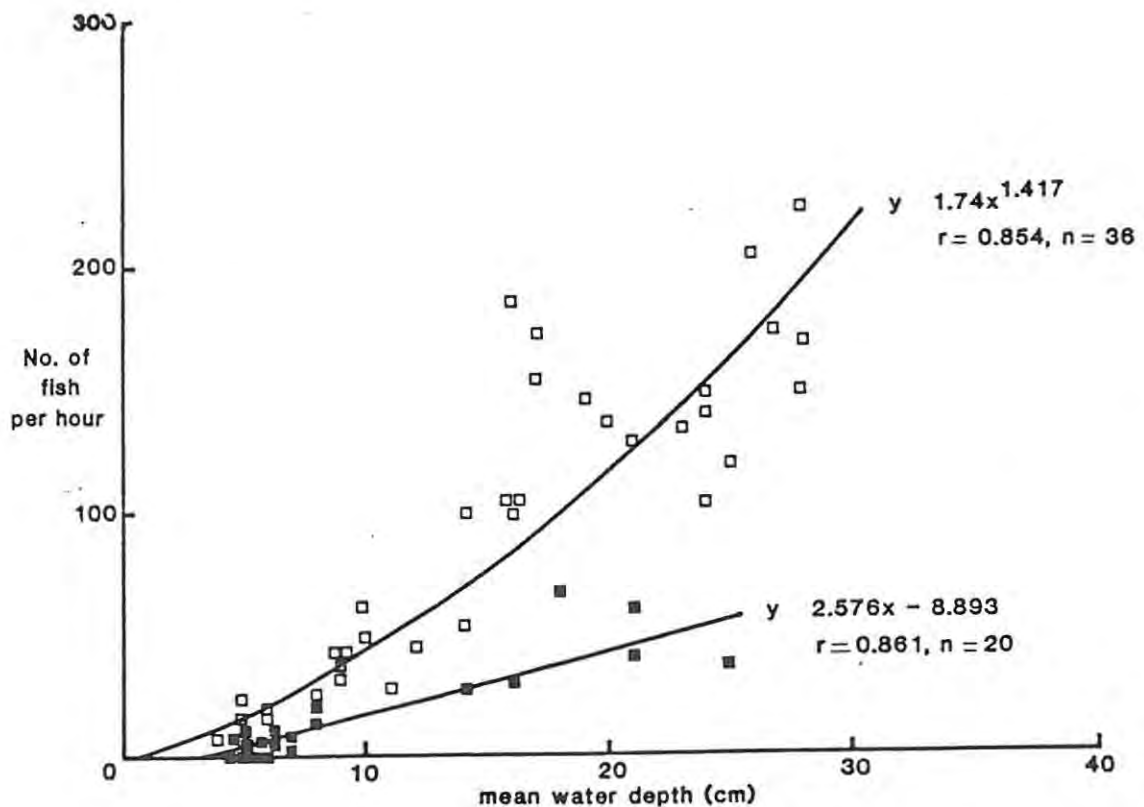


Figure 42: Net numbers of fish migrating up the Serpentine per hour relative to water depth during the day ($\square$) and at night ($\blacksquare$).

Observations around both the traps and the "detritus barriers" suggested that the latter neither scared fish nor attracted them. In the case of the traps, which rested on the bottom of the Serpentine, shoals were occasionally seen to swim up to the wings and then move away again. This observation suggests that estimates of the number of fish involved in migration might be conservative.

An estimate of the of the total number of juvenile marine/estuarine fish migrating into Eilandvlei during February 1984 was made subject to the limitations outlined above. Over this month in the southern Cape there are approximately 14 hours between sunrise and sunset with about 10 hours of darkness. Water level data from the netting area were matched with the hours of daylight and darkness, and the curves in Figure 42 were then used to estimate that approximately 52000 fish migrated up the Serpentine in this month.

Of the 2527 marine/estuarine fish caught during the day, 84% were found to be L. richardsoni. Altogether the Mugilidae comprised 99% of the daytime catch. No L. lithognathus were captured and only one M. falciformis and four R. holubi were recorded. At night however 3% of the 358 marine/estuarine fish captured were L. lithognathus, 11% M. falciformis and 18% R. holubi. Mullet comprised 71% of the catch but the most commonly occurring species was L. dumerili which constituted 40% of the total catch. The catch compositions during both the day and night are shown in Figure 43.

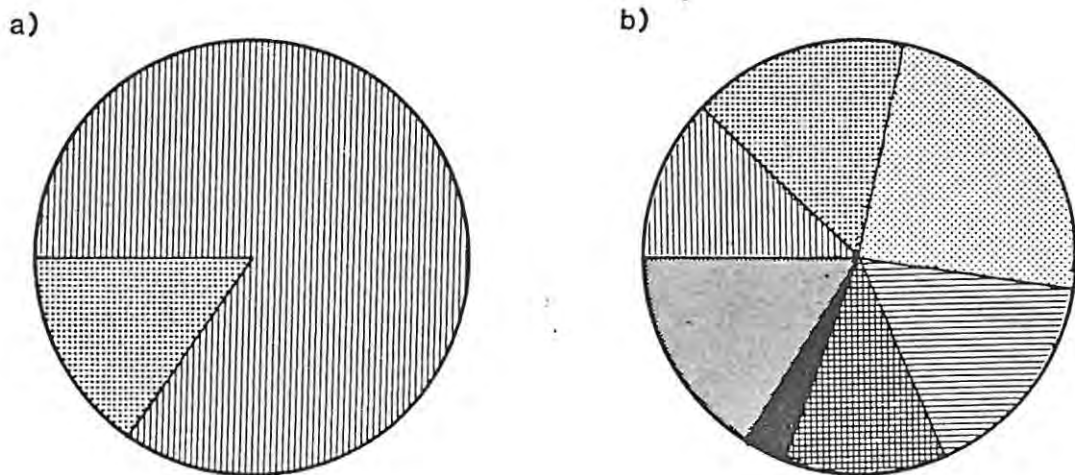


Figure 43: Catch composition of the traps used in the Serpentine during the day (a) and at night (b). Key; ||||| = Liza richardsoni, ||||| = Mugil cephalus, . . . = Liza dumerili, / / / = Myxus capensis, / / / = Rhabdosargus holubi, ■ = Lithognathus lithognathus, / / / = Monodactylus falciformis.

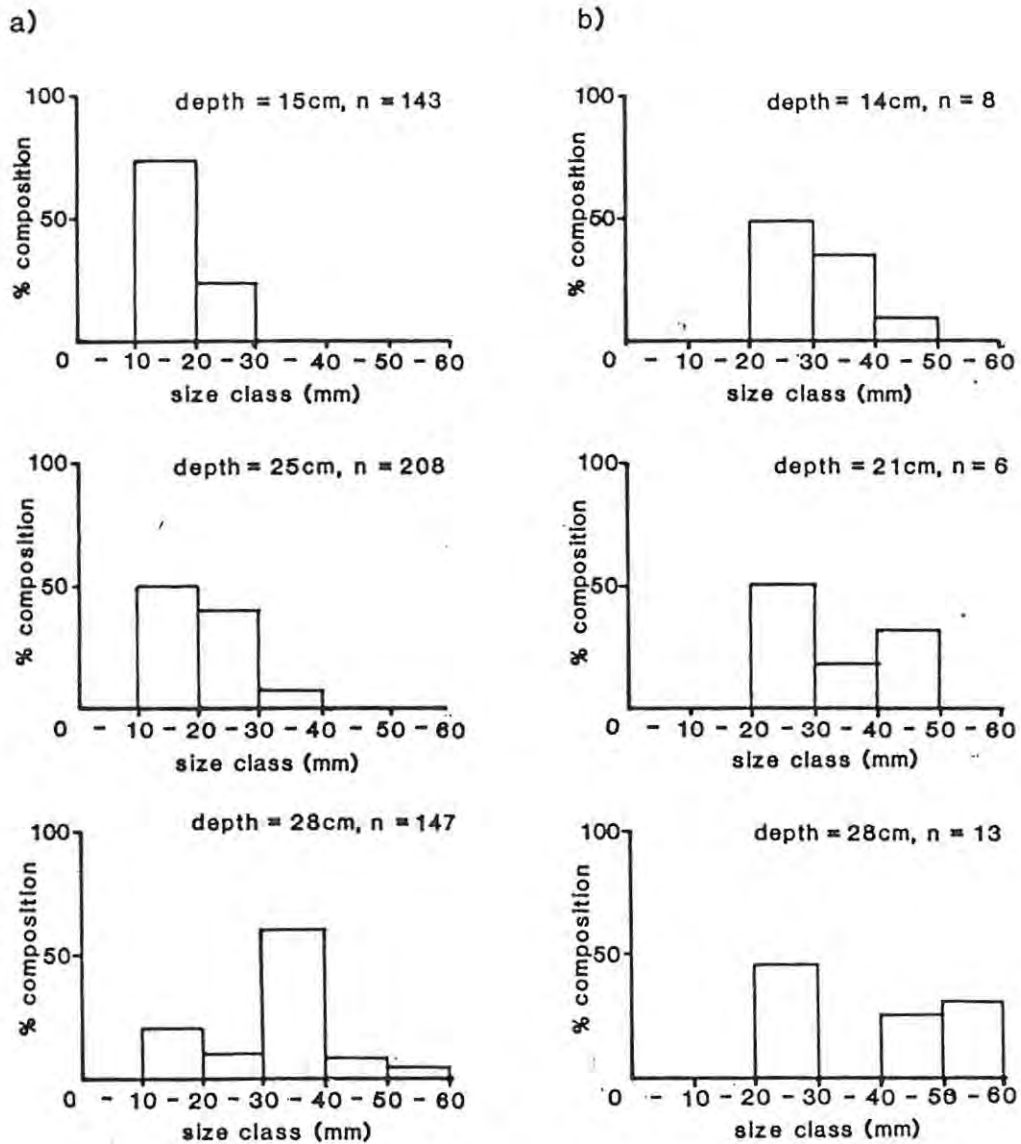


Figure 44: Size composition of (a) *Liza richardsoni* captured during the day and (b) *Rhabdosargus holubi* captured at night at three different water depths.

A characteristic of both day and night migration was that a higher proportion of larger individuals were caught on the high tide. This is illustrated in Figure 44a which represents the changes in size composition of L. richardsoni captured during the day at three different water depths. Figure 44b represents the same trend with R. holubi captured at night.

A literature review suggests that this investigation is possibly the first attempt to quantify the magnitude of juvenile marine/estuarine fish migration in an estuary. Several authors such as De Silva and Silva (1979) and Torricelli et al (1982) have determined the seasonality and diel activity of certain migratory species. They used seine and dip net which are active sampling methods and are therefore more selective than the passive sampling used in this study. The advantages of the traps used in the Serpentine are that they sampled its entire width and there was minimal human interference around them. The effectiveness of the traps was endorsed by observations suggesting they captured the majority of fish shoals seen in the area.

Bias in the results may have been caused by changes in the water flow patterns around the sluice frightening fish away. Alternatively the shade inside the traps might have been attractive to fish looking for shelter. Several workers including Orth and Heck (1980) have shown that juvenile fish seek the cover of marginal vegetation in order to avoid predators. It follows that the 52000 fish calculated to have migrated up the Serpentine may have not have been accurately estimated. As mentioned earlier, this figure is most probably an underestimation. However, Blaber (1973) estimated that between August 1971 and January 1972, 55000 juvenile R. holubi entered the Kleinmond estuary in the eastern Cape. A recruitment of 52000 fishes of 7 species into the Touw river system over one month does not therefore seem unrealistic.

Several authors, eg. Wallace (1975) working in Natal, De Silva and Silva (1979) in Sri Lanka and Torricelli et al (1982) in Italy have shown recruitment into estuaries to be seasonal. According to Kok (cited by Allanson and Whitfield, 1983) February is a peak recruitment month to the Wilderness lakes system. The figure of 52000 fish

migrating up the Serpentine during February 1984 does not therefore represent an average monthly figure, but is only applicable to the time over which the sampling was carried out.

Throughout the investigation it was apparent that with the exception of L. dumerili which was captured mainly at night, the mullet species tended to migrate during the day. This is in contrast to the observations of De Silva and Silva (1979) working on M. cephalus. Torricelli et al (1982) however, recorded two peaks in the catches of six species of juvenile mullet, one after sunset and a slightly reduced peak in the morning.

Blaber (1976) observed that L. dumerili tends to feed more at night than other mullet species and this may account for its abundance in night catches. More likely, it is because larger juvenile fish are more vulnerable to predation by swimming in shallow water during the day. According to Wallace (1975) L. dumerili does not recruit into estuaries until about 50mm in length. This is in agreement with this study where no individuals smaller than the 40-50mm size group were captured.

Each of the other mullet species were well represented in the 10-20mm size group. This is in agreement with the observations of De Silva and Silva (1979) and Wallace and van der Elst (1975) for the minimum size of mullet recruiting into other South African estuaries. Results were also in agreement with those of Blaber (1974) in that the smallest R. holubi captured were in this size class. Day et al (1981) report that the smallest M. falciformis found in estuaries are around 15mm in length. This was also found to be true for this species in the Serpentine.

Like L. dumerili, the more deep-bodied and laterally compressed species such as the Sparidae and M. falciformis, were commonly captured at night and only in the deeper water during the day. These species may find it more difficult to negotiate shallow water than their more elongate counterparts. Their predominance in the night catches may be a predator avoidance mechanism.

De Silva and Silva (1979) found that tides had little influence on the migratory behavior of M. cephalus. However, Torricelli et al (1978) noticed that catches of five species of mullet, including M. cephalus increased around high tide. The increase in the number of juveniles migrating up the Serpentine around high water was independent of flow direction and may have been a function of the shallowness of the sampling station at low tide. Vulnerability to bird predation tends to increase with decreasing water depth (Kushlan, 1976b), so small fish might avoid swimming in exceptionally shallow water.

Finally, it must be emphasized that the strong correlation between migration and water depth may have been a function of the shallowness of the sampling area. The water level of Eilandvlei over the sampling period was the lowest observed in five years (Chapter 5) and the Serpentine was also unusually shallow. This may also explain why only two fish greater than 100mm SL were captured. If migration was hindered by water depth, then the number of juvenile marine/estuarine fish recruiting into the lakes over February may have been lower than for the same month in years when water levels were higher.

The implications of these results upon migration in the Eilandvlei/Langvlei and Langvlei/Rondevlei channels are that because of the shallowness of the former, marine/estuarine fish probably only enter these lakes during flood conditions or when the lagoon mouth is closed and lake levels rise. As was suggested in Chapter 5, part III, this explains why there were less marine/estuarine fish in the upper lakes. Once fish have recruited into them, they may experience difficulty in leaving until water levels once again rise. This explains why both the mean size and total biomass of the same fish in these lakes was greater than in Eilandvlei.

Having established the pattern of migration in the Serpentine the possible effects of the sluice gate on fish movements can be discussed. Data concerning its effect on these migrations suggest that there are at least three hydraulic conditions which can influence the movement of fish. These are described in Figures 45, 46 and 47.

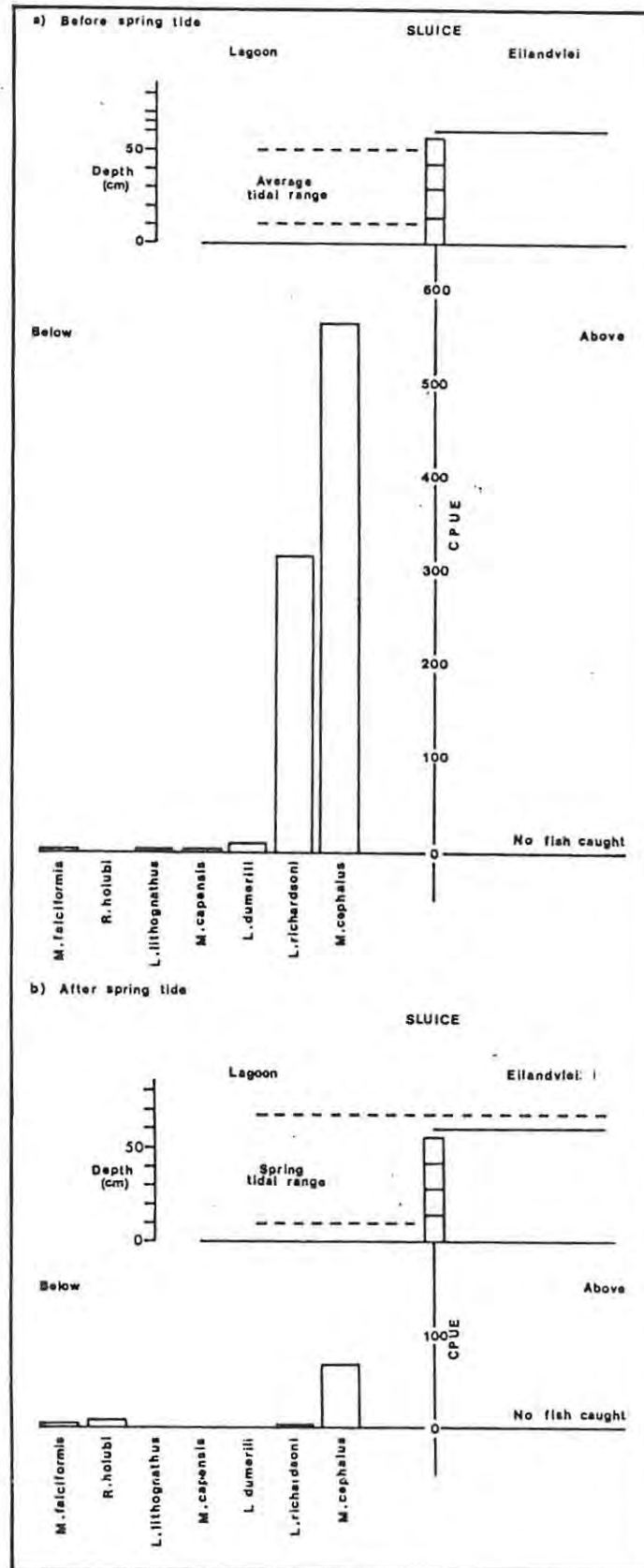


Figure 45: The sluice can act as a partial barrier to fish migrations. Mean CPUE of juvenile marine/estuarine fish (<5cm SL) caught within 3m of either side of the sluice over a three day period before (a) and after (b) spring tide. CPUE = random sweeping with dip net over a 5 minute period. For further explanation see text.

Figure 45 illustrates the condition where the sluice can act as a partial barrier to fish migrations. Figure 45a is representative of the situation before the spring tide of 17 October 1982. There was a constant flow of water over the sluice from Eilandvlei, and at no time were tidal levels below the sluice greater than those above it. Over this period there was a striking build-up of fish as they were unable to penetrate into the lakes. However, towards the peak of spring tide there was a stage when the sluice was topped by water from below, yet a downstream flow was maintained. Under these conditions some fish were observed swimming over the sluice and up towards Eilandvlei. This dispersion probably accounts for the lower number of fish caught below the sluice after spring tide (Figure 45b). Just before peak tide was reached the flow reversed and observations suggest that this inhibits upstream migration until the falling tide once again re-establishes a net downstream flow. These conditions are summarized in the series of diagrams below:

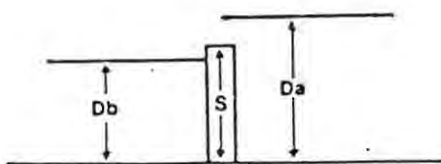
D_a = depth of water above sluice

D_b = depth of water below sluice

S = height of sluice

(i) $D_a > S > D_b$

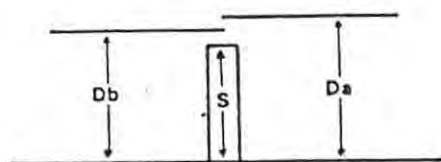
← Flow



- no migration occurred because fish could not negotiate the height of the sluice. Flow downstream.

(ii) $D_a > D_b > S$

← Flow



- migration occurred, fish could easily negotiate the sluice. Flow downstream.

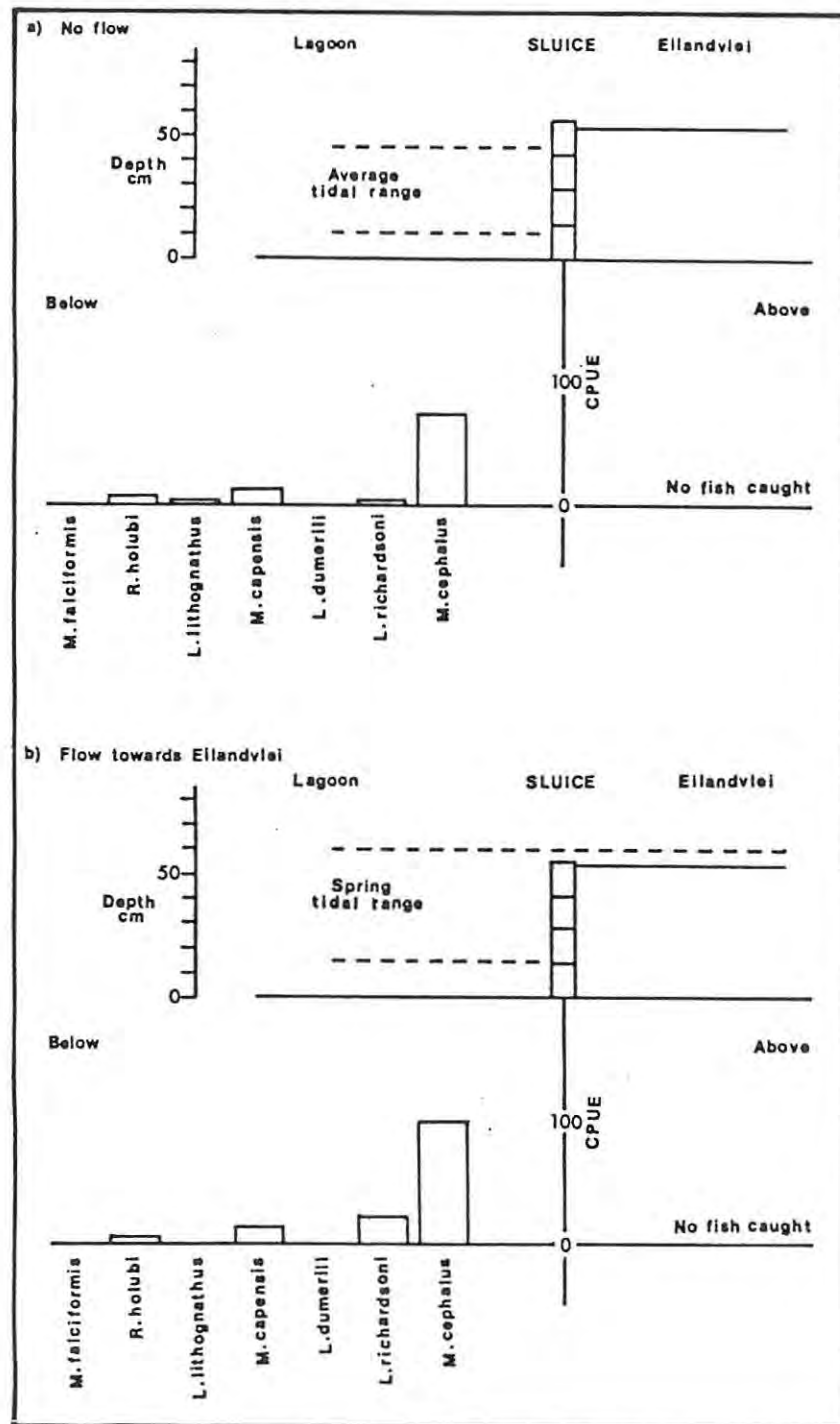


Figure 46: The sluice can act as an absolute barrier to fish migrations. For further explanation see text.

(iii) $D_b > D_a > S$

- no migration even though fish can negotiate the sluice. Flow upstream.

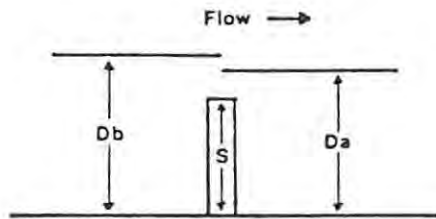


Figure 46 illustrates the condition where the sluice can act as an absolute barrier to fish migrations. Figure 46a is representative of the situation before the spring tide of 15 November 1982. There was no flow from either side of the sluice and a build up of fish below it indicated that it could not be negotiated. Figure 46b represents the hydraulics of the sluice at spring tide and the distribution of fish after it. Water topped the sluice at high tide and there was a flow towards Eilandvlei. This was not coupled with migration, again suggesting that a down estuary flow is required to illicit a directional response.

Figure 47 illustrates how the sluice can be operated to have a minimal effect on fish migrations. Data on two different occasions before spring tide were compared. In Figure 47a a build up of fish below the sluice was associated with a flow over it as tidal levels did not reach the top of the sluice. Figure 47b shows a constant flow under the sluice being maintained by wedging the bottom slat 10cm above its concrete floor. Under these circumstances fish migrations appeared to be minimally affected.

These results show that the hydraulics of the sluice may play a key role in determining the number of fish penetrating the lakes. The only acceptable manner in which it can be operated is to wedge the bottom slat above its concrete floor.

If the sluice is in such a condition, the direction and velocity of water flow under it will depend upon the relationship between the depth of water below it to the depth of water above it. Rulifson (1977) has

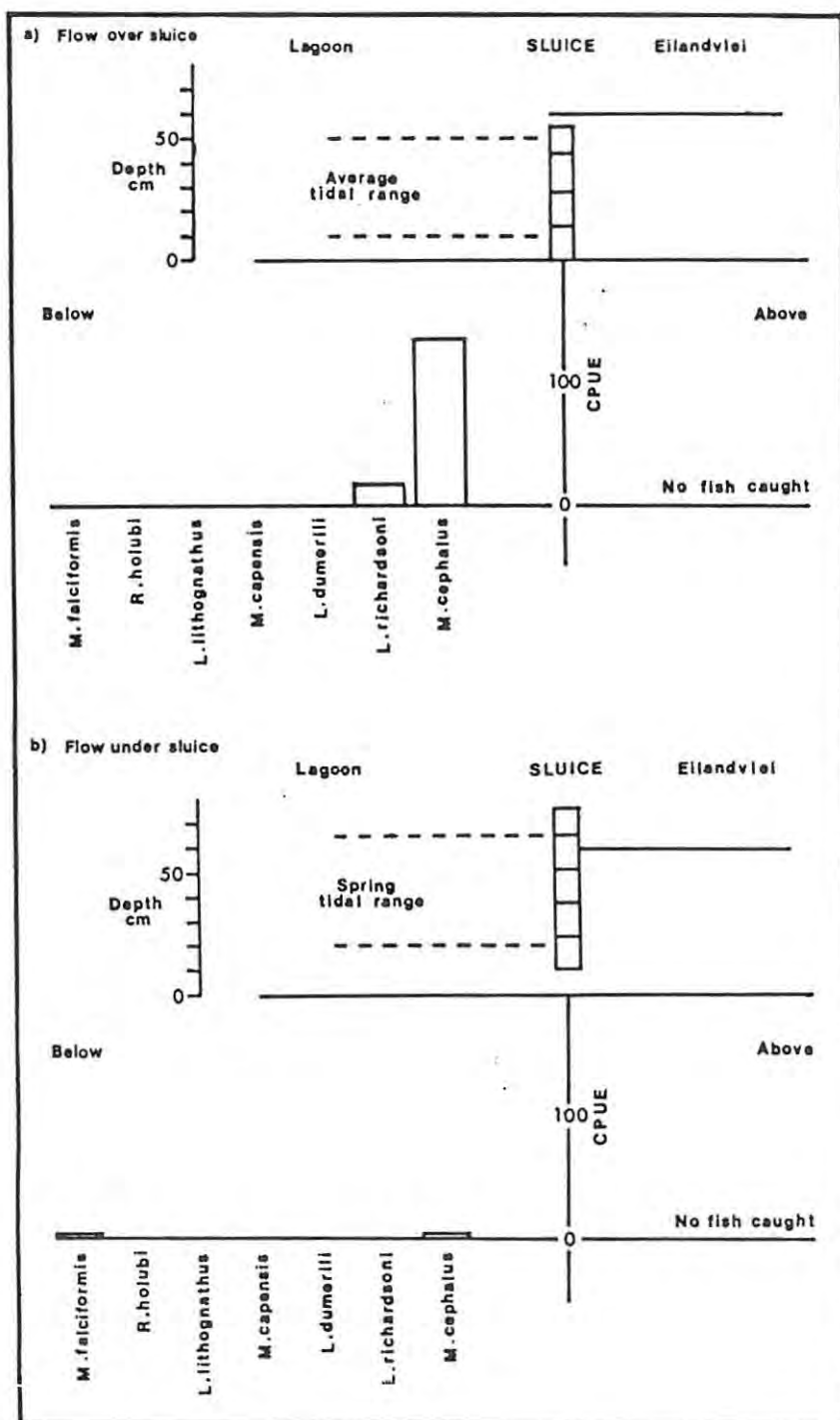


Figure 47: The sluice can have a minimal effect on fish migrations. For further explanation see text.

shown that juvenile M. cephalus (14-70mm SL) start to experience difficulty in swimming when water velocity exceeds five times their body length per second ($5L\ s^{-1}$). The average maximum velocity against which these fish could swim for 30 seconds was $12.71L\ s^{-1}$. Taking this data as representative of all mullet species, this suggests that the maximum permissible water velocity through the bottom of the sluice for a mullet 20mm SL would be $25cm\ s^{-1}$.

Observations around the sluice suggested that a down estuary flow was required to illicit a directional response in migratory juveniles. This has been suggested by Thomson (1954) who also suggests that wind direction and a salinity gradient may play a role in directing the migration of mullet in estuaries. He quotes Roule (1916) who believed that other chemical stimuli may be important. Both Wallace (1974) and Whitfield and Blaber (1978b) have suggested that organic cues from seawater inflows and freshwater drainage may also serve as an orientation function. Contrary to the observations around the sluice, data from the traps did not suggest that fish required water flow to orientate themselves. Catadromous and anadromous fish probably utilize a series of complex and interacting stimuli (which may vary between species) when undergoing migration.

To conclude, it appears that when the system is subject to low water levels, fish migration in the Serpentine is dependent on tidal fluctuations. The effect of the sluice on these migrations can at all times be controlled by man. It is his responsibility to ensure that, should the sluice be operational, it should be used in such a manner that fish can still move up the Serpentine.

PART IV

GENERAL DISCUSSION

A major morphological characteristic of the Wilderness lakes is its segmentation. According to Orme (1973) this has occurred in all of the major Zululand lagoons but is most developed in the Kosi system and in lake St Lucia. In Mozambique the chain of barrier lagoons connecting Lagoa Poelala to the sea is probably also a segmented system.

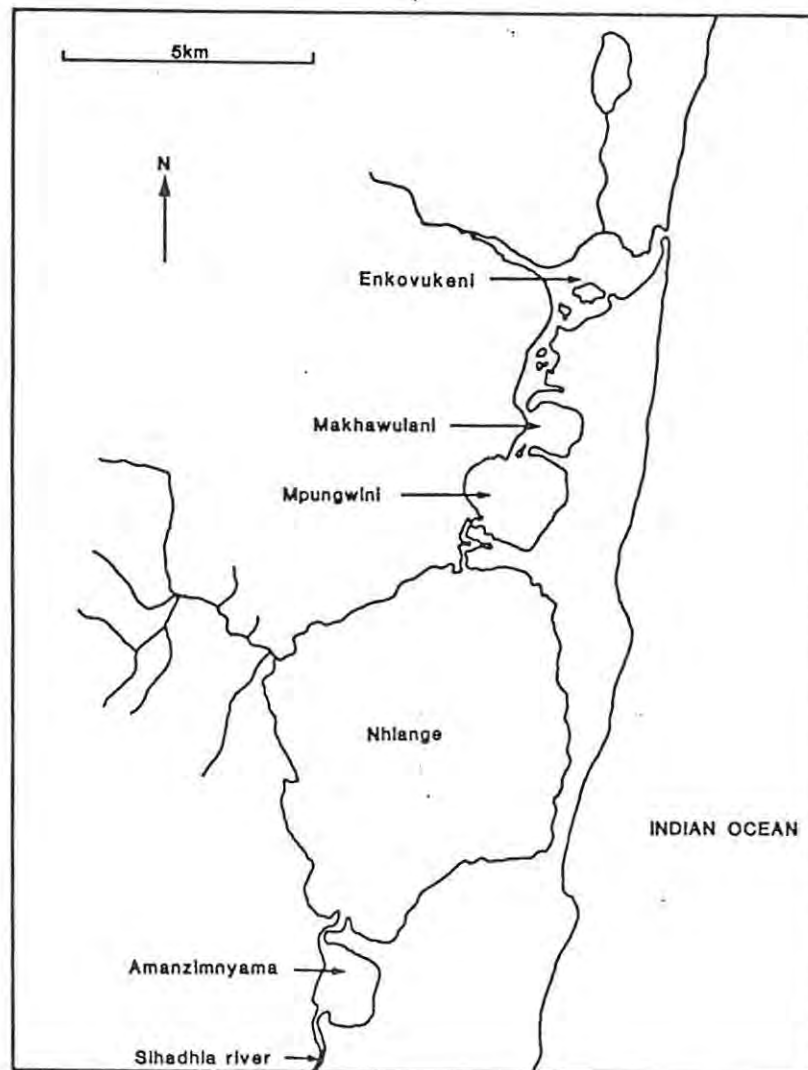


Figure 48. Map of the Kosi system.

The constrictions imposed by segmentation in the Wilderness system are similar to those of the Kosi system (Figure 48). Broekhuysen and Taylor (1957) maintain that the shallows between the estuary mouth and lake

Makhawulani are approximately 1.0 - 2.0m deep with a tidal range of 10 - 15cm. In this respect these shallows are similar to the Serpentine in the Wilderness lakes system. Just as tidal fluctuations are absorbed by Eilandvlei in the Wilderness lakes, so they are absorbed by lake Makhawulani in the Kosi system.

The two channels between lake Makhawulani and lake Mpungwini in the Kosi system are blocked by a shallow sandbank covered by only a few centimetres of water (Broekhuysen and Taylor, 1957). This is similar to the situation in the Eilandvlei/Langvlei channel in the Wilderness lakes system. The channel between lake Mpungwini and lake Nhlangwe in the Kosi system corresponds to the Langvlei/Rondevlei channel in the Wilderness lakes system. It is 2.0 - 3.0m deep (Broekhuysen and Taylor (1957) and like the Langvlei/Rondevlei channel affords a relatively unrestricted flow of water through it.

In the Kosi system the main feeder rivers flow through all the lakes to find the sea. However, the main axis of the Wilderness lakes system is at an angle to the Touw river. This is a major morphological difference for it means that the channels in the Kosi system are regularly subjected to strong currents. Blaber (1978) recorded maximum average summer current speeds in the Nhlangwe/Mpungwini, Mpungwini/Makhawulani and Makhawulani/estuary channels to be 0.61m s^{-1} , 0.27m s^{-1} and 0.23m s^{-1} respectively. These channels are therefore scoured annually during the summer rainfall season. As the main axis of flow through the Wilderness system is not through the lakes, its channels are rarely subject to scouring.

Analysis of water level fluctuations following a flood in the Wilderness lakes system (chapter 1.1. Part II) illustrates that whilst water flows freely along the Serpentine and Langvlei/Rondevlei channels, it is severely inhibited by the Eilandvlei/Langvlei channel. This is because the latter is both shallow and severely choked by macrophytes. The mean biomass of Potamogeton pectinatus recorded in this channel was 1468gm^{-3} which was more than double that of the Langvlei/Rondevlei channel and nearly five times as great as in the Serpentine. In the Kosi system regular scouring in all the channels probably prevents macrophyte encroachment.

The successive floods in the southern Cape during late 1980 and 1981 resulted in an approximate 50% decrease in the salinity of Eilandvlei, Langvlei and Rondevlei. I shall therefore discuss the salinity budget of these lakes in relation to the segmentation of the system.

Investigations into tidal flux of salt in the Serpentine showed that over one lunar tidal cycle 386 tonnes of salt were deposited in Eilandvlei (Table 7). It is unlikely that any of this salt would ever enter Langvlei as tidal fluctuations in Eilandvlei are negligible and the Eilandvlei/Langvlei channel inhibits water flow too severely. However, when the mouth is closed, a major transfer of salt from the lagoon to all three lakes takes place. This occurs because in the region of the Touw/Serpentine junction, discharge from the Touw river mixes with saline water from the lagoon. Salt is then carried up the Serpentine towards the lakes. The data used in formulating a simple model predicting such a movement showed that over an eight month period there was a net gain of 24506 tonnes of salt to all the lakes (Table 8).

These calculations suggest that salt input to the lakes occurs largely when the mouth is closed. This unusual phenomenon is important for it means that, providing the sluice is used according to original management policy, ie only when the mouth is open, its impact on the salt budget of the lakes should be minimal.

Several authors have discussed the effect of segmentation on the physico-chemical properties of different systems. In the St Lucia system Day *et al* (1953) and Millard and Broekhuysen (1970) have shown variations in temperature, salinity and pH between the north and south basins of the main lake. In the Kosi system differences in the salinity of each lake have been documented by several workers and their results have been summarized by Begg (1978). Differences in the concentrations of various cations and anions in two of the Kosi lakes have been recorded by Allanson and van Wyk (1969) who also showed differences in the oxygen and temperature regimes, as well as in the light climate. Further afield, Hedgepeth (1947; quoted by Day, 1951) has shown that owing to a constriction in the Laguna Madre, Texas, it can be divided into two areas of differing salinity. It is therefore apparent that

constrictions can result in the evolution of different physico-chemical environments within different basins of a segmented lagoon.

In the Wilderness lakes system a principal components analysis performed on physico-chemical data showed that there are few differences between the waters of the lakes whilst the Touw river station, which is strongly influenced by humic stained acidic waters, was shown to be very different (chapter 2, Part III). The waters of Wilderness lagoon exhibited some of the properties of both the Touw river and the lakes. This is to be expected for, depending on the state of the tide, it might be subject to near marine or near freshwater conditions. Both Broekhuysen and Taylor (1957) working on the Kosi system and Millard and Broekhuysen (1970) working at St Lucia found large physico-chemical differences between the lower estuary and the rest of the system.

During the present study the aquatic macrophyte senescence ended (Chapter 3, Part III). By February 1983 the mean biomass of submerged vegetation in both Eilandvlei and Langvlei was greater than 1000gm^{-2} dry mass. In comparison with the 1978 data for Eilandvlei (Howard-Williams, 1980), this represents an increase in biomass of 45%. There was no growth recorded in Langvlei in 1978. The re-growth of these macrophytes under a completely new salinity regime illustrates how the system can recover from apparently cataclysmic changes.

Whitfield (1984, 1985) showed that although there were changes in the diversity of the fish fauna in Swartvlei prior to and during the macrophyte senescence, there were no real changes in the number of fish species over this period. If the same is true in the Wilderness lakes system, the number of species recorded during the present study must have been similar to those present before it and can be considered representative.

In comparison with other southern African coastal lakes, the fish fauna of the Wilderness lakes system is poor. A total of 32 species of fish were captured in the system (chapter 5, Part III) whilst 163 species have been recorded from the Kosi system (Blaber and Cyrus, 1981).

Whitfield (1980c, 1983) recorded 108 and 45 species from the St Lucia and Swartvlei systems respectively.

Several authors e.g. Wallace and van der Elst (1975), Blaber (1981) and Whitfield (1983) have discussed the numbers of fish in southern African estuaries in terms of the zoogeographical affinities of different species. Their conclusions are that because of the environmental stresses imposed upon tropical and subtropical Indo-Pacific species, many of these fishes, whilst common in the estuaries of Mozambique, Natal and Transkei, do not occur off the Cape coast.

Apart from the zoogeographical affinities of fish, the small size of the Wilderness lakes system may limit the number of species. Whitfield (1983) states that smaller estuaries generally have a lower species diversity than larger ones primarily because they are usually open to the sea for shorter periods. Additionally the time of year that an estuary opens is of paramount importance in determining the magnitude of recruitment. (Blaber, 1974; Wallace and van der Elst, 1975 and Whitfield, 1978). Similarly, Whitfield (1980a) has shown that the number of fishes present in a periodically closed estuary are dependent on both the time that the mouth opens and the duration of the open phase.

Over the sampling period the mouth was only closed during late July and early September which is not a peak recruitment period (Allanson and Whitfield, 1983). Conditions were therefore ideal for the system to receive maximum recruitment and attain a high species diversity. The low diversity in comparison with other estuarine systems may therefore be largely attributed to the relatively low species diversity of marine/estuarine fishes in the adjacent coastal waters.

Having established that conditions for recruitment were ideal over the study period, the first major constriction encountered by fish entering the system is the Serpentine. Analysis of gill net data collected from this channel show that the diversity decreased from west to east. The species recorded in the west of the Serpentine and which were not recorded further east were mainly predators such as A. hololepidotus, T. feliceps and L. amia. In the lagoon these species were generally

only found in deepest water. This is in agreement with the results of Whitfield and Blaber (1978a) and Marais and Baird (1979) who state that these species prefer deep and turbid water environments in estuaries. It therefore seems that these fish are unable, or unwilling to negotiate the 5.6km of shallow water in the Serpentine.

Eilandvlei was found to be the system's major nursery area for marine/estuarine fishes. The question arises as to why fish should negotiate the Serpentine, which may be dangerous in terms of predation by birds, if Wilderness lagoon is available to them? The scarcity of submerged aquatic plants in Wilderness lagoon, which provide both food and shelter for juvenile fishes (Adams, 1976a, 1976b; Hanekom and Baird, 1984), may have encouraged the observed migration into Eilandvlei.

In addition, Blaber (1980b) has suggested that clear water environments such as are present in Wilderness lagoon, are avoided by many Indo-Pacific juvenile fishes who prefer more turbid waters which help them avoid predation. Movement of juvenile fish in the Serpentine has been discussed with reference to water flow between the Wilderness lagoon and Eilandvlei (Chapter 6, Part III). I have suggested that there is little restriction of water flow along the Serpentine because it is relatively free from macrophyte encroachment. It follows that fish migration should be relatively uninhibited and this is reflected by the estimated 50000 juvenile fishes which migrated up the Serpentine into the lakes during February 1984.

The fish migration in the Serpentine could be adversely affected if the sluice was operated incorrectly. However, by wedging the bottom slat above the floor of the sluice's concrete superstructure, a continual flow of water can be maintained. Providing that water velocities under the sluice do not exceed 25cm s^{-1} , fish of 20mm SL should be able to negotiate it.

The majority of fish entering Eilandvlei do not move up into Langvlei or Rondevlei. However, the principal components analysis performed on physico-chemical data suggested that there was little difference between the waters in each lake. Additionally aquatic macrophytes,

which have been shown to be attractive to juvenile fish (Branch and Grindley, 1979; Orth and Heck, 1980) grow prolifically in both Langvlei and Eilandvlei. In fact, Langvlei supports a more luxuriant growth than Eilandvlei and so in this respect may offer a more suitable habitat.

Davies (1981, 1985) has shown the important association between macrophytes and macroinvertebrates in the Wilderness lakes system. Although the macrophyte communities collapsed during his study, he showed that the P. pectinatus beds in Eilandvlei supported up to 297g m^{-2} dry mass of invertebrates in May 1979. According to Howard-Williams (1980) the mean above ground biomass of macrophytes in Eilandvlei at this time was 900g m^{-2} dry mass. Over the same period there were no aquatic plants recorded in Langvlei so information on invertebrates associated with submerged plants in this lake is lacking. However, in February 1983 the average biomass per transect in Eilandvlei and Langvlei was 1120g m^{-2} and 1170g m^{-2} respectively. Examination of submerged plant material during the study suggested that the macrophyte communities in both lakes supported a wealth of invertebrates.

The conclusions arising from these observations are that the environmental conditions within these lakes are similar. In spite of this however, juvenile marine/estuarine fish do not utilize the other lakes to any significant extent. A possible explanation for this may be related to the inaccessability of the upper lakes.

Investigations showed that fish mobility in the Serpentine was inhibited in shallow water and that even in 10cm water depth, relatively few juvenile fish were involved in migration. A survey of the Eilandvlei/Langvlei channel showed that there was a sill at 1.0m above msl. For most of the sampling period water levels in Eilandvlei and Langvlei lay below the 1.1m above msl level which is the level that allows for 10cm of water over the sill. However, marine/estuarine fish are commonly found in the upper lakes of the Kosi system even though the water depth at the sill between lake Makhawulani and lake Mpungwini is only a few centimetres. This could be because seasonal rainfall annually increases water depths, therefore increasing the accessibility of the channel. In addition, average summer current velocities of 0.27c ms^{-1} (Blaber, 1978) probably prevent macrophyte

growth in this channel. Macrophyte encroachment in the Eilandvlei/Langvlei channel is well developed and is probably the major factor inhibiting fish movement.

Obviously some fish are able to move up to Langvlei when water levels are high. The question then arises as to what happens to these fish? On the basis of water flow data and macrophyte biomass it appears that the Langvlei/Rondevlei channel imposes less of a constriction than the Eilandvlei/Langvlei channel. Having reached Langvlei it is easier for fish to swim into Rondevlei than to return to Eilandvlei. Once in Rondevlei, marine/estuarine fish probably experience difficulty in leaving the system as no river enters this lake and no positive salinity gradient exists. This may account for the presence in Rondevlei of some of the largest marine/estuarine fish within the system (chapter 6, Part III).

Whitfield (1984; 1985) has shown the resilience of estuarine fishes within Swartvlei to environmental change. This study has shown that after apparently disastrous changes in the light climate of the Wilderness lakes, aquatic macrophytes were able to recolonize the system. The segmentation of the lakes has restricted water flow between them although it has not yet caused the evolution of noticeably different environments within them. However, macrophyte encroachment in the channels has played a role in structuring the fish communities of the Wilderness lakes; the channel between Eilandvlei and Langvlei plays a key role in restricting the nursery function of the system to Eilandvlei.

Finally, it is worth considering the effect of dredging the Eilandvlei/Langvlei channel to facilitate water exchange between these two lakes. This would potentially increase the area of readily available nursery waters for juvenile marine/estuarine fish. It was stated earlier that Langvlei supports more prolific macrophyte beds than Eilandvlei, and that there is very little difference between the chemical environments within these lakes. In view of the nursery function of macrophytes (Adams, 1976a, 1976b; Orth and Heck, 1980; Hanekom and Baird, 1984), it could be argued that Langvlei offers a more attractive nursery area than Eilandvlei. However, although

macrophyte beds in Eilandvlei are not as prolific as in Langvlei, they are still extensive and must readily contribute to the food chain directly via detritus pathways, or indirectly by supporting epifaunal and epiphytic communities. In addition to a vegetated littoral, Eilandvlei also offers both sandy and muddy beaches as well as a greater range of water depths. Environmental heterogeneity is therefore greater in Eilandvlei and, in association with an abundant food supply, must make this lake the most effective nursery area in the Wilderness lakes system.

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