

Fish effects on charophyte establishment in a shallow, eutrophic New Zealand lake

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Abstract Fish exclosures were deployed within shallow, eutrophic Lake Rotoroa, Hamilton, New Zealand to assess the influence of an alien-dominated fish population on establishment by charophytes. Replicated mesh exclosures were placed at sites differing in wave exposure and received transplanted charophyte oospores and plants, with identical material placed outside. Charophyte establishment from oospores and plant biomass were greater inside exclosures compared with outside. Wave exposure did not depress germling response and the effect of fish exclosures on charophyte establishment was least apparent at the most exposed site. Exclosures did not have a statistically significant influence on the light climate, and epiphytic algal development was similar or higher inside the exclosures. However, sediment mobilisation was lower inside the exclosures. Results suggest that fish were primarily responsible for the poor performance of unprotected charophytes in Lake Rotoroa, with fish effects on plants operating via direct disturbance or grazing.

Keywords charophytes; oospores; germlings; biomanipulation; alien fish

INTRODUCTION

The “alternative stable states” hypothesis recognises that shallow, eutrophic lakes can exist in one of two conditions; either with abundant submerged plants and relatively high water clarity or without conspicuous vegetation and with highly turbid waters (Scheffer 1989; Scheffer et al. 1993). Plant presence and clear water is viewed as desirable by water-body managers, but this condition has proven difficult to achieve for turbid, shallow lakes. In particular, certain feedback mechanisms that act to maintain the turbid state need to be minimised or overcome (Scheffer et al. 1993).

In recent years a role for fish populations in maintaining turbid conditions in shallow lakes has been identified. Excessive densities of benthivorous and planktivorous fish in European lakes have been implicated in the resuspension of lake sediments and the promotion of phytoplankton (Meijer et al. 1990), whereas associated substrate disturbance is suggested to prevent colonisation by submerged vegetation (Ten Winkel & Meulemans 1984). Herbivorous fish have also contributed directly to the loss of vegetation elements (van Donk & Otte 1996). The deliberate reduction of fish stocks in lakes, termed “biomanipulation”, is now a recognised management tool to increase water clarity and facilitate plant recovery (Scheffer et al. 1993).

Much of the evidence for direct fish effects on lake vegetation has been derived from enclosure or exclosure experiments which concentrate on the fate of transplanted or extant plants (e.g., Crivelli 1983; Vermaat et al. 1990; Wright & Phillips 1992; van Donk et al. 1994). Investigations of fish effects on plant establishment from seed banks are more limited, despite the likely importance of these processes for restoration of submerged vegetation (de Winton & Clayton 1996; de Winton et al. 2000a). Ten Winkel & Meulemans (1984) observed that cages placed to exclude fish enabled charophytes to establish from oospores in the sediment of a Dutch lake. In contrast, Sager et al. (1998) concluded that wave exposure in shallow North American marshes

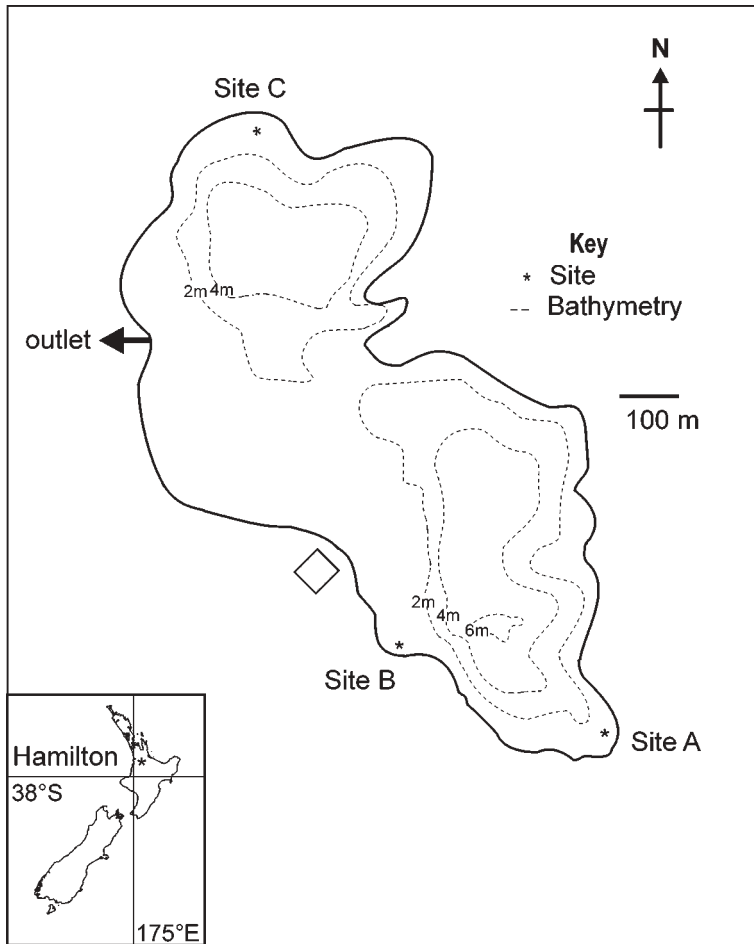


Fig. 1 Location of fish exclusions at Sites A, B, and C in Lake Rotoroa, Hamilton, New Zealand.

was more important than fish activity in reducing plant establishment from a transplanted propagule bank. In the latter study it was found that high wave exposure eroded the transplanted propagule bank material, while high levels of suspended solids provided a poor light environment for propagule establishment and led to propagule burial at sheltered sites.

Sudden declines in submerged vegetation abundance have occurred in a number of shallow New Zealand lakes, in association with deteriorating water quality and ecological value (de Winton & Champion 1993). In most cases lakes have remained de-vegetated and where plant expansion has taken place, this has proceeded slowly over a number of years (Champion et al. 1996; de Winton et al. 2000b; Champion & Burns 2001). Obstacles to plant recovery have been identified, including insufficient light availability (Tanner et al. 1993) or low numbers

of viable propagules in lake sediments (de Winton & Clayton 1996; de Winton et al. 2000). However, the role of fish in influencing vegetation establishment has not been investigated, despite evidence of its importance overseas. As management agencies in this country show increasing interest in restoring aquatic habitats, it has become more important to identify the barriers preventing submerged vegetation recovery.

New Zealand waters lack bream (*Abramis brama*) and roach (*Rutilus rutilus*), the fish species most often implicated in plant loss from European waters, however, other alien benthivorous and herbivorous fish species have been introduced to many shallow lakes. These species frequently occupy a dietary niche that is underrepresented within the native fish fauna. Alien fish were originally introduced to establish "coarse" angling in habitats that were unsuitable for trout, or for ornamental ponds, and

have become widespread. With the exception of grass carp (*Ctenopharyngodon idella*) used for aquatic weed control (Clayton et al. 1995) and aspects of herbivory by rudd (*Scardinius erythrophthalmus*) on aquatic plants (Lake et al. 2002), the effects of alien fish on submerged vegetation in this country are little known.

In this paper we examine the effect of fish occurrence on the establishment from oospores and survival of charophytes in Lake Rotoroa, a shallow, eutrophic New Zealand lake with a fishery dominated by alien species. The managers of Lake Rotoroa identified a water clarity goal of 2.5 m Secchi disc depth and sought to establish extensive beds of charophytes to improve and protect lake water quality (Hamilton City Council 1994). Although biomanipulation was raised as a possible means of achieving these goals, there was little evidence to support this course of action. This study was initiated to detect whether the fish species present in this lake influenced establishment of charophytes. As wave exposure has also been identified as an important factor for the establishment of propagules (Sager et al. 1998), we investigate the importance for charophyte establishment of relative wave exposure within the lake.

METHODS

Study site

Lake Rotoroa (37°48'S; 175°16'E) is a small (54 ha) water-body located within the city of Hamilton, New Zealand and is managed by the local city council as a park reserve. The lake is shallow with >54% of lake area being <2 m deep (Fig. 1) and has a catchment area of 138 ha, comprised of 25% residential housing and 35% recreational reserve (Tanner et al. 1990).

The lake is described as eutrophic (de Winton et al. 2000b) based on mean water quality parameters of chlorophyll *a* (15.5 mg m⁻³), Secchi disc depth (1.57 m), total phosphorus (P) (24.7 mg m⁻³), and total nitrogen (N) (713 mg m⁻³) for the period mid 1999–mid 2000.

European perch (*Perca fluviatilis*) were introduced to Lake Rotoroa in 1907 to establish a sport fishery. Brown bullhead catfish (*Ameiurus nebulosus*) probably entered the lake from the hydrologically linked Waikato River in 1976/77 and rudd (*S. erythrophthalmus*) were illegally released in c. 1979. Tench (*Tinca tinca*) were legally released in 1990 to provide a new sport fishery (Kane 1995). Fish species within Lake Rotoroa (Table 1) and their diets are described by Kane (1995) from surveys carried out in 1993/94. Fish included benthic feeders (catfish, tench, juvenile perch, and rudd) herbivores (adult rudd), and piscivores (adult perch and native eels). Alien species listed above numbered >90% of the large fish (>100 mm FL) that were caught at that time (Kane 1995).

The lake vegetation and its management before 1987 is documented by Tanner et al. (1990) who describe an extensive submerged vegetation covering 80% of the lake area comprising native charophytes, but invaded by a succession of alien, hydrocharitacean weeds. Alien species *Lagorsiphon major* and *Elodea canadensis* dominated the vegetation in 1977, but were then largely replaced by *Egeria densa* by 1986. In the 1970s and 1980s, the herbicide diquat was applied to reduce nuisance weed beds, with the effect of enhancing charophyte abundance. In mid 1986 charophytes comprised 52% of the vegetation (Tanner et al. 1990).

During the late 1980s, the lake vegetation underwent a dramatic decline, concomitant with decreasing water clarity (Clayton & de Winton 1994).

Table 1 Fish species recorded from Lake Rotoroa (Kane 1995).

Species	Common name
* <i>Carassius auratus</i> (Linnaeus)	goldfish
* <i>Gambusia affinis</i> Baird and Girard	mosquitofish
* <i>Ameiurus nebulosus</i> Le Sueur	brown bullhead catfish
* <i>Perca fluviatilis</i> (Linnaeus)	perch
* <i>Scardinius erythrophthalmus</i> (Linnaeus)	rudd
* <i>Tinca tinca</i> (Linnaeus)	tench
<i>Anguilla australis</i> Richard	shortfinned eel
<i>Anguilla dieffenbachia</i> Gray	longfinned eel
<i>Gobiomorphus cotidianus</i> McDowall	common bully

*Alien species.

Between 1994 and 1998, submerged plants were estimated to occupy <1% of the lakebed, but an expansion of charophyte vegetation took place from late 1998 onwards (de Winton et al. 2000b). This vegetation development mirrored changes in water clarity with Secchi disc depths showing a mean increase of 0.05 m per year over 1992–97, and a larger mean increase of 0.11 m per year from 1997 to 2000 (de Winton et al. 2000b). At the time of this investigation charophytes occupied c. 15% of the lake area, were observed to a maximum depth of 1.9 m, and hydrocharitacean species were not recorded (de Winton et al. 2000b).

Experimental design

We used fish enclosures to detect the effects of fish on establishing charophytes in Lake Rotoroa. Enclosures were deployed at three sites (Fig. 1) chosen to provide different degrees of wave exposure. Relative exposure at each site was calculated using a method modified from Keddy (1982) as the sum of wind direction \times fetch for each of eight compass directions, where the wind direction (% of records) was based on 8760 wind records from June 1999 to June 2000 (Ruakura Climate Station) and fetch was the distance to shore (km). On this basis, the three sites were ranked from most sheltered, intermediate in exposure, to most exposed.

Three fish enclosures were deployed at each site in October 1999, within 1.1–1.3 m depth. No plants were observed in the immediate vicinity and sediment substrates were observed to be fine (no conspicuous sand or hard substrates). Enclosures (2.5 \times 2.5 m) were constructed from Donaghys Quad Hail Net[®] (7 mm mesh aperture) supported by surface floats and anchored into the lakebed. The netting was cleaned at monthly intervals to maximise water exchange. A 0.3 m tall barrier above the perimeter of the floats prevented waterfowl from perching on the structure.

Sediment known to contain abundant viable oospores was collected from Lake Okataina (38°09'S, 176°23'E) and Lake Tarawera (38°13'S, 176°24'E), Rotorua District, and stored at 20°C for 2 weeks. Each sediment was mixed in a concrete mixer and decanted into 395 ml pots. Ten pots of each lake sediment were placed in each enclosure and also at an equivalent depth outside the enclosure. Charophyte establishment was assessed after 15 weeks. Germlings from each pot were detected by eye, sorted into species according to oospore and germling characteristics, counted, and dried (80°C) to constant weight (± 0.0001 g).

Plants of *Chara corallina* were collected from Lake Rotoroa, planted in pots of lake sediment and grown in outdoor tanks for 3 weeks to facilitate rhizoid anchorage. Uniform-size plants were selected, comprising 3–4 stems of 50–80 mm in height. Three plants were placed inside and outside each enclosure, with an additional 19 plants of similar size dried to constant weight as above to estimate starting biomass. Transplanted plants were recovered after 3 weeks, individually dried, and weighed as above.

Key water quality parameters inside and outside the enclosures were monitored at 2-week intervals (turbidity, photosynthetically active radiation (PAR)) or 4-week intervals (chlorophyll *a*). Measurements of PAR were made subsurface and at 0.43 and 0.86 m depth (Licor LI-188 B Quantum photometer) and mean light attenuation (K_d) was calculated according to Kirk (1994). A depth integrated water sample was taken to 0.8 m depth. Turbidity of two subsamples was measured by a nephelometric turbidimeter (Hach 2100P). Chlorophyll *a* samples (400 ml) were transported on ice, filtered (GF/C glass fibre), ground, and analysed by a spectrophotometric method (Pridmore et al. 1983).

A sediment trap (78 mm diam.) was placed at the centre of each enclosure and outside each enclosure for the duration of the experiment and the accumulated sediment was dried (80°C) to constant weight (± 0.01 g). A substrate for epiphytic algae was provided by placing plastic tags (9750 mm²) just above the sediment surface, both inside and outside each enclosure. Upon retrieval after 3 weeks, both surfaces of the tags were scrubbed with a fine brush, the material homogenised and analysed for chlorophyll *a* as outlined above.

Germling number per pot, germling dry weight per pot, and transplant dry weight per pot were \log_{10} transformed to stabilise variance among samples, and statistically significant differences ($P < 0.05$) were identified by a split-split plot ANOVA (Genstat 5). The block stratum was the nine chosen areas (three sites \times three enclosure—open lake pairs), the main plot stratum was the two treatments of enclosure or open lake and the subplot level was individual pots (to identify sediment type effects). An ANOVA was used to identify significant differences ($P < 0.05$) in water quality between enclosures and the open lake, and within site differences were also considered in the analysis. An ANOVA was also used to analyse sedimentation data, while a *t*-test was employed to identify differences in epiphytic algal development.

RESULTS

Environmental conditions

Relative wave exposure ranged from most shelter at Site A, intermediate exposure at Site B, and greatest exposure at Site C (Fig. 1). Relative exposure differed by 80% between Sites A and B, and 20% between Sites B and C.

With one exception, mean light attenuation (K_d) was similar within and outside the exclosures, with K_d lower inside exclosures compared with outside (ANOVA, $P < 0.001$) on one date only (Fig. 2). Although mean turbidity of exclosures was frequently 0.3–0.5 nephelometric turbidity units (NTU) lower than external values, differences in chlorophyll *a* levels of water samples were not significant (Fig. 3). No consistent site differences in these parameters were detected. Epiphytic algal development (chlorophyll *a*; Table 2) did not differ significantly between the inside and outside exclosures at Site A or Site B (*t*-test, $P = 0.05$), but was significantly higher within Site C exclosures compared with outside (*t*-test, $P < 0.05$). Overall, sedimentation (Table 2) was significantly greater outside the exclosures (ANOVA, $P < 0.001$), although differences were not detected at Site B (ANOVA, $P = 0.05$). A missing sediment trap lowered statistical power for this latter site (Table 2).

Only occasional small fish (<50 mm length, species unidentified) were observed inside the exclosures. Lake level fluctuated by 0.203 m, with an overall reduction in water level over the course of the trial.

Germling response

Germling response from the Okataina sediment was dominated by *C. corallina* (92% of germlings), whereas the Tarawera sediment response was predominantly *C. globularis* (99% of germlings). Differences in germling number and biomass were identified between the two sediment types (ANOVA, $P < 0.05$). The original sediment level in pots was discernible at the end of the trial and erosion or deposition was not observed.

Germling number and biomass were consistently greater inside the fish exclosures than outside (Fig. 4 and 5). The mean reduction in germling number per pot from outside compared with inside the exclosures ranged from 42 to >99% across the three sites (Fig. 4). The mean reduction in germling biomass per pot from outside compared with inside the exclosures ranged from 66 to >99% across the three sites (Fig. 5). The differences between germling

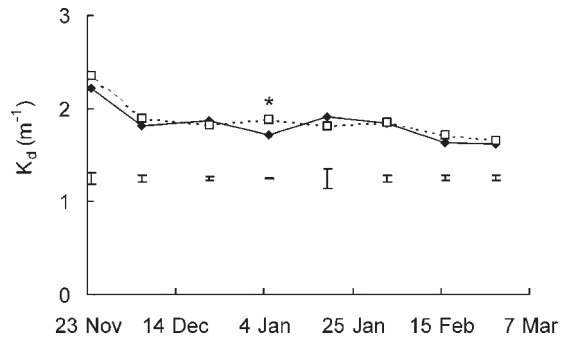


Fig. 2 Mean K_d (m^{-1}) inside fish exclosures (◆) and outside (□) over fortnightly sampling intervals. Error bars are 1 SED, $n = 9$. Asterisk marks an occasion when the two treatment values differed (ANOVA, $P < 0.001$).

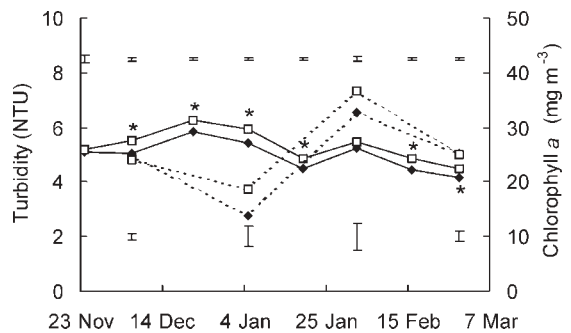


Fig. 3 Mean turbidity (nephelometric turbidity units (NTU), —) and chlorophyll *a* values ($mg\ m^{-3}$, ---) from inside (◆) and outside (□) fish exclosures. Error bars for turbidity values (top) and chlorophyll *a* values (bottom) are 1 SED, $n = 9$. Asterisk mark occasions when differences in turbidity were identified between the two treatments (ANOVA, $P < 0.05$).

establishment inside and outside exclosures were significant (ANOVA, $P < 0.001$), with the exception of germling number arising from Okataina sediment and the germling biomass of Tarawera sediment (ANOVA, $P = 0.05$) at the most exposed site, Site C (Fig. 4 and 5).

Germling number and biomass of pots placed outside the exclosures differed significantly among the three sites (ANOVA, $P < 0.05$), with mean germling number and biomass being greater at the exposed Site C than at the sheltered Site A (Fig. 4 and 5). Conversely, no comparable site differences were identified for pots from within the exclosures (ANOVA, $P = 0.05$).

Table 2 Mean epiphytic algal development per tag (μg chlorophyll *a*) and sedimentation per trap (g dry weight) placed inside fish enclosures or outside at Sites A, B, and C in Lake Rotoroa, New Zealand ($n = 3$, *except $n = 2$ at Site B, outside). (SE, standard error.)

Site	Treatment	Chl. <i>a</i> ($\mu\text{g} \pm \text{SE}$)	Sediment (g dry weight $\pm \text{SE}$)
A	Inside	20 (± 4)	14.2 (± 1.0)
	Outside	17 (± 3)	46.9 (± 8.1)
B	Inside	37 (± 3)	11.7 (± 0.2)
	Outside	29 (± 6)	*21.8 (± 8.1)
C	Inside	72 (± 6)	8.6 (± 0.2)
	Outside	31 (± 4)	41.0 (± 3.6)

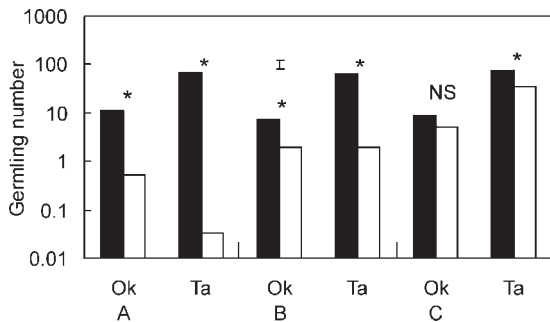


Fig. 4 Mean germling number per pot of Okataina (Ok) and Tarawera (Ta) sediment placed inside fish enclosures (■) and outside (□) at Sites A, B, and C in Lake Rotoroa, New Zealand. Error bars are 1 SED for comparisons within sites, $n = 18$. Asterisk indicate significant differences (ANOVA, $P < 0.05$) between enclosure and outside values; NS indicates no significant difference (ANOVA, $P > 0.05$).

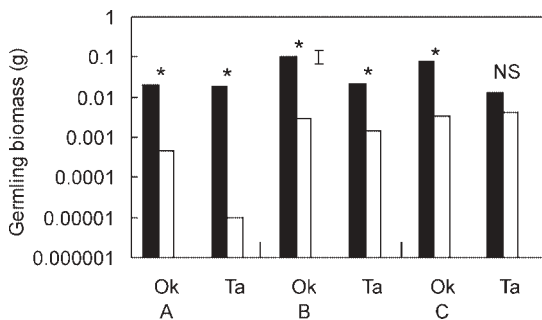


Fig. 5 Mean germling biomass per pot (g) of Okataina (Ok) and Tarawera (Ta) sediment placed inside fish enclosures (■) and outside (□) at Sites A, B, and C in Lake Rotoroa, New Zealand. Error bars are 1 SED for comparisons within sites, $n = 18$. Asterisk indicate significant differences (ANOVA, $P < 0.05$) between enclosure and outside values; NS indicates no significant difference (ANOVA, $P > 0.05$).

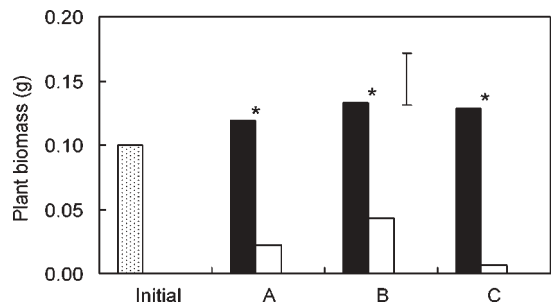


Fig. 6 Mean biomass (g dry weight) per pot of transplanted *Chara corallina* placed either inside fish enclosures (■) or outside (□) at Sites A, B, and C in Lake Rotoroa, New Zealand, together with the initial biomass of transplanted plants. Error bars are 1 SED for comparisons within sites, $n = 18$. Asterisk indicate significant differences (ANOVA, $P < 0.05$) between enclosure and outside values at each site.

Transplant performance

The biomass of *C. corallina* plants transplanted into the fish enclosures was significantly greater (ANOVA, $P < 0.05$) than transplanted plants placed outside the enclosures at all three sites (Fig. 6). This reduction in plant biomass outside enclosures ranged from 70 to 95% across the three sites. No significant site differences were identified (ANOVA, $P > 0.05$). Enclosure plants had increased in biomass (Fig. 6), whereas outside plants were often missing entirely (one-third of plants) or were noticeably reduced in biomass.

During the trial, *Nitella hookeri*/*N. cristata* (a species pair difficult to distinguish) had also colonised several enclosures from vegetative fragments. No colonisation was observed immediately outside the enclosures.

DISCUSSION

Restricted fish access resulted in consistently greater charophyte germination, growth, and survival, suggesting that fish do reduce the potential for plant re-colonisation within Lake Rotoroa.

Reduced wave exposure by the exclosures does not appear to have been a major factor in influencing charophyte performance. First, where differences in charophyte establishment were detected among the three sites (outside exclosures only), the most exposed site had the greatest germling response. In addition, germling response differed least between the exclosures and open areas at the most exposed site (Site C). These results suggest wave exposure was not a major inhibiting factor for charophyte establishment at the experimental sites in this lake.

We also did not detect effects of exclosures upon water quality parameters that were likely to mediate the enhanced charophyte performance. In our trial the exclosures did not present a significantly better light environment than external areas. Although turbidity of exclosures was slightly lower than external values, these differences (0.3–0.5 NTU) were extremely small when considering the wide range of turbidity of natural waters. Light attenuation values provide a more meaningful measure of conditions for plant germination and growth. In contrast, Sager et al. (1998) found that plastic encased exclosures that enhanced propagule establishment also modified wave exposure/water exchange to the point where total suspended solids, chlorophyll *a*, and light attenuation were dramatically reduced.

Although we did find bottom sediment mobilisation and/or deposition was higher outside the exclosures, this disturbance was apparently local since it did not impact significantly on the light climate. Nor was there any observable erosion or burial of the sediments in the transplanted pots. The local sediment mobilisation and/or deposition outside the exclosures suggested a higher frequency or extent of sediment disturbance when exposed to fish activity. Elsewhere, activity by benthivorous fish in small, shallow lakes is seen as a major cause of sediment resuspension (Meijer et al. 1990). This is also in keeping with observations by SCUBA divers in Lake Rotoroa of pitting of the sediment in a manner characteristic of fish disturbance (de Winton et al. 2000b). The loss of transplanted plants from outside the exclosures also indicates direct uprooting or grazing, as plants would have persisted under stress (i.e., unsuitable growth conditions) for longer than the 3-week growth period.

Nest building by freshwater fish is a source of disturbance of submerged vegetation in temperate Northern Hemisphere lakes (Carpenter & McCreary 1985), however no nests or egg masses were observed in this trial.

Grazing by herbivorous waterfowl is cited as one factor preventing plant re-establishment in shallow lakes (Lauridsen et al. 1994), but we do not consider it to be important in this water-body. Low densities (0.5 ha^{-1}) of coot (*Fulica atra*) and black swan (*Cygnus atratus*, 0.1 ha^{-1}) were recorded at Lake Rotoroa during the past 5 years (New Zealand Ornithological Society monthly counts). These waterfowl densities are 1–2 orders of magnitude less than levels suggested to influence macrophyte establishment (Lauridsen et al. 1994; van Donk & Otte 1996).

Our results did not support the theory that fish predation of snail grazers promotes epiphytic algal development and leads to suppression of submerged plant growth (Brönmark & Weisner 1992). Smothering by epiphytic algae did not explain the lower charophyte response outside exclosures, as epiphytic algal development outside exclosures was either similar to, or was lower than, exclosure values. Although fish activities may also indirectly affect plant presence by decreasing water clarity (Meijer et al. 1990), our experiments would not detect such influences due to the exclosure design. Other workers have also established from exclosure/enclosure trials that fish can reduce plant biomass directly without affecting water clarity (Crivelli 1983; Ten Winkel & Meulemans 1984; Vermaat et al. 1990).

We conclude that fish activities are the major factors responsible for the lower charophyte performance outside exclosures. This finding is in contrast to Sager et al. (1998), who found wave exposure, not fish (common carp) access, to be an overriding influence for propagule establishment, although their conclusion probably reflects the larger size, shallow depths, and higher relative exposure of their study sites compared with Lake Rotoroa. It is not possible to confirm which fish species in Lake Rotoroa were responsible, however we suggest the impact on plants was mediated directly via uprooting, shading by deposited sediment, mechanical damage of plants, grazing, or some combination of these mechanisms.

From other studies, there is considerable evidence that fish can compromise the condition of shallow, eutrophic lakes. Similarly, our results indicate that the alien fish communities in shallow New Zealand

lakes may not be compatible with management goals to protect and enhance water quality. In particular, the early establishment of charophytes is sensitive to fish influences and yet may be critical for the restoration of shallow lakes.

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