CYCLES OF MACROPHYTES AND PHYTOPLANKTON IN PUKEPUKE LAGOON FOLLOWING A SEVERE DROUGHT

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SUMMARY: A three year survey of the aquatic vegetation of a New Zealand dune lake is described. Pukepuke Lagoon is a shallow (max. depth 85cm.), slightly saline lagoon with 15ha of open water. Its inflows drain intensively farmed land and are rich in nutrients, especially phosphorus. Dense macrophyte crops characterised the lagoon each spring but the component species differed each year. After a severe drought which dried most of the lagoon bed in the 1969-70 summer, *Veronica anagallis-aquatica* and *Ranunculus fluitans* were the dominant species in 1970; then with normal water levels *Chara globularis* became dominant throughout 1971, followed by *Potamogeton crispus* in 1972. Factors that enabled the dominant species to gain an early competitive advantage are discussed. Drying of the lagoon bed in 1970 is regarded as the major disrupting feature that initiated the sequence of plant species described. Phyto-plankton crops, estimated from chlorophyll *a* pigment, were low during macrophyte growth phases but reached peaks in the summer of 1971-72 and 1972-73; the former being responsible for the destruction of *Chara*. The competitive balance between phytoplankton and macrophytes is a delicate one but the shallow water of Pukepuke Lagoon tends to favour the macrophytes.

INTRODUCTION

The clogging of shallow ponds or canals by dense growths of aquatic vegetation is a phenomenon that is generally regarded as undesirable, but under certain circumstances, such as for waterfowl management, it may be beneficial. Whichever point of view is adopted, it is desirable to know something about the factors that stimulate certain types of dense weed growth or, conversely, can lead to the clearance of aquatic macrophytes. This paper discusses a sequence of events in the re-establishment of the flora of a shallow dune lake following a severe drought which exposed most of the lake bed. Its aim is to document some profound changes in the abundance of macrophytes and phytoplankton that occurred in Pukepuke Lagoon between February 1970 and February 1973 and to make some suggestions about the causes of these changes and their regularity. These observations provide some direct background data for several research projects on waterfowl, eels and zooplankton at the lagoon. They are also relevant, in a wider sense, to eutrophication and its consequences in shallow ponds.

THE LAGOON

Pukepuke Lagoon (Fig. 1) covers an area of 15 ha of open water surrounded by raupo (*Typha meulleri* Rohrb.) and flax (*Phormium tenax* J. R. et G. Forst) swamp within the Pukepuke Wildlife Management Reserve. It is regarded as a basin lake formed between unconsolidated and consolidated sand dunes (Cunningham *et al.* 1953) 3.3km inland from the west coast beach and 14.5km north of Foxton (40°19'S, 175°16'E). The lagoon is shallow with a maximum depth of 85cm. and with a uniform sandy substrate overlain by soft ooze that varies in thickness from a few centimetres to well over 50 cm. at the deepest point.

Two inlet drains bring water into the lagoon from a catchment of about 26 km² of farmland. One drain enters from the north, the other from paddocks to the east of the lagoon where a series of drains collect water that is pumped up to the lagoon level. The pump operates automatically, governed by the water level. One outlet drains the lagoon from the north side. Four experimental ponds of about 0.2ha each have been constructed close to the lagoon (Fig. 1). Pond NP was estab-

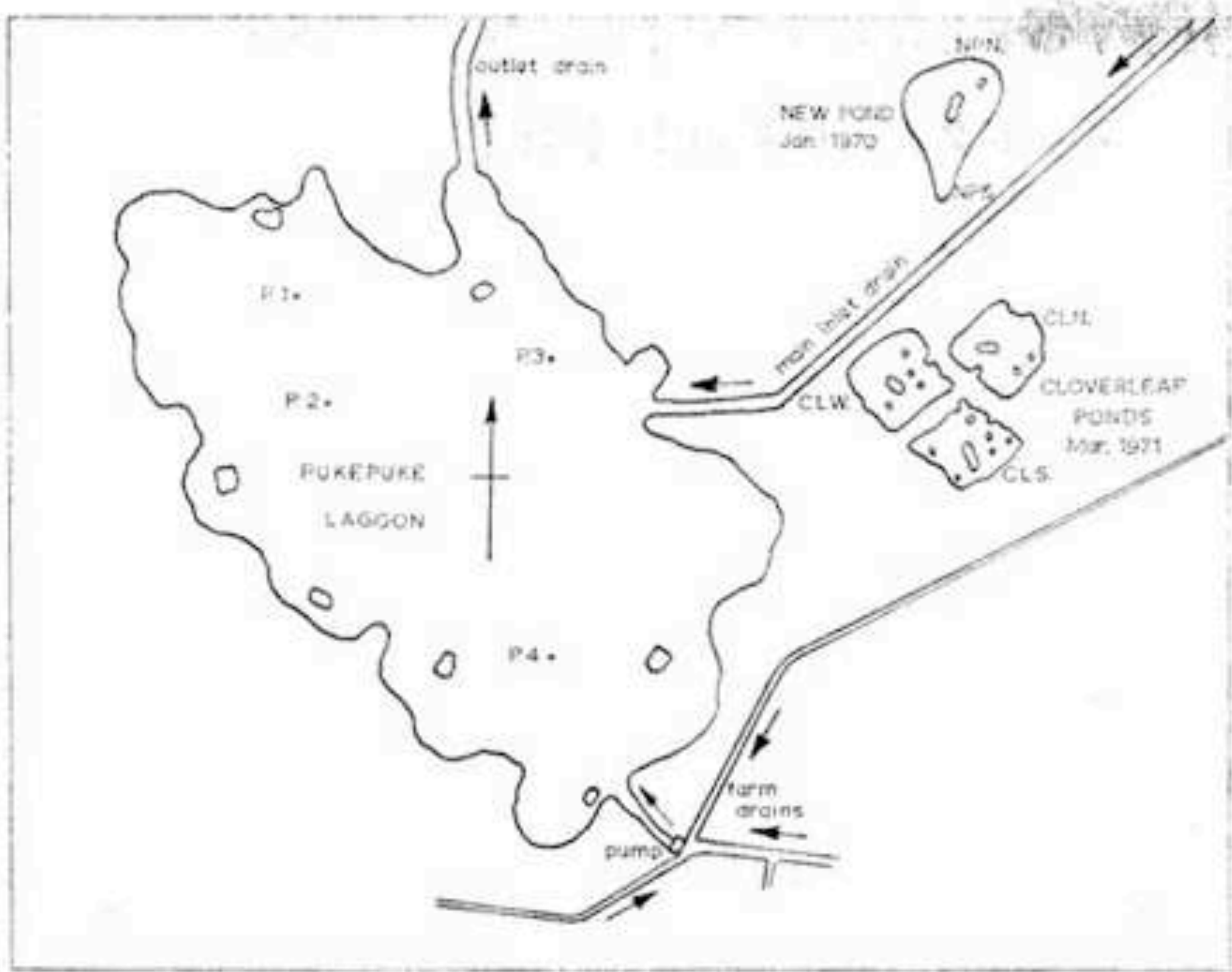

FIGURE 1. *Pukepuke Lagoon and experimental ponds showing sampling sites.*

lished in January 1970 and three CL ponds in March 1971. These have no inlets or outlets.

Table 1 shows that the lagoon water is slightly saline (58-115 mg/1 Cl) with a high total hardness (168-360 mg/l as $CaCO_3$). The latter is probably derived from the quantity of shell in the substrate and the former windblown from the sea. Plant nutrients are readily available, especially phosphorus (0.050-0.767 mg/l reactive P as PO_4), and alkaline conditions prevail for most of the year (pH 7.5-9.8).

TABLE 1. *The range of Variation of Certain Chemicals in Pukepuke Lagoon between September 1970 and June 1972.*

(All values except pH in mg/l).

	Range	Mean	Number of Analyses
pH*	7.5-9.4	8.4	16
Cl^-	58-115	85	9
Alkalinity (as $CaCO_3$)	152-252	199	9
Ca Hardness (as $CaCO_3$)	52-124	88	9
Mg Hardness (as $CaCO_3$)	72-290	147	9
Na^+	30-80	54	5
K^+	1.8-11.3	5.6	5
Fe (total reactive)	0.48-0.90	0.78	6
$Si0_2$	8-18	12.2	5
SO_4^{--}	39.9-60.8	53.0	4
NO_3 -N	nil-0.20	0.11	9
Free NH_3 -N	0.01-0.24	0.16	9
Albuminoid -N	0.76-2.83	1.34	9
Reactive P as PO_4	nil-0.45	0.23	7
Total Solids	353-546	438	9

* Field measurements.

METHODS

Visits to the lagoon were made on or about the 20th day of each month. Observational data on macrophyte growth were noted each time but quantitative samples were not attempted until late in the study (from October 1972) when a modified Gerking (1957) sampler of 0.1 m^2 area was tried. Relatively few species of macrophyte were involved, so that identification in the field was no problem.

No attempt was made to identify the phytoplankton. Instead, beginning in April 1971, regular estimates of the amount of chlorophyll *a* pigment in the water were made by the spectrophotometric method described by Strickland and Parsons (1968). Although not a very critical method, it serves a useful purpose by quantifying the standing crop of photosynthetic organisms. Water samples for these estimates were taken with a modified van Dohrn sampler held vertically so that it took a column of water 5cm in diameter from the surface to a depth of 27cm. After mixing and sieving through a 175 μm mesh, samples of 200 ml were returned to the laboratory in a cool box and filtered within about six hours. The filters (0.45 μm pore size) were frozen for one to ten days before extraction of the pigment.

CHANGES IN THE FLORA

A general limnological study began at the lagoon in February 1970 when the water level was exceptionally low. By March 1970, a severe drought had exposed almost the entire lagoon bed, leaving only a small area of thick black, moist ooze at the deepest point. During this dry phase (the worst remembered by local residents) an abundant growth of *Veronica anagallis-aquatica* L. seedlings arose from the dry, sandy portions of the lagoon bed (about 40% of its area).

Figure 2 summarises the following sequence of events. As the water level rose with autumn rains in April-May, these seedlings continued to flourish, now under water, and were joined by ***Ranunculus fluitans*** Lam. Both grew vigorously until by November 1970 they covered about 70% of the lagoon with emergent, flowering stems, leaving an open space at the deepest part around stations P. 1

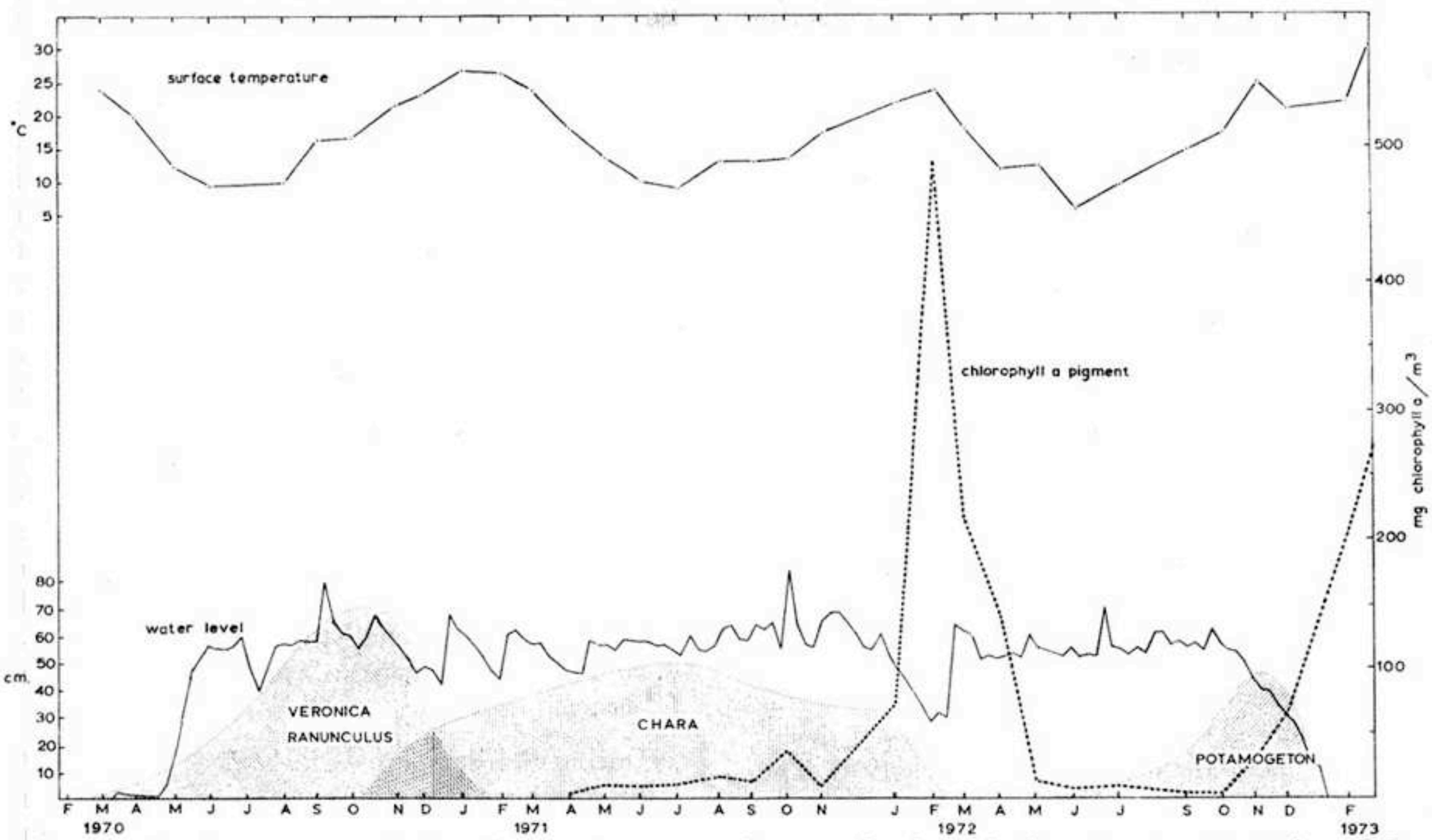

FIGURE 2. *A summary of the changes in macrophyte and phytoplankton crops at station P.3, Pukepuke Lagoon, between February 1970 and February 1973. Water temperatures and chlorophyll a pigment are mean values from four stations. Weekly water levels at station P.3 are transposed from a staff gauge in the outlet drain.*

and P. 2 (Fig. 1). This deeper area, although clear of dense macrophytes (*Veronica* & *Ranunculus*) nevertheless supported a sparse flora of *Potamogeton pectinatus* L., an entirely submerged plant with narrow, ribbon-like leaves.

A charophyte, *Chara globularis* Thuill was first noted at station P. 3 in November 1970. While the vascular plants decayed during January and February 1971, *C. globularis* became more conspicuous over most of the area formerly occupied by *Veronica* and *Ranunculus*. Dense mats of *Chara* coalesced to almost completely occlude the sandy substrate by March 1971. It always remained about 20 cm below the water surface, possibly due to grazing by waterfowl (Fig. 2).

During the second year of the study, *C. globularis* dominated the lagoon. Duckweed (*Lemna* sp.), a free floating hydrophyte, was an important temporary constituent of the flora during late summer and autumn 1971, reaching its peak in March when it covered about 30% of the free water with a mobile carpet. In the spring of 1971 both *V. anagallis-aquatica* and *R. fluitans* again became emergent and flowered but the density of these plants was far lower than in 1970. Unfortunately no quantitative measurements were taken at that time to indicate the relative importance of these species. Then, in the summer of 1971-72, *Chara* degenerated, and it had disappeared from the lagoon by March 1972. Coincident with the decay of *Chara* was a dense bloom of phytoplankton which began in January 1972 and reached a peak in February (Fig. 2). This was the first occasion that the water had been obviously discoloured due to phytoplankton.

By the end of the bloom in May 1972, when the water again became clear enough to see a Secchi disc at the bottom, the lagoon bed was practically devoid of macrophytes with the exception of a few scattered *Potamogeton pectinatus* at P.1 and P.3. Over the winter months the lagoon remained almost clear of macrophytes and with a low standing crop of phytoplankton. During spring both *P. pectinatus* and *Potamogeton crispus* L. gradually increased in abundance until, in November 1972, these two macrophytes occupied about 90% of the lagoon water. Emergent inflorescenses of *P. crispus* were so dense that they prevented normal wave action. Neither *V. anagallis-aquatica* nor *R. fluitans* were present within the main lagoon at this time. Table 2 shows dry weights of plant material from 0.1 m^2 samples taken towards the end of 1972. At this time the dominant macrophyte was *P. crispus*. Filamentous algae coated many of the vascular plants in spring, forming large mats in some areas, particularly around the main inlet drain (station P.3).

In the summer of 1972-73 the district again suffered a drought and Pukepuke Lagoon levels dropped almost to the point reached in 1970. The dense clogging growth of *P. crispus* noted on 19 December 1972 had disappeared by 8 February 1973 leaving only a few blackened stem fragments.

TABLE 2. *Mean Dry Weights (g) of Living Macrophytes per 0.1m² from Pukepuke Lagoon Between October 1972 and February 1973.*

	Oct.*	Nov.**	Dec.**	Feb.**
Potamogeton crispus	7.001	6.334	13.345	0
P. pectinatus	1.930	0.465	0.265	0
Ruppia polycarpa	0.269	0.131	0.069	0
Lemna sp & *Azolla*	0	0.005	0.138	0
Filamentous algae	5.663	2.910	0.784	0
Total	11.619	9.875	14.601	0
Depth at sampling stations (cm)	58	44-71	28-56	0-24

* Two samples.
** Four samples.

DISCUSSION

1. Changes in the Macrophyte Communities

In the three years of this study three entirely different communities of macrophytes have dominated the lagoon. Under normal circumstances, the status of various component plants might be expected to show seasonal variations, but the basic floral constituents should remain similar from year to year (Sculthorpe 1967).

The departure from this normal pattern that occurred at Pukepuke between 1970 and 1973 was due, in part, to the extreme lowering of the water level in 1970, but unfortunately there is no record of the flora immediately prior to the drought. The only previous account is that of Cunningham *et al.* (1953) who noted that in January 1949 "the floor of Lake Pukepuke was completely covered . . . with species of *Potamogeton* and *Chara*". The dominant plants in 1971, *V anagallis-aquatica* and *R. fluitans* were not mentioned in 1949. Also, in this study, these two species had disappeared from the main Lagoon area by 1972, indicating that they were probably temporary constituents of the flora. Thus the initial and most striking effect of the drought was to eliminate the established hydrophytes and favour *V. anagallis-aquatica* and *R. fluitans*.

During the dry periods in both 1970 and 1973, large numbers of seedlings appeared on the firm, dry, sandy substrate. They were predominantly *Veronica,* with *Ranunculus* appearing later as rain began to raise the water level and moisten the substrate. In 1970 these species continued to flourish under water and by spring had choked the areas of the lagoon that had been dry the previous summer. A central area, where the deep ooze had not dried out completely, remained uncolonised by these species, supporting instead a sparse flora of *Potamogeton pectinatus*. This distribution indicates that the ability of *V. anagallis-aquatica* and *R. fluitans* to initiate growth while the lagoon bed was free of water was the main factor leading to their dominance.

Both *V. anagallis-aquatica* and *R. fluitans* were conspicuous elements of the aquatic flora of the experimental ponds during each year of the study. In the Cloverleaf ponds *Veronica* was dominant in pond CLS while *Ranunculus* dominated pond CLN. Both ponds dried up each summer. Also, in seasons of normal water level (1971, 1972), *V anagallis-aquatica* was present around the shore of the main lagoon where it thrived on wet mud in a semi-aquatic situation. This is precisely the habitat described for the species by Mason (1970).

In the second season *V. anagallis aquatica* and *R. fluitans* were supplanted by *Chara globularis* as the dominant plant. Once it gained ground cover, which happened during autumn when the perennial vascular plants had died back, very little light was able to penetrate to the substrate. The thick, mat-like form of *C. globularis* and its ability to propagate vigorously in winter were probably the main factors leading to its successful dominance for 15 months. But why did it not reappear after the phytoplankton bloom? Conditions in the lagoon seemed ideal throughout autumn and winter 1972 with clear water and a very sparse flora of *P. pectinatus*.

According to Fritsch (1948), *Chara* species are typical of clear waters with sandy substrates and can thrive where the substrate contains much decomposing organic matter. They usually form extensive subaquatic meadows. Forsberg (1964) describes a "*Chara*-lake" as being poor in other vegetation, with a high calcium content and pH often above 8. In these respects, Pukepuke Lagoon is a suitable habitat. However, Forsberg (1964) has found that charophytes are sensitive to phosphorus, which behaves as a maximum factor (thus, he claims, explaining the absence of these algae in very eutrophic waters). His conclusions were based on a survey of many "*Chara*-lakes" and on experiments in which he grew *Chara globularis* in tap water with varying concentrations of additional phosphorus, finding that inhibition of growth occurred at 0.30 mg/l of phosphorus.

If these findings are applicable to the situation at Pukepuke Lagoon, perhaps it was a change in phosphorus concentrations that rendered the water unsuitable for *C. globularis* in 1972. However, data from water chemical analyses do not support this suggestion. During the period of dominance by *C. globularis,* analyses of Pukepuke Lagoon water were done by the Wellington City Council Laboratories on five occasions. The concentrations of "reactive" phosphorus shown in Table 3 indicate that the range was very much higher than the maximum limiting value given by Forsberg (1964). Evidently other factors interact with phosphorus concentrations at Pukepuke Lagoon to provide a suitable habitat for *C. globularis* or perhaps the amount of available phosphorus in these hard, alkaline waters is over-estimated because of acidification during analysis. Whatever the reason, the Pukepuke data do not support the view that high phosphorus content limits the growth of *C. globularis*. Nor do the chemical data suggest why *C. globularis* failed to return in 1972 (see Table 3).

TABLE 3. *Concentrations of "Reactive" Phosporus in Pukepuke Lagoon, 1971-72.* (*PO_4 as mg/l*).

	Filtered	Unfiltered
During *Chara* dominance		
22/ 3/71	0.37	
20/ 5/71	0.45	
20/ 7/71	nil	
21/10/71	0.29	
20/ 1/72	0.05	0.45
After *Chara* dominance		
18/ 4/72	0.18	0.52
20/ 6/72	0.23	0.27
28/ 7/72		0.12
24/ 8/72		0.18
24/10/72		0.13
21/11/72		0.59
19/12/72		0.77

The appearance of *Potamogeton crispus* and its rise to dominance in 1972 was as striking as the events of the previous two seasons. Not recorded in the Lagoon in either of the two preceding years, it clogged about 90% of the total area of open water in November-December and was destroyed entirely by lowered water levels and drying of the lagoon bed in February 1973.

Although the composition of the macrophyte flora has changed dramatically each year, there are two generalisations that apply throughout. First, the Lagoon has always been choked with hydrophytes in spring and early summer and second, the diversity has remained low with only one or two species being prominent at any time.

The first feature is to be expected in a shallow pond with copious decaying organic matter and an inflow from farmland. Throughout this study it has been apparent that the main lagoon produces larger standing crops of both phytoplankton and macrophytes than the small experimental ponds. A comparison of some chemical parameters as shown in Figure 3 indicates that the higher phosphorus levels in the main lagoon might well be a very important factor in the promotion of such vigorous growth. Incidentally, the present phosphorus concentrations are very much higher (23 times) than the 0.013 mg/l value found by Cunningham *et al.* (1953) for January 1949. This could be related to the more intensive farming that has developed since then.

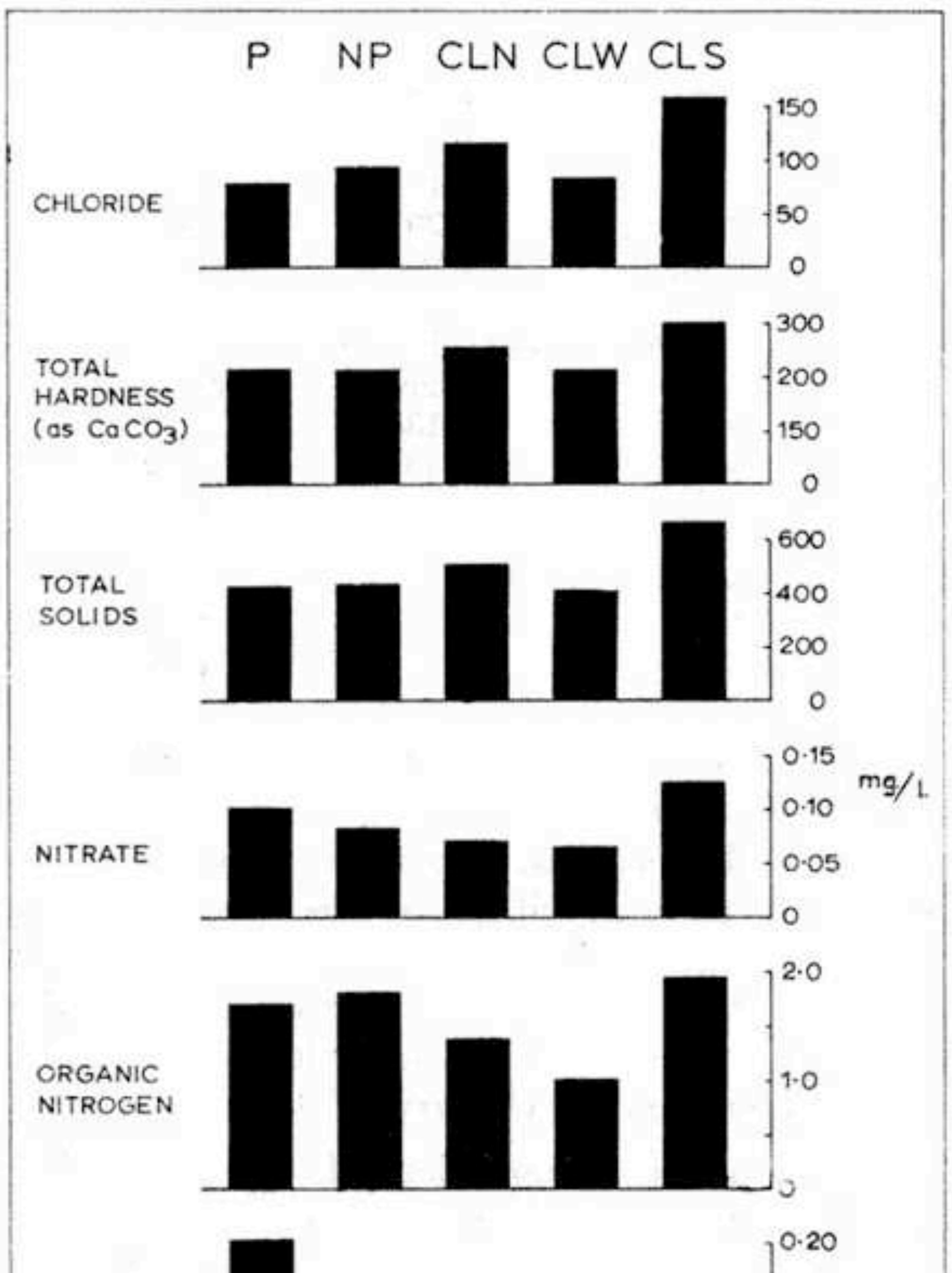

FIGURE 3. *The mean concentrations of certain chemicals in Pukepuke Lagoon (P) compared with the experimental ponds (designated as in Fig. 1.), September 1970 to June 1972.*

Concerning the second point, it is known that numerous submerged plants tend to form extensive pure stands. Sculthorpe (1967) notes that, at a favourable site, one species may gain an early initiative and increase faster than any competitor, thus gaining seasonal predominance. He cites rates of vegetative reproduction and antagonism between species as being perhaps the most important factors responsible for this phenomenon. The present observations at Pukepuke support the view that an early advantage is crucial. The factors responsible for this advantage were obvious in 1970 (related to substrate drying) but not in the succeeding years.

We have been examining the rise to dominance of three different macrophyte communities but have not considered the factors that might have been responsible for their extinction. The decline of the *Veronica/Ranunculus* community and the build-up of *Chara* were simultaneous. Possible reasons for this have been discussed. The disappearance of *Chara* after 15 months of dominance occurred in mid-summer and was linked to two events. First, a major flood in October 1971 raised the water level and the lagoon became turbid due to suspended material carried in from the farm drains. For the first time in the study, transparency was reduced and a Secchi disc could no longer be seen at the bottom. The *Chara* mat became covered with a layer of silt which must have further reduced the light intensity reaching its photosynthetic cells. On this occasion many pieces of blackened, decaying *Chara* were found in sweep net samples. Some small fragments of decaying *Chara* were found in November, but transparency had improved and the *Chara* mat seemed alive and photosynthetic. It was the second event, a dense bloom of phytoplankton, that directly caused the decay of the *Chara*. From January to April 1972, the bloom reduced light penetration to the extent that a Secchi disc could not be seen beyond 30cm between February and April. Decomposition of *Chara* was rapid—possibly fast enough to return nutrients to the water in time for the phytoplankton to utilise them. The significance of the flood in October is uncertain since the *Chara* mat appeared normal again in November (the lagoon was not visited in December). However, it migh have provided sufficient excess nutrient from farm runoff to initiate the rise of phytoplankton.

2. *Changes in Phytoplankton*

Estimates of chlorophyll *a* pigment in the Lagoon waters since April 1971 suggests a tendency for a marked rise in standing crop of phytoplankton during summer (Fig. 2). In 1972 the peak value for chlorophyll *a* was 37 times the average value over the preceding eight months. However, this tendency was not as regular as the data in Figure 2 might suggest. For instance, although measurements were not taken in 1970/71, the water clarity in that summer indicated that a bloom did not occur. Also, the data for 1972/73, which show a bloom arising in November and reaching a peak in late February, can not be regarded as "normal" due to the rapidly falling water level and consequent decay of *Potamogeton* at the time the phytoplankton increased. Thus several more years will be necessary to establish whether the summer peak is a normal occurrence or whether it depends on the density and type of macrophytes present.

Many studies of the phytoplankton of temperate lakes indicate an upsurge of planktonic algae in spring, a decrease over mid-summer and sometimes a further peak in autumn (Lund 1965). There is no evidence for this pattern at Pukepuke where it seems the spring flush of growth is taken up by the macrophytes. Lund draws attention to the competitive effects between phytoplankton and macrophytes in shallow bodies of water, stating that "competition is likely to be most severe during the main period of growth of macrophytes in early summer in temperate lakes . . ." At Pukepuke phytoplankton crops were low during winter, regardless of whether macrophytes were present or not. A consistent competitive effect was seen in spring when macrophytes prevailed, but in summer the competitive outcome was less regular and, from the limited data so far available, tends to favour the phytoplankton.

Mitchell (1971) has described an irregular alternation between phytoplankton and macrophytes for Tomahawk Lagoon near Dunedin (a shallow coastal lagoon very similar to Pukepuke). During Mitchell's study phytoplankton dominance lasted for two seasons before a changeover to macrophytes took place over the 1964-65 summer. While the phytoplankton dominated, light intensities reaching the bottom were probably too low for macrophyte growth. Although Mitchell measured transparency, chlorophyll pigment, productivity, pH and various inorganic ions during the changeover and thereafter, he could offer no direct explanation for the inhibition of phytoplankton growth except that the density of phytoplankton was related to the presence of macrophytes. The macrophytes declined in Tomahawk Lagoon after about 16 months of dominance and phytoplankton blooms occurred again in the 1966-67 summer.

When the overall patterns of the two lagoons are compared it becomes apparent that phytoplankton tend to dominate for long periods at Tomahawk Lagoon whereas macrophytes dominate Pukepuke Lagoon. The balance between these two forms of vegetation is a delicate one and in this comparison may be simply a function of depth—Tomahawk Lagoon being about twice the depth of Pukepuke Lagoon. In the deeper water the competitive advantage is more often with the phytoplankton. Much more information is required before we can explain the important changeovers.

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