**Summary**  
*Egeria densa* Planch., a submerged aquatic plant, was introduced into New Zealand through the aquarium trade and has naturalised to become widespread in much of the North Island. Its establishment has been associated with the collapse of submerged vegetation in many shallow lakes.

Two alternative stable states may exist in such shallow lakes, either a turbid state dominated by phytoplankton or a clear water state dominated by macrophytes. These conditions only change should disturbance of a stabilising factor occur.

Lake Omapere in Northland lost its submerged vegetation in 1985 and switched back from a turbid state to a clear water state in 1993. The interaction of water quality and the lake biota was investigated for a ten year period from 1992 to present. During this time a second collapse of submerged vegetation and switch to a turbid water state occurred.

The freshwater mussel *Hyridella menziesii* (Gray) is a filter-feeder and is believed to have instigated the switch from turbid to clear water conditions. Establishment of macrophytes, predominantly *E. densa*, further stabilised this state by protecting bottom sediments from wave disturbance, hence preventing nutrient suspension. However, after several years, the tall dense surface-reaching beds of *E. densa* appear to have facilitated benthic anoxia causing major mortality of plants and *H. menziesii* and nutrient release from benthic sediments. This disrupted the stabilising effects of both mussels and macrophytes, initiating a switch back to a turbid condition.

Evidence suggests that the alien macrophyte *E. densa* may have directly contributed to the loss of submerged vegetation in many other lowland lakes in New Zealand.

**Keywords**  

**INTRODUCTION**  
*Egeria densa* Planch. is a submerged macrophyte in the family Hydrocharitaceae, with a native range of tropical South America. This species has been spread throughout the world as an aquarium plant and it is now naturalised in most continents including Australia and also New Zealand. In New Zealand this species was first collected as a naturalised plant in 1946 and it is now widespread throughout most of the North Island and also in a few scattered localities in the South Island.

Spread of this species is solely by vegetative means as only male plants appear to have been introduced into New Zealand. *E. densa*, and several other alien species in the family Hydrocharitaceae and also the dicotyledon *Ceratophyllum demersum* L. have a major impact on native vegetation once introduced into a waterbody. Commonly monocultures of *E. densa* result, especially between 1 and 6 m water depth.

The impact of this species is particularly severe in shallow lakes (maximum depth ≤5 m), and by the mid-1970s most shallow lakes within the Waikato Region and other North Island lakes, e.g. Lake Omapere in Northland, were dominated by this species. Surface-reaching beds occurred over much of the water body, displacing a diverse native vegetation community. Despite this loss of plant diversity the dense beds of *E. densa* provided a variety of benefits to the ecosystem including stability of bottom sediments, shelter, spawning and feeding sites for fish and invertebrates, a major food source for black swan (*Cygnus atratus* (Latham)) and a substrate for epiphyton, thus increasing or maintaining primary production and nutritive sources for other lake organisms.

Over the next 30 years virtually all of these *E. densa* dominated lakes lost their submerged vegetation and are now virtually devegetated, with turbid, planktonic algal-dominated waters. Causes of the declines have been attributed to many factors including reduction in water clarity (through flooding, mining activities and catchment clearance), increased organic content of bottom sediments, increased toxins including boron, phenolics and arsenic, disturbance of macrophyte beds by storms,2997, swan and/or coarse fish grazing, disease, changes in water level or combinations of these (de Winton and Champion 1993).

state dominated by aquatic vegetation and a turbid state characterised by high algal biomass. Changes from one state to another are driven by perturbations to the stabilising factors. An important stabilising factor in clear water lakes is the submerged vegetation, which stabilises bottom sediments thereby reducing resuspension of sediments and influx of nutrients into the water column, which is often associated with abundant phytoplankton. Conversely, in turbid lakes abundant phytoplankton reduce the penetration of light required for macrophyte growth (Scheffer et al. 1993).

This paper reports on the changes in water quality and biota in one shallow lake, Lake Omapere in Northland, in relation to changes in lake condition occurring from 1985 to present.

MATERIALS AND METHODS

Study area and background information  Lake Omapere is a large shallow lake almost circular in shape, occupying an area of 11.62 km² within a small catchment, predominantly vegetated by pasture. The lake is shallow with a maximum depth of 2.6 m and an annual lake height fluctuation of approximately 1 m.

_E. densa_ colonised Lake Omapere in the mid 1970s possibly spread by boat trailers associated with water skiing activities on the lake. In December 1984, _E. densa_ formed a monoculture over the majority of the lake (Tanner et al. 1986) and formed surface-reaching weed beds. However in December 1985, a thick algal bloom was reported on the lake, and the extensive macrophyte beds were no longer present. The algal species comprising the bloom were _Anabaena circinalis_, _A. flos-aquae_ and _Microcystis aeruginea_. These are all cyanobacteria (blue-green algae) that can produce toxins.

Methods The water quality of Lake Omapere was monitored twelve times per year from February 1992 to June 1996. Following this samples were taken approximately three times per year up to the present time. Samples were taken at two sites on the lake and the following parameters measured in the field; water depth, Secchi depth (water transparency), water temperature and dissolved oxygen (DO) profiles at 0.25 m depth intervals. Water samples were taken at two depths, equating to 25% and 75% of the lake depth, at two sites for subsequent evaluation of volatile (organic) suspended solids, inorganic suspended solids, chlorophyll a, total nitrogen (TN) and total phosphorus (TP). Additional surface water samples were preserved on site with Lugols iodine to enable assessment of phytoplankton species/ abundance.

Macrophytes were noted as re-establishing in Lake Omapere in 1994 and from 1995 onwards macrophyte cover, height, vigour and composition were estimated at approximately 500 m intervals along two perpendicular transects spanning the lake. Biomass was estimated by sampling all macrophytes within a total of six 1 m² quadrats cut along the two transects.

Freshwater mussel (_Hyridella menziesii_ (Gray)) numbers were estimated on three occasions by sampling living mussels within five replicate 0.1 m² quadrats sampled at six sites along the two transects.

RESULTS

All water quality parameters (suspended sediments, TN, TP and chlorophyll a showed the following trends. Relatively high values declined from 1992 to late 1993. Low values were maintained from that time to winter 2001 apart from a major increase sampled in March 1998. From December 2001 until present very high values for each parameter have been determined. As an example, Figure 1 shows the changes in chlorophyll a over the monitoring period. Secchi depth showed an opposite trend to the other parameters, with the highest water clarity occurring from late 1993 to winter 2001. DO in the water column remained saturated from 1992 to 2000. In the summers of 2000 and 2001 bottom anoxia was recorded, but not in 2002.

Planktonic algal species were dominated by diatoms from 1992 through to 2000, with _Aulacosira granulosa_ the dominant species. Cyanobacterial species became conspicuous in 2000 with short-lived blooms of _M. aeruginea_ in March of that year and _A. circinalis_ in early February 2001. A combination of these species formed a dense bloom from November 2001 to present.

_E. densa_ began to recolonise Lake Omapere in 1994, and was first assessed by scuba in March 1996, with approximately 5% of the lake bottom occupied by this species along with two indigenous macrophytes _Chara corallina_ and _Potamogeton ochreatus_. _E. densa_ covered much of the lake bottom from September 1995 to present.
1998 onwards and surface-reaching beds of this macrophyte occupied the entire lake from November 2000 to February 2001. From then until present *E. densa* has declined in height and density, losing 73% of its biomass over the summer of 2001 and a further 81% of the remnant biomass in 2002. Figure 2 shows the changes in *E. densa* biomass from March 1996 to January 2002. Large accumulations of this plant were noted around the shores of Lake Omapere in these summers.

*H. menziesii* numbers were estimated at 42 m⁻² in November 2000, reducing to 8 m⁻² estimated in April and May 2001. Large numbers of floating dead mussels were noted in February 2001.

**DISCUSSION**

A switch from a turbid water condition to a clear water condition in 1993/4 and a return to a turbid water condition in 2001/2 within Lake Omapere is indicated by changes in water quality parameters (Figure 1).

In late 1993 water clarity markedly improved and turbidity (a combination of suspended sediments and phytoplankton) reduced to a low level. This permitted sufficient light penetration to allow re-establishment of bottom-rooted macrophytes.

*H. menziesii* is a filter-feeder and its impact on phytoplankton and filtering rates have been studied by various researchers (James 1985, 1987, Ogilvie and Mitchell 1995, James et al. 1998). James et al. (1998) estimated that these mussels at a density of 6 m⁻² could filter a volume of 14.3 L h⁻¹. The population assessed in November 2000 averaged 42 mussels m⁻². This number would thus filter 100 L h⁻¹. Assuming a depth of 2 m, then 1 m² of bottom sediment would be overlain by 2000 L of water. Forty two mussels could process this volume in 20 hours. This would be a sufficient rate to exceed the growth rate of planktonic algae (with doubling times normally around one week). Therefore, *H. menziesii* could have been a key factor in the switch from a turbid to clear water condition.

*E. densa* increased rapidly in Lake Omapere after its re-establishment in 1994. Unlike indigenous vegetation, this species can form dense tall beds and is able to form surface-reaching beds as occurred in 2000/2001. Even before this, vegetation had established to a height of 1.5 m across much of the lake bottom by 1998. This macrophyte growth conferred further stability to the clear water condition by protecting bottom sediments from resuspension through wave action. These macrophyte beds are likely to have kept available nutrients in the water column at a low level and therefore prevented the development of dense phytoplankton blooms.

However there were indications of destabilisation e.g. the presence of iron (ferrosoferric hydroxide) floc and elevated TN, TP and inorganic suspended sediments in November 1998 and a short lived cyanobacterial bloom (*M. aeruginea*) in 2000. Both these events are indicative of bottom anoxia, with release of ferrous iron and nutrients a consequence of low redox potentials. This nutrient release may stimulate algal blooms, but grazing by filter feeding freshwater mussels would help to rapidly reduce this plankton to low levels. In February 2001 a DO <1 mg L⁻¹ was measured in the benthic zone of Lake Omapere. At that time *E. densa* formed dense surface-reaching beds. High TN and TP concentrations were recorded in the water column but no algal bloom was noted. It is hypothesised that the dense beds of this macrophyte created a barrier between surface and bottom waters, preventing dispersal of oxygenated water through the water column. This barrier to oxygen mixing and high rates of benthic respiration could have combined to cause benthic anoxia.

The benthic anoxic event had major consequences for the biota of Lake Omapere. Plants of *E. densa* were in an unhealthy condition with many leaves detached and with dead blackened roots. The biomass of this plant had reduced by 73% by May 2001, but it still maintained a vegetation cover over much of the lake bottom.

*H. menziesii* numbers declined by approximately 80% and their filtering rate for the lake water volume would have been reduced from 20 hours to 100 hours m⁻². This reduced filtering ability and the increased available nutrients in the water column would have allowed increased phytoplankton growth. A dense bloom eventuality occurred (with chlorophyll concentrations often in excess of 200 mg m⁻³) dominated by either *A. circinalis* or *M. aeruginea*. This was maintained in Lake Omapere throughout the summer of 2001/2.

It is suggested that the shading impact of this prolonged algal bloom, rather than further deoxygenation effects, has resulted in the further decline of *E. densa*.

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**Figure 2.** Biomass of *Egeria densa* Planch. in Lake Omapere (tonnes dry weight). Error bars indicate standard deviation.
Once the bottom cover afforded by this plant has been lost then bottom resuspension by wave action is likely to maintain high levels of nutrients in the water column sustaining turbid water conditions from phytoplankton blooms in addition to suspended sediments.

*E. densa* may be the cause of submerged vegetation decline and loss of clear water conditions in Lake Omapere; through the loss of filter-feeding *H. menziesii* and vegetation cover resulting from impaired dissolved oxygen mixing. Lake Omapere is the only shallow New Zealand lake to have changed back to an *E. densa* dominated clear water lake following a prior collapse of *E. densa* dominated vegetation and a switch to a turbid water state. Perhaps in the other lakes, the initial event resulting in vegetation collapse also completely extirpated *H. menziesii* populations in those lakes. They were certainly present in great numbers in many shallow Waikato lakes, but are now rarely found there (de Winton and Champion 1993).

This study shows how biotic rather than physicochemical factors can also influence the limnology of shallow water lakes, with the lake switching from a hypertrophic turbid lake to a mesotrophic clear water lake under the same nutrient regime. This study also illustrates how an alien plant can completely disrupt an aquatic ecosystem.

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REFERENCES


