Effects of fluctuations in water level and growth of *Lagarosiphon major* on the aquatic vascular plants in Lake Rotoma, 1973–80

J. S. CLAYTON†
Botany Department
University of Auckland
Private Bag
Auckland, New Zealand

Abstract Fluctuations in water level and the growth of the introduced exotic *Lagarosiphon major* (Ridley) Moss have significantly influenced the submerged vegetation of Lake Rotoma over the period 1973–80. Low lake levels temporarily reduced the proportion of native vascular plants by removing available shallow-water habitats through erosion, siltation, or desiccation. High lake levels have allowed native vascular plants to re-establish from seed and rhizomes. Fluctuations in water level appear to have reduced the long-term replacement of native species by *L. major*, which has none the less spread progressively around the lake. Water-level fluctuations enhanced its rate of fragmentation, and thus its dispersal and establishment. The annual increase in the proportion of *L. major* has been primarily at the expense of the shallow-water characean algae, but also partly by competitive displacement of native vascular plants. The south-west inlet of Lake Rotoma had an exceptionally high plant density, with up to 3518 g/m^2 dry weight of *L. major* (believed to be a world record for submerged plant biomass); this is attributed to local enrichment and protection from wave exposure.

Keywords Lake Rotoma; water level fluctuations; aquatic plants; biological surveys; *Lagarosiphon major*; Hydrocharytaceae; biomass; *Elodea canadensis*; freshwater weeds; freshwater lakes.

Received 8 January 1981; revised 31 July 1981
†Present address: Ruakura Soil and Plant Research Station, Ministry of Agriculture and Fisheries, Private Bag, Hamilton, New Zealand

INTRODUCTION

Concern has been expressed about the explosive growth of introduced aquatic plants in the Rotorua and Waikato lakes (Chapman & Brown 1966). A history of their infestation has been given by Chapman (1970b). Only fragmentary evidence remains of the native vegetation within this group of lakes, since exotic species have largely displaced the native flora (Brown 1975).

In 1973 a study was begun on the vegetation of Lake Rotoma (38°02′S, 176°35′E), in the Rotorua Lakes district, since this was one of the few remaining such lakes where eutrophication and human influence were minimal and predominantly native vegetation was present (Clayton 1981). Some exotic species had already been introduced, however, and this therefore provided an opportunity to follow their establishment and growth.

This paper reports on the changes in vascular plant frequencies in Lake Rotoma between 1973 and 1980, with emphasis on the spread of the exotic *Lagarosiphon major* (Ridley) Moss over this period.

METHODS

During the first 3 months of 1973, 50 transects were placed systematically around the lake at right angles to the shore (Clayton et al. 1981, fig. 1). A total of 5708 quadrats of 625 cm^2 (25 cm square) were examined for the presence of rooted species (Clayton 1978).

Samplings from the 50 transects were repeated each year at the same site from 1973 to 1976, and again in 1980. To record changes in vascular plant frequencies it was only necessary to sample each transect to the maximum depth of the vascular hydrophytes. For comparison, the number of quadrats containing each vascular species was totalled each year and divided by the total number of quadrats sampled in 1973. This placed each species on an equivalent percentage basis relative to the total lake vegetation. The percentages given for the vascular plants each year are low, on account of the preponderance of characean algae in the lake vegetation.

The biomass of *Lagarosiphon major* was measured in June 1980. Samples (1 m^2) were cut from the densest parts of the oldest known stands, which were selected subjectively using scuba. Particular care was taken to sample only 1 m^2 and to remove silt from the roots. Wet weights and dry weights (constant at 105°C) were determined for each sample.

N, P, K, Mn, Fe, Cu, and Zn contents were analysed in the Plant Analysis Laboratory at Ruakura Agricultural Research Centre, on mixed random samples of dried leaves taken from each *L. major* sample. N and P were determined by Kjeldahl digestion from a procedure adapted from Gehrke et al. (1972). K was measured by flame photometry (Clinton 1967), and trace elements by atomic absorption spectroscopy (Allan 1970).

RESULTS AND DISCUSSION

Lake vegetation (1973)

During the 1973 study characean algae formed the dominant plant community within Lake Rotoma. *Chara fibrosa* f. *acanthopitys* (A.Br.) R.D.W. and *Nitella leptostachys* var. *leonhardii* (R.D.W.) R.D.W. dominated within the 48 transects which contained plants. Tall-growing native vascular plants — *Myriophyllum elatinoides* Guad., *M. propinquum* A. Cunn., and *Potamogeton cheesmanii* A. Bennet—were present on 17 of the 50 transects, and were located predominantly in the north-east and south-west of the lake. They formed a discontinuous cover above an understorey of charophytes. A low mixed community (LMC) consisting of *Glossostigma elatinoides* Benth., *G. submersum* Petrie, *Lilaeopsis lacustris* Hill, and *Elatine gratioloides* A. Cunn., as described by Chapman et al. (1971a,b), was restricted to 4 transects in the north-east of the lake in shallow water.

At the start of the study there were 29 transects containing the exotic *L. major.* It was the most widespread and abundant vascular plant, although it was often present only as isolated shoots or small clumps. The transects containing the largest and most developed growths of *L. major* coincided with nearby boat access sites to the lake, which was consistent with observations on other lakes in this area (Brown 1975).

Changes in native plants, 1973–80

A decline in water level between 1973 and 1974 was accompanied by a reduction of the LMC from 1.00% to 0.07% of the vegetation (see Fig. 1). Rapid recolonisation of newly flooded areas followed the subsequent rise in water level, and resulted in the highest recorded percentage of LMC (1.23%) in 1975. From 1975 to 1977 the water level was reasonably stable, but competitive replacement at the lower limits of the LMC by tall species, both native and exotic, appeared to be responsible for the reduction of this community to 0.79% of the total lake vegetation by 1976.

From 1977 to 1979 no quantitative data were collected. Qualitative observations on the survival of the restricted north-east LMC site over this period showed a further reduction until it became visually indistinct. This can reasonably be associated with the progressive lowering of the water level until 1979. The 0.58% in 1980 was interpreted to be a recent development following the subsequent rise in water level early in 1980, rather than a general decline since 1976.

The effect of water-level fluctuation was more pronounced on the LMC than on other vascular plants, presumably because the plants of this community had the shallowest depth range of all plants recorded in 1973 (Clayton 1978). The lowering of the lake level resulted in generally increased wave action on previously less exposed vegetation, which was often eroded away. Occasionally intact areas of the LMC were stranded above the receding water, depending on the rate of water level decrease and the intensity and duration of wave action. The exposed plants of the LMC would generally flower and set seed before becoming buried by storm drift, desiccated from exposure, or replaced by terrestial weeds such as lupin, thistles, and grasses. This seeding appeared to be significant in allowing re-establishment of this community whenever water levels subsequently increased.

The decline in water level from 1973 to 1974 was also accompanied by a decline in all *Myriophyllum* species from 2.98% to 1.30% of the total lake vegetation. The subsequent increase in water level (1974–75) was accompanied by an increase in the proportion of *Myriophyllum* to 1.70%. The recolonisation potential of *M. elatinoides* was probably due to its deeply buried rhizomes and roots, which grew deeper in the substrate than those of any other species in the lake. Erect shoots died back as a result of declining water levels, but regrowth from rhizomes was rapid following an increase in water level. From 1975 to 1976 the stable water level prevented regrowth of further rhizomes, which remained uncovered by water. During this period *Myriophyllum* decreased from 1.70% to 1.26% of the lake vegetation, probably because of partial displacement by *L. major.* The increase in *Myriophyllum* species from 1.26% in 1976 to 2.05% in 1980 was interpreted from qualitative observations to be a recent event following the increase in water level from 1979 to 1980.

Shoot fragments of *L. major* were observed to establish widely on inundated ground following an increase in water level, but localised areas of *Myriophyllum* and the LMC species re-established more quickly from rhizome and seed. Despite *L. major* taking longer to establish from fragments of vegetation, its competitiveness subsequently resulted in partial displacement of the native species from shallow water.

Potamogeton cheesmanii generally grew in deeper water than the LMC and *Myriophyllum* species, and the large decrease in water level from 1973 to 1974 was associated with a smaller frequency reduction than that recorded for other native plants. The reduction in *P. cheesmanii* in 1976 could have been caused by unfavourable seasonal growth, competitive replacement by *L. major*, or possibly an interaction of these and other influences. The high incidence of *P. cheesmanii* in 1980 was interpreted from qualitative observations to be a recent event following the increase in water level from 1979 to 1980, rather than a general increase since 1976.

In theory, the loss of available growing space calculated from the decline in water level from 1973 to 1974 was sufficient to cause complete removal of the LMC, a 45% reduction in *Myriophyllum* species, and an 18% reduction in *P. cheesmanii*. The actual declines were 93%, 56%, and 14% respectively, which supports the hypothesis that the decline in native plants from 1973 to 1974 was essentially caused by the reduction in water level over this period. Although there is evidence that these native plants do not spread easily, their ability to re-establish from seeds and rhizomes following an increase in water level was found to be important in ensuring their long-term survival under a fluctuating water-level regime. The effect of competition from *L. major* was reduced by fluctuating water levels, which allowed rapid re-establishment of native species in shallow water following a water-level increase. Consequently the native vascular plants were almost as well established in 1980 as in 1973.

Elodea canadensis Michx. was uncommon in 1973, when it constituted only 0.21% of the lake vegetation. After 1 year it had increased to 0.37%. The greatest measured increase took place between 1974 and 1975, with more than a fourfold increase in population to 1.63% of the total vegetation, but with subsequent decline it was almost as uncommon in 1980 as in 1973.

The initial rapid expansion by this plant was due primarily to its development in the south-west inlet between 1974 and 1975. The subsequent decline by 1980 was attributed to its replacement by *Lagarosiphon major*. The greatest spread of *E. canadensis* was across the bed of the inlet, where nutrient enrichment, lower light penetration, and fine silt sediments were apparently conducive to its rapid development. Subsequent extension of *L. major* from the sides of the inlet across the bottom of the channel initially resulted in coexistence of both species in 1976, and in almost complete replacement of *E. canadensis* by 1980. *E. canadensis* also extended from the south-west inlet into the area sampled by Transects 45 and 46 in deeper water below the established *L. major* community. Transect 24 was the only other location showing a similar growth habitat below *L. major*.

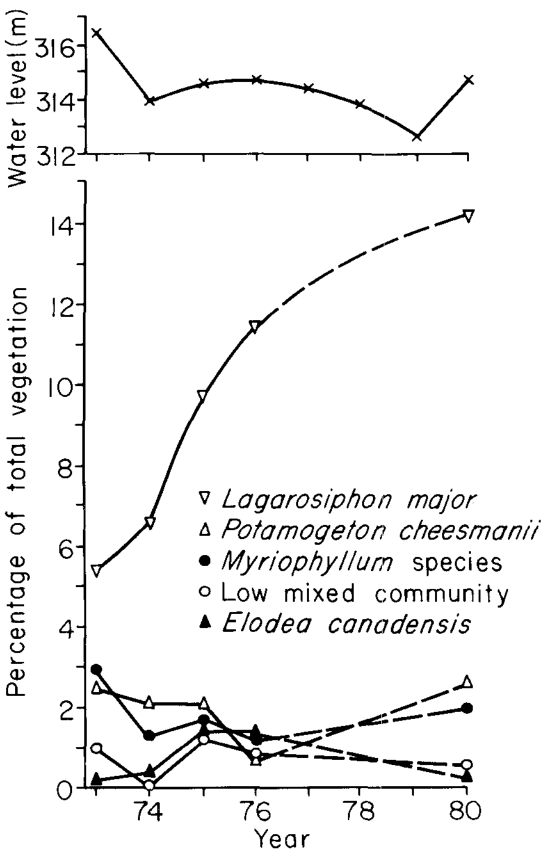

Fig. 1 Annual variation of vascular hydrophytes and average Jan–Mar water level, Lake Rotoma, 1973–80.

Clayton (1978) noted the widespread establishment of isolated shoots and small patches of *L. major* within the predominantly native vegetation of Lake Rotoma in 1973. In 1973 *L. major* was recorded from 29 transects and 308 quadrats (5.4% of the lake vegetation); it increased its distribution and abundance each year, and by 1980 it was recorded from 46 transects and 819 quadrats (14.35%). It was absent from only 4 transects, 2 of which were devoid of plants over the study period as a result of cliff erosion and sediment instability.

Table 1 Average wet and dry weights of *Lagarosiphon major* from samples selected for maximum biomass during June 1980, Lake Rotoma. Element analyses are for mixed samples of dried leaves.

Sample location	Plant height (m)	Wet weight (g/m^2)	Dry weight (g/m^2)	Major elements (% DW) N	P	K	Trace elements (ppm) Fe	Mn	Zn	Cu
Transect 23	2.0	10 510	1280	2.20	0.13	1.10	508	251	31	2
Transect 37	1.5	15 040	1830	1.90	0.11	1.15	868	308	32	4
Transect 47	3.0	24 220	3140	1.50	0.13	1.17	3326	1240	112	5

Unlike *E. canadensis* or the native species, *L. major* never decreased between 1973 and 1980 because of its ability to occupy a wider range of habitats, including water deeper than that required by native vascular species and a wider range of sediments than *E. canadensis.* Furthermore, *L. major* was able to competitively displace native species and *E. canadensis.*

The highest rate of spread for both *E. canadensis* and *L. major* took place between 1974 and 1975, and is attributed to the unstable water level. A 3 m reduction in water level between January 1972 and April 1974 resulted in the erosion and redistribution of large established beds of *L. major.* Dispersion took place into deeper water, and the subsequent rise in water level allowed recolonisation to take place in shallow water. The overall effect was to extend the lower depth distribution of *L. major* more rapidly than would otherwise have been possible.

It is probable that *L. major* was first introduced into Lake Rotoma around 1969. This is consistent with reliable information from a local resident that *L. major* was observed within the south-west inlet and along the southern roadside in 1970, and that considerable growth had taken place at the north-east end of the lake fronting the road access by 1971 (S. Hutchinson, pers. comm.). Similarly, it was found in an Ekman dredge sample in 1 m of water immediately beyond the boat access of the south-west inlet in May 1970 (D. J. Forsyth, pers. comm.). This is also consistent with the 1973 field data, which indicated that *L. major* was probably first introduced at the boat access points adjacent to Transects 23 and 49. Dissemination from the original points of introduction and establishment soon took place, since *L. major* appeared on the western side of Lake Rotoma in 1972, and local cottage owners had first sprayed the localised growth adjacent to their boat jetties with diquat in 1973.

The population of *L. major* in the south-west inlet was examined separately. In 1973 it made up 30% of the total vegetation in this area, increasing to 50% by 1976 and to 60% by 1980. This was the largest concentration within the lake. This local success could be a consequence of more favourable growing conditions, since the maximum depth across the bottom of the inlet does not exceed 6.5 m, the maximum potential depth for this plant (Coffey 1970). Furthermore, this area was a likely site of introduction, which would have allowed more time for development. Local enrichment of the inlet water is also apparent, possibly from residential septic tanks.

The large weed beds in the south-west inlet and near Transects 23 and 32 were sprayed with diquat by the Department of Lands and Survey during March 1978 (A. Harding, pers. comm.), but by 1980 there was not only complete recovery but also further development relative to the 1976 distribution. The apparently rapid replacement of *E. canadensis* by *L. major* in the south-west inlet may have been due in part to the 1978 spraying, by providing a competitive advantage to *L. major,* which would have had more vegetative fragments for regrowth.

Although *L. major* is now found all round the lake, considerable scope still exists for its further expansion in terms of increased density and extension of beds to the limiting depth of 6.5 m. However, as habitat saturation approaches, the rate of spread must decline, as has occurred in nearby Lake Okataina.

Biomass of *Lagarosiphon major*

Table 1 gives biomass data for *L. major* from the 3 sampled locations in Lake Rotoma. During quadrat sampling most of the plant roots were included in the sample and washed free of silt and sand, to give a measure of biomass rather than standing crop.

The dry weight of submerged plants is usually 10–15% of the fresh weight. Dry weights of *L. major* from Lake Rotoma varied from 11.0% to 13.4% of the fresh weights (average 12.3%). The samples contained a high proportion of old, tough stems.

The highest known biomass values for submerged aquatic plants have been recorded in New Zealand. Most values in the literature are less than 500 g dry weight per m^2 (Wetzel 1975), but Sculthorpe (1967) reported a world record standing crop of 1000 g/m^2 for *L. major* taken from Lake Rotoiti by Fish (1963), and Brown (1975) reported 1496 g dry weight per m^2 for *E. canadensis* from Lake Rotokahahi (Rotorua Lakes District). Brown (1975) suggested that the reason for *E. canadensis* having a higher weight per unit area than any reported for *L. major* might be a more compacted community structure. The results from Lake Rotoma indicate that insufficient biomass measurements have been made to allow reliable comparison between species. Exotic macrophytes do exceed 1000 g/m^2 dry weight in other of the Rotorua and Waikato lakes, and in the Clutha catchment of the South Island following the recent establishment of *L. major* (B. T. Coffey & J. S. Clayton, unpubl. data).

The dry weight value of 3140 g/m^2 in Lake Rotoma (see Table 1) was the mean of 3 samples from the south-west inlet. The maximum dry weight obtained was 3518 g/m^2, even though the area had been sprayed with diquat only 2¼ years before the samples were taken. Complete recovery of biomass had taken place, and the further spread of *L. major* may have been enhanced following the spraying.

The higher biomass values from the south-west inlet (Transect 47) may reflect greater plant height relative to other sampled sites (see Table 1); more sheltered conditions resulting in less pruning by wave action; locally enriched water and/or sediments; and increased density of stems as a result of the regrowth following diquat spraying. If the differences in plant height are allowed for, then the biomass values from Transects 36 and 47 are comparable. The northern lake site (Transect 23) had the lowest plant density, most probably on account of greater wave exposure and hence periodic thinning from wave action.

Aquatic plants reflect the nutrient status of the water and sediments of their habitat (Sculthorpe 1967). The element analyses on samples of dried *L. major* leaves from each site (see Table 1) were made to establish whether any important differences existed between sites. All the elements were above the concentrations regarded as limiting to plant growth (Carpenter & Adams 1977), so *L. major* appears not to be limited by availability of these nutrients. Similarly, Brown & Dromgoole (1977) found no correlation between standing crop in dense *L. major* stands and trophic status or water chemistry in Lakes Rotoiti, Okataina, and Tarawera. Although McColl (1972) classified Lake Rotoma as oligotrophic from physical and chemical measurements made on the water, he subsequently found that sediment samples from Lakes Rotoma and Okataina contained significantly higher amounts of P than sediments from the mesotrophic lakes in this area (McColl 1977).

The higher concentration of trace elements in the plant samples from the south-west inlet is indicative of the locally more enriched conditions from runoff, sewage seepage, and reduced water exchange with the open lake. Density of *L. major* plants is probably limited by available growing space in the southern sites sampled (Transects 37 and 47) and by wave exposure in the northern site (Transect 23). Brown & Dromgoole (1977) reported the rate of growth and spread of *L. major* to be related to the trophic status of the water and sediments. The more rapid development of *L. major* in the south-west arm of Lake Rotoma may well reflect enhanced tropic status there.

ACKNOWLEDGEMENTS

I am grateful to Professor J. M. A. Brown and Dr B. T. Coffey for helpful criticism of the paper, and to Mrs M. Fransen for technical assistance. Dr D. J. Forsyth provided data from Ekman dredge samples taken in 1970. Mr A. Harding was responsible for the Lands and Survey lakeweed spraying, and gave information on the areas and dates of spraying in Lake Rotoma. Mr S. Hutchinson, a local resident, provided valuable information from skindiving observations.

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