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THE INVASION OF LAKE TAUPO BY THE SUBMERGED WATER WEED *LAGAROSIPHON MAJOR* AND ITS IMPACT ON THE NATIVE FLORA

Summary: The waterweed *Lagarosiphon major* (Hydrocharitaceae) was first recorded in Lake Taupo in 1966, and by 1979 it had occupied most, if not all, the potentially colonisable sites in the lake. The aim of this study was to examine the distribution, abundance and growth forms of *L. major* in Lake Taupo and to assess the effects of this plant on the native aquatic vegetation. Studies involved underwater mapping of the 161 km length of littoral zone of the lake and detailed analyses at 42 sites around the lake at which *L. major* biomass, height and density were measured together with the species composition of each site. Five growth forms of *L. major* were identified, ranging from absent to beds of continuous cover greater than one metre in height. The relationship between these growth forms and height and biomass was established. Height and biomass were negatively related to fetch, and positively related to littoral slope angle and proportion of fine sediment. The number of native species decreased markedly as *L. major* height and biomass increased. The most noticeable decrease was at 4 m depth. Large weed beds of *L. major* attract herbivorous birds and detritivores which also adversely affect the native flora. Until recently the implications of the spread of *L. major* for the conservation of the indigenous flora has been overlooked.

Keywords: submerged waterweed, invasion, aquatic weed, density, biomass, Lagarosiphon, littoral zone, Hydrocharitaceae.

Introduction

The invasion of New Zealand's freshwaters over the last century by adventive aquatic plants has had a number of repercussions, the most obvious of which was an increased public awareness of 'aquatic weed problems'. These problems were generally seen as restrictions on human activities such as recreation, drainage and hydro-electric power generation (Chapman, 1970; Brown, 1975; Coffey, 1979; Johnstone, 1982). However, in some cases adventive aquatic macrophytes were actively planted to enhance wildlife values and recreation, specifically fishing and hunting (Tanner *et al.,* 1986; Chapman, 1967; Thompson, 1922). The effects of these adventives on New Zealand's native aquatic flora have not received the same attention as have the invasions of terrestrial adventives on the land flora. Native aquatic species have been completely replaced by adventives in some places (e.g. lower Waikato area, Howard-Williams *et al.,* 1987).

The purpose of this paper is to provide an example of how these invasions can affect native plant communities. The specific aims of the study were to examine the distribution, abundance and growth forms of the water weed *Lagarosiphon major* (Ridl.) Moss in Lake Taupo, and to assess the effects of this plant on the native aquatic flora.

Lagarosiphon major originates from Southern Africa where it inhabits high mountain streams and ponds (Wager, 1927). The first reported field population of the plant in New Zealand was in 1950 in the Hutt Valley and by 1957 it was established in nuisance proportions in Lake Rotorua. The first record of *L. major* in Lake Taupo was in 1966 (Wilson and Gibbs, 1966) where it was almost certainly introduced to the Taupo boat harbour by recreational boat traffic.

Prior to this the lake had been invaded by *Elodea canadensis* L. which dominated the vegetation at the boat harbour and at the south end of the lake where it occurred in conjunction with *Ranunculus* sp. and *Myriophyllum* spp.. Within two years of the first record of *L. major* in the boat harbour it had largely replaced *E. canadensis* there (Coffey, 1975). By 1968 it was present at the south end of the lake although *E. canadensis* was still dominant (Oayton, 1979),. but by 1975 *L. major* had largely replaced *E. canadensis* there also. By 1980 when the first part of our study was conducted, the plant occurred in almost every site around the lake where we believed suitable conditions existed.

Methods

Two types of field method were employed: a whole lake survey for distribution and mapping; and a selected site analysis. All field operations were conducted with SCUBA.

Whole lake survey

We surveyed the 161 km littoral zone of Lake Taupo to a depth of seven and occasionally ten metres using a variety of techniques. Diver operated 'manta-board' surveys involved a continuous series of short *(ca.* 200m) tows run in conjunction with a boat echo sounder. At the end of each tow, the diver surfaced and reported on the species composition and abundance of the vegetation to the boat assistant who also plotted the position on the 1:50,000 bathymetric map of Lake Taupo (Irwin, 1972). The echo sounder trace from each tow provided further information on vegetation height and location. Over extensive shallow shelving areas where large aquatic plant populations occurred, the boat towed the diver in a zig-zag fashion between the one and ten metre depth contours. To avoid missing large areas of optimum *L. major* growth by the zig-zag technique, a double zig-zag was run where growths were extensive (e.g. Waihi Bay).

The manta-board surveys covered 35% of the lake shoreline (ca. 56 km). Where there were long stretches of littoral zone with few aquatic plants (e.g. under rocky cliffs or along the exposed beaches of the east coast) we mapped the vegetation from surface observations from the boat, following along the 4-5 m depth contour with the aid of the echo sounder. Wherever a clump of vegetation was seen, a diver' made a spot dive for species identification. In the clear waters of Lake Taupo (extinction coefficient 0.1 m^{-1}) we could distinguish, from the boat, small patches less than 0.1 m across or individual plants to depths of 4 m.

Preliminary surveys led to the identification of five types of *L. major* growth form in the lake:

Growth form
1: plants absent;
2: scattered individual plants less than 0.5 m high;
3: patches and small clumps less than 1 m high;
4: closed canopy beds less than 1 m high but continuous for more than 10 m.
5: closed canopy beds growing to over 1 m in height and sometimes exceeding 2 m.

For small areas of *L. major* (<50 m in length), one rating was given to each area. Where more extensive areas occurred each zig-zag was recorded separately or, where a single tow occurred, the locality where the rating changed was noted. These data were used to compile a complete littoral map of the adventive species in Lake Taupo. Some communities of native species, particularly those in water greater than 7 m deep, may have been missed when the vegetation was mapped from boat surface observations.

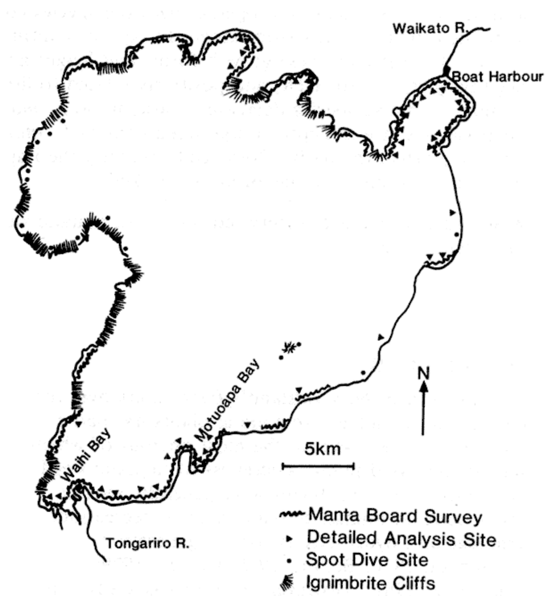

Figure 1: *Study areas in Lake Taupo showing locations of manta board surveys, spot dives and detailed analysis sites. No macrophytes occur beneath the ignimbrite cliffs.*

Detailed site analysis

One year following the whole lake survey, 42 sites around the lake (Fig. 1) were analysed for vegetation structure and selected environmental variables. At each site we measured direct fetch, effective fetch and aspect. Direct fetch was the longest distance in a given direction that the wind could blow unimpeded on to the study site. Effective fetch was the cosine corrected fetch value for angles up to 450 on either side of the line of direct fetch and takes into account the effect of the shape of the opposite shore (US Army Corps of Engineers, 1977). At water depths of 2, 4 and 6 m a sediment sample from the surface and 0.3 m below the sediment surface was collected. Slope was measured with an angle meter and a vegetation species list was made across a 10 m wide strip at right angles to the shore. The stand structure of *L. major* was analysed by placing a transect parallel to the shore at 2, 4 and 6 m. Plant height, density (number of stems per 0.1 m^2 quadrat placed 0.5 m below the maximum height of the plants in the quadrat), and biomass were recorded. Biomass was sampled by handcutting from a circular steel ring quadrat of area 0.25 m^2 pushed through the vegetation. Where tall solid beds of *L. major* were encountered, a large 2 m high net was attached to the top of the ring quadrat to avoid losses.

Sediment samples were size fractionated by weighting proportions of the fraction of oven dried (80∞∞C) sediment which passed through the following sieve meshes: pebbles, > 20 mm; gravel, 20-2 mm; coarse sand 2-0.2 mm; fine sand 0.2-0.02 mm; mud < 0.02 mm (Tinsley 1970). Percent organic matter was determined by ashing at 500∞∞C.

Results

General distribution

The distribution of submerged aquatic plants in Lake Taupo is very patchy (Fig. 2). Approximately 55 km of shoreline, particularly on the western side have vertical ignimbrite cliffs which extend into the water making them unsuitable for plant growth. The major areas of colonisation are the extensive shallow littoral shelves at the south end of the lake. Continuous sediment inputs and currents make the Tongariro River delta the only area at the south end where aquatic plants are absent. However, even where there is apparently suitable substrate, the distribution is localised. Where aquatic plant beds occur at the north end of the lake they are in bays rather than on points, and in large bays they are found where there is some protection from waves from the south or southwest. South westerlies are the strongest winds on the lake (NZ Meteorological Service data). Native aquatic plants occur mostly where *Lagarosiphon major* is found, and *L. major* is invariably restricted to sites which are protected from south westerly winds (Fig. 2).

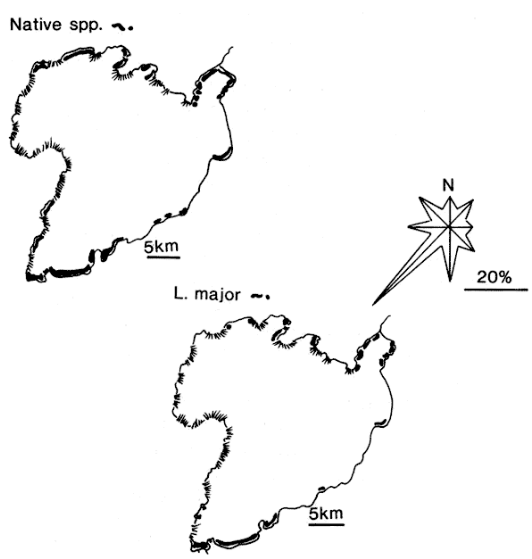

Figure 2: *Distribution of native aquatic species in Lake Taupo (above) and Lagarosiphon major (below). A wind rose for Taupo is also shown.*

Site analysis

Where growth form 5 of *L. major* occurs, the littoral zone of Lake Taupo is dominated by this plant between water depths of 2 to 6.5 m.

Table 1: *Characteristics of the* L. major *population at three depths in Lake Taupo. Data from* 32 *sites around the lake, with 10 samples* at *each depth* at *each site*. *x = mean, x_{max} = mean maximum values. Data in brackets = SE.*

Characteristic		Depth (m) 2	4	6
Biomass	x	165 (35)	480 (52)	101 (30)
gm^{-2}(dry)	x_{max}	708 (69)	1178. (139)	541 (109)
Height	x	0.36 (0.06)	0.80 (1.21)	0.32 (0.08)
m	x_{max}	1.21 (0.05)	2.86 (0.25)	1.14 (0.08)
Densitl	x	76 (22)	185 (29)	65 (15)
N m^{-2}	x_{max}	450 (24)	357 (18)	310 (26)

Biomass, height and density data for the *L. major* stands around the lake (see Fig. 1) are given in Table 1. Maximum biomass, height and density occur at the 4 m depth zones with some values well in excess of 1000 g m^{-2} dry wt for biomass, 2.5 m height and 350 shoots m^{-2} density. Values of biomass were also significantly ($p < 0.05$) higher at 2 m than at 6 m. The tall, closely packed stands (growth form 5) of *L. major* were invariably monospecific with virtually no space available for any other species.

There was a significant relationship of *L. major* biomass with both slope ($r= 0.60$, $n = 32$, $p < 0.001$) and the proportion of fine sediment ($r = 0.43$, n =

32, $p < 0.02$) which was improved by a $10g_{10}$ transformation of the environmental data ($r = 0.62$ and 0.52 respectively).

Although the distribution maps of the plant showed that it occurred only in areas sheltered from south west winds, the relationship between fetch and biomass or height was more complex (Fig. 3).

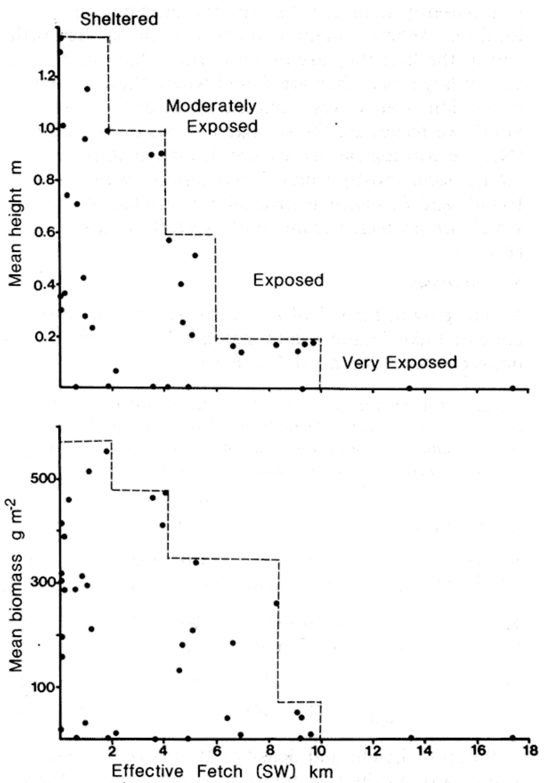

Figure 3: *Mean height and biomass of Lagarosiphon major at each site as a function of effective fetch.*

Maximum biomass and plant heights were found in sheltered areas and no high values were recorded in exposed areas (south west effective fetch of > 8 km). However, low biomass and height were found throughout the fetch range. No *L. major* was recorded at effective fetches of more than 10 km (SW). On the basis of Fig. 3 it is possible to classify four types of coast with respect to degree of exposure: sheltered shores, with less than 4 km effective SW fetch; moderately exposed shores with 4-8 km effective SW fetch; exposed shores with 8-10 km effective SW fetch and very exposed, > 10 km SW effective fetch.

Multiple regressions of the height and biomass of *L. major* versus original or log transformed data of slope, fine sediment content and effective fetch showed that 60% of the variance in both mean height and biomass could be explained by these three parameters. Height and biomass were positively related to slope and fine sediment and negatively related to fetch. The equations were as follows:

L. major height (m) = 0.245 + 0.023 (slope °) + 0.0073 (Fine sediment %) - 0.034 (effective fetch km, ... 1
($r^2 = 0.60$, $p<0.001$)
L. major biomass ($g\ m^{-2}$ dry) = - 28 + 291 ($\log_{10}$ slope °) + 83.2 ($\log_{10}$ Fine sediment %) -17.8 (Effective fetch km).. 2
($r^2 = 0.61$, $p<0.001$)

where the range of slope angles are 1-27° from horizontal, and log transformation gave a slightly higher r^2 than the original data for equation 2. Although each of the independent variables contributed significantly ($p<0.05$) to the regression equations there was an interaction between fetch and fine sediment. This complicates the interpretation of these equations but they are still valid as predictors of height and biomass in Lake Taupo.

The relationship of biomass, density and height with the field growth form ratings (1-5) of *L. major* are shown in Fig. 4. At growth form 5 mean biomass was in excess of 400 $g\ m^{-2}$ and height was more than 1 m. These parameters declined to rating 2 where biomass was less than 10 $g\ m^{-2}$ and the few odd shoots found were only 11 cm high on average.

An analysis of the species composition at each depth zone in the 32 stands (Fig. 4) shows that where *L. major* occurred in growth form 5 an average of only 2.5 native species per stand was recorded, with none deeper than 2 m depth.

As the abundance decreased from growth form 5 to 2 the number of native species recorded in each stand increased. Where *L. major* occurred in growth form 4 the number of native species increased at 2 and 6 m depths with an average of 5 and 2 species respectively and in some stands natives were found even at 4 m depth. At *L. major* growth forms 3 and 2, native species increased further to an average of 9.4 per stand. Where *L. major* was absent (growth form 1) species diversity was less than at ratings 2 and 3. This

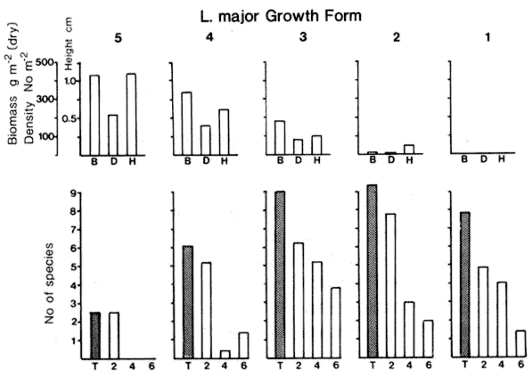

Figure 4: *Top: Mean Biomass (B), Density (D) and Height (H) of Lagarosiphon major for each of the five growth forms. Bottom: Mean number of native macrophyte species recorded at sites with the five L. major growth forms, T = total number of species at the site;* 2, 4, 6 = *number at* 2 *m,* 4 *m and* 6 *m respectively.*

is probably due to the fact that at the stands where *L. major* was not found, environmental conditions were unfavourable for macrophyte species in general. For instance, the proportion of coarse sediment (>0.2 mm) was 78.6 ± 5.85 in these stands as opposed to a mean proportion in the stands where *L. major* occurred of 16.1 ± 2.9. Coarse sediment is generally unfavourable for macrophyte growth.

The number of native species occurring in sites occupied by *L. major* was better related to *L. major* height than to biomass. The equations were:

$$N = 10.2 - 6.44\ (H) \qquad (3)$$
$$N = 9.6 - 0.018\ (B) \qquad (4)$$

where N = total number of native species, H = *L. major* height (m), B = *L. major* biomass (g m^{-2}). The correlation coefficient for Eq. 3 was - 0.561 ($p< 0.001$) and for Eq. 4 it was - 0.415 ($p< 0.05$), for 30 degrees of freedom.

Discussion

The invasion of sites within Lake Taupo by *L. major* was rapid. The time from the first recorded population in 1966 from the north end of the lake to its appearance at the south end was less than 2 years. The flora of the lake in 1966 was obviously susceptible to invasion and the barriers to invasion at all non-rocky sites with a fetch of less than 10 km (Fig. 3) were all likely to be botanical, as environmental conditions favouring the growth of native species were similar to those favouring *L. major* in this lake.

A botanical barrier to invasion is found where safe sites do not exist. A safe site (Harper, 1977) is a place where an invader can settle, grow and reproduce. The rapidity with which the *L. major* invasion occurred showed that botanical barriers did not exist and that safe sites for this species were abundant throughout the vegetated area, including those sites already colonised by the adventive *E. canadensis*. In oligotrophic lakes such as Lake Taupo, *E. canadensis* seldom forms dense monospecific stands and tends to co-exist with, rather than replace, native species (Brown, 1975; Coffey, 1975; Howard-Williams *et al.,* 1986). Two significant areas of native communities in the north-west comer of the lake have no *L. major* associated with them. One of these is a deep water (+ 7 m) characean community, and the other is a very sparse area of *Myriophyllum triphyllum* on a shallow (ca. 1 m) shelf, subject to wave action from the south.

The ability of *L. major* to form tall closed canopy stands in sheltered sites in Lake Taupo is the reason for its success here. Maximum height and biomass occur in sites with fine sediment and steep slope (> 70 from horizontal). This contrasts with the finding of Duarte and Kalff (1986) for Lake Memphremagog (Canada) where maximum macrophyte biomass was inversely related to the slope. They argue that gently sloped littorals allow the deposition of fine material while steep slopes are areas of erosion and sediment transport. However, in Lake Taupo, with its very different morphometry, the steepest littoral slopes were often in sheltered waters (effective fetch <4 km) while areas exposed to long fetches had wide wave-cut terraces with coarse sediments on shallow slopes. We could not determine a correlation between fine sediment content and slope angle in Lake Taupo.

The dense tall stands of *L. major* clearly have a very significant effect on native species numbers (Fig. 4) but even where the plant occurs in growth form rating 3 it has the potential to increase. In this form the plant occurs as isolated clumps amongst native vegetation and represents a 'guerilla' invasion *(sensu* Harper and Bell, 1979) where the plant exists as discrete units in small hollows and in the shelter afforded by stones and logs. The barrier to further spread is likely to be wave action as all the stands where the fetch is greater than 4 km *Lagarosiphon* occurs in growth forms of 3 or 2. Given prolonged periods of calm weather or high water levels this guerilla invasion may be replaced by a 'phalanx' type invasion (see Harper and Bell 1979) if the *L. major* clumps can coalasce. The native species would then be severely reduced. Low stature but continuous beds of *L. major* (growth form 4) could, once established, persist in some of these areas for a long time.

The stability of the growth forms of *L. major* is currently under investigation. The data available (C. Howard-Williams unpublished) indicate that at any one site growth form 5 is the least stable. The tall beds can collapse in the space of a few weeks, and then either persist as growth form 4 for up to 12 months or rapidly re-establish as growth form 5. Reasons for the variability are related to storm events and to natural senescence. The high variability in plant height or biomass and fetch, for instance, (Fig. 3) probably results from such temporary instabilities in growth form. These variations will be site specific and occur at different times at different parts of the lake. It is unlikely that the constants in equations 1 and 2 would differ greatly if the data analysis was done at a different time.

The native flora of the lake has been directly replaced or reduced in many areas by *L. major*. There are also indirect interactions by which *L. major* adversely affects native plant communities. The most obvious of these is the grazing effect of swans. Tall stands of *L. major* and other adventives which grow to the water surface form a major food source for the black swan *(Cygnus atratus)* whose appearance on the lake has been attributed to the adventive macrophyte stands (Bull, 1983). This bird appears in large numbers at the south end of Lake Taupo where 600-800 individuals can occur (D. Stack, Department of Conservation, pers. comm.), and these have kept Waihi Bay (Fig. 1) essentially clear of surface macrophyte growths for several years. However they also move to Motuoapa Bay (Fig. 1) when Waihi Bay has been grazed to the maximum feeding depth (ca. 1.0 m). Here they uproot native plants growing in shallow water (0.5 to 1.0 m depth). Rafts of uprooted native macrophytes can be seen floating amongst feeding swails in Motuoapa Bay and the virtual disappearance of *Potamogeton* spp. from the sheltered south end of Motuoapa may be due to swan grazing. The apparent advantages of the swans in keeping the water surface free of aquatic weed growth may be offset by their detrimental effects on native aquatic plants in nearby areas.

Dense populations of the freshwater crayfish *(Paranephrops planifrons)* have been shown to limit the downward extent of native macrophyte communities, especially characean meadows and deepwater bryophytes (Coffey and Clayton, 1988). Characeans are a preferred source of food for the crayfish, relative to vascular hydrophytes and the damage caused by these animals on characean meadows is due to browsing and trampling (Coffey and Clayton, 1988).

A peculiar feature of the vegetation of Lake Taupo is the frequent absence of characean meadows below large *L. major* beds in spite of an abundance of photosynthetically active radiation here (e.g. 49% of subsurface irradiance occurs at 7 m depth). Where wire cages of small (1 cm diameter) mesh were placed on the lake bed below the *L. major* zone these became colonised by characeans to depths of 20 m (C. Howard-Williams, unpublished data). The absence of this valuable native flora community here is almost certainly due to feeding activities of *P. planifrons*. which are particularly abundant below large beds of adventives such as *L. major*. The wire cages excluded these animals and allowed characeans to develop. When larger holes developed in the cages, and *P. planifrons* was able to move in, the characeans disappeared. Further evidence for crayfish damage to characean meadows is given in Coffey and Clayton (1988).

Proposals for the commercial release of grass carp to control adventive aquatic plants such as *L. major* in New Zealand should also be viewed in the context of the native flora of the lakes. The food preference studies carried out on these fish in New Zealand (Rowe and Schipper, 1985) show that many native aquatic plants are eaten by grass carp and some of the native species are even listed as 'much preferred food'. The possible impact of grass carp in New Zealand's native flora needs further consideration.

The effect of the adventive aquatics such as *L. major* is to directly displace the native flora over large areas of the lake littoral zone, and by attracting large herbivores such as swans, and detritivores such as crayfish, which adversely affect the native flora, the effect of the adventives is compounded.

The few remaining Northland lakes (Tanner *et al.,* 1986), Westland lakes and other isolated South Island lakes such as Lake Christobel, where adventive aquatic plants do not occur, are a fragile reminder of New Zealand's native aquatic condition. Every care should be taken to preserve these from exotic water plant invasions, and to preserve existing remnant populations in our other lakes from further degradation.

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