THE HISTORY AND PRESENT VEGETATION OF THE MACROPHYTE SWAMP AT PUKEPUKE LAGOON

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SUMMARY: Pukepuke Lagoon is one of a series of shallow dune-lakes in the Manawatu district of New Zealand. Its open water area has been reduced by about 90% during the last century by sand drift from adjacent dunes, man-made changes to the local drainage, and the spread of macrophytes) especially *Typha,* Superimposed upon these changes are others due to the influx of exotic plants and animals.

The vegetation of the macrophyte swamp is described in terms of the supposed sequence of hydroseral development. A reciprocal average ordination is used to describe the extensive *Typha* stands. The first axis of the stand ordination correlates with water depth, pH and the depth of the underlying organic matter. The second axis probably reflects stand disturbance. A species list is presented.

INTRODUCTION

This paper is the first in a series which will describe studies carried out during 1968-1973 on the ecology of raupo *(Typha orientalis)* B.C. Presl. at Pukepuke Lagoon. It outlines the history and management of the study area, and describes the current vegetation of the lagoon and swamp ecosystems, to provide a background for more detailed studies on *Typha*. Subsequent papers will cover: (1) *Typha* shoot growth and survivorship, (2) rhizome growth, (3) decomposition of dead material, and (4) stand productivity and energy flow. Authorities for botanical nomenclature are given in Appendix II.

LOCATION AND STATUS

Pukepuke Lagoon lies at latitude 40°20' S, longitude 175° 16' E on the coastal sand-dune country of Manawatu, North Island, New Zealand (Fig 1). It is one of a series of shallow lakes and swamps, formerly more extensive, lying along the boundary between the Motuiti and Waitarere dune phases (Cowie, 1963), between the Rangitikei and Manawatu river mouths about 3 km from the sea, and 6.5 m above mean sea level. Although it is locally known, and officially gazetted, as *Pukepuke Lagoon,* the open water is not a *lagoon* in the generally understood sense, having no presen: or original connection with the sea. The catchment covers about 30 sq km with Omanuka Lagoon at its head. The hydrology of the area has been described by Mark-Brown (1978).

The lagoon and environs, totalling 86 hectares, is administered as a Wildlife Management Reserve by the Wildlife Service of the Department of Internal Affairs. It was studied as a representative basin by the Hydrology Section of the Ministry of Works and Development between 1969 and 1978 and has been the location of a wide variety of wildlife and wetland-related research projects (e.g. Caithness and Pengelly, 1973; Lavers, 1973; Craig, 1974; Baker-Gabb, 1978; Tilley, 1980).

FIGURE 1. *Map of the southern half of North Island showing the position of Pukepuke Lagoon. Area covered by Holocene sand dunes shaded, (Redrawn from Cowie, 1968).*

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CLIMATE

Climatological data have been collected at the lagoon since 1969 (Mark-Brown, 1978), and longer records are available from Tangimoana (EO5321; 1923-1949) and Ohakea (EQ5231; 1940 to present) situated 6 km to the north and 18 km to the northeast respectively. (Bureau of Meteorology, Wellington, New Zealand).

These data show that the coastal region of Manawatu has warm summers and mild winters. The mean monthly temperature of the warmest months-January and February-is about 17° C, and that of the coldest-July-about 8° C. Mean annual rainfall in the area around Pukepuke Lagoon is about 940 mm, evenly distributed but with a slight preponderance during winter. Average rainfall is less than potential evapotranspiration in summer, when soil moisture deficits are common. Due to the sandy nature of the soils and the low lying topography, variations in ground-water levels closely follow variations in rainfall, although with a lag of about one month in winter (McFadgen, 1972).

The region is subjected to strong and frequent northwest winds, which are at their strongest in spring and early summer (Cowie and Smith, 1958). These winds have controlled the alignment of both the Motuiti and Waitarere dune systems, implying that they have been a dominant force in the formation of the landforms around the lagoon for at least a millenium.

HISTORY

The coastal plain of Manawatu comprises a series of four Holocene dune phases of different ages, arranged roughly parallel to the present coastline and stretching inland for 19 km at their widest extent. The chronosequence of soil types and the natural vegetation of the area have been described by Cowie (1963, 1968) and Saunders (1968), and by Carnahan (1957) and Esler (1969, 1970, 1978) respectively.

The sand dunes of the Motuiti phase were probably advancing inland at 1200 AD, and stabilised by vegetation soon after 1400 AD (Cowie, 1963, 1968; McFadgen, 1972). Archaeological evidence suggests a sudden rise in water-tables associated with coastal progradation about 1600 AD (McFadgen, 1972), and it was probably then that the small dune-flat lakes on this surface extended to form larger lakes, such as Pukepuke Lagoon. Subsequently these lakes and swamps have been transgressed along their western margins by dunes of the Waitarere phase, blocking their natural drainage and pushing them inland.

Movement of the Waitarere dunes may have been a direct consequence of the destruction of plant

FIGURE 3. *Aerial view of Pukepuke Lagoon, looking west.*

cover *(Spinitex hirsutus)* on the foredunes by cattle during settlement of the area by Europeans early last century (Cockayne, 1911; Wilson, 1959; Cowie, 1968). Although sand drift was largely checked by the planting of marram grass *(Ammophila armaria)* early this century (Wilson, 1959), extensive areas of unstable sand remained. For example, aerial photographs of the area west of Pukepuke Lagoon show that, in 1942, 54% of a 133 ha representative area was bare sand; by 1958, this was reduced to 22 %; and by 1968, to 6%. The decline in water area, and the changes in lagoon ecology and morphology since the earliest European surveys of the area (1872), are detailed in Appendix 1 and Figure 2. They are similar to those documented for other lakes and lagoons in the area (e.g. Lake Kaikokopu: Downes, 1909; Wilson, 1959), and can be summarised as follows:

(1) Before 1840. Lagoon covering about 162 ha and relatively stable. Maori population in area utilising abundant eel *(Anguilla spp.)* and wildfowl populations.

(2) 1840-1910. Waitarere dunes unstable. Lagoon area reduced by sand drift and outlet drain blocked. Flooding of adjacent pastures led to efforts to drain the lagoon and stabilise the dunes.

(3) 1910-1930. Period of extensive drainage changes, dune stabilisation and commencement of dairying. Flax *(Phormium tenax)* cut in adjacent swamps. Lagoon about 49 ha in area.

(1) 1930-1940. A local sand drift apparently split the lagoon into two separate areas.

(5) 1940-1970. Lagoon progressively reduced in area by spread of marginal macrophytes, especially *Typha*. Further drainage changes. Total water area reduced to c. 15 ha.

(6) 1970-present. Lagoon administered as a Wildlife Management Reserve. Spread of marginal vegetation checked. Scientific programme commenced by Wildlife Service.

VEGETATION

In this section, the present vegetation of Pukepuke Lagoon is described under three headings: (1) the supposed sequence of hydroseral development; (2) the effects of introduced plants and animals; (3) the composition of the *Typha-dominated* area. This latter account is based on a reciprocal average (RA) ordination of 50 quadrats located in *Typha* stands.

The hydrosere

The natural vegetation of the lagoon and associated swamp can be described in terms of a classic hydrosere, in which successive plant communities are arranged as a series of concentric zones around the open water area. However, while such a simplification is convenient for description, it is rarely discernable on the ground (Figs. 3, 4).

Most of the lagoon is less than 0.6 m in depth, with the maximum being 1.2 m. Submerged aquatic plants include *Potamogeton spp. (P. cheesman* ii, P. *crisp us,* P. *pectinatus), Ruppia polycarpa. Zannichellia palustris, Myriophyllum elatinoides, Ranunculus fluitans,* and the alga *Chara* spp. Floating plants include members of the Lemnaceae and *Azolla rubra*. As the water level drops in summer, semi-aquatics and adventive ruderal plants colonise the exposed mud and sand. Extensive marginal communities of *Callitriche stagnalis. Nasturtium officinale. Ranunculus sceleratus, Veronica anagallis-aquatica, Polygonum hydropiper* and P. *decipiens* become established in some years, and remain alive as a semi-floating mass as the water level rises again in winter. In such circumstances, *Veronica* (in particular) may contribute significantly to the standing crop of macro-

FIGURE 4. *Vegetation of Pukepuke Lagoon taken from colour and false colour aerial photographs in September 1970.*

phytes. Gibbs (1973) has described these changes, and the associated phytoplankton blooms, following the almost complete drying of the lagoon in February, 1970.

The relative contribution to the total submerged productivity made by phytoplankton, submerged aquatics and temporarily flooded ruderals appears to be determined primarily by hydrologic factors, and varies markedly seasonally and annually. In winter and spring, when flushing occurs through the basin, the submerged macrophytes are favoured. In summer when water-levels recede and water temperatures increase, phytoplankton development occurs, sometimes to such an extent that light levels may be reduced for the submerged macrophytes (K. Potts, pers. comm.). When water levels continue to drop to the extent that large areas of damp surface are exposed, ruderal communities become established. With subsequent reflooding, these communities come into competition with submerged macrophytes.

The emergent macrophyte vegetation bordering the open water areas is dominated by *Typha* and the large tussock-forming sedge, *Carex secta*. The latter may invade open water as seedlings by establishing on the damp surfaces exposed at times of low water level. *Typha* seedlings also occur on exposed mud, but few seem to survive subsequent immersion and the spread of this species is predominantly by rhizome extension from marginal stands.

The marginal *Typha*/*Carex* stands normally contain standing water throughout the year, but further back, periodic or seasonal surface drying becomes more frequent. Here, large vigorous herbs such as flax and *Cyperus ustulatus,* and scramblers such as *Calystegia sepium, Solanum dulcamara* and *Galium palustre* occur. The extensive areas of flax and cabbage tree *(Cordyline australis)* probably represent a late stage of hydro sera I development. At the north-western end of the swamp, old dying tussocks of *Carex secta,* over-topped by vigorous *Typha,* frequently support flax seedlings, suggesting an autogenic explanation for the successional sequence *Carex-Typha-Phormium*. Elsewhere, sand accretion, causing a reduction in water depth, appears to be the main factor determining the abundance of flax and cabbage trees.

On the western margin of the swamp, there is an area where the *Phormium*/*Cordyline* association contains scattered shrubs of *Coprosma robusta,* C. *propinqua, Olearia solandri* and *Muehlenbeckia com-*

plexa, indicating a transition to shrub-swamp. The terminal swamp-forest stage is not represented although some evidence of its former presence (kahikatea, *Podocarpus dacrydioides* twigs) has been observed in peat deposits thought to have been marginal to the lagoon in 1872, and its composition can be judged from the few extant bush remnants on similar sites in the area (Esler and Greenwood, 1968; McFadgen, 1972; Esler, 1978).

The effect of introduced flora and fauna

During the latter par~ of this century, as the lagoon and swamp have shrunk due to drainage and hydro seral colonisation, the area has also been invaded by an alien flora and fauna. Of the 176 species of vascular plants recorded at Pukepuke, 120 (68%) are adventive (Appendix II). The proportion of adventive plant species in the swamp and open-water vegetation is lower (c. 45%; A. Esler, pers. comm.). Although in most parts of the system native monocotyledons still predominate, several adventive species are now common, particularly in shallow water where *Ranunculus sceleratus, R. fluitans, Bidens frondosa* and *Veronica anagallis-aquatica* frequently form a marginal fringe to the lagoon.

Prior to improved fencing in 1970, cattle did extensive damage, especially during drought periods. Now, the dense macrophyte vegetation of the undrained swamp ecosystem is protected from the direct effects of grazing by introduced mammals, although sambar deer *(Cervus unicolor)* are present in the area in low numbers.

The most important effect of the development of adjacent areas for pastoral farming has undoubtedly been via drainage changes and eutrophication. The latter results mainly from the use of superphosphatic fertilisers within the catchment. It seems likely that both these effects have contributed to the dramatic spread of *Typha* since about 1940. *Typha* is known to be highly responsive to phosphate fertilisation (Boyde and Hess. 1969).

The dramatic changes in the native bird populations in the area since European settlement are beyond the scope of this paper. However, we note that New Zealand scaup *(Aythya novaeseelandiae)* and brown teal *(Anas aucklandica chlorotis),* now absent, were formerly abundant, and that the grey duck *(Anas s. superciliosa)* has been progressively replaced by the introduced mallard *(Anas p. platyrhynchos)*. The effects of such changes on the trophic structure, and hence on the vegetation of the lagoon-swamp ecosystem, can only be surmised. However, black swan *(Cygnus atratus),* pukeko *(Porphyrio p. melano-(us),* New Zealand dabchick *(Podiceps rufopectus),* Australasian harrier *(Circus approximans)* and the Australian bittern *(Botaurus stellaris poiciloptilus)* utilise dead *Typha* for nesting, while during summer, *Typha* provides invaluable escape cover for unfledged duck and swan and for all moulting adult waterfowl. Only pukeko is known to feed directly on the living shoots and rhizomes of *Typha*.

The Typha stands

Examination of Figures 2, 3 and 4 shows that the extensive areas dominated by *Typha* are not all of the same age. Despite periodic cutting by duck-shooters, and grazing by cattle at times of drought *Typha* invaded the open water at an average rate of c. 0.28 ha/year from 1942 to 1968 (representing a 40% reduction of open water area). Since then the Wildlife Service has followed a cutting, excavating and spraying programme to maintain the lake margins, and created several new water bodies in areas of former swamp. This programme is aimed at halting or reversing plant succession to improve the area as a wildlife reserve.

Thus, superimposed upon the general hydroseral changes occurring in the *Typha* stands with time since initial colonisation, are changes related to cutting and other disturbances. There is also a seasonal pattern in the above-ground biomass, mainly due to the deciduous nature of *Typha* itself. Consequently, an adequate description of the *Typha* area requires spatial and temporal coverage. Seasonal changes in *Typha* biomass and population structure in stands of different ages will be dealt with in a later paper, but here, we describe the broad pattern of variation in the species composition of stands in which *Typha* occurs.

Fifty quadrats, each 2 x 2 m in area, were located along five transects in the vegetation of the northern half of the Pukepuke system (Fig. 4). The transects were aligned across the swamp (NE-SW) and their starting points were chosen on aerial photographs so as to give a complete coverage of the area. Quadrats were placed at 10 m intervals along them, except that any quadrat falling in 'open water' (lacking emergent macrophytes) was relocated in the nearest macrophyte stand. In each quadrat, a visual estimate of the 'cover' of each species was made using a five point scale (*). Such a course scale seemed appropriate when comparing plants with such different growth forms as *Spirodela, Calystegia* and *Typha*. The following environmental measures were made at

*Scale used: 1 = trace present – 5%; 2 = 5 – 25%; 3 = 25 – 50%; 4 = 50 – 75%; 5 = 75 – 100%. Percentage cover was assessed as a vertical projection of the vegetation onto the swamp surface.

TABLE 1. *Percentage frequency of occurrence, in 50* 2 *x* 2 m *quadrats, of species occurring in more than one stand of macrophyte vegetation at Pukepuke Lagoon* (1).

Species	% occurrence
Typha orientalis	98
Lemna minor	76
Phormium tenax	54
Carex secta	48
Calystegia sepium	48
Bidens frondosa	38
Spirodela punctata	26
Solanum dulcamara	16
Cordyline australis	14
Senecio spp. (2)	14
Cortaderia toetoe	12
Juncus spp. (3)	10
Blechnum minus (4)	10
Rumex conglomeratus	8
Cyperus ustulatus	8
Solanum nigrum	8
Carex maorica	6
Coprosma spp. (5)	6
Wolfjia australiana	6
Scirpus lacustris	6
Carex lessoniana	6
Nasturtium officinale	4
Lotus pedunculatus	4
Galium palustre	4

Notes: (1) Species occurring once only were: *Agrostis stoloni1era, Sonchus oleraceus, Ranunculus repens* and an unidentified fern.
(2) Recorded as S. *lautus*, but possibly S. *spathulatus*.
(3) Probably mainly *J. pallidus,* but *J. articulatus* also present.
(4) This is the plant originally referred to as the swamp form of *B. capense*.
(5) *Coprosma robusta,* C. *propinqua* and hybrids between these.

several (usually four) locations in each stand and the results averaged:

(1) pH of surface water (using an Eel portable Ph meter).
(2) water depth.
(3) depth of organic matter (i.e. depth to the firm sand base, using an auger).

The frequencies with which different species were recorded are given in Table 1. *Typha* was present in all except one of the 50 quadrats.

The 'species in quadrats' cover-data table was analysed using reciprocal average (RA) ordination (Hill, 1973). This technique provides both site and species ordinations (Fig. 5, A and B respectively). The first two axes (eigenvectors) of the ordination accounted for 74 % of the total variance, thus providing a satisfactory summary of the raw data.

The environmental measures are summarised in Table 2, A correlation matrix was calculated using the environmental measures and the RA axis loadings for each stand. For the first axis, this showed signifycant positive correlations of vegetation composition (as reflected by axis loading) with water depth and pH, and a significant negative correlation with the depth of the organic matter. Thus, the changing species composition along this axis-accounting for 41 % of the total variance---reflects decreasing water depth and pH and increasing organic matter build-up with time and distance from the open water margins.

In contrast, the second axis accounted for only 33 % of the total variance and showed no significant correlations with any of the measured environmental variables. The species ordination suggests that this second order variation may be due to the occasional presence of some species, particularly ruderals and exotic weeds, which may largely reflect the degree of disturbance.

The RA results can be summarised as indicating one overall pattern of variation related to hydroseral development, with a super-imposed secondary pattern, possibly related to disturbance. The primary pattern can be clearly seen by plotting the smoothed mean cover values for species in groups of five stands lying adjacent to each other on the first axis (Fig. 6). The main indigenous macrophytes *(Phormium, Typha* and *Carex secta)* all 'peak' at different points along this axis. Likewise the floating duckweeds *Lemna minor* and *Spirodela punctata* tend to segregate; although the former is present throughout, it rarely forms extensive mats like those of *Spirodela* near the lake margins, and is most abundant in pools in the older *Typha* stands. Experimental studies, in which these two species were grown in culture solutions in growth chambers, showed that *Lemna* preferred lower pH's, and was tolerant of greater shading and dilution of the culture medium than was *spirodela* (*). These trends are consistent with the suggested interpretation of first axis of the RA ordination.

*Culture solution was that used by Bollard (1966) and Bieleski (1968). Estimated pH optima: *Lemna minor* 5.0; *Spirodela punctata* 5.5. Reduction of light intensity frpm 700 to 60 foot ..candles (at 23 °C) reduced growth rate by 55% and n'et production by 74% (after 16 days) in *Lemna,* but by 72% and 91 % respectively in *Spirodela*. In 0.1 strength culture solution *Lemna* survived but *Spirodela* died.

TABLE 2. *Summary of environmental variables in stands of macrophyte vegetation with* Typha *presellt at Pukepuke Lagoon.*

(1) Gibbs (1973) gives a pH range of from 7.5 to 9.4 (mean 8.4) for the open lagoon water. Similarly, Mark' Brown (1978) gives values from 7.6 to 10.5. Considerable diurnal and seasonal variation in pH values within macrophyte stands is to be expected, but note that the higher values recorded for the open water are in accord with increasing pH values along axis 1 of the RA ordination.

FIGURE 5. *Site (A) and species ordination (B) of 50 quadrats in* Typha *dominated vegetation in the northern Half of the Pukepuke swamp. 'A' and 'B' in Figures 3 and 4, demarcate the southern edge of the area sampled for the ordination study. Legend to (B): 1.* Carex lessoniana; *2.* Coprosma *spp.*; 3. Calystegia *spp*; 4. *Ferns*; 5. Blechnum minus; 6. Cordyline australis; *7.* Cyperus ustulatus; *8.* Juncus *spp., 9.* Cortaderia toetoe; *10.Carex* maoriea; 11. Scirpus lacustris; 12. Wolffia australiana. a. Ranunculus repens; *b.* Sonehus oleraceous; *c.* Rumex *$Pp.; d.* Nasturtium *spp.; e.* Solanum nigrum; *f.* Lotus pendunculatus; *g.* Galium *spp.; h.* Senecio ?lautus: *i.* Bidens frondosa; *j.* Agrostis stolanifera; *k.* Solanum dulcamara.

FIGURE 6. *Approximate percentage cover values for selected species along the first axis of the RA ordination. Points are smoothed mean values for adjacent groups of five stands. Smoothing accomplished using* $x = a + 2b + c/4$ *where a. band* c *are mean cover values in adjacent stand groups.*

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APPENDIX I

Summary of the historically recorded changes in the areas of lagoon and swamp at or near Pukepuke. and brief notes on associated environmental changes.