

Impacts of introduced brown and rainbow trout on benthic invertebrate communities in shallow New Zealand lakes

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SUMMARY

1. Brown and rainbow trout have been introduced to many inland waters in New Zealand, but research on the impacts on native communities has focused mainly on streams. The purpose of this study was to compare the benthic communities of trout and troutless lakes. Based on previous studies in North America and Europe, we predicted that the benthic biomass, and especially the abundance of large invertebrates, would be lower in lakes with trout as compared to those without. We surveyed the invertebrate fauna of 43 shallow, high-elevation lakes (26 with and 17 without trout) in four geographic clusters on the central South Island and then conducted a detailed quantitative study of invertebrate biomass and community structure in 12 of these lakes.

2. Benthic community composition and diversity of lakes with and without trout were nearly identical and biomass was as high or higher in the lakes with as without trout. There was no evidence that trout have caused local extinctions of benthic invertebrates. Although the proportional abundance of large-bodied aquatic was slightly lower in lakes with than without trout, the abundance of several groups of large-bodied benthic taxa (dragonflies, caddisflies and water bugs) did not differ.

3. Our findings are in contrast to those in North American and Europe where trout introductions into previously troutless lakes have led to declines in the abundance of benthic invertebrates, especially large-bodied taxa. We propose that the modest effects of trout in New Zealand could be explained by (i) the high areal extent of submergent vegetation that acts as a benthic refuge, (ii) low intensity of trout predation on benthic communities and/or (iii) characteristics of the benthic invertebrates that make them relatively invulnerable to fish predation.

4. Regardless of the relative importance of these hypotheses, our results emphasise that the same invertebrates occurred in all of the lakes, regardless of size, elevation and presence of trout, suggesting habitat generalists dominate the benthic fauna in shallow New Zealand lakes.

Keywords: benthos, introduced species, invertebrates, lakes, predation, submergent vegetation, trout

Introduction

The introduction of non-native species by humans is a major threat to native biodiversity (see reviews by Lodge, 1993; Vitousek *et al.*, 1996; Mooney & Cleland, 2001; Davis, 2003). Among the best-documented cases

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that directly link introductions of non-native species to extinctions or declines of indigenous species are those in which top predators have been introduced into spatially restricted environments such as islands and lakes (e.g. Gill & Martinson, 1991; Kauffman, 1992; Fritts & Rodda, 1998; Sax, Gaines & Brown, 2002). Introduced predators and/or the subsequent decline of key indigenous prey species can lead in turn to cascading effects on community structure and ecosystem function (e.g. Vander Zanden, Casselman & Rasmussen, 1999; Mack *et al.*, 2000; Schindler, Knapp & Leavitt, 2001).

Rainbow [*Oncorhynchus mykiss* (Walbaum)] and brown trout (*Salmo trutta* Linnaeus) have been introduced deliberately for recreational and commercial fishing throughout the world (MacCrimmon & Marshall, 1968; MacCrimmon, 1970; Elliott, 1994). In New Zealand, these two species were introduced in the late 1880s and are now the top predators in many streams and lakes throughout the country (Townsend, 2003). The invasion success of trout in New Zealand is well documented and perhaps not surprising given the ability of trout to eliminate potential competitors (mainly galaxiid fishes) and the relatively benign parasite/pathogen/predator threats in New Zealand waters (Moyle & Light, 1996; Townsend, 1996). Studies on the effects of trout in New Zealand have focused on streams where trout impacts on native fish and invertebrates have led to (i) changes in invertebrate behaviour, drift and spatial distributions (e.g. McIntosh & Townsend, 1994, 1996), (ii) fragmentation of native fish populations (Townsend & Crowl, 1991; McIntosh, 2000), (iii) altered community composition (Flecker & Townsend, 1994) and (iv) top-down effects on stream ecosystem structure and function including trophic cascades that change primary production and the movement of energy and nutrients (Huryn, 1998; Nyström, McIntosh & Winterbourn, 2003; Nyström & McIntosh, 2003; Simon & Townsend, 2003; Greig & McIntosh, 2006).

In contrast, there is relatively little known about the impacts of introduced trout on the ecology of New Zealand lakes. During the spread of rainbow and brown trout after introductions in the late 1800s, there was evidence that native galaxiid fishes (e.g. koaro, *Galaxias brevipinnis* Günther) declined in lakes on the North Island (McDowall, 1987, 1990), as did two large-bodied freshwater invertebrates (crayfish, 'koura,' *Paranephrops planifrons* White; and crabs,

Halicarcinus lacustris Chilton) (McDowall, 1987, 1990; Rowe, 1993). However, there has been little subsequent research to systematically compare the faunas of lakes with and without trout. There is some evidence that trout can impact zooplankton in New Zealand lakes (Jeppesen *et al.*, 1997), but we know of no research that has explicitly focused on trout impacts on lake benthic communities.

The purpose of this study was to compare the benthic invertebrate communities of New Zealand lakes with and without introduced rainbow and brown trout. Research in North America and Europe on the impacts of trout on lake benthos suggested the potential for two types of impacts. First, it is well documented that both brown and rainbow trout are size-selective predators (Ware, 1972; Wurtsbaugh, Brocksen & Goldman, 1975; Bannon & Ringler, 1986; Angradi & Griffith, 1990; Keeley & Grant, 2001; Nyström *et al.*, 2001). Moreover, the introduction of a variety of species of trout, including brown, rainbow, cutthroat [*Oncorhynchus clarki* (Richardson)] and brook trout (*Salvelinus fontinalis* Mitchell), into previously fishless alpine lakes in North America and Europe has resulted in the local decline or elimination of large-bodied invertebrates and amphibian larvae (Larson *et al.*, 1992; Liss *et al.*, 1995; Carlisle & Hawkins, 1998; Drake & Naiman, 2000; Cavalli, Miquelis & Chappaz, 2001; Knapp, Matthews & Sarnelle, 2001; Dunham, Pilliod & Young, 2004; Orizaola & Brana, 2006). Thus, we predicted that lakes with trout would have reduced abundances of large invertebrates compared to those without trout. Such impacts would be of special concern in New Zealand where there are endemic species, genera and families of aquatic invertebrates that have special significance for understanding global affinities and evolutionary trends within and between taxonomic groups (Forsyth & Lewis, 1987; Collier, 1993). Endemic groups with restricted ranges can be especially vulnerable to the effects of introduced predators and are of special concern for conservation strategies designed to minimise the impacts of introduced species (Polhemus, 1993; Dobson, Bradshaw & Baker, 1997). Our second prediction was that the overall biomass of benthic invertebrates should be lower in lakes with than without trout. Research on shallow lakes and ponds in North America and Europe has described how trout-induced reductions in benthic biomass have led to trophic cascades resulting in

higher algal biomass and increased rates of nutrient cycling (Leavitt *et al.*, 1994; Nyström *et al.*, 2001; Schindler *et al.*, 2001). We viewed a comparative study of the benthic biomass in relatively small New Zealand lakes with and without trout as a first step towards assessing whether trout have the potential to bring about comparable top-down effects on trophic structure. Such information has important management implications given that there are ongoing stocking programmes and range expansions of trout into previously troutless lakes in New Zealand.

Methods

Study sites

We surveyed the benthic communities in 43 high-elevation lakes to the west and north of the Canterbury plains (from Lake Coleridge in the south to Tarndale Lakes in the north) on the South Island of New Zealand during October 2001 to March 2002 (Fig. 1). All of the study sites were relatively shallow, natural inland lakes at moderate to high elevations (approximately 500–1100 m) that were geomorphically derived from glacial (kettles) and fluvioglacial processes (depressions dammed by moraines or alluvial fans) (Timms, 1983; Mosley, 2004). We limited the geographic range of our study to minimise the complicating effects of

regional differences in geology and water chemistry (Lowe & Green, 1987; Timperly, 1987) and geographic shifts in invertebrate species pools (Timms, 1982; Winterbourn, Gregson & Dolphin, 2000).

Few lakes in New Zealand have escaped trout introductions and those that have are relatively small or relatively remote compared to lakes with trout. We first located lakes without trout and then chose nearby lakes with trout for comparison. Lakes without trout either (i) had natural barriers to prevent immigration from stream outlets and were remote to the extent that they have escaped stocking, or (ii) were protected zones specifically excluded from stocking programs. The lakes with trout were well-known recreational fisheries with self-recruiting rainbow and/or brown trout populations (see Appendix 1). Although several of the lakes have historically had ongoing stocking programmes, many have self-recruiting populations. Published information on the trout species in each lake (North Canterbury Fish and Game Management Plan, 1997) was verified with direct observations from the shoreline and while snorkeling. Because of high water clarity, the presence and species of trout were easily observed while sampling benthos.

The lakes were shallow (<10 m maximum depth), isothermal and well oxygenated as a result of mixing by persistent strong winds (Timms, 1982, 1983). The physical and chemical attributes of shallow inland

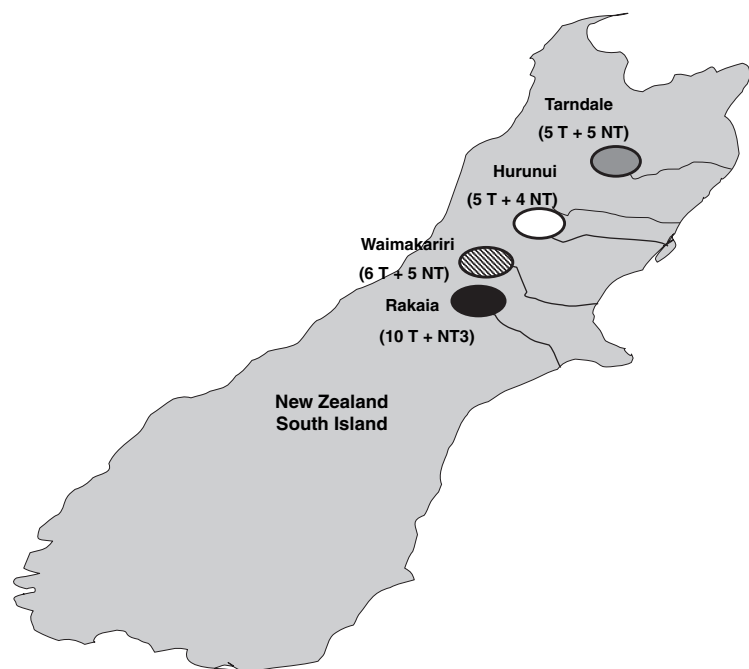


Fig. 1 Locations of the four geographical clusters of lakes surveyed in this study [after Livingston *et al.* (1986) and North Canterbury Fish and Game Management Plan (1997)]. T, lakes with trout; NT, lakes without trout.

lakes in this region have been well studied and they are characterised as circumneutral, oligotrophic to mesotrophic and moderately soft (Timperly, 1987; Jeppesen *et al.*, 2000). Although physical and chemical data are published for many of the lakes (Livingston, Biggs & Gifford, 1986), there was no information for several of the smallest basins. Thus, we collected water samples near the outlet of each lake (or if no outlet, at the prevailing downwind end of the lakes) as an integrated measure of whole-lake chemistry. The pH and conductivity were measured on site using Oakton (Series 20) portable meters. Total phosphorus was estimated chemically using a standard colorimetric procedure (Strickland & Parsons, 1968). Lake depth and area were either taken from published information from inventories of South Island Lakes (Livingston *et al.*, 1986; North Canterbury Fish and Game Management Plan, 1997) or estimated on site during sampling (Appendix 1).

The lakes can be roughly divided into four clusters from south to north based on catchment and geographic proximity (Fig. 1). Although we purposefully chose relatively small lakes with trout, they were still significantly larger and deeper on average than those without trout (Table 1). This difference in size and depth was exaggerated by four relatively large (100–200 ha) lakes in the Waimakariri and Hurunui clusters (Pearson, Taylor, Sheppard and Lyndon) (Appendix 1). We conducted the statistical analyses with and without these lakes and found no difference in the results; thus, they were included in the analysis presented here. Lakes without trout were higher in elevation and slightly more acidic than trout lakes. However, none of the other chemical variables including phosphorus (as a coarse measure of trophic status) differed significantly between trout and troutless lakes (Table 1). Bullies (Gobiidae: *Gobiomorphus cotidianus* McDowall, *Gobiomorphus breviceps* Stokell, *Gobiomorphus alpinus* Stokell = Tarndale ecophenotype of *G. cotidianus*) were present in all of the lakes (S. A. Wissinger and H. S. Greig, pers. obs.). Long-

finned eel (*Anguilla dieffenbachia* Gray) and koaro (*G. brevipinnis*) migrate into most New Zealand lakes with stream connections (Rowe & Graynoth, 2002) and a land-locked population of koaro is in Lake Marion, a faunal preserve. We directly observed koaro in both land-locked (Blackwater, Little Blackwater) and lakes with stream connections in the Waimakariri cluster (H.S. Greig and S.A. Wissinger, unpubl. data).

Taxonomic surveys of macroinvertebrate communities

We sampled all shore-accessible habitats in each of the 43 lakes in spring (October to December 2001) and again in mid-late summer (January to March 2002) to account for seasonal differences in community composition. We did not sample inlet or outlet stream habitats and for lakes with adjacent lacustrine wetlands, we did not sample the wetlands beyond the lakeside edge that was exposed to trout predation. A standard d-frame net was swept through different types of shoreline emergent vegetation, nearshore unvegetated habitats and submergent vegetation. In the largest lakes, offshore submergent vegetation was inaccessible by wading and was sampled to up to 3 m depth using snorkeling gear. Macroinvertebrates were sorted from detritus on site and preserved in 90% ethanol. Taxonomic identification to genus and often species was based on Winterbourn *et al.* (2000) and other references for New Zealand aquatic invertebrates (Crustacea, Chapman & Lewis, 1976; Chironomidae, Stark, 1981; Boothroyd, 2000; Oligochaeta, Brinkhurst, 1971; Mollusca, Winterbourn, 1973).

Benthic biomass and species abundances

In the second part of the study, we compared the abundance (number m⁻²) and biomass [ash-free dry mass (AFDM) m⁻²] of macroinvertebrates in six trout and six troutless lakes in the Waimakariri and Tarndale clusters. These lakes were chosen to reduce the size disparity between the two groups in the

Table 1 Summary of physical and chemical characteristics of the trout and troutless lakes included in this study

Trout	Elevation (m)	Area (ha)	Depth (m)	Conductivity (µS cm ⁻¹)	pH	Total [P] (µg L ⁻¹)
Yes	707 ± 37	40.4 ± 50*	10.9 ± 4.5*	57.3 ± 23.2	7.1 ± 0.41	21.9 ± 11.8
No	800 ± 59	10.8 ± 14	5.5 ± 1.9	40.8 ± 23.3	6.8 ± 0.64	20.5 ± 15.7

Values are means ± 1 SD. Asterisk indicates significant difference based on a *t*-test ($P < 0.05$).

43-lake survey. Benthic invertebrates were sampled quantitatively in mid-summer (January and February 2002) in three different habitats within each lake. Preliminary sampling suggested that we could account for most of the within-lake variability in community composition by dividing lakes into three zones; (i) a shoreline zone dominated by emergent vegetation at the terrestrial ecotone, (ii) an adjacent zone of bare sediments or only sparse submergent vegetation and (iii) extensive beds of submergent vegetation including characean algae (*Chara* spp., *Nitella* spp.) and vascular plants (mainly *Elodea canadensis* Richardson, *Myriophyllum tryphyllum* Orchard, *Potamogeton cheesemanii* A. Bennett, *Isoetes alpinus* Kirk). Visual observations from adjacent hill-tops indicated that 75–90% of the central basins of these lakes were covered with this submergent vegetation. The emergent zone on gently sloping shorelines was dominated by *Typha orientalis* C. Presl, *Juncus effusus* L., *Juncus articulatus* L., *Carex secta* Boott, *Schoenus pauciflorus* Hook. f., and/or *Eleocharis acuta* R. Br. Shorelines with a relatively steep gradient had a relatively narrow emergence zone dominated by overhanging tussock (*Chionochloa rubra* Zotov), spike rush (*Eleocharis sphecelata* R. Br) and flax (*Phormium tenax* JR Forst & G. Forst).

We established four sample sites (approximate north, south, east and west) at each lake and used two types of sampling devices in each of the three vegetation zones (shoreline, nearshore sparse/bare and offshore submergent vegetation); thus we collected 24 quantitative samples per lake. We estimated the abundance of small-bodied macroinvertebrates (oligochaetes, chironomids, clams, snails and epibenthic crustaceans) at each site using a 0.01 m⁻² cylinder [polyvinyl chloride (PVC) pipe; 1 m length] that was pushed down over the vegetation and into the substrate. The contents of the cylinder were capped, transferred to a standard d-frame net, washed and invertebrates sorted from substrata and preserved in 90% ethanol on site. The abundance of large-bodied taxa (caddisflies, odonates, beetles, hemipterans and lepidopterans) was estimated from samples taken with a 0.1 m⁻² box sampler (see Wissinger, 1988). A d-frame net was repeatedly drawn through the box following a standardised protocol that was based on preliminary data for reaching the 99% removal rate for biomass (S.A. Wissinger, unpubl. data). Invertebrates and detritus were transferred to sorting pans

and invertebrates were removed and preserved in 90% ethanol on site.

In the laboratory, invertebrates were identified, counted and sorted into major categories for AFDM determination. Each group was dried at 50 °C for 48 h (Lab-Line 3505 oven; Melrose Park, IL, U.S.A.), weighed, ashed (M15A-SA Furnace; Blue M Electric, Blue Island, IL, U.S.A.) at 500 °C for 2 h, and re-weighed to the nearest 0.0001 g (Sartorius MCI 210S analytic balance, Goettingen, Germany).

Statistical analysis

We searched for patterns in the distribution of invertebrates across lakes using Bray-Curtis polar ordination on presence-absence data for all taxa (Beals, 1984). We chose this ordination technique because of its non-restrictive assumptions (does not assume random sampling, multivariate normality and non-clustering of observations) compared with eigenvector techniques (e.g. principle components analysis; see Gauch, 1982; Austin, 1985; McGarigal, Cushman & Stafford, 2000). The original ordering of data in the Bray-Curtis ordination was based on per cent dissimilarity (Gauch, 1982). Subsequently, we used canonical correspondence analysis (CCA) to estimate the degree to which community structure was related to environmental variables measured at each lake (Table 1; see TerBraak, 1994; Okland, 1996). The environmental matrix used to constrain the ordination of the invertebrate matrix included the four following environmental variables in order to reduce the ratio of variables to sample-units: (i) lake area (highly correlated with lake depth), (ii) elevation, (iii) total phosphorus and (iv) pH (highly correlated with total conductivity). Biplots were constructed to express the importance of environmental variables in explaining structure in the invertebrate matrix. Both multivariate procedures were conducted using PC-ORD (McCune & Mefford, 1999). For both ordinations, we included only the subset of taxa for which we were confident of our taxonomic precision (77 of the more than 90 total taxa). The biomass and numerical data from the quantitative samples were analysed using two-way ANOVA (lake habitat × presence of trout) after testing for departures from normality and homoscedasticity using residual and normal quantile plots of the dependent variables.

Results

Patterns in community composition

Over 90 benthic macroinvertebrate taxa were encountered (Appendix 2). Taxonomic precision was highest (species) for large-bodied taxa and lowest (genus or 'operational taxonomic unit') for chironomids, annelids and microcrustaceans, for which species richness is probably underestimated. A core group of large-bodied species occurred in all or nearly all of the 43 lakes including odonates (*Xanthocnemis zealandica* and *Procordulia grayi*), caddisflies (*Triplectides cephalotes*, *Oecetis unicolor* and *Paroxyethira hendersoni*), water bugs (*Sigara arguta*, *Microvelia macgegori* and *Diaprepocoris zealandiae*), beetles (*Liodessus plicatus* and *Rhanthus sutularis*), molluscs (*Potamopyrgus antipodarum*, *Gyraulus corinna* and *Musculium novaezealandiae*) and an aquatic lepidopteran (*Hygraula nitens*). Most other taxa were only missing from one or two lakes within a cluster and their presence-absence was not correlated with trout. The mean taxonomic richness of benthic invertebrates in lakes with (61 ± 4 SD) and without (57 ± 5 SD) trout was remarkably similar.

The distribution pattern of the few non-ubiquitous species fell into two main categories. First, several groups of taxa typically found in stream habitats in

New Zealand such as mayflies (*Deleatidium* sp. and *Nesameletus ornatus*), stoneflies (*Zelandobius furcillatus* group) and several predominantly lotic caddisflies (*Pycnocentroides aureolus* and *Pycnocentria evecta*), were encountered in wave-swept, open-substrate habitats at the leeward end of the prevailing fetch in the largest lakes. Secondly, several taxa were specific to particular geographic clusters. For example, a semi-aquatic water bug (*Saldula* sp.) was found in the emergent zone of lakes in the three northern clusters, but not in the Rakaia cluster; and an emergent-zone beetle (*Liodessus deflectus*) was recorded mainly in lakes in the Waimakiriri and Hurunui clusters. Finally, several chironomid taxa were specific to particular clusters and two orthoclads were only encountered in two high tarns in the Waimakiriri cluster. The latter were the only two taxa found in lakes without trout that were not also present in lakes with trout!

The Bray-Curtis ordination emphasised that the overall distance measures for species composition across all lakes along the primary axes were extremely small (Fig. 2). Axis 1 represented a gradient from large, low-elevation to small high-elevation lakes, which roughly correlated with presence – absence of trout. Axis 2 represented a geographic gradient from

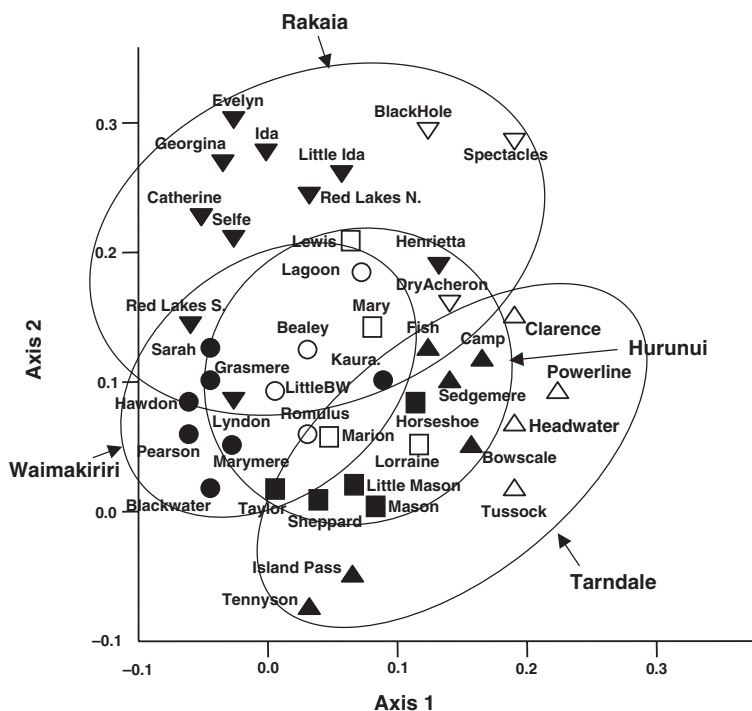


Fig. 2 Bray-Curtis unconstrained ordination based on presence-absence of 77 taxa in 43 lakes. Symbol types correspond to geographical clusters (▽, Rakaia; □, Waimakiriri; ○, Hurunui; △, Tarndale). Open and closed symbols indicate lakes with and without trout, respectively.

lakes in the south (Rakaia cluster) to those in the north (Tarndale cluster) of our study area (Fig. 2). The first two axes explained 51% of the variation in the species matrix. The importance of lake size and elevation in explaining differences in the presence-absence of species was illustrated when we constrained the ordination with the environmental variables matrix using CCA (Fig. 3). The correlation between species and environment was high (Pearson correlation coefficient = 0.83) and the biplots suggest that lake area and elevation were the two variables to which individual species distributions were most highly correlated. Of particular note were the large weightings along the first axis for the predominantly lotic taxa (mayflies and stoneflies) that were encountered in the wave-swept zone of large lakes (see above). Despite the high species-environment correlation, the cumulative variance in community structure explained by the environmental matrix (eigenvalue/total variance) was relatively low for the first two axes (10% + 6% = 16%); perhaps as expected, given the overall high similarity in species composition among lakes (Fig. 2).

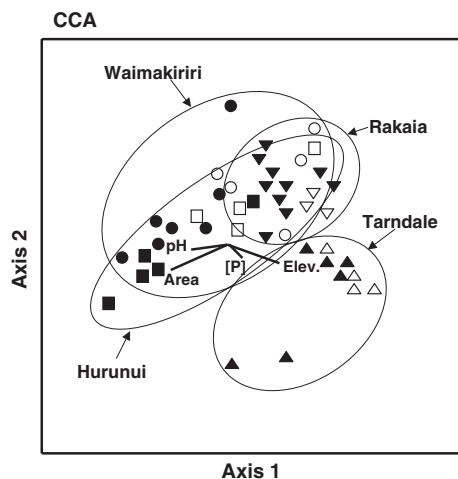


Fig. 3 Biplot of canonical correspondence analysis (CCA) for 43 lakes constrained by major environmental variables measured in this study. The environmental matrix was collapsed to four variables to eliminate the redundancy of correlated variables (depth is correlated with lake area and conductivity is highly correlated with pH). Length of lines expresses the importance of environmental variables in explaining the structure in the invertebrate matrix. Symbol types correspond to geographical clusters (see Fig. 2 legend). Open and closed symbols indicate lakes with and without trout, respectively.

Invertebrate biomass and proportional abundances of species

Nearly identical patterns of abundance were obtained from densities (number m^{-2}) and biomass (AFDM m^{-2}) measurements, so we mainly present biomass data below to minimise redundancy. Total biomass of benthic invertebrates was higher in trout than troutless lakes (Fig. 4; ANOVA main effect of trout $F_{1,30} = 4.7$; $P = 0.04$). Within lakes, biomass was higher in the submergent macrophyte beds than in the open shoreline and emergent vegetation habitats, which did not differ (two-way ANOVA subhabitat main effect $F_{1,30} = 16.1$; $P < 0.001$; habitat differences based on Scheffé's test between groups in one-way ANOVA on combined data for habitats). The high biomass values for the submergent macrophyte zone were largely attributable to the higher abundance of molluscs in submergent vegetation compared with open and emergent habitats (habitat main effect $F_{2,30} = 26.7$; $P < 0.001$). Over 90% of mollusc biomass was attributable to one species, *P. antipodarum*, whose density in submergent vegetation averaged approximately 200 000 m^{-2} and ranged as high as 500 000 m^{-2} (Fig. 5). Across all habitats, *P. antipodarum* was more abundant in trout than troutless lakes (trout main effect $F_{1,30} = 7.8$; $P = 0.008$). When we excluded this species from the analysis, the total AFDM m^{-2} in lakes with and without trout did not differ ($F_{1,30} = 1.1$; $P = 0.30$).

The biomass of large-bodied benthic taxa [Odonata + Trichoptera (not including Hydroptilidae) + Hemiptera + Coleoptera + aquatic Lepidoptera] did not differ between trout and troutless lakes ($F_{1,30} =$

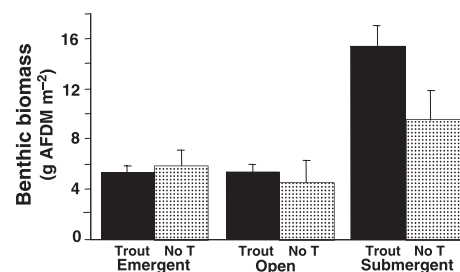


Fig. 4 Mean (\pm SE) biomass (ash-free dry mass) of benthic invertebrates in the three subhabitats in trout and troutless (No T) lakes on the South Island of New Zealand. Emergent = shoreline emergent vegetation zone; open = littoral zone of sparse or no vegetation; submergent = submergent vegetation zone.

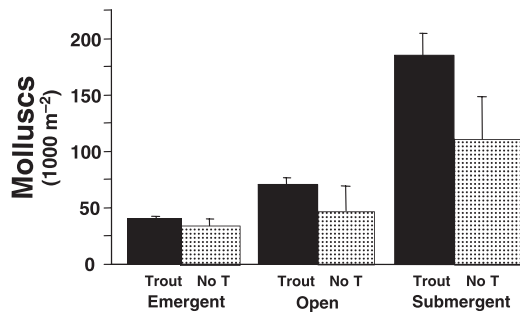


Fig. 5 Mean (± 1 SE) density (no m^{-2}) of molluscs (mainly *Potamopyrgus antipodarum*) in the three subhabitats in trout and troutless (No T) lakes on the South Island of New Zealand. Emergent = shoreline emergent vegetation zone; open = littoral zone of sparse or no vegetation; submergent = submergent vegetation zone.

3.2; $P = 0.08$); but as a percentage of total biomass, large-bodied taxa were more abundant in lakes without than with trout ($F_{1,30} = 6.9$; $P = 0.01$; Fig. 6). Across all lakes, the absolute and percentage biomass of large-bodied taxa were greater in the submergent and emergent habitats than on open substrate habitats ($F_{2,30} = 12.7$; $P < 0.001$ and $F_{2,30} = 3.7$; $P = 0.03$, respectively). The relatively high biomass of large-bodied taxa in troutless lakes was due mainly to odonates and coleopterans, both of which were significantly more abundant in lakes without than with trout (main effect of trout on odonates $F_{1,30} = 6.6$; $P = 0.004$; on coleopterans, $F_{1,30} = 6.2$; $P = 0.02$, Fig. 7a,b). Dytiscid coleopterans were especially abundant in the emergent zone in lakes without trout ($P < 0.05$ for Scheffé's test between groups in one-way ANOVA; Fig. 7b). Odonates were significantly more

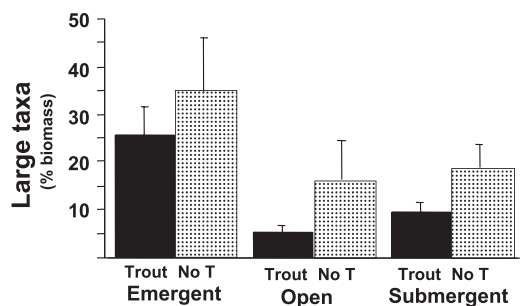


Fig. 6 Mean (± 1 SE) percent biomass (ash-free dry mass) of large-bodied taxa (odonates + beetles + water bugs + caddisflies + lepidopteran) in three subhabitats of lakes with and without trout (No T) lakes on the South Island of New Zealand. Emergent = shoreline emergent vegetation zone; open = littoral zone of sparse or no vegetation; submergent = submergent vegetation zone.

abundant in emergent and submergent macrophytes than in open substrata (Scheffé a posteriori test $P < 0.05$ from protected one-way ANOVA; Fig. 7a). The trout effect on odonates was because of lower abundances of damselflies (mainly *X. zealandica*) in lakes with, compared to those without, trout. The biomass of dragonflies (*P. grayi* and *P. smithi*) did not differ between trout and troutless lakes ($P \gg 0.05$).

Biomass of the other two dominant groups of large-bodied taxa, hemipterans and trichopterans) did not differ between lakes with and without trout (Fig. 7c,d; main effect of trout $F_{1,30} = 0.02$; $P = 0.88$; $F_{1,30} = 0.08$; $P = 0.76$, respectively). Leptocerid caddisflies were among the most conspicuous benthic invertebrates in both trout and troutless lakes. *Triplectides* spp. (mainly *T. cephalotes*) were abundant in emergent and submergent vegetation in all lakes and *Hudsonema amabile* was typically among the biomass dominants in open, near-shore habitats in lakes with and without trout. The most frequently encountered hemipteran, *D. zealandiae* was broadly distributed across all habitats in both trout and troutless lakes. A second common species, *S. arguta* occurred in all habitats in lakes without trout, but was restricted mainly to nearshore emergent habitats in lakes with trout.

Biomass of most small-bodied taxa did not differ among habitats or between trout and troutless lakes. They included oligochaetes (Lumbriculidae and Tubificidae), epibenthic microcrustaceans (mainly Ostracoda, Cladocera and Copepoda) and non-chironomid dipterans (Tipulidae and Stratiomyidae; all main and interaction effects $P \gg 0.05$). Chironomidae was the one small-bodied group for which there was a trout effect; biomass values were slightly higher in lakes with than without trout (main effect of trout $F_{1,30} = 6.6$; $P = 0.02$; Fig. 8).

Discussion

Researchers who have studied the effects of introducing trout to previously troutless lakes have reported a decrease in the overall abundance of benthic and planktonic invertebrates as well as shifts in community composition, especially the disappearance or decline of large-bodied invertebrate taxa (Leucke, 1990; Liss *et al.*, 1995; Carlisle & Hawkins, 1998; Drake & Naiman, 2000; Knapp *et al.*, 2001; Parker *et al.*, 2001; Tate & Hershey, 2003). In contrast, we found no difference in the overall benthic biomass in trout and

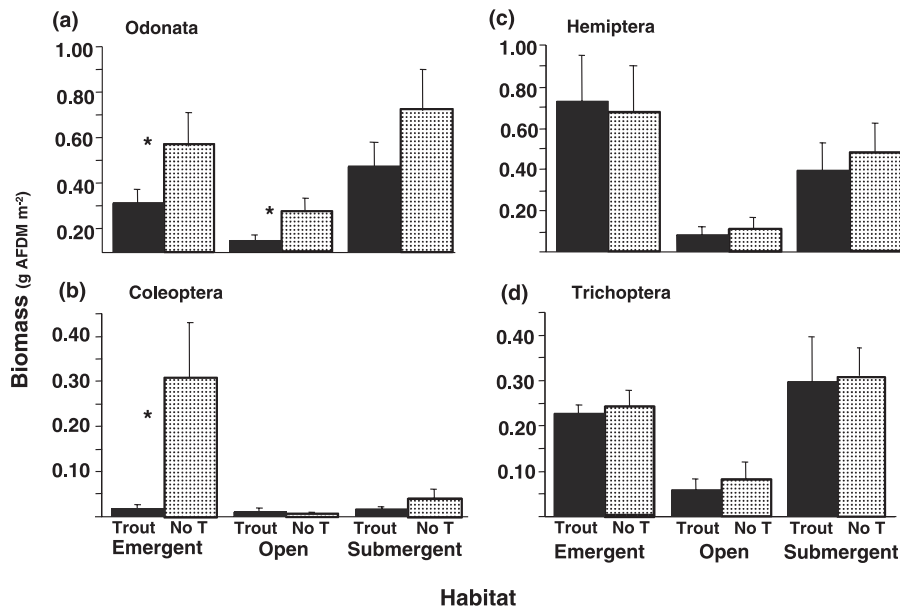


Fig. 7 Mean (± 1 SE) biomass (ash-free dry mass) of (a) Odonata, (b) Coleoptera, (c) caddisflies (Trichoptera) and (d) beetles (Coleoptera) in New Zealand lakes with and without trout (No T). Emergent = shoreline emergent vegetation zone; open = littoral zone of sparse or no vegetation; submergent = submergent vegetation zone. Asterisks indicate significant differences in biomass between trout and troutless lakes ($P < 0.05$) based on Scheffé's test on one-way ANOVAs.

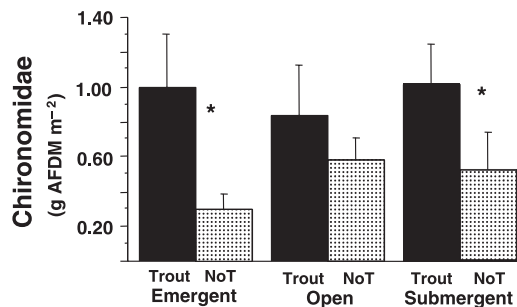


Fig. 8 Mean (± 1 SE) biomass (ash-free dry mass) of chironomids in three subhabitats in trout and troutless (No T) lakes on the South Island of New Zealand. Emergent = shoreline emergent vegetation zone; open = littoral zone of sparse or no vegetation; submergent = submergent vegetation zone. Asterisks indicate significant differences in biomass between trout and troutless lakes ($P < 0.05$) based on Scheffé's test on one-way ANOVAs.

troutless lakes in New Zealand and relatively minor differences in community composition. All of the large-bodied benthic taxa were present in all lakes; and within lake clusters, all but a few taxa encountered in troutless lakes were also found in those with trout. Thus, we found no evidence that the introduction of trout has led to the local extinction of native species in our study areas in New Zealand and has, at the most, had a modest effect on community struc-

ture. Lakes with trout had lower abundances of damselflies and beetles, but the absence of measurable effects of trout on the abundance of leptocecid caddisflies, dragonflies and water bugs is in contrast to (i) documented declines in these groups after trout introductions to lakes in North America and Europe (see references above) and (ii) a wealth of evidence for fish-induced species replacements in these taxa between fish and fishless habitats (Wellborn, Skelly & Werner, 1996). Below, we discuss several non-mutually exclusive hypotheses for why brown and rainbow trout have apparently had a minimal impact on the benthic communities at our study sites in New Zealand.

Does submergent vegetation act as a benthic refuge in New Zealand lakes?

Most previous studies that link trout introductions to changes in benthic communities have been conducted in lakes that either do not have dense stands of submergent vegetation, or in which the vegetation is restricted to a relatively narrow band in the littoral fringe (Donald, 1987; Leavitt *et al.*, 1994; Bradford *et al.*, 1998; Carlisle & Hawkins, 1998; Drake & Naiman, 2000; Knapp *et al.*, 2001; Schindler *et al.*,

2001; Jeppesen *et al.*, 2002). In contrast, the central basins of the lakes we studied are covered by beds of submergent plants and/or characean algae. There is an extensive literature that describes the broad areal extent, high biomass, distinct zonation and surprising depths to which submergent vegetation extends in New Zealand lakes (characeans and vascular plants up to 40 m; and bryophytes to 70 m; Kelly & McDowall, 2004; de Winton & Schwarz, 2004). The pervasiveness of submergent vegetation in the deep central basins of New Zealand lakes is attributed to the extremely high water clarity and persistently strong winds that prevent stratification (de Winton *et al.*, 1991; Schwarz, Hawes & Howard-Williams, 1996). In contrast, the central basins of geomorphically comparable lakes in North America are typically not densely vegetated and characterised as being 'plantless, muddy-bottom deposits' (Brinkhurst, 1974). There are a few clear-water lakes in North America with deep beds of macrophytes (e.g. Frantz & Cordone, 1967) and there are some extremely deep lakes in New Zealand that exceed the extinction point for light penetration; but, in the lakes that we studied, the areal extent of submergent vegetation is qualitatively different from that in the North American lakes where trout impacts on benthos have been found.

In our study (Fig. 4) and previous studies of benthic communities in New Zealand lakes, the highest invertebrate densities and biomass are in these central-basin submergent macrophyte beds (Fig. 4; Biggs & Malthus, 1982; Talbot & Ward, 1987; James *et al.*, 1998; Weatherhead & James, 2001; Kelly & McDowall, 2004; Kelly & Hawes, 2005). In contrast, the central-basin benthic fauna of comparably deep North American and European lakes has low diversity (dominated by oligochaetes, molluscs and chironomids) and does not include many of the large-bodied taxa that we encountered at our study sites (e.g. caddisflies, hemipterans, odonates and beetles) (Brinkhurst, 1974; Lalonde & Downing, 1992; Tolonen *et al.*, 2001; Johnson & Goedkoop, 2002).

Thus, one hypothesis for the minimal impact of trout on benthic biomass and community composition in New Zealand lakes is that beds of submergent vegetation act as an extensive refuge for large-bodied invertebrates. There is a wealth of empirical and theoretical evidence that supports the idea that refuges increase the equilibrium number in prey populations (see review by McNair, 1986), which in

turn should decrease the likelihood of local extinction of otherwise vulnerable prey. It is well established that structural complexity created by submergent vegetation can ameliorate the top-down effects of fish on benthic invertebrates (Crowder & Cooper, 1982; Diehl, 1988, 1992; Carlisle & Hawkins, 1998; Markland, Blindow & Hargeby, 2001), and this is one explanation for why New Zealand lakes with trout have much higher benthic biomass (review by Kelly & McDowall, 2004, this study) than those in North America (Larson *et al.*, 1992; Liss *et al.*, 1995; Bradford *et al.*, 1998; Carlisle & Hawkins, 1998). Trout can glean invertebrates from the edges of submergent beds, but might be unable to effectively reduce benthic biomass or cause species extinctions. Competition-induced migration of aquatic stages to the tops and edges of these refugia, as well as flushes of emerging aquatic insect adults (see Rowe, 1987), could provide a high, stable source of benthic production that underlie high growth rates of trout in New Zealand lakes (Deans, Unwin & Rodway, 2004). If this scenario is correct, decreases in water clarity (one condition necessary for extensive deep-water vegetation) associated with eutrophication could have catastrophic effects on the recreational fishery in New Zealand lakes (e.g. see Jeppesen *et al.*, 2005).

Do trout in New Zealand exert weak predation pressure on benthos?

Independent of the vegetation hypothesis above, there are several potential explanations related to trout abundance and demography for the apparently weak top-down effects of trout in New Zealand lakes. A quantitative study of trout densities was beyond the scope of our study, but we did conduct visual searches in these extremely clear lakes to confirm fisheries data for the presence and species of trout. Moreover, in the lakes in which we quantified benthic biomass, trout were frequently observed from the shoreline and while snorkeling. Nonetheless, we cannot eliminate the hypothesis that the modest trout impact on benthic invertebrates is in part a result of low trout densities.

The most striking observation about the brown trout and rainbow trout that we observed was the lack of size-structure and preponderance of large adults. From the shoreline and while snorkeling, we frequently observed large trout and small native benthic

fishes (bullies, *Gobiomorphus* spp.), but rarely observed juvenile size classes of trout in either the pelagic or littoral zone (S.A. Wissinger & H.S. Greig, unpubl. data). Many self-sustaining populations of rainbow and brown trout in New Zealand lakes rely on inlet and outlet streams for spawning sites and nurseries (Hayes, 1988; McDowall, 1990) and the benthivorous juveniles remain in these nursery streams where they have higher growth and survival than those in open lake basins (Percival & Burnet, 1963; Hayes, 1995; Graynoth, 1999). The ontogenetic shift from benthivory to piscivory in both rainbow and brown trout occurs at a relatively small size in lakes and fish that re-enter the lake system after that shift might exert a minimal impact on lake benthos (Mittlebach & Persson, 1998; Keeley & Grant, 2001). Dietary data for brown trout in Europe (e.g. Saksgard & Hesthagen, 2004; Hyvarinen & Huusko, 2006; Jensen *et al.*, 2006) suggest that adults in lakes are often predominantly piscivorous and/or primarily feed at the surface on terrestrial and emerging insects (also see Smith, 1959). The extremely high clarity of the lakes we studied should favour piscivory and surface feeding over benthivory (Rowe *et al.*, 2003). The relatively large size of most fish and a tendency towards piscivory might partly explain why the impact of trout on New Zealand lake zooplankton communities is modest (Jeppesen *et al.*, 1997) compared with that observed in North America and Europe (e.g. Leavitt *et al.*, 1994; Nybert, 1998; McNaught *et al.*, 1999; Donald *et al.*, 2001; Knapp *et al.*, 2001; Parker *et al.*, 2001).

In addition to the absence of population size structure, there is also a difference in the individual size of adult trout in these lakes compared with those in high elevation lakes in western North America where trout effects on benthos are best described. Regardless of species (in addition to brown and rainbow, stocked species include brook [*S. fontinalis* Mitchell], cutthroat [*O. clarki* (Richardson)] and related oncorhynchids), trout in those lakes are typically much smaller and more likely to feed on zooplankton and epibenthic invertebrates than the large brown and rainbow trout in New Zealand lakes (e.g. Leucke, 1990; Carlisle & Hawkins, 1998; Schindler *et al.*, 2001).

Hypotheses related to differences in the characteristics of trout in New Zealand versus North America and Europe are not mutually exclusive from the

submergent macrophyte hypothesis; i.e. both structural differences in benthic habitats and species-specific or lake-specific variation in trout foraging behaviour could explain the weak top-down effect that trout appear to have on benthic invertebrates in New Zealand lakes. Understanding the relative importance of these two hypotheses would have important consequences for building general models that incorporate benthos into whole lake food webs (Vadeboncoeur, Vander Zanden & Lodge, 2002; Vander Zanden & Vadeboncoeur, 2002; Sierszen, McDonald & Jensen, 2003; Rowe & Schallenberg, 2004).

Are New Zealand lentic invertebrates relatively invulnerable to trout?

In addition to the explanations above, it is also possible that one or more attributes of the invertebrates in New Zealand make them less vulnerable to trout predators compared with those in North America and Europe. Most invertebrate taxa at our study sites were present in all or most of the lakes in our survey, regardless of differences in the presence of trout, elevation, lake area and depth, geographic location and water chemistry. Many of these same ubiquitous taxa are reported in species lists from studies on small permanent ponds to extremely large lakes to the north and south of our study area on the South Island (e.g. Forsyth, 1978; Timms, 1982; Talbot & Ward, 1987; Weatherhead & James, 2001). The absence of species replacements between trout and troutless lakes is a striking result of our survey that is in contrast to what is found in North America where different species within genera or different genera within families of invertebrates occur in fish and fishless lakes within the same region (Wellborn *et al.*, 1996).

Damselflies exemplify the degree to which North American and New Zealand faunas differ in terms of habitat diversification within a taxon. All of the lakes in our study were dominated by one endemic coenagrionid species (*X. zealandica*) that is widely distributed across habitat types (lakes, permanent wetlands, brackish marshes and streams) in New Zealand (Rowe, 1987). In contrast, there has been rapid evolutionary diversification of coenagrionids in North America, so that within a genus (e.g. 33 species of *Enallagma*), different species with different behaviours, physiologies and morphologies are found in

lakes with and without fish (McPeck, 1990; McPeck & Brown, 2000). Similarly, one lestad damselfly (*Austrolestes colenstonis*) occurs in the emergent vegetation of both trout and troutless lakes in New Zealand, whereas different *Lestes* species in North America occur in lentic habitats with than without fish (Stoks, McPeck & Mitchell, 2003). The dominance of a few generalist taxa in New Zealand lakes is not limited to damselflies; the dragonflies, caddisflies, water bugs, beetles and molluscs that dominate in both trout and troutless lakes all have ecologically equivalent counterparts in North America for which there are typically species replacements between habitats with and without vertebrate predators (Wellborn *et al.*, 1996; Wissinger *et al.*, 2006).

A similar observation has been made about stream invertebrates in New Zealand, which are often generalists rather than the trophic and habitat specialists that replace each other along stream size continua in North America and Europe (Winterbourn, Rounick & Cowie, 1981; Winterbourn, 1987, 2000). That both stream and lake invertebrate communities in New Zealand are dominated by generalists might suggest that there are phylogenetic constraints to diversification related to the endemic nature of the fauna (Forsyth & Lewis, 1987). Winterbourn (1997) has argued that the unpredictable nature and intensity of disturbance has selected for trophic opportunism and flexible life histories that allow New Zealand stream taxa to inhabit a wide range environments. The observation that generalist species are most abundant in the most highly disturbed streams (Townsend, Dolédec & Scarsbrook, 1997) is consistent with Winterbourn's idea that ecological conditions in New Zealand (rather than phylogenetic constraints) have favoured the evolution of a generalist stream fauna. It is difficult to envision how physical disturbance has constrained the diversification of invertebrates in permanent lentic habitats. However, it is possible that the selection pressure on invertebrate diversification exerted by native New Zealand galaxiids and/or more recently by introduced salmonids differs from that exerted by North American and European fishes (especially percids and centrarchids) (also see Leucke, 1990). Experiments that compare anti-predator responses of lake invertebrates to trout versus native fishes would be a first step towards understanding the behavioural ecology of fish-benthic invertebrate interactions in New Zealand lakes (as in

McIntosh & Townsend, 1995). A comparison of the between-habitat genetic variation within a habitat generalist in New Zealand (e.g. *X. zealandica*) to that observed between populations of habitat specialists in North America (e.g. *Enallagma* spp.) might provide insight into the relative importance of phylogenetic and ecological constraints on diversification and community evolution (McPeck & Miller, 1996; Webb *et al.*, 2002).

In conclusion, we view this study as a first attempt at characterising the nature of trout – benthic community relationships in New Zealand lakes. Our results beg the question: to what degree are the apparently weak top-down effects of trout on lake benthic communities in New Zealand a result of the (i) structure of the lakes? (ii) biology of the trout? and/or (iii) characteristics of the invertebrate fauna? Experimental tests (whole lake and mesocosms) of these potential explanations should have important consequences for understanding interactions between introduced salmonids and native species, and for the long-term health of the sport-fishing industry in New Zealand.

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Appendix 1 Physical and chemical characteristics, and trout status of lakes and temporary tarns included in this study. See Fig. 1 for cluster locations. Trout species (B, brown trout; R, rainbow trout) based on North Canterbury Fish and Game Management Plan (1997) and visual observations. Elevation, area and depth for most lakes from Livingston *et al.* (1986). See text for an explanation of chemical measurements (Cond., conductivity; TP, total phosphorus).

Lake name	Cluster	Northing	Easting	Terrestrial vegetation	Trout	Elevation (m)	Area (ha)	Depth (m)	[TP] ($\mu\text{g L}^{-1}$)	pH	Cond. ($\mu\text{S cm}^{-1}$)
Sarah	Waimakiriri	5794630	2410331	Tussock	B, R	577	20	6	8.6	7.4	60
Hawdon	Waimakiriri	5788647	2416386	Tussock	B, R	579	30	4	13.2	7.3	40
Marymere	Waimakiriri	5787171	2416757	Tussock	B	619	22	4	18.0	7.3	50
Romulus	Waimakiriri	5792730	2408440	Pasture	No	640	12	3	12.5	8.0	60
Pearson	Waimakiriri	5789142	2410989	Pasture	B, R	611	178	16	14.5	7.2	50
Grasmere	Waimakiriri	5792962	2410276	Pasture	B, R	584	63	12	17.1	7.3	70
Little Blackwater	Waimakiriri	5787670	2422550	Pasture	No	680	10	2	20.2	7.3	60
Blackwater	Waimakiriri	5787371	2422518	Pasture	B, R	610	16	3	25.2	7.0	30
Kaurapataka	Waimakiriri	5823781	2403384	Forest	B	505	55	8	8.3	6.2	20
Lagoon	Waimakiriri	5794275	2395595	Tussock	No	1160	8	3	3.7	5.9	10
Bealey	Waimakiriri	5796500	2394860	Tussock	No	1020	2	2	3.9	6.2	20
Taylor	Hurunui	5826343	2447074	Tussock	B, R	588	185	40	11.4	7.8	65
Sheppard	Hurunui	5827201	2448181	Tussock	B	587	115	21	10.4	7.6	60
Mary	Hurunui	5827983	2448382	Tussock	No	590	2	3	11.7	7.4	70
Little Mason	Hurunui	5829091	2441724	Tussock	B	674	20	2	12.5	7.5	70
Big Mason	Hurunui	5831085	2441877	Tussock	B	675	53	38	10.4	7.5	70
Marion	Hurunui	5836371	2447238	Forest	No	640	17	4	36.5	7.0	50
Lorraine	Hurunui	5845220	2468120	Pasture	No	540	16	5	45.3	7.4	80
Lewis	Hurunui	5869545	2460740	Forest	No	840	2	3	21.2	5.8	15
Horseshoe	Hurunui	5845404	2470742	Pasture	B	500	4	5	29.0	7.6	90
Fish	Tarndale	5898494	2504367	Tussock	B, R	1008	15	3	33.6	6.3	20
Headwater	Tarndale	5897740	2504540	Tussock	No	1060	1	2	58.2	6.1	10
Tussock	Tarndale	5897050	2502660	Tussock	No	1050	1	2	48.3	6.1	15
Camp Tarn	Tarndale	5897780	2505280	Tussock	No	1037	10	3	31.1	6.3	20
Bowscale	Tarndale	5897679	2506221	Tussock	B, R	1027	48	5	29.3	6.2	20
Sedgemere	Tarndale	5896860	2503029	Tussock	B, R	1010	12	2	16.8	6.1	20
Island Saddle	Tarndale	5893020	2494340	Pasture	B	1180	2	3	23.3	7.1	50
Powerline	Tarndale	5888490	2490350	Pasture	No	1080	2	2	15.3	7.3	50
Clarence Flats	Tarndale	5888320	2490300	Tussock	No	1060	2	2	16.3	7.2	45
Tennyson	Tarndale	5889564	2487549	Tussock	B, R	1100	65	10	15.5	7.0	30
Lyndon	Rakaia	5766444	2404582	Pasture	B, R	830	95	28	7.4	7.1	30
DryAcheron	Rakaia	5755090	2401650	Pasture	No	616	1	3	25.6	7.5	60
Spectacles	Rakaia	5766250	2393170	Pasture	No	590	4	4	30.0	7.4	60
BlackHole	Rakaia	5755750	2400840	Pasture	No	600	1	8	30.4	7.4	50
Red Lake North	Rakaia	5763490	2397450	Pasture	B	665	2	4	22.5	7.0	60
Red Lake South	Rakaia	5763240	2397850	Pasture	B	660	2	3	21.5	7.2	60
Henrietta	Rakaia	5774257	2388180	Tussock	B, R	575	4	2	24.4	6.9	100
Catherine	Rakaia	5775219	2393004	Tussock	B, R	669	16	10	15.8	7.3	70
Selfe	Rakaia	5773065	2389721	Tussock	B, R	574	33	29	35.7	7.2	100
Ida	Rakaia	5773667	2391253	Tussock	B, R	675	12	9	42.2	7.1	80
Little Ida	Rakaia	5773770	2390510	Tussock	B, R	676	4	5	45.0	7.0	85
Evelyn	Rakaia	5771731	2391272	Tussock	B, R	586	15	3	32.3	7.1	55
Georgina	Rakaia	5764613	2393892	Tussock	B, R	542	20	12	42.1	7.0	55

Appendix 2 Invertebrate taxa in trout and troutless lakes in the central South Island of New Zealand. Predominant vegetation zone(s) of occurrence: emergent, shoreline emergent zone; open, open substrate or sparsely vegetated littoral zone; submergent, submergent vegetation

	Trout	Troutless	Vegetation zone		
			Emergent	Open	Submergent
Ephemeroptera					
<i>Deleatidium</i> spp.	✓	✓		✓	
<i>Nesameletus ornatus</i> (Eaton)	✓	✓	✓	✓	
Odonata					
<i>Austrolestes colenisonis</i> (White)	✓	✓	✓		
<i>Xanthocnemis zealandica</i> (McLachlan)	✓	✓	✓		✓
<i>Procordulia grayi</i> (Selys)	✓	✓	✓	✓	✓
<i>Procordulia smithi</i> (White)	✓	✓	✓	✓	✓
Plecoptera					
<i>Zelandobius furcillatus</i> group	✓	✓		✓	
<i>Austroperla cyrene</i> (Newman)	✓			✓	
Trichoptera					
<i>Pycnocentroides aureolus</i> (McLachlan)	✓			✓	
<i>Pycnocentria evecta</i> McLachlan	✓			✓	
<i>Hudsonema amabile</i> (McLachlan)	✓	✓	✓	✓	✓
<i>Triplectides cephalotes</i> (Walker)	✓	✓	✓	✓	✓
<i>Triplectides obsoletus</i> (McLachlan)	✓	✓	✓	✓	✓
<i>Oecetis unicolor</i> (McLachlan)	✓	✓	✓	✓	✓
<i>Oecetis iti</i> McFarlane	✓	✓	✓	✓	✓
<i>Oxyethira albiceps</i> McLachlan	✓	✓	✓	✓	✓
<i>Paroxyethira tillyardi</i> Mosely	✓	✓	✓	✓	✓
<i>Paroxyethira hendersoni</i> Mosley	✓	✓	✓	✓	✓
Lepidoptera					
<i>Hygraula nitens</i> (Butler)	✓	✓	✓		✓
Hemiptera					
<i>Sigara arguta</i> White	✓	✓	✓	✓	✓
<i>Diaprepocoris zealandiae</i> Hale	✓	✓	✓	✓	✓
<i>Microvelia macgregori</i> (Kirkaldy)	✓	✓	✓		
<i>Anisops wakefieldi</i> White	✓	✓	✓		✓
<i>Anisops assimilis</i> White	✓	✓	✓		✓
<i>Saldula</i> sp.	✓	✓	✓		
Coleoptera					
<i>Liodessus plicatus</i> (Sharp)	✓	✓	✓		
<i>Liodessus deflectus</i> Ordish	✓	✓	✓		
<i>Antiporus strigosulus</i> (Broun)	✓	✓	✓		✓
<i>Antiporus femoralis</i> (Boheman)	✓	✓	✓		✓
<i>Lancetes lanceolatus</i> (Clark)	✓	✓	✓		
<i>Rhantus suturalis</i> Macleay	✓	✓	✓		✓
<i>Onychohydrus hookeri</i> (White)	✓	✓	✓		
<i>Limnoxenus zealandicus</i> (Broun)	✓	✓	✓		
Scirtidae no. 1	✓	✓	✓		
Staphylinidae no. 1	✓	✓	✓		
Diptera					
<i>Limonia</i>	✓	✓	✓		
<i>Zelandotipula</i>	✓	✓	✓		
Ceratopogonidae no. 1	✓	✓	✓	✓	
Stratiomyidae	✓	✓	✓		✓
<i>Chironomus zealandicus</i> Hudson	✓	✓	✓		✓
<i>Cladopelma curtivalva</i> (Kieffer)	✓	✓	✓	✓	
<i>Parachironomus cylindricus</i> (Freeman)	✓	✓			✓
<i>Paucispinigera</i> sp.	✓	✓	✓		
<i>Polypedilum pavidus</i> (Hutton)	✓	✓	✓		✓

Appendix 2 (Continued)

	Trout	Troutless	Vegetation zone		
			Emergent	Open	Submergent
<i>Tanytarsus verspertinus</i> Hutton	✓	✓	✓	✓	✓
<i>Tanytarsus funebris</i> Freeman	✓	✓	✓	✓	✓
<i>Tanytarsus</i> sp. no. 3	✓		✓		
<i>Ablabesmyia mala</i> (Hutton)	✓	✓	✓		✓
<i>Gressittius antarcticus</i> (Hudson)	✓	✓	✓		
<i>Macropelopiini</i> sp. no. 1	✓	✓	✓		
<i>Macropelopiini</i> sp. no. 2	✓	✓	✓	✓	✓
<i>Cricotopus planus</i> Boothroyd	✓	✓	✓		✓
<i>Cricotopus zealandicus</i> Hutton	✓	✓	✓		✓
<i>Metriocnemus</i> sp.					
<i>Paratrichocladius pluriserialis</i> (Freeman)	✓	✓	✓		
<i>Lymnophyes</i> sp.	✓	✓	✓		
Orthocladiinae no. 1		✓	✓	✓	✓
Orthocladiinae no. 2		✓		✓	✓
Acari					
<i>Hydrozetes lemnae</i> (deCoggi)	✓	✓	✓		
<i>Hydrachna maramauensis</i> Stout	✓	✓	✓	✓	✓
<i>Eylais waikawae</i> Stout	✓	✓	✓		
<i>Piona pseudouncata</i> (Piersig)	✓	✓	✓		
<i>Piona uncatata exigua</i> Viets	✓	✓	✓	✓	✓
<i>Arrenurus lacus</i> Stout	✓	✓	✓	✓	✓
Mollusca					
<i>Potamopyrgus antipodarum</i> (Gray)	✓	✓	✓	✓	✓
<i>Gyraulus corinna</i> (Gray)	✓	✓	✓	✓	✓
<i>Glyptophysa variabilis</i> (Gray)	✓	✓	✓	✓	✓
<i>Physella acuta</i> (Draparnaud)	✓	✓	✓	✓	✓
<i>Austropeplea tomentosa</i> (Pfeiffer)	✓	✓	✓	✓	✓
<i>Lymnaea stagnalis</i> (Linnaeus)	✓	✓	✓	✓	✓
<i>Musculium novaezealandiae</i> Deshayes	✓	✓	✓	✓	✓
<i>Hyridella menziesi</i> (Gray)	✓	✓	✓	✓	✓
Crustacea					
<i>Simocephalus vetulus</i> (Schödler)	✓	✓	✓		
<i>Chydorus sphaericus</i> (O.F. Müller)	✓	✓	✓		✓
<i>Camptocercus australis</i> Sars	✓	✓	✓		
<i>Herpetocypris pascheri</i> Brehm	✓	✓	✓	✓	✓
<i>Cyprretta viridis</i> (Thomson)	✓	✓	✓	✓	✓
<i>Cypridopsis vidua</i> (O.F. Müller)	✓	✓	✓	✓	✓
<i>Eucypris</i> sp.	✓	✓	✓	✓	✓
<i>Cypricercus</i> sp.	✓	✓	✓	✓	✓
<i>Cyprinotus incongruens</i> (Ramdohr)	✓	✓	✓	✓	✓
<i>Candonocypris</i> sp.	✓	✓	✓	✓	✓
<i>Acanthocyclops</i> sp.	✓	✓	✓	✓	✓
Annelida					
<i>Lumbriculus variegatus</i> (Müller)	✓	✓	✓	✓	✓
Tubificidae no. 1					
Tubificidae no. 2	✓	✓	✓	✓	✓
Lumbricidae no. 1	✓	✓	✓		
<i>Alboglossiphonia multistriata</i> (Mason)	✓	✓	✓		✓
<i>Placobdelloides maorica</i> (Benham)	✓	✓	✓	✓	✓
Collembola	✓	✓	✓		
Turbellaria	✓	✓	✓	✓	✓