

The Rise and Fall of Water Net (*Hydrodictyon reticulatum*) in New Zealand

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ABSTRACT

During the late 1980's to early 1990's a range of aquatic habitats in the central North Island of New Zealand were invaded by the filamentous green alga, water net *Hydrodictyon reticulatum* (Linn. Lagerheim). The alga caused significant economic and recreational impacts at major sites of infestation, but it was also associated with enhanced invertebrate numbers and was the likely cause of an improvement in the trout fishery. The causes of prolific growth of water net and the range of control options pursued are reviewed. The possible causes of its sudden decline in 1995 are considered, including physical factors, increase in grazer pressure, disease, and loss of genetic vigour.

Key words: algal control, algal invasions, ecological impacts.

INTRODUCTION

Description

Water net is a green filamentous alga. It is distinctive in that the individual cells are joined to form a six-sided mesh structure (usually visible to the naked eye) which makes up cylindrical colonies. In New Zealand nets have measured >1 m long, and resemble a green fish net stocking. The cells are multi-nucleate and each cell is capable of forming a new colony (~1,000 cells) vegetatively, which enables this species to grow very rapidly when conditions are favourable. Sexual reproduction resulting in formation of resistant spores has been described by Marchant and Pickett-Heaps (1972).

Global Distribution

Water net has a world wide distribution but rarely forms persistent nuisance growths as other species of filamentous algae, such as *Cladophora*, *Oedogonium* and *Spirogyra*, that tend to be dominant (Pocock 1960). In the United States it is widespread and present in a range of habitats and climatic zones where Dineen (1953) described seasonally prominent growths of water net in a Minnesota pond (with ice cover in winter) and Kimmel (1981) described it as common in Florida wetlands. However it is rarely a nuisance in the U.S. in comparison with other filamentous algae (J. D. Madsen, pers. comm., U.S. Army Corps of Engineers). In Central

Europe, Thomas (1963) reported it as a nuisance in Lake Zurich. In England, Flory and Hawley (1994) described a recent water net bloom (present since 1993) which had a surface bloom visible of 14 ha in Loe Pool, Cornwall. It was also abundant (50% cover on the river bed) in the slow flowing Tamar River, near Tavistock, England (author's observation, 1996) however, generally in England it is a minor component of the suite of filamentous algae (P. Barrett, pers. comm., Aquatic Weed Research Unit, Reading). In North Africa it was reported to be common as well as in Asia where it was reported to occur frequently in paddy fields (Pocock 1960). In Australia water net has been recorded but is not frequently found (J. John, pers. comm., School of Environmental Biology, Perth, Australia).

WATER NET IN NEW ZEALAND

Naturalization and Spread

Water net was first reported naturalized in New Zealand in 1986, near Tauranga, in an ornamental pond formed by damming a small stream (Coffey and Miller 1988). A quarantine facility for the importation of tropical fish and plants, which connected to the same stream also had dense growths of water net in outdoor culture troughs fed by geo-thermal bore water. The owner had been attempting to control the algal problem in his culture troughs for some years prior to 1986. A likely source of water net was from South-east Asia as a contaminant (vegetative cells or resistant spores) with a shipment of tropical fish. More widespread distribution in New Zealand prior to this date was discounted by Hawes et al. (1991a) who cited its distinctive macroscopic features which make it readily identifiable and its absence from the extensive algal checklists that include most water bodies around the country. By February 1989, water net had spread 35 km from the initial infestation site to Lake Rotorua and the west end of Lake Rotoiti (Figure 1). Over the next 2 years it expanded its range rapidly through the Bay of Plenty and Waikato Regions (Hawes et al. 1991b) and by 1994 it had spread to its maximum extent as shown in Figure 1.

Mechanisms of Spread

The capability of water net to establish from a single cell of a colony or from spores (Pocock 1960) makes it very difficult to contain once established in the field. Water net spread rapidly to lakes reservoirs, rivers, streams, ponds, wetlands, ornamental ponds and patches of damp ground, where it produced seasonally conspicuous growths. Potential

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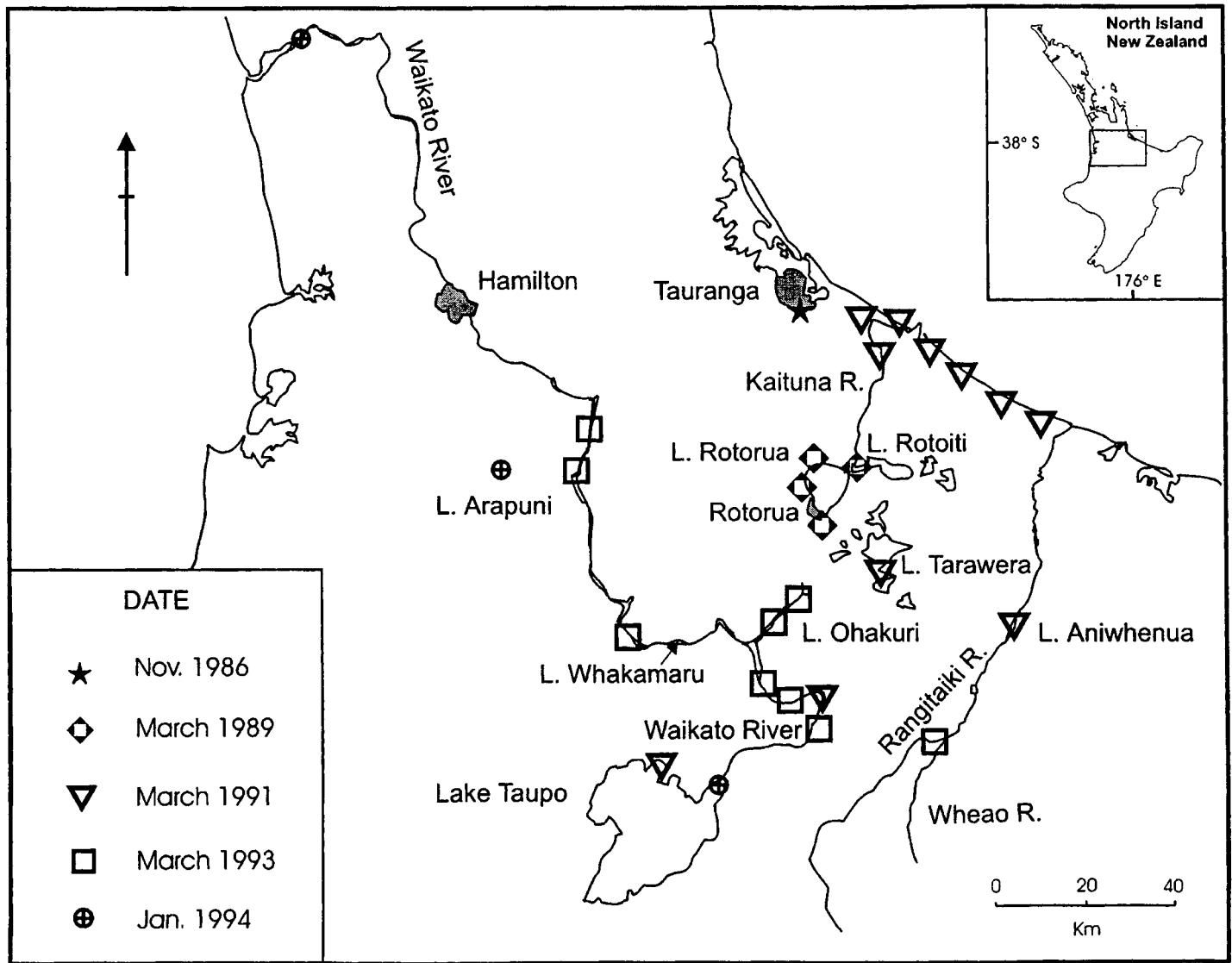


Figure 1. The spread of water net in the North Island, New Zealand, with dates indicating when water net was first noted.

agents for dispersal include, wind and water movements, wildfowl, insects, livestock and humans. The aquarium and pond plant industry, the movement of machinery used in and around waterways, and boating and fishing are all likely to have contributed to its dispersal. Its occurrence in isolated small water bodies (particularly cattle water troughs) suggests that mechanisms such as wind, insects or wildfowl were active in spreading the alga.

Causes of Prolific Growth

The magnitude of the nuisance caused by water net in New Zealand was unparalleled elsewhere in the world, which suggests a particularly vigorous strain or environmental factors favouring prolific growth occurred in New Zealand. Differences between United Kingdom and New Zealand water net isolates were observed at the genetic level. Both isozymes and RAPDs (random amplified polymorphic DNAs) have been used to distinguish between the United Kingdom and New Zealand strains, and to investigate the degree of varia-

tion among some field samples of New Zealand water net, using the method in Hofstra et al. (1999). Isozyme band patterns were different for United Kingdom (UK-a, UK-b and UK-c) and New Zealand (culture and field) isolates for two enzyme systems PGM (phosphoglucumutase) and MDH (malate dehydrogenase). Two different PGM patterns distinguished United Kingdom from New Zealand isolates, whereas a second MDH band pattern was observed for the UK-b isolate (Figure 2). RAPD band patterns, like the isozyme data, readily enabled isolates from these two countries to be distinguished. RAPD fragments produced using 10 random primers showed a large degree of variation between individual samples (Figure 3). A neighbour joining tree based on the RAPD data shows two clusters, separating the New Zealand isolates from the UK-B and UK-C isolates. Although the UK-A isolate is clustered with the New Zealand samples, the tree also illustrates a large degree of variation between all isolates, including those from New Zealand field sites but the majority of variation was partitioned between

Enzyme Systems and Banding Patterns

| | PGM | MDH |
|------------|-----|-----|
| ↑ (-) | | |
| Sample | | |
| NZ culture | * | * |
| NZ field | * | * |
| UK-a | * | * |
| UK-b | * | * |
| UK-c | * | * |

Figure 2. Isozyme band patterns for two polymorphic enzyme systems, PGM (phosphoglucosmutase) and MDH (malate dehydrogenase), in water net samples from New Zealand and the United Kingdom. The * denotes the band patterns observed in each sample.

individuals rather than between clusters. The level of variation shown between the New Zealand field isolates would be expected in a sexually reproducing population. However, further study with multiple samples from field populations would be necessary to confirm the level of variation at the population level.

Water net showed a seasonal growth pattern with high growth rates from August until March, with daily growth rates of up to 0.33 g dry weight (DWT d⁻¹ measured over 14 days in the mesocosm studies (Hall and Payne 1997). From May to July (winter) little or no growth was recorded with water net biomass disappearing from surface waters during this period. This seasonal pattern was not linked to dissolved inorganic nitrogen (DIN) or dissolved reactive phosphorus (DRP) patterns (Hall and Payne 1997) but was likely to be due to seasonal irradiance levels and/or temperature.

The ability of water net to over-winter vegetatively was investigated by enclosing a column of water (1-1.8 m deep) from the sediment to water surface using mesocosms (1.5 m diameter) constructed of 92% shade cloth. The mesocosms was erected in summer (February 1996) with two each in the, lower Kaituna River, Lake Aniwhenua, Lake Ohakuri, and Lake Whakamaru (Figure 1). Each mesocosm had 100 g wet weight of water net added when they were installed. Water net grew in all mesocosms for the remainder of the summer but was no longer visible from early winter (May 1997). Six sediment cores were taken using a 50 ml syringe with the end removed from each mesocosm in winter (July), and spring (September and October) prior to re-establishment of the population. Three cores from each site were incubated at 25 C with a 12 hour light/dark cycle in 500 ml erlenmeyer flasks with 250 mls of WC media (Guillard and Lorenz 1972). Flasks were examined for water net after 3 and 10 days. The remaining cores were examined under 100x magnification for water net fragments. Vegetative water net fragments (1-2 mm long cells) were found in winter and spring cores from all sites except Lake Whakamaru. Viability of over-wintering vegetative fragments was confirmed by the establishment of

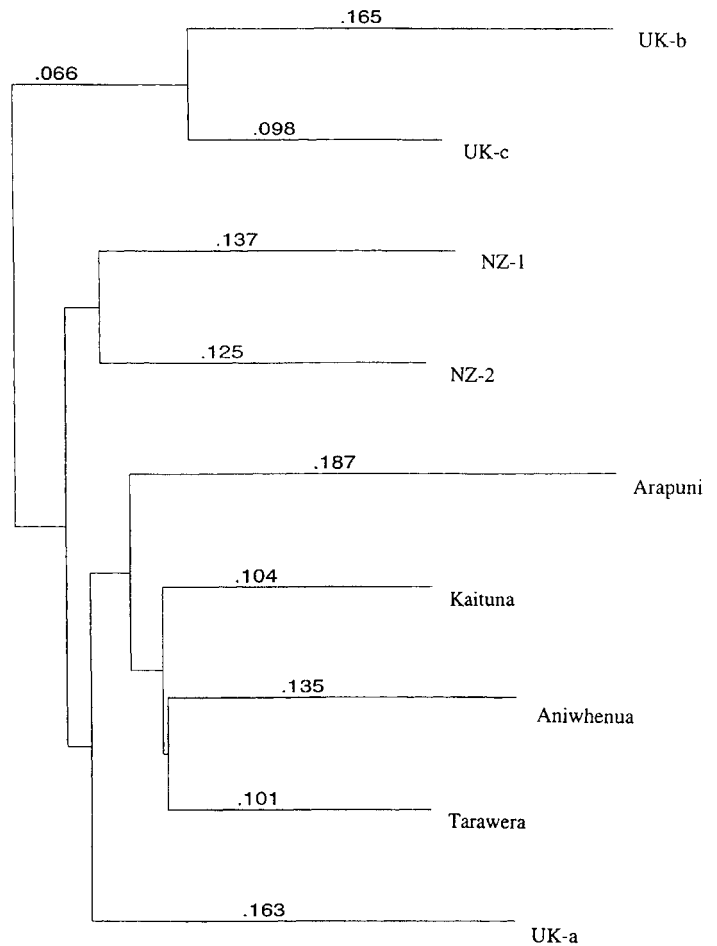


Figure 3. Water net neighbour-joining tree based on RAPD (random amplified polymorphic DNA) data. The New Zealand culture samples were NZ-1 and NZ-2, New Zealand field samples were from Lakes Arapuni, Aniwhenua, Tarawera, and the Kaituna River. The United Kingdom cultured samples were represented by UK-a, UK-b, and UK-c. The numbers beside the branches refer to the length of that branch. The tree was generated using Jaccard's algorithm in the RAPDistance package (Armstrong et al. 1995).

healthy water net in the cultures set up from the sediment core material.

Hawes and Smith (1993) showed that the strain of water net introduced into New Zealand could grow over a wide range of temperatures from 6-40 C with the highest growth rate at 25 C. Cells remained viable in the minimum tested temperature of 5 C. They also showed water net is a shade adapted species with light saturation occurring between 100 and 160 $\mu\text{mol m}^{-2} \text{s}^{-1}$ depending on temperature. Hawes and Smith (1993) reported optimal nitrogen content of the water net cells could be maintained in laboratory culture at ambient DIN concentrations as low as 100 $\mu\text{g L}^{-1}$ and storage of cellular nitrogen was considered unlikely, since growth rate was linearly related to internal nitrogen concentrations. These results were consistent with field observations which showed that a DIN concentration of 30 $\mu\text{g L}^{-1}$ could support healthy growth (Hall and Cox 1995). Further investigations using the field based mesocosm experiments along a DIN gradient showed that water net growth was saturated at approximately 200 $\mu\text{g L}^{-1}$ DIN (Hall and Payne 1997), which

is low in comparison to 700 $\mu\text{g L}^{-1}$ DIN for *Cladophora* (Gordon et al. 1981). The New Zealand strain of water net has a high affinity for DIN with a calculated half saturation constant (K_s) of 29 $\mu\text{g L}^{-1}$, and can grow rapidly at low cellular N:P ratios (Hall and Payne 1997). The ability of water net to take up DIN at low concentrations and to grow at low tissue N concentrations may account for the development of the nuisance blooms of water net in the central North Island, New Zealand. This is a region where there is no record of filamentous algal blooms and where nitrogen frequently limits algal growth (White et al. 1985). Field observations (Hall and Cox 1995) and mesocosm studies (Hall and Payne 1997) suggested that DRP was unlikely to be controlling the growth of water net in this region. This was supported by the laboratory studies of Hawes and Smith (1993) who suggested that optimal growth would be supported by filterable reactive phosphorus (FRP) concentrations of 5 $\mu\text{g L}^{-1}$.

Impacts and Responses

Extensive surface floating mats (up to 30 ha) of water net degraded the aesthetic values of a number of New Zealand water bodies and interfered with recreational activities by clogging jetties, marinas, and water intakes of boat engines, interfering with swimming, fishing lines, and by accumulating in large drifts on beaches with subsequent decay producing foul odours. Tourist activities, such as sight-seeing excursions on a range of craft (including a large paddle steamer, a hovercraft, float planes and small boats), fishing excursions and other passive lake shore activities based on the city foreshore of Lake Rotorua were affected, particularly in 1990-1991 prior to implementation of effective control measures. Water net impacts elsewhere included clogging of screens and filters at the Wheao and Lake Aniwhenua hydro-electric power stations.

As water net continued to spread, concerns for biological, recreational and economic impacts were widely expressed in the media and even in parliament. National newspapers predicted a looming "eco-disaster"² due to de-oxygenation, entrapment of fish and smothering of submerged plants. Lack of a single organization with clear responsibilities for combating water net presented initial accountability and management problems. This was overcome by the formation of a Water Net Technical Committee in January 1991, which included representatives of research and management agencies. In mid-1991 the government commissioned an independent review on water net to determine whether a National Pest Strategy was required; however, it was concluded that the Water Net Technical Committee was effectively coordinating research and management of the water net (East 1992).

Management Options

A range of management options were investigated by the Water Net Technical Committee.

Removal. Physical removal of water net was the most common method of control deployed to alleviate the large surface

floating mats that accumulated. Residents around Lake Rotorua spent considerable time and effort raking the alga from the water and foreshore in front of their properties. Machinery was more effective with the most commonly used being a back hoe (with a free draining bucket) to collect and load water net onto trucks. In the 1990-1991 season approximately 1,000 m^3 water net was removed from 400 m along the Rotorua City lake front reserve area alone. A conveyor type mechanical harvester with a 2-m collection width was later evaluated for collecting water net strandings. The initial attempts showed sufficient promise to warrant a local operator supported by public money to build one with a 3-m collection width. This machine proved to be five times more efficient than the back hoe in collecting water net in shallow water and was used regularly by the local council. Various pumping systems were also tested but were limited by the fundamental problem of separating the water net from large volumes of water as screens and mesh bags quickly became clogged.

The large amounts of water net collected proved costly to dispose of, so its suitability as an animal feed or compost was considered. While the amount of metabolizable energy (11.5 MJ kg^{-1} dry matter) was equivalent to spring pasture and crude protein (14.3 g per 100g dry matter) was not prohibitively low, there were problems with high concentrations of Mn (4986 mg kg^{-1}), Fe (3474 mg kg^{-1}), Zn (20 mg kg^{-1}) and B (32 mg kg^{-1}) for use as an animal feed or a food crop fertilizer. These initial results along with reports of potential accumulation of toxic levels of heavy metals (Rai & Chandra 1992), and it being an unsuitable source of protein in fish meal diets for *Tilapia* spp. (Appler 1985), did not favour continuing this line of enquiry.

Natural growth regulators. Extracts of decomposing barley straw liquor (from rates of 2.57 to 10 kg DWT straw m^{-3}) have been reported to inhibit the growth of several planktonic and filamentous algae (Gibson et al. 1990, Newman and Barrett 1993). Welsh et al. (1990) reported inhibition of algal growth in an English canal (turnover time 5.3 hr) using 440 g DWT barley straw m^{-3} . Barrett et al. (1998) described its successful use (up to 28 g m^{-3} , with 6-12 g m^{-3} added about twice a year) in reducing numbers of suspended algae in a Scottish potable supply reservoir. Filamentous algae were controlled (excluded) in an Irish canal with barley straw at a rate of 10 g m^{-3} (Caffrey and Monahan 1998). In New Zealand, we conducted three laboratory, one outdoor tank and 3 field trials from 1991-1994, to assess the effectiveness of barley straw in controlling growth of water net (Wells et al. 1994). The laboratory and outdoor tank trials showed inconsistent effects on water net growth (of aerobically decomposing barley straw). Effects ranged from varying degrees of inhibition through to enhanced growth. Similarly, Norton et al. (1997) found no negative effect on water net from aerobically decomposing barley straw. Furthermore in situ field bio-assays did not show a reduction in water net growth of a magnitude sufficient to warrant its use by water managers (Wells et al. 1994).

Algicides. A range of algicides were screened on water net in outdoor and glasshouse facilities which included, chelated copper (copper-triethanolamine), terbutryn (1,3,5-triazine-2,4-diamine, n-(1,1-dimethylethyl)-n-ethyl-6), simazine (6-chloro-N2, N4-diethyl-1,3,5-triazine-2,4-diamine), diuron (3-(3,4-dichloro-

²New Zealand Herald, 12th December 1991, page 1.

ophenyl)-1,1 dimethyl urea), a quaternary ammonium compound (ADMA 246-621 benzyl chloride), hydrogen peroxide (H₂O₂) and endothall (7-oxabicyclo[2.2.1]heptane-2,3-dicarboxylic acid) (Hawes et al. 1991b, Wells 1994, Wells and Clayton 1993). Chelated copper was the most promising as it has a history of use in natural waters, and it caused a loss of buoyancy and arrested growth of water net at concentrations above 0.25 mg l⁻¹ and at 10 mg l⁻¹ killed all the algal biomass. It was used in a 1 ha field trial (Wells 1994) at Lake Aniwhenua with a surface application to give 0.3 mg l⁻¹ (calculated total water column treatment, 1.5 m deep). It killed water net surface mats and mid-water growths on macrophytes, however the macrophytes were also killed. The copper did not affect water net on the bottom. Copper concentrations in the water, returned to pre-treatment levels within 6 to 12 hours, did not cause detectable elevated sediment copper levels, and caused no observed toxic effects on a range of surface caged invertebrates (snails, mussels and damselfly larvae) or resident fish in the treated area (Wells, 1994).

Biological control. Large densities of gastropods occurred amongst water net populations in the field and some were seen eating it. The feeding rates of three species of New Zealand freshwater gastropods (*Potamopyrgus antipodarum*, Gray, *Limnaea tomentosa*, Pfeifer and *Limnaea stagnalis*, Linn.) were measured to evaluate whether they could be used as biocontrol agents (Wells and Hall 1995, Wells and Clayton 1999). The three species of gastropods actively sought out water net in preference to other common algal species tested and consumed 0.74, 1.29 and 0.93 g DWT per 100 g live weight of snails day⁻¹ respectively (Wells and Clayton 1999). High densities of gastropods (2280 g live weight m⁻²) in the field amongst a high water net biomass (200 g DWT m⁻²) with a high water net growth rate (20% day⁻¹) as reported by Wells et al. (1994) were calculated to have the potential to consume c. 9% of the production of water net per day at a feeding rate of 3.59 g water net DWT m⁻² day⁻¹. However a commonly found density of water net (c. 10 g DWT m⁻²), with the same gastropod consumption rate would exceed water net production and consume c. >10% of the standing crop on day one. Gastropods were an effective means of controlling water net at sites where their densities could be manipulated such as in ornamental ponds, particularly early in the season when water net biomass was low.

Habitat manipulation. In Lake Rotorua water net grew entangled with the apical tips of the egeria (*Egeria densa* Planchon) in weed beds and on the sediment in shallow, sheltered water inshore of the beds. It was hypothesized that the weed beds (475 ha, Wells and Clayton 1991) provided a suitable habitat for water net by providing a supportive structure and anchorage beneath the water surface where the dampening effects of wave action from the 10 km wave fetch were buffered by the presence of the weed beds. In October (spring) 1991, 64 ha of egeria adjacent to the Rotorua City lake front reserve was treated with diquat (6,7-dihydrodipyridido (1,2- α 2',1'-c) pyrazinediiumbromide) herbicide to remove the weed bed which had a 90% water net cover. Following this treatment water net abundance was reduced at this site and declined to less than 5% cover (Wells and Clayton 1993). After the removal of the egeria beds there were no further large scale strandings of water net on the Rotorua

City foreshore adjacent to this area and there was about a 90% reduction in expenditure on removal of nuisance accumulations from lake front. Elsewhere in the lake, water net accumulations on-shore continued to be as problematic as they had been in 1990-1991 (Wells and Clayton 1993).

Ecological Benefits

The ecological impacts of water net blooms (1989-1994) were studied at Lake Aniwhenua (Wells and Clayton 1999) by sampling a range of invertebrates, macrophytes and sport fish such as rainbow trout (*Oncorhynchus mykiss* Richardson) during and after the bloom period. Water net did have some localized negative impacts on the biota of the lake. For example, macrophyte beds that became smothered were prone to collapse and subsequent decay. Dense accumulations of water net against the shore caused temporary localized anoxic conditions while decaying in shallow water, that affected benthic species. Surprisingly, many invertebrates and trout appeared to have benefited from the water net blooms. For example, *Ceriodaphnia* sp. were small enough to swim through the mesh of most water net nets. They were often present at high densities (5.5 × 10⁴ m⁻²) amongst the water net which provided a degree of protection from predatory water boatmen (*Anisops assimilis* White) and juvenile goldfish (*Carassius auratus* L.). Gastropods in particular were also exceptionally abundant (*P. antipodarum* densities of 1.8 × 10⁵ m⁻²) and they consumed water net at a rate of c. 1.3 g DWT g⁻¹ live weight d⁻¹, (Wells and Clayton 1999). Small snails comprised the major portion of the diet of adult rainbow and brown trout (*Salmo trutta*, L.) in Lake Aniwhenua. A marked peak in the sports fishery, with 4-8 kg fish commonly caught (Thomas 1996), coincided with the water net bloom period. It is interesting to note that small snails such as *P. antipodarum* are of questionable food value for trout as they provide a low energy diet of 30-40 J g⁻¹ (i.e. < 20% of the available energy in broken *P. antipodarum*) for rainbow trout and only 3-4 J g⁻¹ for brown trout (McCarter 1986). But the increased abundance of *P. antipodarum* amongst the water net blooms may have made feeding easier and improved the energetics favourably enough to compensate for a low-energy diet (Wells and Clayton 1999).

The Decline of Water Net

The spring and summer of 1994-1995 was the first time since the introduction of water net to New Zealand that its distribution did not expand and in fact most populations failed to re-establish in spring and none attained nuisance proportions. From late 1988 to spring 1994, water net was prominent within Lakes Aniwhenua, Rotorua and Rotoiti (three popular recreational lakes), but has been virtually absent since, despite low levels of the alga being still present in or near these water bodies. Water net still persists (1998) at scattered field sites but is no longer a management problem.

The failure of water net populations to re-establish nuisance growths in the summer of 1994-1995 may have been determined by a combination of factors affecting the overwintering of vegetative material and/or its re-establishment in spring. We have shown that water net is capable of overwintering vegetatively on the sediment surface. The amount

of inoculum remaining in spring may be a key factor in the re-establishment of nuisance populations. A similar explanation has been proposed for sea lettuce (*Ulva* spp.) abundance in harbours where intermittent blooms are reported (Kamermans et al. 1998). Although rapid growth of sea lettuce is experienced under favourable conditions of temperature, light and nutrients, a high over-wintering biomass is a good predictor of summer blooms. Therefore it is possible that a reduction in the water net over-wintering biomass may have resulted in the failure to re-establish significant water net growths in the spring. Similarly, the conditions in spring operating on the inoculum potentially available for re-growth may not have been favourable for rapid growth.

Possible factors contributing to low over-wintering biomass or spring re-growth include a change in physical factors (e.g. temperature, light, nutrients), an increase in grazer pressure, disease, and loss of genetic vigour. In the summer of 1995-1996 (after the collapse of nuisance blooms) field growth trials were repeated at four sites within experimental mesocosms where water net had previously been abundant, to determine if conditions for growth of water net were still favourable. Results showed that growth rates were similar to previous years when water net had attained bloom proportions (Hall and Payne 1997). This confirmed that temperature and nutrients remained conducive to rapid growth at the sites tested and that other factors were preventing the seasonal re-establishment of the population.

Grazing, particularly during minimum winter biomass or in early spring could prevent effective spring re-growth. Gastropods were commonly found throughout all sites with water net and they were attracted to the alga. Grazing rates measured in laboratory trials were extrapolated to field situations and at times of low biomass were theoretically capable of reducing the water net standing crop by >10% day⁻¹. Other potential but unconfirmed grazers might include some species of non-biting midges (Chironomidae) and fish.

A disease initially seemed to be a likely reason for the decline. However, there was never any evidence of a diseased algal population or premature un-seasonal declines. Similarly, none of the growth trials (field, or climate control rooms) ever exhibited disease-like symptoms and remnant water net populations remain apparently uninfected within areas which had supported dense water net populations. Furthermore, if disease or an increase in the numbers of grazers were responsible, then it would be expected that frontier expansion of the water net boundary would have continued unabated.

Loss of genetic vigour to explain the simultaneous decline across all sites seems unlikely when mesocosm experiments are considered, since subsequent to the water net decline, maximal water net growth rates were achieved in all outdoor mesocosm sites when using genetically equivalent samples of water net kept in pure culture. Furthermore, both isozymes and RAPDs (random amplified polymorphic DNAs) band patterns in New Zealand isolates was consistent with a sexually reproducing population and this would not be supportive of a loss of genetic vigour hypothesis.

The likelihood of a resurgence in water net to nuisance levels is difficult to assess as no one likely cause for the decline fits the observations, however, in the past four years

there has been no evidence of a repetition of former production of abundant biomass. Despite repeated instances of aquatic macrophyte declines reported in the literature the exact reasons for even predictable declines is poorly understood (Chambers et al. 1993). For example, some Eurasian watermilfoil (*Myriophyllum spicatum* L.) populations characteristically decline after 10-15 years of dominance (Carpenter 1980) but rather than disappearing, Eurasian watermilfoil has been shown to persist at lower levels of abundance and become integrated into a more diverse plant community (Treibitz et al. 1993). These authors similarly reported that the 'boom bust' growth pattern of Eurasian watermilfoil appeared to be independent of any major changes in trophic status, management or lake usage. New Zealand would appear to present an interesting case of geographic isolation, where the global spread of water net has been surprisingly late. The boom/bust behaviour of water net in New Zealand may have been characteristic of this algal species as an adventive to other continents in the past and is consistent with macrophyte introductions and declines reported elsewhere.

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