

The recovery and dynamics of submerged aquatic macrophyte vegetation in the Wilderness lakes, southern Cape

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Keywords: biomass, Characeae, fluctuations, macrophytes, monitoring, *Najas marina*, *Potamogeton pectinatus*, succession, vegetation dynamics, Wilderness lakes

ABSTRACT

Between 1979 and 1981, the submerged aquatic macrophyte vegetation in the Wilderness lakes died back significantly, and in some areas disappeared altogether. This study documents the senescent phase and describes the recovery of the plant populations between May 1982 and May 1983. In two lakes, namely Langvlei and Eilandvlei, the plant biomass approximately doubled between the winters of 1982 and 1983. Seasonal changes in species composition are documented and possible factors accounting for the collapse and recovery of the plant populations are discussed.

UITTREKSEL

Gedurende 1979–1981, het die makrofitiese onderwaterplantegroei in die Wildernismere aansienlik teruggesterf en in sommige gebiede heeltemal verdwyn. Hierdie opname beskryf die verouderende fase en die herstel van die plantbevolkings vanaf Mei 1982 tot Mei 1983. In beide Langvlei en Eilandvlei het die plantbiomassa nagenoeg verdubbel tussen die winters van 1982 en 1983. Seisoenale veranderinge in die spesiesamestelling word beskryf en faktore wat moontlik verantwoordelik kon wees vir die ondergaan en herstel van die plantbevolkings word bespreek.

INTRODUCTION

Several authors (Howard-Williams 1980; Jacot Guillarmod 1982; Weisser & Howard-Williams 1982) have studied the aquatic macrophyte communities in the Wilderness lakes. Their work, which was conducted prior to a major die-back of aquatic plants throughout the lakes, provide base-line data for describing vegetation changes arising from a combination of seasonal and successional processes (Miles 1979).

Between 1975 and 1979, submerged macrophytes were an important biological component of the Wilderness lakes, producing in excess of 750 t of dry plant mass per annum (Howard-Williams 1980). The most important species were *Potamogeton pectinatus*, *Chara globularis*, *Lamprothamnium papulosum* and *Ruppia cirrhosa*. The aquatic macrophyte population beds in this system died back significantly between 1979 and 1981. This study describes the senescent phase and documents seasonal changes in species composition and biomass which occurred during part of the recovery period (1982–1983).

STUDY AREA

The Wilderness lakes comprise a segmented barrier lagoon system lying parallel to the southern Cape coast. There are three interconnected lakes (Rondevlei, Langvlei and Eilandvlei) linked to the Wilderness Lagoon and the Touws River by a narrow winding channel known as the

Serpentine (Figure 1). The Wilderness Lagoon is shallow, varying in depth from 1 m in its lower reaches to 3.5 m in the vicinity of the Serpentine entrance. The lakes are all deeper than the lagoon, with a maximum depth of 6.5 m in Eilandvlei, 4.0 m in Langvlei and 6 m in Rondevlei.

The whole lake system (91 km²) is situated on a series of Quaternary sands known as the Wilderness-Knysna embayment. Immediately inland of this embayment is a 200 m high Tertiary platform (foothills of the Outeniqua Mountain range) consisting of folded sediments of the Table Mountain Sandstone group, which forms part of the catchment area of streams and rivers that feed the lakes and Wilderness Lagoon. The lake system is estuarine in nature and only periodically open to the sea at the Touws River Mouth.

An important characteristic of the Wilderness lakes is its reversed salinity gradient (Allanson & Whitfield 1983). Rondevlei, which only receives fresh water from precipitation and is the lake furthest from the sea, has the highest salinity, whereas Eilandvlei, which is also influenced by fresh water input from the Touws River has the lowest salinity. Evaporation at Rondevlei (1 100–1 200 mm per annum) generally exceeds precipitation and this leads to increasing salinity during dry periods. Heavy rainfall years have the opposite effect. A series of floods in 1981 resulted in a dilution of salt present in all three lakes. At Rondevlei the salinity decreased from 16 g kg⁻¹ to 10 g kg⁻¹ between September 1980 and September 1981, whereas over the same period in Langvlei and Eilandvlei salinity decreased from 10 g kg⁻¹ to 5 g kg⁻¹ and 9 g kg⁻¹ to 4 g kg⁻¹ respectively (Allanson & Whitfield 1983).

The waters throughout the system are generally well oxygenated, though low oxygen concentrations (< 2 mg l⁻¹) are occasionally recorded in deeper areas of all three lakes during the summer months (December–February).

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MS. received: 1992-05-19.

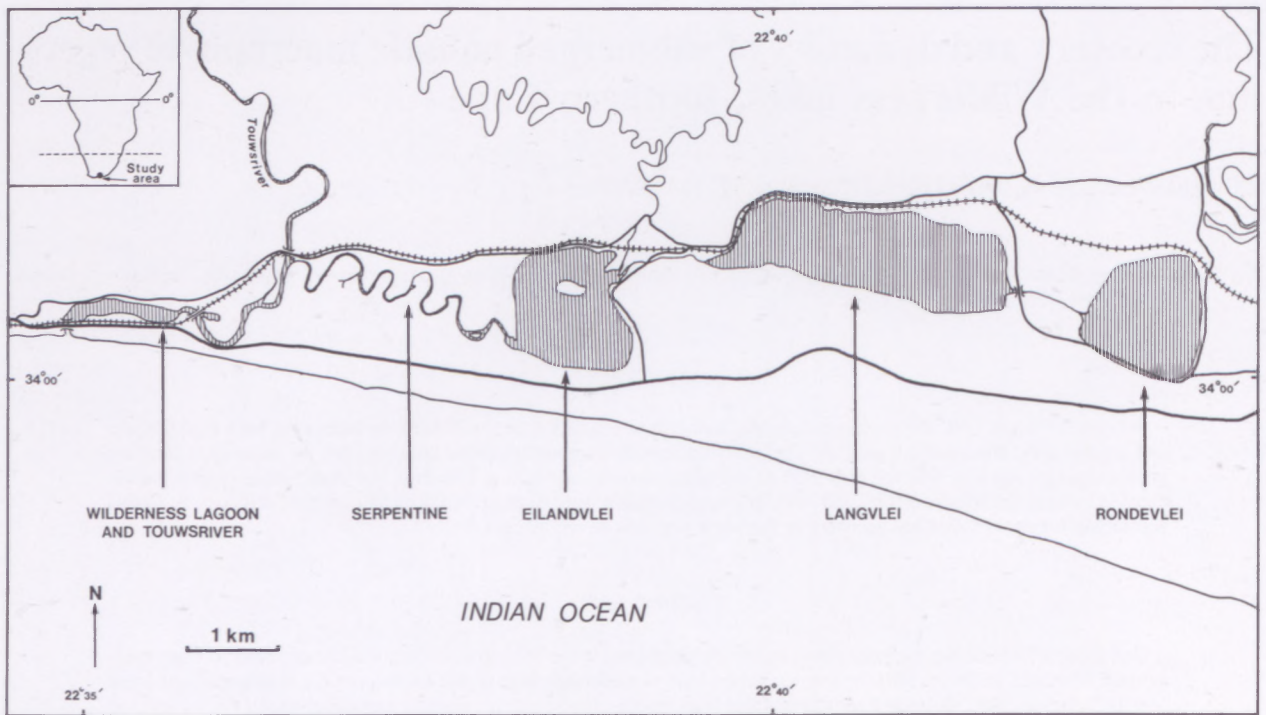


FIGURE 1.—Map of the Wilderness lakes showing localities mentioned in the text.

Surface water temperatures in the central region of the lakes range from between 14°C in midwinter (July) to 26°C in midsummer (January). The pH values range between pH 7 and pH 9 despite the acidic (pH 5–6) nature of the rivers and streams entering the system. Nutrient levels are generally low, with total phosphorus and nitrate (NO_3N) values seldom exceeding values of 100 $\mu\text{g l}^{-1}$ and normally <40 $\mu\text{g l}^{-1}$. Chlorophyll *a* values are also generally less than 15 $\mu\text{g l}^{-1}$ though readings as high as 146 $\mu\text{g l}^{-1}$ have been recorded during phytoplankton blooms in Langvlei (Allanson & Whitfield 1983).

MATERIALS AND METHODS

Aquatic macrophyte distributions in the Wilderness Lake System prior to the die-back were mapped according to a method described by Weisser & Howard-Williams (1982). During the senescent phase (1979–1981), the degree of aquatic macrophyte die-back in each part of the system was visually monitored by boat at monthly intervals. The recovery phase was more intensively monitored and sampling commenced in May 1982. Six littoral transects were positioned at approximately equidistant intervals around Eilandvlei and five around Langvlei. 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 submerged macrophyte sampler described by Howard-Williams & Longman (1976) was used to sample a 0.0625 m^2 area at variable intervals along the length of each transect. Samples were returned to the laboratory for sorting and drying. Results are expressed as g m^{-2} dry weight. The total species biomass along each transect was established by multiplying the mean biomass for each plant species by the total transect length. The above procedure was repeated in May, August and November 1982, and in February and May 1983. In this study, the period December–February is regarded as summer, March–May as autumn, June–August as winter and September–November as spring.

The standing biomasses of submerged macrophyte populations in Rondevlei and Wilderness Lagoon were too low to sample effectively with the macrophyte collector. Therefore only changes in species composition in these two sections of the Wilderness lakes were recorded.

Past distribution patterns of aquatic macrophytes in the Wilderness lakes were obtained from direct inspection of historical aerial photographs using a Wild Aviopret Stereoscope (Weisser & Stadler 1983).

RESULTS

Eilandvlei

In 1975 most of Eilandvlei (Figure 2) supported a littoral plant community dominated by *Potamogeton pectinatus*, which occurred in water up to 3 m deep. At depths greater than 3 m, no macrophytes were recorded. Zones of Characeae and *Ruppia cirrhosa* occurred on the landward side of the *P. pectinatus* zone (Figure 2).

Between 1976 and 1978, the *P. pectinatus* zone (Figure 3) receded by almost 40 m at the southeastern side of the lake. This decline continued during 1979, so that by January 1980 no mature plant canopy was evident. A series of severe floods in 1981 caused silt-laden waters (400–500 $\text{mg dry mass l}^{-1}$) to enter Eilandvlei from the Duiwe River, increasing water turbidity.

The recovery of submerged aquatic plant beds commenced during 1982 with *Najas marina* occupying large areas previously colonized by *P. pectinatus* (Figures 2 & 4). Changes in species composition were most apparent in the northeastern section of Eilandvlei. In May 1982 the mean dry biomass (six sampling transects around the lake) of *N. marina* was 635 g m^{-2} (S.D. ± 1032), that of *P. pectinatus* 109 g m^{-2} (S.D. ± 81) and Characeae 4 g m^{-2} (S.D. ± 5). The average transect length in Eilandvlei

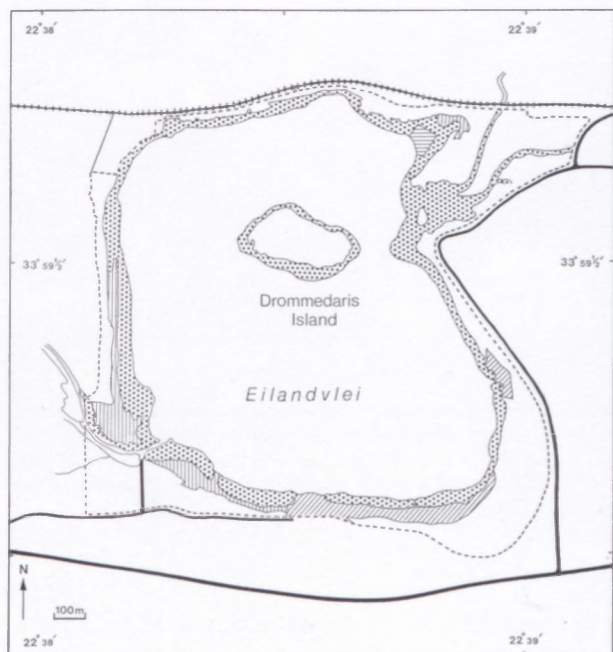


FIGURE 2.—Distribution of submerged aquatic macrophytes in Eilandvlei during 1975 (adapted from Weisser & Howard-Williams 1982). Dashed line = limit of study area; stippled areas = *Potamogeton pectinatus*; areas with vertical lines = Characeae; oblique lines = *Ruppia cirrhosa*; horizontal lines = *Najas marina*.

increased from 19 m in September 1982 to 27 m in March 1983.

Proportional contributions of different aquatic plant taxa to biomass in different seasons during 1982 and 1983 are shown in Figure 5. *N. marina* beds were a major component of the aquatic plants in the winter of 1982 but during the spring these beds started to recede and were replaced by *P. pectinatus*. Characeae beds also showed signs of recovery. By the summer of 1982/83 large amounts of filamentous algae (*Enteromorpha* sp.) started to grow both epiphytically and epipsammically. The smothering effect of this alga on other submerged plants 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 did not disappear entirely.

Langvlei

In 1975 the entire bottom of Langvlei was covered by dense Characeae beds (Figure 6) comprising *Chara globularis* and *Lamprothamnium papulosum*. Both species occurred throughout the lake, but the western region was colonized almost exclusively by *L. papulosum*, and *C. globularis* dominated the deeper central areas. These extensive Characeae beds were still evident during April 1978, but by March 1979 had virtually disappeared. Aerial photographs taken of Langvlei during December 1981 (Job 391, 1:10 000) showed an absence of any aquatic macrophyte canopy or submerged Characeae beds. In 1975 the lake bottom was clearly visible at 4 m. Thereafter, the water transparency decreased as a result of a dinoflagellate bloom (Weisser & Howard-Williams 1982). The mean Secchi disc value for the period January–December 1978 was 0.8 m (Coetzee & Palmer 1982).

During 1982, water transparency in Langvlei increased again, resulting in a recovery of littoral submerged plant beds but not those in deeper water (Figure 7). Five littoral transects around the lake in May 1982 revealed a *Potamogeton pectinatus* mean dry biomass of 750 g m^{-2} (S.D. ± 1138), Characeae 48 g m^{-2} (S.D. ± 54) and *Najas marina* 1 g m^{-2} (S.D. ± 2). A band of *N. marina* was present along the northern shore of Langvlei during the winter of 1982 but was replaced by *P. pectinatus* in the spring of that same year. The latter species contributed more than 70% to the total submerged biomass in the lake in all seasons (Figure 8).

The extensive charophyte meadows, which covered the deeper areas of the lake prior to the vegetation die-back, did not reappear. *P. pectinatus* spread into these areas during the summer of 1982/83, and by autumn 1983 this species covered virtually the entire water surface area of some regions of the lake. Filamentous algae were recorded in the lake during the spring and summer of 1982/83, but they did not proliferate as in Eilandvlei.

Rondevlei

In 1975, submerged macrophyte beds were absent in Rondevlei, possibly due to the relatively high salinity (22 g kg^{-1}) prevailing at the time. During 1978 the submerged



FIGURE 3.—Photograph of Eilandvlei in March 1978 showing bands of *Potamogeton pectinatus* (arrowed) surrounding both Drommedaris Island and the lake. These aquatic plant beds had disappeared by January 1980.

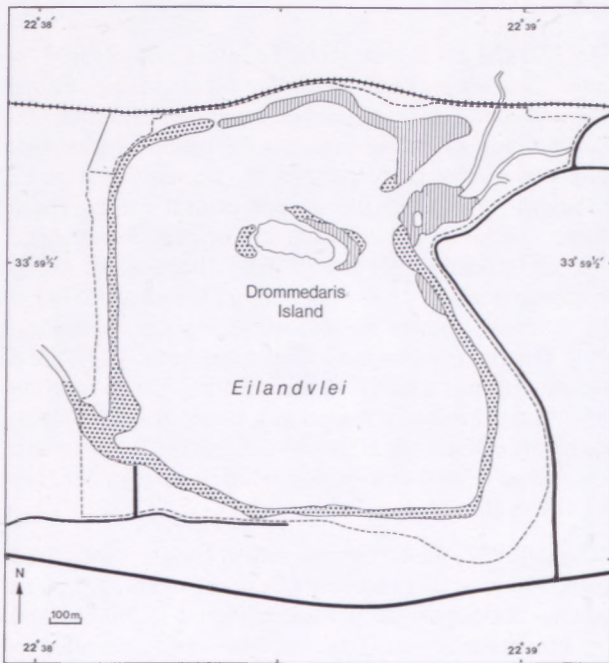


FIGURE 4. — Distribution of submerged aquatic macrophytes in Eilandvlei during 1982. Areas with vertical lines = *Najas marina*; stippled = *Potamogeton pectinatus*.

vegetation of Rondevlei comprised a peripheral band of the dominants *Ruppia cirrhosa* and *P. pectinatus* (Weisser & Howard-Williams 1982) extending to a depth of 1.3 m. In March 1979 the submerged macrophytes of Rondevlei had diminished considerably compared to March 1978, and the few scattered remaining plants did not reach the surface. Aerial photographs taken during December 1981 (Job 391, No. 291/3) confirmed the macrophyte senescent phase. This situation persisted until 1982 when evidence of a recovery was recorded. In May 1982 sparse patches of *R. cirrhosa* covered approximately 30% of the littoral zone to a depth of about 1 m. By May 1983 these patches, together with *P. pectinatus*, had expanded to cover approximately 90% of the littoral zone.

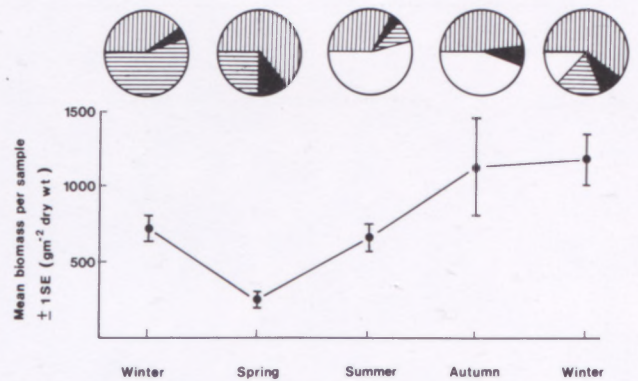


FIGURE 5. — Seasonal changes in composition (pie chart) and biomass (graph) of submerged aquatic plants in Eilandvlei during 1982 and 1983. Pie chart legend: vertical lines *Potamogeton pectinatus*; horizontal lines = *Najas marina*; black = Characeae; white = *Enteromorpha*.

Wilderness Lagoon

In March 1978, the submerged plants in the Wilderness Lagoon comprised *Potamogeton pectinatus*, *Ruppia cirrhosa*, *Zostera capensis* and filamentous algae (Weisser & Howard-Williams 1982). Isolated patches of *P. pectinatus* were recorded growing in the Wilderness Lagoon during 1982/83, and epipsammic *Enteromorpha* mats proliferated during lagoon mouth closure. These mats covered up to 60% of the water surface at such times, but were dissipated and washed out to sea whenever the estuary mouth opened. *Z. capensis* was not recorded from the Wilderness Lagoon during 1982/83.

DISCUSSION

Aquatic macrophyte populations of brackish waters are characterized by a low species diversity and vulnerability to changes in environmental conditions, whether natural or anthropogenically induced. Howard-Williams & Liptrot (1980) for example suggested that if human activities cause the decline of a macrophyte species in estuarine waters,

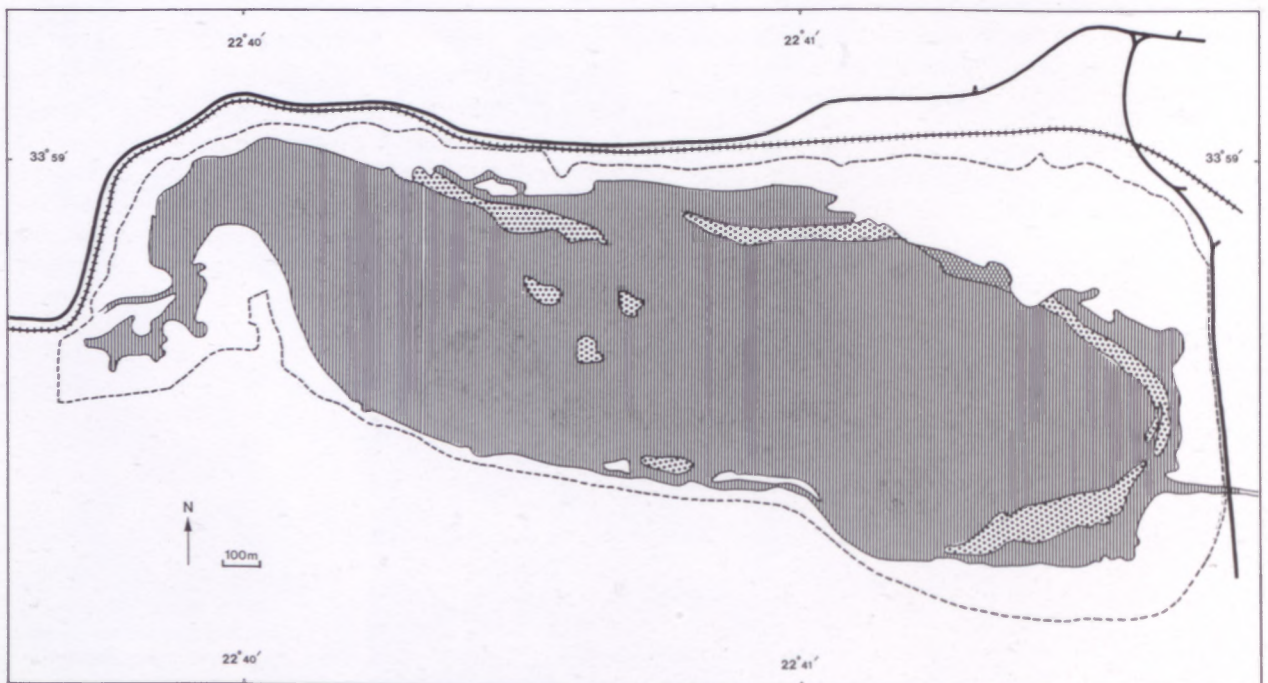


FIGURE 6. — Distribution of submerged aquatic macrophytes in Langvlei during 1975 (after Howard-Williams & T. Longman in Weisser & Howard-Williams 1982). Vertical lines = Characeae; stippled = *Potamogeton pectinatus*.

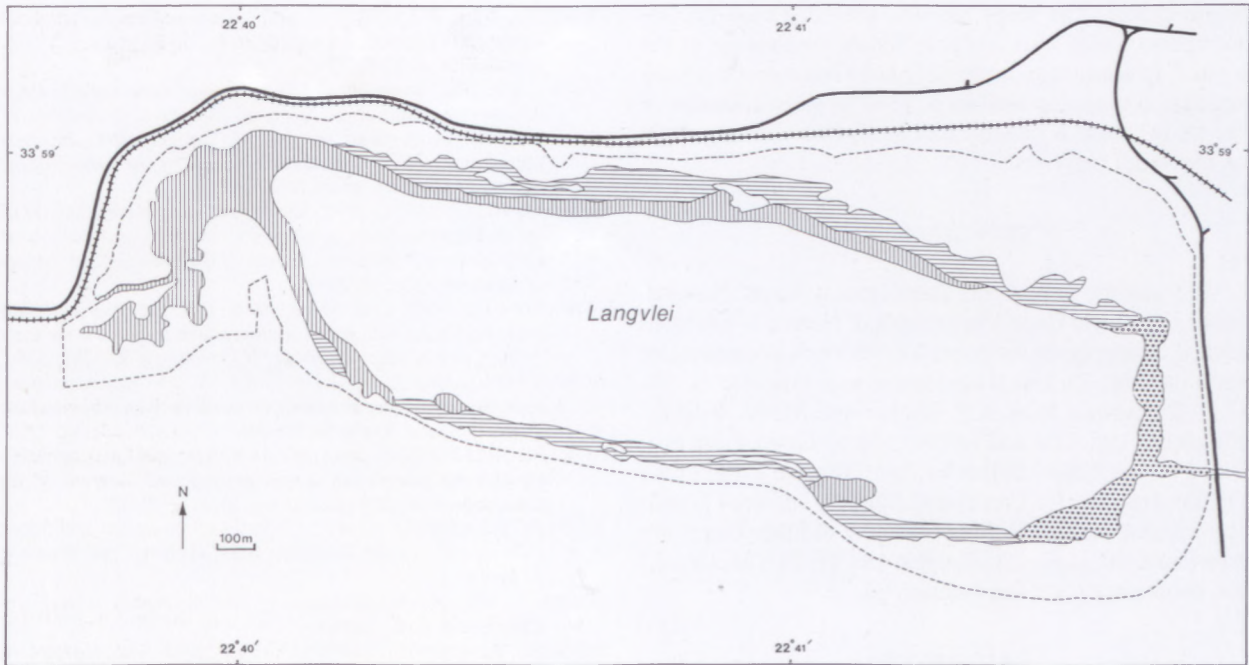


FIGURE 7.—Distribution of submerged aquatic macrophytes in Langvlei during 1982. Areas with vertical lines = *Najas marina*; horizontal lines = *Potamogeton pectinatus*; stippled = *Ruppia cirrhosa*.

there are generally few replacement taxa. This hypothesis is supported by the current study which found that, during the senescent phase, no new macrophyte species invaded the previously occupied littoral zone. Recolonization potential was limited to five species and contrasts to the situation pertaining in most terrestrial environments e.g. tropical forests.

The rapidity with which vegetation changes proceed in brackish waters is noteworthy. In this study community 'succession' was most prevalent in Eilandvlei (Figure 5). Nevertheless, in both Eilandvlei and Langvlei, seasonal changes in mean standing crops followed a similar pattern and were of the same order of magnitude. Mean biomass per square metre approximately doubled between the winter of 1982 and the winter of 1983 in both lakes.

However, the rate of expansion of plant beds towards the centre of the lake in Langvlei was more rapid than in Eilandvlei, a much deeper system. Average water transparencies (Secchi disc) in Langvlei were 1.7 m and in Eilandvlei 1.2 m over the period April 1982 to January

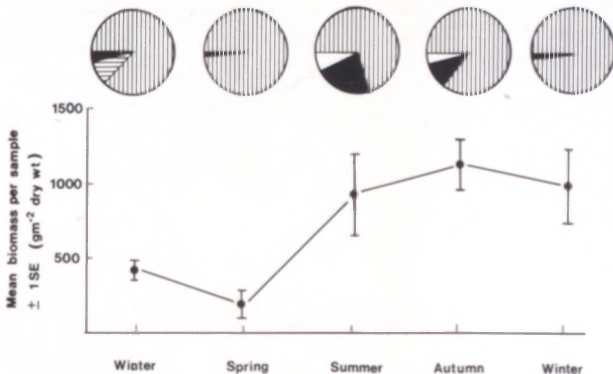


FIGURE 8.—Seasonal changes in composition (pie charts) and biomass (graph) of submerged aquatic plants in Langvlei during 1982 and 1983. Pie chart legend: vertical lines = *Potamogeton pectinatus*; horizontal lines = *Najas marina*; black = Characeae; white = *Enteromorpha*.

1983, indicating better light penetration in Langvlei. In nearby Swartvlei, it has been shown that the distribution of *Potamogeton pectinatus* is closely associated with water depth and degree of penetration of photosynthetically active radiation within the water column (Howard-Williams & Allanson 1981).

Evidence from Langvlei suggests that aquatic vegetation proceeds through cycles; from an aquatic macrophyte dominated system through a phytoplankton dominated system and back to a macrophyte dominated system. However, the dominant submerged plants at the beginning of the study (Characeae) were not well represented at the end of the study period, when *P. pectinatus* was dominant.

The cause(s) of most of the submerged macrophytes dying in the Wilderness lakes has not been identified and may well differ from one part of the system to another. According to Weisser & Howard-Williams (1982) the high-water level management policy, planktonic algal blooms, development of periphyton on submerged plants and uprooting of plants by wave action during strong winds may all have contributed to declines in submerged macrophytes within the system. It is interesting to note that a similar collapse in aquatic macrophytes was recorded from nearby Swartvlei in 1979 (Davies 1982; Whitfield 1984), and 10 years later these Characeae and *P. pectinatus* beds had still not fully recovered (A.K. Whitfield pers. obs.). In Natal, Breen & Weisser (1986) recorded the disappearance of previously abundant *Potamogeton schweinfurthii* and *P. pectinatus* in Lake Mzingazi, but could not identify any definite factor(s) which caused the die-back. Breen & Weisser (*op. cit.*) did, however, suggest that rapid changes in lake water levels may have contributed to the collapse.

This investigation has shown that aquatic plant communities of the Wilderness lakes are highly variable, both on a spatial and temporal scale, and that this dynamism is due to a complex interplay of environmental and

biotic factors. The study has also provided base-line information which will facilitate future monitoring of the system. In conclusion we would like to recommend regular vegetation mapping and aerial photographic coverage of the study area as a valuable tool in the future management of the Wilderness lakes.

ACKNOWLEDGEMENTS

We thank the Lake Areas Development Board, National Parks Board and Cape Department of Nature & Environmental Conservation for permission to work in areas under their control. Technical assistance was provided by Mr G.L. Christmas, Miss A.P. Backer and Mr K. Wagner. Financial, logistical and infrastructural support was provided by the CSIR, Estuaries Joint Venture Programme (FRD), Institute for Freshwater Studies, National Botanical Institute and J.L.B. Smith Institute of Ichthyology. We also thank Mr M.G. O'Callaghan and Mr D.J. McDonald for commenting on the manuscript.

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