them. In the Czech Republic alone, the 1992 budget has set aside some 13 billion crowns for environment-saving measures, but at least three times as much money would be needed to bring about a sufficiently fast and visible improvement. This example shows that even the most economically developed regions of post-Communist Central Europe cannot make a breakthrough in environmental improvement without substantial financial and technical assistance from abroad. This should preferably be in the form of long-term credits with low interest rates for the purchase or development of modern technologies and machinery, and for the restoration of damaged ecosystems. Lecturing, transfer of know-how and elaboration of management plans by Western firms are useful, but expensive, and thus little effective. Often local firms or specialists could accomplish most of these tasks more cheaply and equally well, and the money could be spent directly on the accomplishment of projects for environmental improvement.

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PLENARY ADDRESS

Processes of Aquatic Weed Invasions: The New Zealand Example

CLIVE HOWARD-WILLIAMS[1]

ABSTRACT

Aquatic weed problems in New Zealand are caused by introduced submerged species, particularly those of the family Hydrocharitaceae. Introduced submerged species have successfully dominated the native flora in the depth range of 1 to 6 m and spectacular invasions are still occurring. Their growth is particularly marked in clear oligotrophic lakes where weed bed heights of > 4 m and biomass values of up to 3000 g m^2 (dry mass) have been recorded. Turbulence due to wave action appears to be the major factor controlling the upper limits in natural growth for some species, but low nutrient level is a barrier for others. Weed movement between lakes is facilitated by interlake recreational boat movements. Native plants can re-establish in oligotrophic lakes if the invading species are controlled (*e.g.* by mechanical harvesting). Published literature shows that well-planned scientific experiments on weed management strategies (with adequate experimental controls) are not common. For instance, data show that large-scale natural declines in weed populations can occur which complicate the interpretation of management methods.

Key words: mechanical harvesting, dispersal, *Hydrilla, Hydrodictyon, Ceratophyllum, Rorippa, Lagarosiphon, Elodea.*

INTRODUCTION

New Zealand has all the world's worst aquatic weeds, and hence has a long history of aquatic weed management. Almost 20% of the country's aquatic and wetland flora are introduced (Johnson and Brooke 1989), and invasions by these species have had a major impact on the fresh waters of New Zealand. The most significant problems are caused by submerged species, in particular coontail (*Ceratophyllum demersum* L.) and members of the Hydrocharitaceae, notably lagarosiphon (*Lagarosiphon major* (Ridl.) Moss), elodea (*Elodea canadensis* L.) and egeria (*Egeria densa* Planch).

Aquatic weed problems in New Zealand lakes are largely manifested as commercial losses to hydropower stations and threats to recreational waters. Some herbicidal control is used by applying Diquat (the only herbicide registered for use in New Zealand's natural waters) from barges with spray booms, and large-scale experiments using triploid grass carp are underway (Clayton et al. 1992, Clayton 1992). However, most of the practical weed control work is done by mechanical means. This includes harvesting and routine control by:

a. Floating booms at an angle across the current to collect floating weed masses and concentrate them at a single site on the shore for removal (Johnstone 1982).
b. Mechanical screen cleaners which rake the penstock intake screens to hydropower stations pulling off vegetation as it accumulates. Johnstone (1981) estimated that partial blockage of screen intakes can result in losses of up to 60,000 MW hr^{-1}

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[1] Freshwater Division, National Institute of Water and Atmospheric Research Ltd., PO Box 8602, Riccarton, Christchurch, New Zealand.

each year in the hydro stations on the Waikato River alone.

c. Lake drawdowns in summer to desiccate weed masses (Johnstone 1982) and in winter to freeze-kill weed masses in the 1- to 4-m depth zone (Howard-Williams *et al.* 1989).

Useful reviews of the control options for New Zealand's aquatic weeds have been published (Johnstone 1982, 1986, and Clayton 1992). This paper takes a general theme of invasion and concentrates on the ecological aspects of the weed invasions themselves using New Zealand lakes as an illustrative case.

INVASIONS

For some reason, when aquatic plants first arrive in New Zealand (and probably many other countries) they do spectacularly well. This is illustrated by two species which are not normally associated with large-scale weed infestations, watercress (*Rorippa nasturtium-aquaticum* (L.) Hayek) and waternet *(Hydrodictyon reticulatum* (L.) Lagerheim).

Watercress was introduced to New Zealand by the French in 1840 as a food plant (Healy 1969) and within a few years, plants which grew to a size unknown in Europe were causing problems to boat traffic on the Avon River. In 1857 a reward was offered for a plan to eradicate the weed, and by 1864 the Provincial Government in Canterbury passed what was called the "Watercress Ordinance" to prevent further obstruction of rivers by watercress and related weeds. The reward, by the way, has never been collected. The plant has long ceased to be a major weed problem and has now assumed the role of a valued food item. Although it frequently covers pasture streams, its high growth rate (RGR = 5% day^{-1}) and high nutrient requirement (*ca.* 700 mg N m^{-2} day^{-1}) mean that it is very effective at nutrient stripping from enriched pasture stream waters (Howard-Williams *et al.* 1982), thus performing a doubly valuable function. This is a case where a problem invasion has resolved itself into a beneficial introduction.

A more recent but similar invasion has been the recent arrival of waternet in field situations in New Zealand (Hawes *et al.* 1991). Waternet was first reported in the field in 1988 (Coffey and Miller 1988) where it occurred in the ponds of a tropical fish importer's property. Within two years it had spread to a wide range of waters throughout the central North Island where it has proliferated to an extent unrecorded in the international literature in large lakes as unialgal stands (Hawes *et al.* 1991). For instance, in late summer (1990) it covered approximately 200 ha of Lake Rotorua, a large windswept lake of 80 km^2, in a major tourist area. Beach fronts were smothered, tourist boats became inoperable, and there are still well-founded fears that the plant could spread further to block the intake screens of some of the hydropower stations.

SUCCESSION VERSUS INVASION

In classical Clemensian succession a plant community gradually alters in a more or less predictable way. The direction of change is dictated by the environmental conditions which are created by the preceding vegetation. Thus new species may gradually "invade a community" to replace the existing ones as the environment gradually changes.

However, rapid and large-scale plant invasions, such as the two I have just referred to, are clearly non-successional. Explanations for such events noted in the ecological literature are: low ecological diversity of the community being invaded; poor adaptation of the original flora to its environment in comparison with the invader; lack of predators of the invader; lower reproductive potential of the native flora relative to the invader and/or environment undergoing rapid man-made change (*e.g.* eutrophication or physical disturbance) which may promote the invader.

Frequently, none of these reasons are adequate to explain a particular aquatic plant invasion and we should look to a more general model to explain invader success. The concept of "the Safe Site" proposed by Harper (1977) may be such a model. A Safe Site is a location in which a plant can invade grow *and* reproduce. Plants can invade a site to grow and reproduce only in the *absence* of environmental barriers (Johnstone 1985). These barriers may be biotic and/or abiotic.

For instance, watercress only invaded New Zealand streams when the native forests were cut to make way for pasture and the major abiotic barrier (shade) was removed. The reason for its success was that when the forests were cleared there were no botanical barriers preventing its spread. This is because New Zealand is the only significant non-polar land mass in the world that is without native rheophytes (emergent, flood-resistant stream plants) (van Steenis 1981). Watercress has never proliferated in the sunlit margins of New Zealand wetlands in the presence of a dense native vegetation.

In the case of waternet, in spite of its successful invasion of eutrophic lakes, this plant has not been able to invade oligotrophic lake systems. For instance, oligotrophic Lake Taupo (70 km from Lake Rotorua) was inoculated by waternet at the same time as Lake Rotorua. It occurred at one locality in Lake Taupo for approximately one year (1990-91) where it dominated the native vegetation to a depth of 20 m. It has subsequently declined and fragments are now rarely found. The barrier to invasion in this case was abiotic, namely the low nutrient status of the waters of Lake Taupo. Dissolved inorganic nitrogen (DIN) in the epilimnion in summer is frequently below 5 mg m^{-3} and dissolved reactive phosphorus (DRP) levels are *ca.* 1 mg m^{-3} (White and Payne 1977). These concentrations are well below threshold limiting concentrations for growth of the plant of 45 mg m^{-3} DIN and 6 mg m^{-3} DRP and even below the Half Saturation Constants (K_S) of 18 and 2 for NO_3-N and DRP (Dr. I. Hawes, unpublished data).

An abiotic barrier may also be the reason why coontail has also never proliferated in oligotrophic Lake Taupo. For instance, the first patch of coontail to invade the northern end of the lake was mapped in a depth of 9 m adjacent to a boat ramp in 1981. Ten years later this small patch was still present as the only colony and has not extended in area.

The first submerged invader to have a major impact in Lake Taupo was elodea in the 1950's. This plant occupied sheltered sites throughout the lake in the depth zone of 1 to 11 m impacting on the native flora of that depth zone. In the 1960's elodea was replaced by lagarosiphon, an exotic species from Southern Africa. This pattern of invasion has been typical of a large number of oligo- and mesotrophic New Zealand lakes. In the last two decades coontail has successfully competed with lagarosiphon in all nutrient rich lakes, and in the last decade egeria has grown at the expense of all the other adventive submerged weeds in meso-eutrophic conditions. However, the last two species have not been as successful in oligotrophic conditions. A schematic diagram of invader sequences in oligotrophic vs meso-eutrophic North Island lakes (Figure 1) shows quite different sequences which relate to species specific abiotic barriers to the invasions.

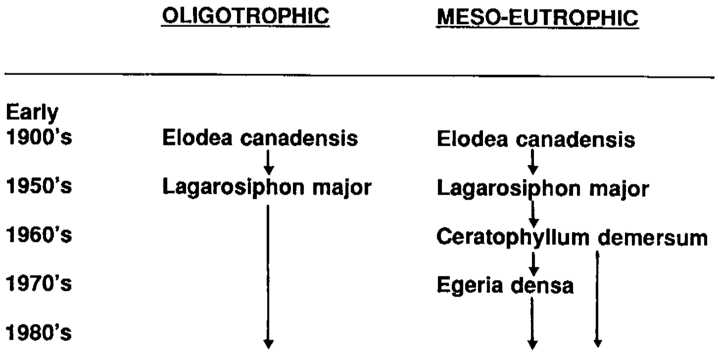

Figure 1. Sequence of dominant aquatic weed species in the invasions of oligotrophic and meso-eutrophic lakes of New Zealand's North Island.

While there may be a relationship of dominant species with eutrophication, there is no relationship between the biomass of submerged species and lake trophic status (Johnstone *et al.* 1985, Howard-Williams *et al.* 1987). In fact, the evidence indicates that submerged weed biomass declines when strongly eutrophic conditions persist. The factor which controls the upper limit of biomass in oligotrophic and mesotrophic lakes is wind and consequent wave action. An excellent example is provided by Lake Taupo which is a large lake with fetches of almost 40 km, but with many sheltered bays. The impact of wave action can be assessed from calculations of effective fetch (U.S. Army Corps of Engineers 1977). A plot of lagarosiphon height *vs* fetch (Figure 2) for Lake Taupo shows that the upper limits of height decline steadily with increasing fetch. Biomass data (Howard-Williams and Davies 1988) show a similar trend. The highest values for mean stand height (> 1 m) were found where effective fetch was less than 2 km. Nuisance growths only occurred at effective fetches of < 2 km. At fetches in excess of 10 km no lagarosiphon was recorded.

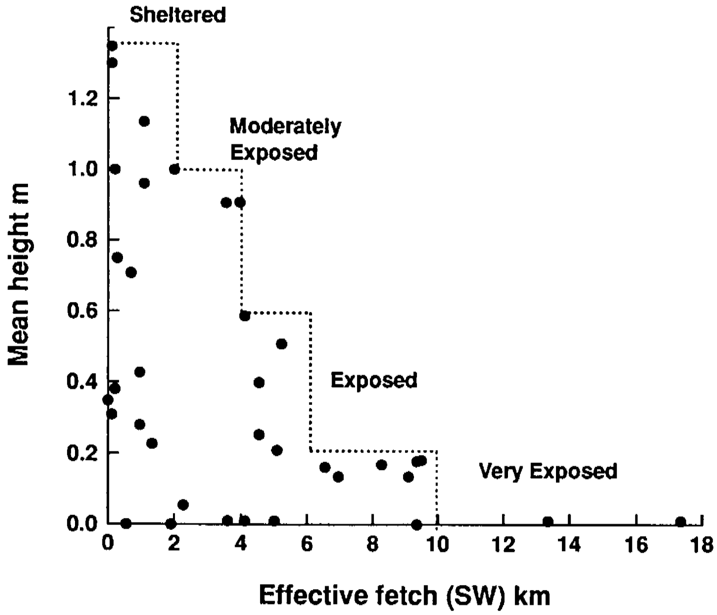

Figure 2. Mean stand height of lagarosiphon in Lake Taupo in a range of effective fetches exposed to the prevailing southwest winds.

BARRIERS TO MOVEMENT

An effective means of transport between lakes is critical if an invading species is to spread from its original infestation site. The Hydrocharitaceae in New Zealand do not produce seed, so dispersal is only by vegetative fragments. There are two aspects which need to be considered for an analysis of between-lake transport: minimum size of a vegetative fragment to be transported, and survival time of a fragment. A vegetative fragment can only germinate if there is a bud. Lateral stem buds were found to be the most resistant to desiccation so the minimum size of stem fragment that would guarantee the presence of a lateral bud can be calculated. The data for the New Zealand Hydrocharitaceae are given in Table 1 and show that for hydrilla and egeria, a stem fragment needs to be over 30 cm in length to ensure the inclusion of a

TABLE 1. MORPHOLOGICAL AND SURVIVAL CHARACTERISTICS FOR DISPERSAL PROPAGULES OF FIVE AQUATIC WEEDS IN NEW ZEALAND. LATERAL BUD FREQUENCY, MINIMUM STEM LENGTH REQUIRED TO ENSURE PRESENCE OF A LATERAL BUD, MINIMUM/FATAL WEIGHT LOSS AND SURVIVAL TIME. (DATA FROM JOHNSTONE *et al.* 1985.)

Species	Nodes/bud	Mean internode length (mm)	Minimum stem length (mm) to include one bud	Minimum fatal weight loss (%)	Time in air to reach fatal weight loss (hours)
L. major	7	34	238	70	20
E. canadensis	7	7	49	56	9
C. demersum	1	59	59	74	36
H. verticillata	5	65	325	46	5
E. densa	11	32	352	65	10

lateral bud (Table 1). Hydrilla is the most sensitive species to desiccation, with a time of only 5 hr before minimum fatal weight loss occurs.

Interlake movement of boats has been implicated almost exclusively in the transfer of aquatic weeds in New Zealand. For instance, in an analysis of 88 lakes in the North Island (Johnstone *et al.* 1985) there were 38 lakes which did not have adventive Hydrocharitaceae or coontail. In 27 of these there was no boating or fishing. Boating and/or fishing took place in the remaining 61 lakes, of which in 50 of these there was at least one of the submerged adventives. The presence of these weeds was significantly ($P < 0.01$) related to human activity (Table 2). In addition to boating and fishing, aquatic weeds have been transferred by float plane and even by weed harvesters! Water birds have not been shown to be effective vectors for the transfer of viable vegetative fragments of vascular plants. All this is of particular significance to the invasion of New Zealand by hydrilla.

TABLE 2. THE RELATIONSHIP BETWEEN THE PRESENCE OF ANY OF FIVE ADVENTIVE WEED SPECIES AND HUMAN ACTIVITY IN 88 LAKES (FROM JOHNSTONE *et al.* 1985).

Boating and/or fishing activity	Total number of lakes	Weed presence	
		Present	Absent
Absent	27	0	27
Present	61	50	11
Total	88	50	38

The dense canopy production by hydrilla, its tolerance of a wide range of habitat conditions (Bowes *et al.* 1977) and its prolific reproductive capacity have allowed hydrilla to displace not only native plants in many countries but even compete successfully with large adventive relatives such as egeria (de Kozlowski 1991) and vallisneria (Haller and Sutton 1975). Hydrilla is not a major problem in New Zealand at present as it is restricted to a small group of four lakes remote from other water bodies of the North Island. It has been there since at least 1963 (Clayton *et al.* 1992), and has not spread. If boats are the principal means of interlake transport, then the sensitivity of the plant to desiccation and the remoteness of the four lakes where it occurs from other water bodies (*ca.* 120 km) means that the chances of its accidental spread are very low (Figure 3).

While large vegetative fragments of vascular aquatic weeds are required for dispersal, this is not the case with algae such as waternet, where even a few cells may be sufficient for interlake dispersal. Procedures for cleaning a large commercial aquatic weed harvester which had been working in a waternet-infested lake provide an example of the ease with which filamentous algae can be transported. The cleaning procedure adopted before the harvester could be transported to another catchment was as follows: thorough water blasting at the haul-out boat ramp with high pressure hoses, followed by a spray of the whole machine with 56 L of quaternary ammonium algicide (QAC) applied by a hand pressure pump with flexible nozzle to reach into all visible cracks and under the machine conveyors. The harvester was then transported to the new location, but a four-day drying out was requested and then a final check before launching. After all this, viable fragments of the weed were found under a conveyor. The machine had to be resprayed with QAC again before the harvester could be used.

EFFECT ON NATIVE SPECIES

In almost every instance where an invasion has occurred the native vegetation has declined markedly. New Zealand has no native canopy-forming submerged aquatic plants. Canopy formations are a characteristic of the Hydrocharitaceae which have successfully dominated in almost every lake they have invaded. Closed stands of 3 to 5 m in height are formed by lagarosiphon and elodea in sheltered areas and stands up to 5 m have been recorded for egeria.

It is generally recognized that there are three "typical" native community types in a depth transect of New Zealand lakes: a low mixed community in the upper littoral zone, a

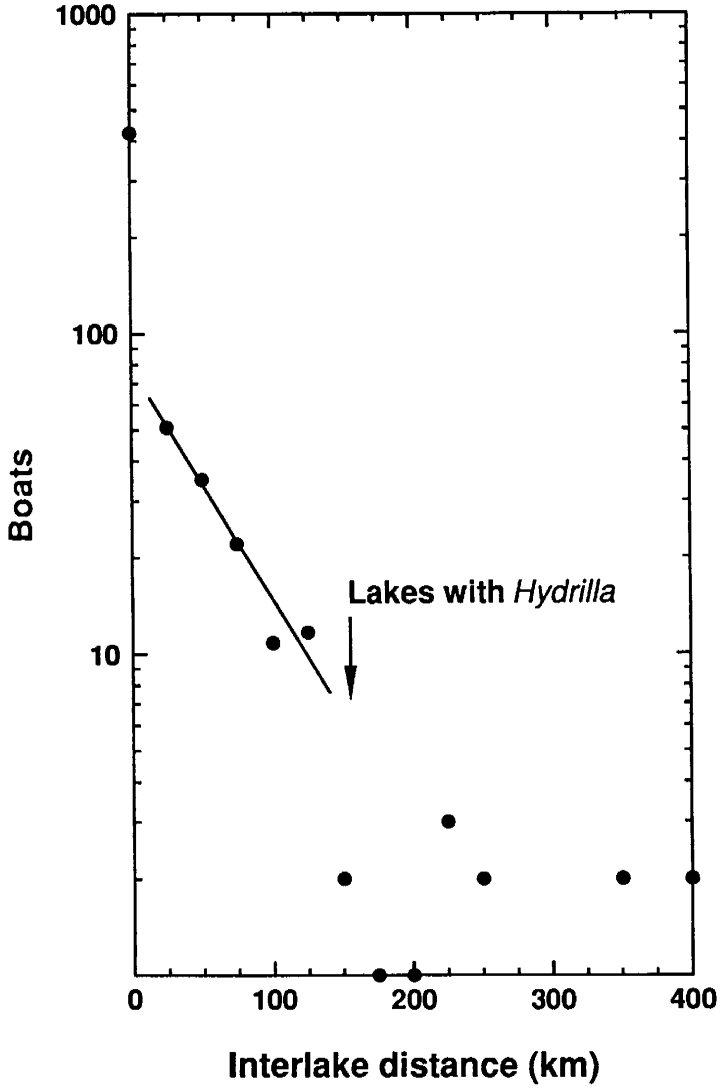

Figure 3. Frequency distribution of interlake distances traveled by boats in New Zealand (n = 564) based on boat ramp surveys. Note: only 14 (2.5%) had come from a lake >125 km distant and only a small proportion of those are likely to carry any weed away from the lakes. (Data from Johnstone *et al.* 1985.)

tall vascular community in the mid-depth range (2 to 8 m) and a characean meadow community to the bottom limit of the littoral zone. Invasion by canopy-forming plants has had a major impact on the tall vascular community. This can be shown quantitatively for data from Lake Taupo by plotting the relationships of number of native species *vs* lagarosiphon height and biomass (Figure 4). As lagarosiphon biomass and height increase, the number of native species declines, and especially so in the 4-m depth zone which is the optimal depth for the tall vascular community.

If the native community is dense, why should it not form a biotic barrier to invasion? Madsen *et al.* (1991) described how Eurasian water-milfoil *(Myriophyllum spicatum* L.) in Lake George (NY) was able to invade healthy native communities in the absence of disturbance. This is also frequently the case with lagarosiphon invasions in New Zealand with the general pattern described as follows: A viable shoot of lagarosiphon (with lateral buds) may settle on a short 'low mixed community' some 15 to 150 cm tall in shallow water (*e.g.* 2 m). Long roots grow to the sediment, bypassing the short-stature native plants. Once the invader begins to grow, side branches fall and produce more roots (*e.g.* Coffey 1980) producing small clumps of lagarisophon. This is known as 'guerilla' invasion (*sensu* Harper and Bell 1979). If these clumps coalesce a wall or 'phalanx' invasion occurs with a downward extension of a tall mass of lagarosiphon smothering the native community. Where wind fetches exceed 4 km (moderate fetch) shoots do not grow tall enough to form a phalanx and lagarosiphon and native species may co-exist.

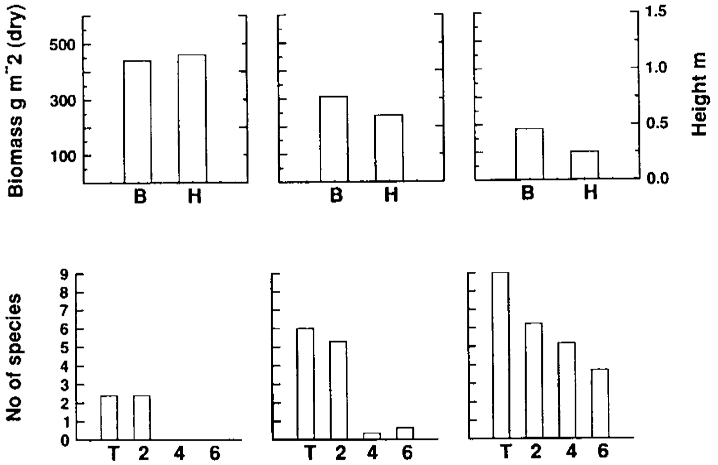

Figure 4. Relationship between biomass (B) and height(H) of the aquatic weed lagarosiphon (top) and the number of native species (bottom) at 2-, 4- and 6-m depth. T = total number of species recorded over all depths. (Data from Howard-Williams and Davies 1988.)

REVERSING AN INVASION

Aquatic weed control can reverse the invasion sequence and there are examples where this has occurred. In Hamilton Lake (NZ) selective herbicide treatments with gel-formulated diquat (Clayton and Tanner 1988) were successful in removing lagarosiphon and egeria and consequently maintaining a bottom cover of desirable characeae.

Mechanical harvesting trials in Lake Aratiatia, an oligotrophic New Zealand hydro-lake, illustrate this process. Figure 5 compares a control (unharvested) site and a harvested site in a lagarosiphon-dominated section of the lake. Regrowth after harvesting was patchy and slow, and also quite substantial natural collapses in unharvested areas occurred,

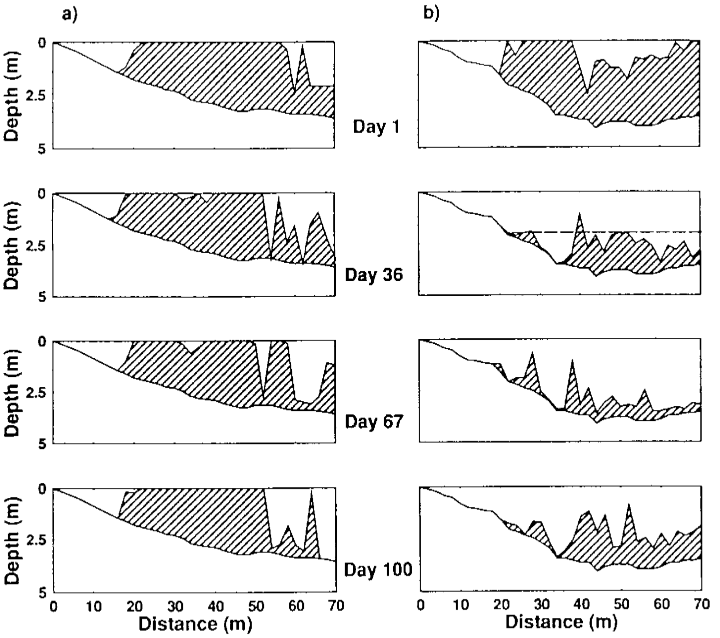

Figure 5. Profiles of weed bed height in two sites in Lake Aratiatia before harvesting (day 1) and after 36, 67 and 100 days harvesting. (a) Control site, unharvested. (b) Site cut by mechanical harvester. Dotted line = depth of cut.

reflecting natural cycles in growth. Patchy regrowth in the harvested area resulted in a rapid recolonization of sections of the transect by native characeae (*Nitella* spp) as illustrated in Figure 6.

Submerged aquatic weeds in particular are prone to marked natural fluctuations in biomass (Loucks *et al.* 1979), and reports in the literature show that such cycles in density can occur over short time scales (weeks), seasonal time scales or years.

In the now classic studies on the Eurasian water-milfoil invasion of Lake Wingra in the 1970s, Carpenter (1979) pointed out that following the natural collapse of the milfoil populations, two of the few remaining robust stands of the weed were those which were regularly harvested and conversely many of the larger stands which collapsed had never been treated with either herbicides or harvested.

The question we need to ask is "How long after an invasion can we afford to wait before being certain that the invader and its problems are here to stay, and that we need to spend big money on its control?" After all, watercress in New Zealand changed from a serious problem weed to a beneficial species.

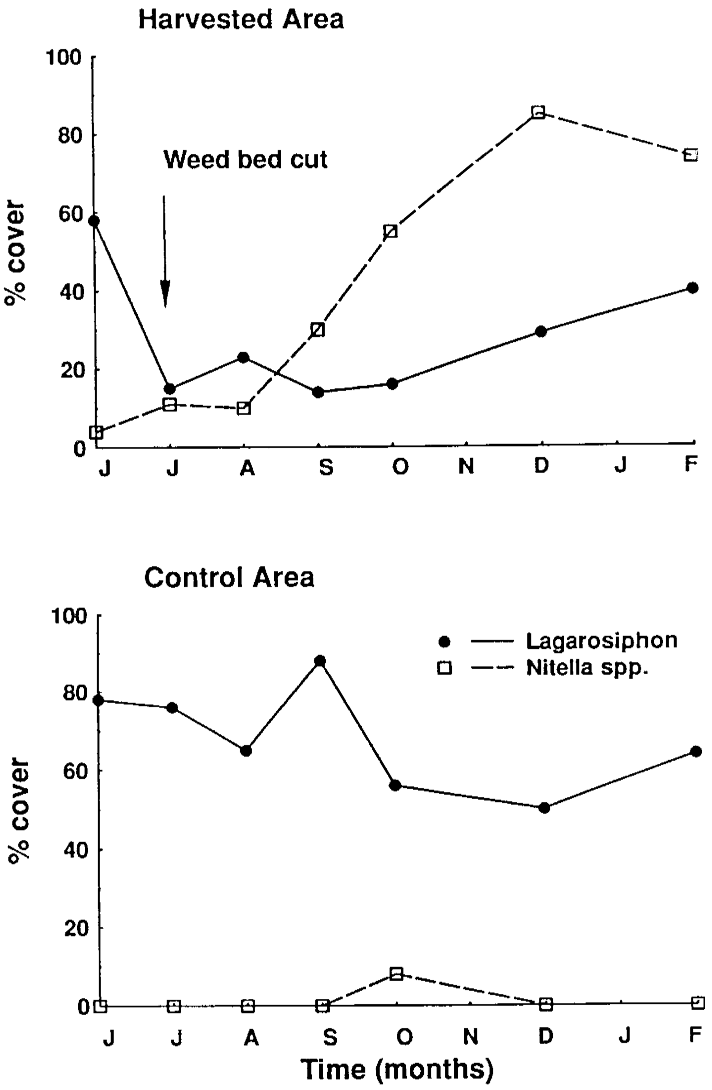

Figure 6. Percent cover of lagarosiphon and native characeae over time in a harvested and non-harvested control area in Lake Aratiatia.

David Sutton, in his presidential address to this society's 30th Annual Meeting in 1991 stated, "Unless we understand better the factors that contribute to causing exotic plants to get out of hand in the first place, there is little likelihood that we are going to make much progress on eliminating or reducing some of our major weed problems."

In this context the example of the recent invasion of waternet to lakes in New Zealand is a good example. Why have native filamentous green algae such as *Cladophora* and *Enteromorpha*, which naturally occur in Lake Rotorua, not proliferated to the same extent as waternet in that lake. Both these genera cause problems elsewhere but the success of waternet at the expense of the other potential competitors is a salutary reminder that we still do not fully understand species specific events of this nature.

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