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IMPACT OF PARTIAL REMOVAL OF THE INVASIVE MACROPHYTE *Lagarosiphon major* (HYDROCHARITACEAE) ON INVERTEBRATES AND FISH

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ABSTRACT

Invasive macrophyte species are a threat to native biodiversity and often grow to nuisance levels, therefore, making control options necessary. Macrophyte control can have pronounced impacts on littoral fish by reducing habitat heterogeneity and the loss of profitable (high density of invertebrates) foraging areas. Yet, there is little known about the impacts of macrophyte removal on invertebrates themselves. We conducted a macrophyte removal experiment, that is the cutting of channels into dense macrophyte beds, to investigate the impact of mechanical macrophyte control on invertebrate and fish communities in a littoral zone dominated by the invasive macrophyte *Lagarosiphon major*. The effect of macrophyte removal had only a temporary effect on macrophyte areal cover (4 months). Nevertheless, the treatment increased light penetration significantly. However, we could not detect any difference in epiphyton biomass. Invertebrate biomass increased in macrophyte stands 4 months after treatment and there was a shift in the invertebrate community composition. Mechanical control had no effect on invertebrate biodiversity. The higher invertebrate biomass did not translate into a higher fish density in the treated areas. The results of this study indicated that partial mechanical removal is a suitable option to control unwanted macrophyte stands. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: *Lagarosiphon major*; invasive species; macrophyte control; invertebrates; littoral fish

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INTRODUCTION

Lagarosiphon major Ridley (Moss) (hereafter lagarosiphon) is an exotic macrophyte species that quickly established throughout New Zealand after introduction in the 1950s. It is a threat to native biodiversity due to its ability to outcompete and replace native macrophyte species (Howard-Williams and Davies, 1988; Rattray *et al.*, 1994). Once a waterbody is invaded, diverse native macrophyte communities are displaced by dense monospecific stands of lagarosiphon within a specific depth range. However, regardless of the negative impacts of this invading species, it is likely to perform the multiple beneficial functions of other macrophytes in lake ecosystems (Carpenter and Lodge, 1986). These functions include the support of a high density of invertebrates (Biggs and Malthus, 1982; Kelly and Hawes, 2005) and the provision of habitat and food for fish and other vertebrates (i.e. waterfowl in New Zealand) (Crowder and Cooper, 1982; Diehl, 1993; Persson, 1993; Bickel and Closs, 2008).

Despite the importance of macrophytes, they can reach nuisance levels, interfering with recreational activities (boating, fishing, swimming), impacting on aesthetic values, interfering with hydroelectric generation and drainage, thus making macrophyte control necessary (Johnstone, 1986; Van Nes *et al.*, 1999). There are several different control methods (mechanical, chemical and biological) available for macrophyte management, each of which has advantages and disadvantages. Furthermore, management goals need to be orientated towards multiple user groups that have different expectations of the amount of vegetation removed (Clayton and Tanner, 1988; Van Nes *et al.*, 1999). There are several anticipated macrophyte management outcomes: total removal (benefits recreational users), partial removal (benefits fisheries), eradication of certain target species (invasive species—restoration of native macrophyte communities), no action (beneficial for wildlife) or even enhancement of

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macrophytes (lake restoration in revegetated waterbodies). In the case of unwanted invasive macrophytes, a total eradication of target species would be the ideal outcome to allow restoration of native macrophyte communities from seed banks. However, a total eradication of macrophytes is often not viable due to the associated economic and ecological costs, considering their important ecosystem functions (Carpenter and Lodge, 1986; Johnstone, 1986; Van Nes *et al.*, 2002).

There is considerable information available on the impact of different degrees of macrophyte management and methods on fish communities, abundance, biomass and fecundity (Bailey, 1978; Maceina *et al.*, 1991; Bettoli *et al.*, 1993; Valley and Bremigan, 2002; Sammons *et al.*, 2003), but very little on the impacts of control on invertebrates (but see: Kaenel and Uehlinger, 1999). Generally, moderate macrophyte cover can provide spatial diversity and is beneficial for fish diversity and sport fish production in contrast to excessive cover and a lack of macrophytes (Crowder and Cooper, 1979; Wiley *et al.*, 1984; Killgore *et al.*, 1998; Bickel and Closs, 2008). Therefore, there might be even positive effects of some vegetation removal on littoral zone fish abundance, growth, weight and fecundity (Killgore *et al.*, 1998; Sammons *et al.*, 2005). Theoretical considerations and modelling suggest that removal of about 20–50% of macrophyte areal cover should be most beneficial for fish growth due to increased predation success (easier access to prey fish) and an increase in prey fish abundance due to prey accessibility along macrophyte edges (Carpenter *et al.*, 1997; Trebitz *et al.*, 1997). Initial experiments conducted in lakes in North America showed a positive response of growth of bluegill (*Lepomis macrochirus* Rafinesque, 1819) and largemouth bass (*Micropterus salmoides* (Lacepède, 1802)) after the cutting of channels into macrophyte beds (Carpenter *et al.*, 1995; Olson *et al.*, 1998). Increased fish growth was attributed to better access to prey, higher predation success and a reduction of population size due to predation (Carpenter *et al.*, 1995; Trebitz and Nibbelink, 1996; Trebitz *et al.*, 1997; Olson *et al.*, 1998).

The aim of this study was to investigate the influence of mechanical macrophyte control, that is the cutting of channels into macrophyte beds, on the biotic and abiotic parameters in the macrophyte beds and especially the distribution of macroinvertebrates and fish. We hypothesized that the cutting of channels into the dense macrophyte beds would increase primary productivity in macrophyte beds by increasing light penetration and therefore enhance invertebrate standing crop biomass. Common bully (*Gobiomorphus cotidianus* McDowall, 1975) is a common prey of brown trout (*Salmo trutta* Linnaeus, 1758) in lake Dunstan. Prey fish distribution in the littoral zone is often best explained by predation pressure and the availability of food (Werner and Hall, 1988; Pierce *et al.*, 1994), therefore the anticipated increase in the amount of food in the treated macrophyte beds was hypothesized to produce localized increases in fish abundance.

METHODS

Study sites and cutting of channels

This study was completed within the littoral zone of lake Dunstan, Central Otago, New Zealand (45°02'S, 169°12'E). Lake Dunstan is a large oligotrophic hydroelectric lake (ca. 30 km², max. depth 60 m, mean depth 12.1 m, mean annual maximum production 1–6 mg cm⁻³ h⁻¹, total phosphorus 3.7 µg L⁻¹, total nitrogen 62 µg L⁻¹, chlorophyll *a* 0.8 µg L⁻¹ from Schallenberg and Burns, 1997), the result of the impoundment of the Clutha and Kawarau Rivers. Lake Dunstan is a comparatively new system only reaching its full operational level in 1993. Source water for the Clutha and Kawarau Rivers is from lakes Wanaka/Hawea and lake Wakatipu, respectively (Figure 1). The study was restricted to the Clutha Arm of lake Dunstan as it is the largest part of the lake (19 km², max. depth 23 m, mean depth 9.3 m, hydraulic residence time 7.7 days) with extensive shallow areas providing a suitable habitat for macrophyte growth. Currently, lagarosiphon occupies virtually all of the suitable littoral habitat within its depth range in lake Dunstan. Ten sites with a similar shore gradient and degree of lagarosiphon biomass were selected along the western shore of the Clutha Arm (all sites at least 50 m apart) in the first week of October 2004. This part of the lake was chosen for the experiment as macrophyte biomass was intermediate relative to the maximum densities recorded elsewhere in the lake thus reducing the cost of cutting and difficulties associated with moving the large barge that was used for collecting the cut macrophytes. Nonetheless, the chosen sites display a macrophyte biomass typically encountered in many parts of the lake Dunstan littoral.

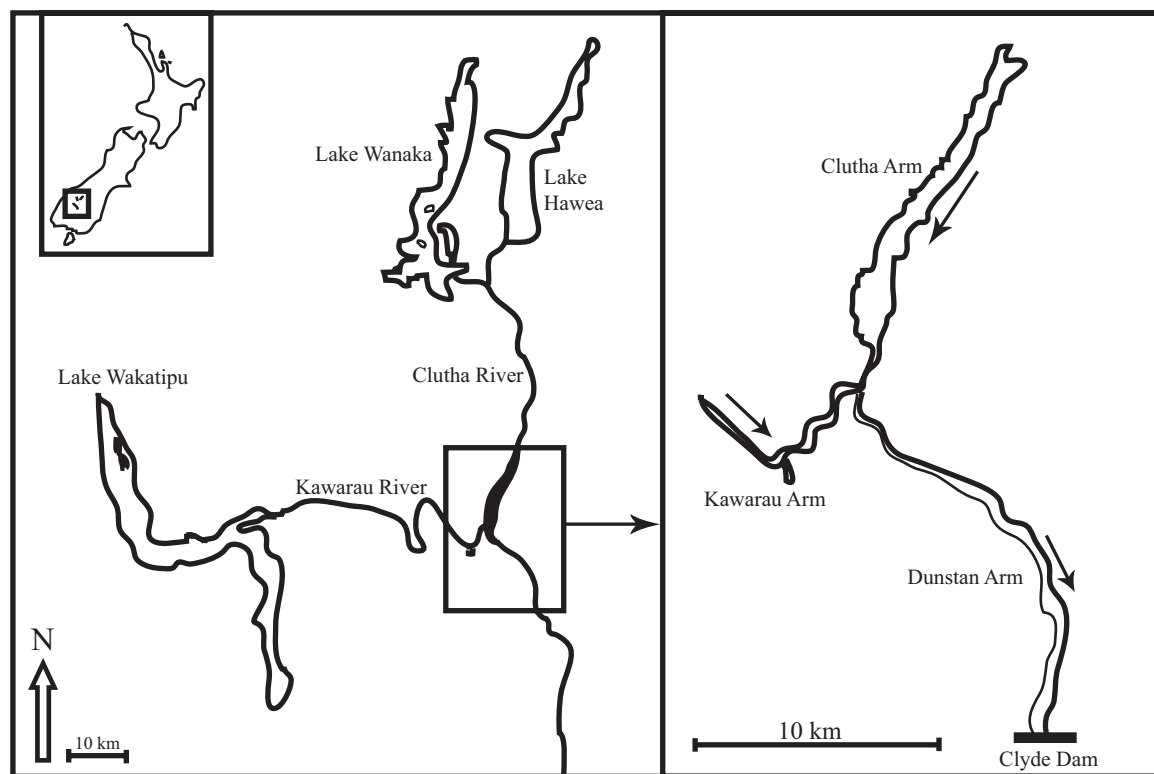


Figure 1. Lake Dunstan is located in the centre of the South Island, New Zealand. Sites were located along the western shore of the Clutha Arm. Arrows indicate direction of flow

At each site two subplots were established (10 m apart) one of which was randomly assigned to cutting (experiment) and the other left untouched (control). In spring 2004 (October) three channels were cut into the treatment plot from the shoreline down to about 3 m depth, which is below the depth of maximum lagarosiphon biomass. Channels were cut manually by a diver and the cut macrophytes were extracted with a Venturi suction dredge and pumped into a barge for later land disposal. Channels were completely cleared of any macrophyte growth and residual stem material. Mean channel length was 3.5 m with an average width of 2 m; channels were separated by 5 m. The height of the lagarosiphon stands varied between 90 and 170 cm (mean 98.1 ± 36.3 cm) which is roughly equivalent to an average macrophyte biomass of $1800 \text{ g dry mass (DM) m}^{-2}$ in this system.

To confirm that the control and experimental plots had an identical invertebrate biomass before the treatment, invertebrate samples were collected at all sites prior to cutting. Approximately 4 months after cutting (second week of February 2005) invertebrates, fish, epiphyton biomass, water chemistry and light availability were sampled (details below). All channel dimensions were re-measured, lagarosiphon regrowth determined (height) and percentage cover visually estimated by a diver. Presence and cover of other macrophyte species was recorded.

Physico-chemical water parameters and epiphyton biomass

Light and physico-chemical water parameters were measured on the bottom of the macrophyte beds (control) or on the bottom of the channels (all about 3 m depth) in each site. Water samples were collected in plastic bottles by a diver and pH, oxygen concentration and water temperature were measured on shore immediately afterwards using an YSI 85 meter (YSI Environmental, Baton Rouge, Louisiana). At each site four water samples were taken, two in

the control and two in the experimental plot at the bottom of two of the three cut channels. All water samples were taken at the same time of the day (0900 h). Light was measured with a LI-COR LI192 light sensor (LI-COR, Lincoln, Nebraska) at noon. In each plot, two measurements were taken (four per site). Mean light availability in the plots was calculated as percent light reaching the bottom (bottom-light surface-light⁻¹100).

As increased light penetration into the macrophyte beds was expected to increase algal productivity epiphyton biomass was measured in the plots. A diver collected three random macrophyte samples per plot (six per site) with mesh bags to assess epiphyton biomass. Epiphyton was washed from the leaves by vigorously shaking the samples in a plastic bag with 500 ml of tap water for 1 min. The effectiveness of this method is discussed in Zimba and Hopsons (1997). The epiphyton water mixture was filtered through precombusted 0.3 µm glass fibre filters (Advantec 75GF, Toyo Inc.). The filters were dried (>48 h at 55°C), weighed, and subsequently ashed (>2 h at 550°C) to assess epiphyton ash free dry mass (AFDM) to account for possible abiotic sediments that settled on the macrophytes. Macrophyte biomass of each sample was measured (DM > 48 h at 55°C) and epiphyton biomass was related to this for each sample (mg epiphyton AFDM g⁻¹ macrophyte DM).

Invertebrate and fish sampling

To assess any possible effects of the channels on invertebrate abundance and biomass, we collected invertebrate samples in each site by SCUBA diving using 250 µm mesh bags (70 × 30 cm²) that were open on one end and could be closed by tightening a strap (Cheruvilil *et al.*, 2000). The mesh bags were carefully lowered over approximately five macrophyte stems to avoid any loss of invertebrates. Five samples were taken randomly within each of the control and experimental plots (10 samples per site). Invertebrate samples were deep frozen at -20°C until processing in the lab. The invertebrates were washed off the macrophytes into a 250 µm sieve, sorted and identified under a dissecting microscope to the lowest possible taxonomic unit. The DM of the macrophytes of each sample was established to relate invertebrate abundance and biomass to sample size (i.e. *N* individuals g⁻¹ macrophyte DM; mg invertebrate biomass g⁻¹ macrophyte DM). Invertebrate biomass was estimated using previously established mean mass values and published values for individual taxa (Stoffels *et al.*, 2003).

To determine if cutting had any effect on fish abundance in the plots, fish were sampled with cubic minnow traps (60 × 30 × 30 cm³). Three traps were set overnight in each plot (six per site) either on the bottom of the macrophyte beds (control) or in one of the channels (experiment). Trap depth was similar for all plots (*ca.* 3 m). CPUE (catch per unit effort) was calculated from the mean abundance as *N* fish h⁻¹ of trapping. Mean fish biomass was estimated from a length—mass regression (Bickel, 2006).

Data analysis

General statistical analyses were performed with SPSS 12.0. If necessary, data were log₁₀ transformed prior to testing to meet the criteria of normality and homoscedasticity. Paired sample *t*-tests were used to investigate differences between treatments for water chemistry, light availability, epiphyton biomass, invertebrate biomass and fish abundance. A repeated measure ANOVA was not used to test for differences before and after treatment. Any differences between before and after treatment would be hard to attribute to treatment effects alone due to confounding effects of seasonal change. Comparison of the samples collected prior to macrophyte removal indicated whether there were differences between control and experimental plots before the treatment.

To investigate the effects of the macrophyte removal on invertebrate communities, NMDS (non-metric multidimensional scaling) ordinations were carried out on untransformed invertebrate abundance data using the Bray Curtis similarity measure. PC-ORD 4.0 (McCune and Mefford, 1999) was used for the ordinations following the recommendations of the authors (McCune and Mefford, 1999). The MDS is presented as a biplot including calculated scores for invertebrate taxa that had more than 25% correlation with either of the ordination axes (Pearson and Kendall Correlations *r*² > 0.25). Multi-response permutation procedures (MRPP) were used to test for significant differences between groups in the ordinations. To analyse taxa richness and diversity in the plots, taxa numbers and the Shannon Wiener diversity index (*H*) were determined with the programme Species Diversity and Richness Version 2.3, PISCES Conservation Ltd., UK.

RESULTS

Channel morphology and macrophyte communities

Prior to treatment of the experimental plots, there was 100% lagarosiphon areal cover in experimental and control plots. Four months after the complete clearing (to the substrate) of the channels in the experimental plots, lagarosiphon had extensively re-established. Average areal lagarosiphon cover in the channels was 75.2% ($\pm 17.6\%$) with an average 72.9 cm (± 10.5 cm) of regrowth (Table I). There was no change in the height of the lagarosiphon stems or areal cover in the control plots during that period (i.e. no net growth; mean = -9 cm ± 29 cm; 100% areal cover). Some native macrophyte species (*Potamogeton cheesemanii*, *Myriophyllum triphyllum* patches of a 'low mixed community') colonized channels in four of the sites but another invasive pest species, *Potamogeton crispus*, also established (areal cover $< 5\%$). Areal cover of native macrophyte species never exceeded 5% in any of the sites.

Abiotic factors and epiphyton biomass

Four months after lagarosiphon removal (February 2005), there was no significant difference in mean water temperature ($t = 0.014$; $p = 0.989$), oxygen saturation ($t = 0.844$; $p = 0.407$) or pH ($t = -1.055$; $p = 0.298$) between control and experimental plots (Table I). Nevertheless, measurements showed a much higher proportion of light (PAR: photosynthetic active radiation) reaching the bottom in the treated macrophyte beds than in the controls ($t = -7.082$; $p = 0.0001$) despite the re-establishment of lagarosiphon. There was a similar amount of epiphyton biomass in the channels and the untreated lagarosiphon beds ($t = -1.326$, $p = 0.21$).

Invertebrate communities and taxon diversity

We found a total of 41 invertebrate taxa (cut: 26 taxa; control: 27 taxa) before treatment and a total of 41 invertebrate taxa (cut: 29; control: 28 taxa) 4 months after the treatment, respectively. Before the experiment there was no difference in the average (over sites) taxa richness (cut: 14.5 ± 3.2 taxa; control: 15.1 ± 1.7 taxa; $t = 0.542$ $p = 0.601$) and diversity (Shannon Wiener H; cut: 1.500 ± 0.237 control: 1.569 ± 0.171 ; $t = 1.565$, $p = 0.152$) between the plots. Average taxa richness (cut: 13.8 ± 2.4 taxa; control: 14.9 ± 3.8 taxa; $t = 1.408$ $p = 0.193$) and diversity (Shannon Wiener H; cut: 1.3 ± 0.2 control: 1.3 ± 0.3 ; $t = 0.337$, $p = 0.744$) were also similar in the experimental plots 4 months after cutting.

An ordination (NMDS) of the invertebrate abundance data for the experimental and control plots showed a significant seasonal separation of invertebrate communities into pre-treatment (spring) and post-treatment (summer) along Axis 1 (MRPP: $A = 0.097$; $p = 0.00002$; Figure 2). There was no separation into control and experimental plots before treatment indicating a similar invertebrate community in all plots prior to the cutting (MRPP: $A = -0.009$; $p = 0.6308$). However, the post-treatment plots revealed a strong separation into cut and uncut plots along Axis 2 of the ordination Diagram 4 months after treatment (MRPP: $A = 0.2571$; $p = 0.00008$). An increase in abundance in three mollusc taxa (*Gyraulus*, *Lymnaea* and *Potamopyrgus*) and Chydoridae was mainly

Table I. Lagarosiphon areal cover, regrowth since removal and native macrophyte establishment in experimental and control plots 4 months after treatment. Mean water temperature and chemistry values (\pm SD). Average light availability (% of surface light reaching the bottom) and epiphyton biomass (mg AFDM g^{-1} DM macrophyte).

| | Lagarosiphon cover (%) | Lagarosiphon regrowth (cm) | Native macrophyte cover (%) | Temp ($^{\circ}$ C) | pH | O ₂ sat. (%) | Light (%) | Epiphyton biomass (mg g^{-1}) |
|--------------|------------------------|----------------------------|-----------------------------|-------------------------|------------------------|--------------------------|--------------------------|----------------------------------|
| Control | 100 (± 0) | -9 (± 29) | 0 | 18.72 (± 1.07) | 7.52 (± 0.44) | 101.82 (± 3.64) | 0.67 (± 1.24) | 0.012 (± 0.004) |
| Experimental | 75.2 (± 17.6) | 72.9 (± 10.5) | < 5 | 18.72 (± 1.19) | 7.65 (± 0.35) | 100.72 (± 2.97) | 27.32 (± 17.20) | 0.015 (± 0.012) |

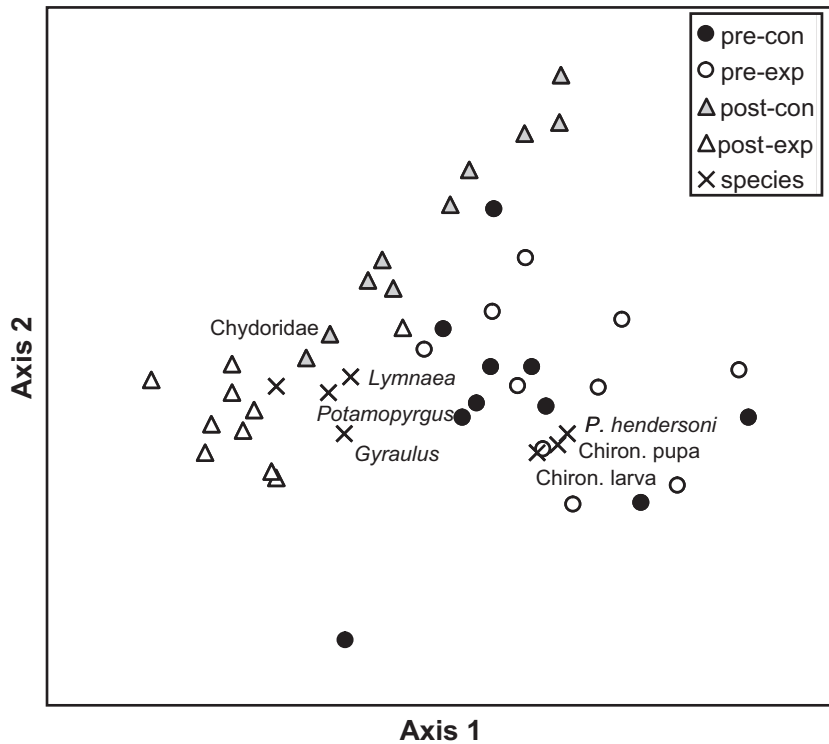


Figure 2. NMDS bi-plot of the invertebrate communities in the different plots (final stress = 12.09; final instability = 0.00048; $p = 0.0099$). Circles indicate pre-treatment plots (black circles control, open circles experiment). Triangles represent post-treatment plots (shaded triangles control, open triangles experiment). Invertebrate taxa that showed a high correlation ($r^2 > 0.25$) with any of the two axes are indicated by X (Chiron., Chironomidae; *P. hendersoni*, *Paroxyethira hendersoni*)

responsible for the grouping of sites in the ordination, as all these were grouped with the post-treatment plots (Figure 2). All these taxa are typical grazers in macrophyte stands. The invertebrate communities before treatment (both experimental and control plots) were characterized by higher abundances of Chironomidae (both pupae and larvae) and a Trichoptera taxa (*Paroxyethira hendersoni*), probably an effect of season on the community composition.

Invertebrate biomass and abundance

There was no difference in total invertebrate biomass between plots before cutting, that is plots had an identical biomass before treatment (Figure 3; $t = 0.696$, $p = 0.506$). Four months after cutting the channels, there was a significant difference in total invertebrate biomass between control and experimental plots ($t = -5.886$, $p = 0.0002$). Mean invertebrate biomass ($\text{mg invertebrate AFDM g}^{-1}$ lagarosiphon DM) in the treatment plots ($29.79 \pm 15.12 \text{ mg g}^{-1} \text{ DM}$) was double of that of the control plots ($14.60 \pm 5.82 \text{ mg g}^{-1} \text{ DM}$). Mollusc taxa accounted for the majority of biomass (AFDM, excluding shellweight) comprising 93.4% of total invertebrate biomass in the pre-treatment and 95.8% in the post-treatment plots. There was a near threefold increase in the abundance of molluscs in the treatment as compared to the control plots (Table II) 4 months after cutting. Most other invertebrate groups showed similar increases in abundance, notably crustaceans which increased \sim fourfold (Table II). Mites were the only invertebrate group that were unaffected by the treatment. Most of these invertebrates are typical grazers in macrophyte stands such as snails (molluscs) and Chydoridae (cladocerans). Predatory invertebrates (Coleoptera and Odonata) were more common in the experimental plots as well.

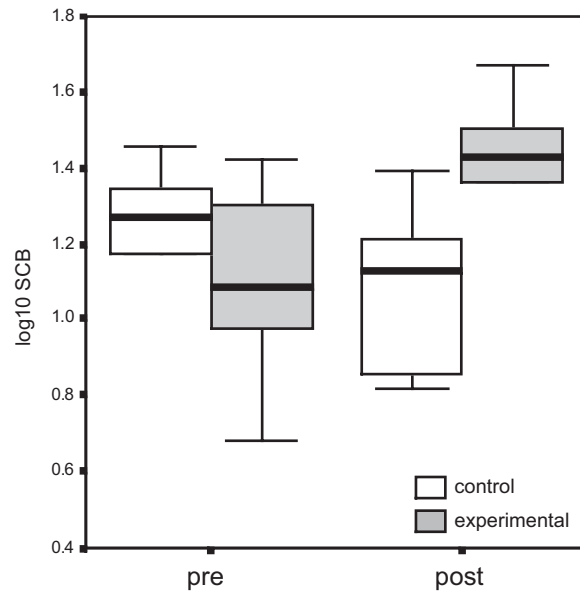


Figure 3. Boxplot showing invertebrate standing crop biomass (SCB) in control and experimental plots before and 4 months after treatment. Prior to treatment (pre) there was no difference in invertebrate SCB between plots. There was a significantly higher macroinvertebrate biomass in the treated (experiment) than in the untreated (control) plots after the cutting (post). Bars represent medians, boxes enclose 50% of all cases (upper and lower quartile) and whiskers show spread of data

Fish distribution

There was a 1.5 times higher average abundance (CPUE) and 1.3 times higher average fish biomass (common bully, no other fish species were caught) in the experimental compared to the control plots (Table III). However, this difference was not significant (CPUE: $t = -1.648$ $p = 0.130$; SCB: $t = -1.245$; $p = 0.242$). Mean fish size (total length) did not vary between treatments ($t = 0.616$; $p = 0.540$). Nonetheless, in 7 out of 10 pair wise comparisons (70%), there was a higher fish abundance in the experimental as compared to the control plots and there were twice as many bullies in experimental than control sites in 4 out of 10 of the sites.

DISCUSSION

The mechanical removal of lagarosiphon was only a temporary success. The previously cleared channels were overgrown by lagarosiphon within 4 months and establishment of native macrophytes was limited to four sites only. However, only a significant reduction in the biomass of invasive macrophytes would be expected to benefit native

Table II. Mean (\pm SD) invertebrate abundance (N invertebrates AFDM g^{-1} lagarosiphon DM) in control and experimental plots (misc insects comprise Odonata, Lepidoptera and Coleoptera)

| Site | Mollusca*** | Trichoptera* | Misc insects* | Hydrocarina n.s. | Chironomidae* | Crustacea** | Total*** |
|--------------|--------------------|------------------|------------------|------------------|------------------|--------------------|---------------------|
| Control | 33.8 (\pm 18.9) | 0.8 (\pm 1.1) | 0.3 (\pm 0.4) | 0.6 (\pm 0.5) | 0.1 (\pm 0.1) | 7.6 (\pm 7.8) | 43.2 (\pm 26.0) |
| Experimental | 95.6 (\pm 28.5) | 2.2 (\pm 2.9) | 0.9 (\pm 1.2) | 0.4 (\pm 0.4) | 0.9 (\pm 0.9) | 31.2 (\pm 23.1) | 131.3 (\pm 28.0) |

Significance levels paired t -test.

n.s. $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table III. Total bully abundance, mean (\pm SD) abundance (CPUE: N fish h^{-1}), biomass ($g h^{-1}$) and mean total length in control and experimental plots

| | N | CPUE ($N h^{-1}$) | Biomass ($g h^{-1}$) | Total length (mm) |
|--------------|-----|---------------------|------------------------|--------------------|
| Control | 41 | 0.17 (\pm 0.08) | 0.86 (\pm 0.74) | 65.1 (\pm 20.8) |
| Experimental | 63 | 0.26 (\pm 0.20) | 1.11 (\pm 0.78) | 62.7 (\pm 18.8) |

species in the long term (Tanner *et al.*, 1990a,b). This rapid recolonization by lagarosiphon occurred despite the complete clearance of any residual stem material. Similar experiments on vegetation removal with other macrophytes indicate that rapid recovery is a common outcome (Fox and Murphy, 1990; Unmuht *et al.*, 1998; Kaenel and Uehlinger, 1999). Furthermore, the availability of free space in the clear-cut channels, abundant light, protection from wave action by the channel walls formed by lagarosiphon stems, and lastly lateral encroachment from the channel walls probably facilitated the recolonization process. Additionally, the channels were limited to the shallow areas of the littoral zone which have the highest degree of regrowth (Unmuht *et al.*, 1998).

The channels greatly increased the penetration of light into the macrophyte beds. Even though lagarosiphon invaded a large proportion of the previously cleared space (75%), growth was less dense compared to control plots. This is presumably the result of a lower macrophyte biomass as compared to mature lagarosiphon stands. However, there was no detectable impact on other chemical or physical water parameters. Reasons for this might include the comparatively narrow nature of weed beds in this part of the lake preventing the build-up of deoxygenated zones in the macrophyte beds and a change in pH through photosynthetic activity as seen in other dense macrophyte beds (Scott and Osborne, 1981; Cardinale *et al.*, 1997; Kaenel and Uehlinger, 1999). Additionally, there is a noticeable downstream water current in this part of the hydro-lake enhancing the exchange of water between the macrophyte beds and surrounding open water.

It was expected that the increase in light availability in the channels would enhance epiphyton production. However, we could not detect a difference in epiphyton biomass between the experimental and control plots. Epiphyton may be limited by other factors than light for example nutrients (Harrison and Hildrew, 1998) or increased grazing pressure due to the higher standing crop biomass of molluscs in the cut areas (epiphyton-grazer interactions: see e.g. Lodge, 1986; Brönmark, 1989; Higgins and Hann, 1995; Jones *et al.*, 1999).

The mechanical harvest of lagarosiphon had strong effects on phytophilous macroinvertebrate community composition and biomass. Total invertebrate biomass and abundance was significantly higher in the cut channels compared to the untreated macrophyte beds. Molluscs dominated the invertebrate community, both in terms of abundance and biomass, and are an important food source for the native fish common bully (Bickel and Closs, 2008) and introduced salmonids in lake Dunstan (Bickel, 2006); mollusc abundance nearly tripled in the treated macrophyte stands. Thus, the macrophyte clearance increased both the availability and total abundance of macroinvertebrate prey. Increases in fish growth, such as those observed in previous studies (Carpenter *et al.*, 1997; Trebitz *et al.*, 1997; Olson *et al.*, 1998), could be explained by either a combination of improved accessibility to prey or increased prey abundance.

Taxa richness and diversity were similar between control and experimental plots indicating that mechanical removal of lagarosiphon had no effect on invertebrate biodiversity 4 months after treatment. Nevertheless, the invertebrate communities differed significantly between treated and untreated plots. Changes in invertebrate communities were presumably a result of differences in habitat structure and complexity (old stems: low degree of ramification, defoliated vs. freshly grown stems) (Schmude *et al.*, 1998) and differences in food (epiphyton-detritus complex) availability and quality (mainly epiphyton in fresh cut vs. more detritus in uncut areas). The main driving factor of separation of communities in the ordination was likely the relative changes in biomass of taxa (and hence abundance) rather than major differences in taxa composition between treatments. Furthermore, taxa richness and species diversity indices were similar between treatments. The difference in invertebrate communities between pre- and post-treatment periods as indicated in the ordination most likely reflects seasonal variation in invertebrate community structure, a pattern to be expected in cool temperate New Zealand environments (Talbot and Ward, 1987).

The higher invertebrate biomass in the treated plots did not result in a significantly higher fish (common bully) biomass. This can partly be attributed to the generally low abundance of common bullies in lake Dunstan (Strickland *et al.*, 2000). Additionally, the creation of macrophyte edges possibly increased predation on bullies by piscivorous fish (brown and rainbow trout in lake Dunstan) (Carpenter *et al.*, 1997; Olson *et al.*, 1998) thus counteracting any increase. Furthermore, abundance itself might be not a very suitable parameter to evaluate the 'fish' response to harvest (Carpenter *et al.*, 1995; Trebitz *et al.*, 1997). Growth rate might be much better suited for this purpose; however, the experimental scale was too small to measure growth responses in highly mobile organisms such as fish. Whole lake experiments would be needed to evaluate the response of larger, more mobile, fish species like trout given their larger home range. Further studies investigating possible predator-prey interactions between different fish species and use of the newly created habitat (macrophyte bed edges) by large predatory fish (trout) would provide valuable insights into the effects of macrophyte management.

Previous studies have demonstrated that mechanical harvest of macrophytes, that is the cutting of channels, can influence fish communities (Carpenter *et al.*, 1997; Olson *et al.*, 1998). The outcome of this small-scale management experiment shows that the mechanical harvest of macrophytes also has direct effects on the availability of invertebrate prey. This suggests that a partial removal of unwanted macrophytes may serve several, often conflicting, management goals aimed at different user groups (Barko *et al.*, 1986; Van Nes *et al.*, 1999) at the same time: (1) a partial reduction of macrophyte biomass can open up water for recreational use (e.g. swimming and boating) and reduce the risk of further spread, but (2) still provide enough macrophyte biomass—including the highly profitable edges that support increased invertebrate and prey fish densities—to support prey for fish communities (including sport fish production) (Crowder and Cooper, 1982; Heck and Crowder, 1991; Diehl, 1993; Persson, 1993; Bickel and Closs, 2008) and structural complexity in the littoral zone (Norton, 1991; Maceina, 1996; Maceina and Reeves, 1996). Further research is needed to confirm this result in other waterbodies.

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