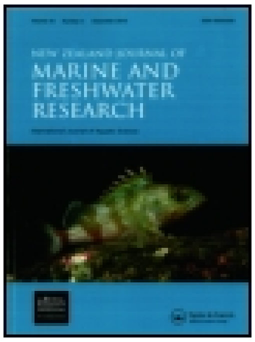

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Effects of hydro-electrically induced water level fluctuations on benthic communities in Lake Hawea, New Zealand

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Abstract Artificially induced lake level fluctuations influence benthic communities in numerous lakes, but their effects are relatively poorly understood. Littoral communities were described from three habitat types in two oligotrophic lakes in New Zealand, one subject to a natural hydrological regime with limited lake level fluctuations, the other subject to >5 m fluctuations as a result of hydro-electric management. The fluctuated lake showed evidence of littoral compression and the replacement of macrophyte beds at shallow and intermediate depths by green filamentous algae. Macroinvertebrate biomass was higher in the fluctuated lake, despite this lake having a lower standing crop of primary producers compared with the unfluctuated lake. Disturbance of the littoral zone may reduce macrophyte biomass but may maintain high levels of primary producer productivity through an increase in benthic algae such as diatoms.

Keywords lake levels; macrophytes; macroinvertebrates; New Zealand

INTRODUCTION

Lake levels of reservoirs are commonly fluctuated to maximise the generation potential of hydro-electric schemes, with potentially profound effects on disturbance regimes (Hellsten & Riihimaki 1996). Most studies to date have concentrated on the effects on lake macrophytes and have assumed that effects on littoral invertebrates and fish are related to loss of macrophytes as habitat (e.g., James et al. 1995; Wagner & Falter 2002). Studies of macrophyte distributions have generally shown substantial reductions in cover owing to direct disturbance (e.g., Clayton et al. 1986; James et al. 1995; Wagner & Falter 2002), except where local disturbance factors such as freezing exceed the effects of the fluctuations (Hellsten & Riihimäki 1996). One of the consequences of increased lake level fluctuations is littoral compression (James et al. 1995). As lake levels rise, aquatic vegetation establishes itself in the newly inundated zone. However, if the lake is drawn down again, then colonists will be removed by dessication (James et al. 1995) or frosting (Viner et al. 1989). In deeper water, raising lake levels can reduce plant communities owing to reduction in light levels (James et al. 1995). If lake levels are fluctuated at a rate which does not allow colonisation of the newly inundated areas as levels increase, or recovery of weed beds in deeper waters as water levels reduce, then the width of the zone of littoral vegetation on the shore can become reduced with potential effects on higher trophic levels such as fisheries (Mylechreest 1978).

Other studies of lake level fluctuations have described effects on substrate composition, shore stability, and nutrient dynamics (e.g., James et al. 1995; Verschuren et al. 2000; Wagner & Falter 2002). Lake beaches and other structures are a result of an interaction between lake levels, sediment supply, and wave action. Any alteration in water level will initiate change in the lake shore (Mark & Kirk 1987). Shoreline exposure can cause excessive beach erosion through slumping, damaging shoreline vegetation and causing loss of beach material into

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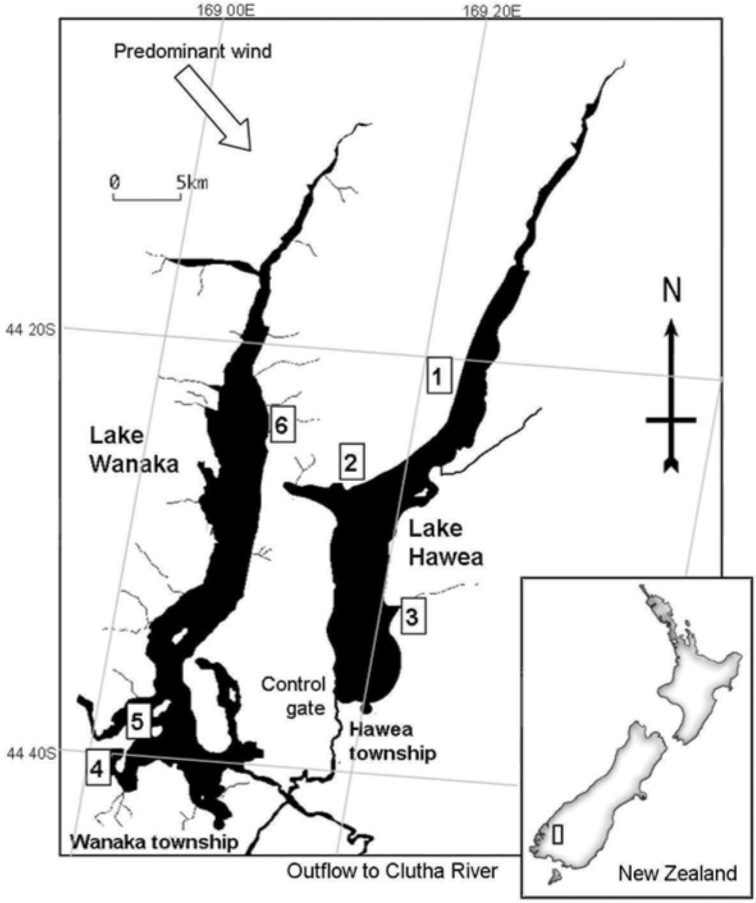


Fig. 1 Location of the two study lakes with major towns shown. Numbers in squares indicate transect locations—Lake Hawea: Terrace Creek (1), Kidds Bush (2), Timaru Creek (3); Lake Wanaka: Paddock Bay (4), Bishops Bay (5), Camp Creek (6).

deeper waters (Mark & Kirk 1987). Erosion of lake margins affects aquatic communities by generating inputs of sediment which may alter aquatic habitat (Clayton et al. 1986; Schwarz & Hawes 1997).

It is clear that lake level fluctuations increase the frequency and intensity of disturbance in the littoral zone (Mylechreest 1978). Predicting the effects of this increased disturbance, by reference to either theory or previous empirical studies, is challenging. Intermediate levels of disturbance have been hypothesised to maximise diversity (Connell 1978), which influences productivity (see Hooper et al. 2005 for review). Direct modelling and empirical studies of disturbance–productivity relationships have found that intermediate levels of disturbance can maximise productivity by maintaining communities at an intermediate level of succession (e.g., Cooper 1973; Rutherford 1993). Recently, a synthetic literature has emerged which places relationships between disturbance, diversity and productivity within a common causal framework (see Cardinale et al. 2005 for review). This research suggests that relationships between diversity and productivity depend on the disturbance context in which they occur. Differing management of lake levels in two neighbouring lakes in the South Island of New Zealand, with one lake fluctuated for hydroelectric generation and the other subject to a natural hydrologic regime, provided an opportunity to test the effects of differing disturbance regime on the benthic communities of lakes.

MATERIALS AND METHODS

Study site

Lakes Hawea and Wanaka (Fig. 1) are a pair of oligotrophic, high-country lakes in the South Island of New Zealand. Predominant winds are from the northwest. Of glacial origin, the two lakes are separated by a narrow neck of land less than 1 km wide. The completion of a control gate structure in 1958 and its subsequent operation have resulted in the level of Lake Hawea being increased by approximately 14 m, and lake level fluctuations increasing from 2.86 vertical metres to up to 21.90 m, although fluctuations in the last decade have not exceeded 7 m (Chisholm et al. 2000). With the exception of this difference in lake level fluctuations, the two lakes are very similar, sharing the same orientation, approximate surface area, depth, and broad patterns of surrounding land use (Table 1). Conditions within the lakes are also similar, with both lakes being oligotrophic and having very high clarity (Table 1).

Lakes Hawea and Wanaka were surveyed in the period 12 to 15 November 2001 (austral spring). At the time of sampling, both lakes were slowly refilling, and lake levels were at 341.10 m a.s.l. (Lake Hawea) and 277.10 m a.s.l. (Lake Wanaka). The areas sampled in both lakes had been inundated for 35 days (Lake Hawea) and >365 days (Lake Wanaka), respectively.

Three transects were established on each lake, paired to represent similar habitat types (Table 2). Three broad habitat types were sampled; exposed cobbly shore, sheltered cobbly shore, and soft shore, representing the majority of the habitat available in both lakes. The slope of the shore above water line was measured using a surveyor's level and staff at 5 m intervals for each transect.

Transects sampled were generally similar, with the different habitats at the different lakes sharing similar shore slope and underlying lithology (low metamorphic grade schist) (Table 2). The soft shore sites were more shallowly sloping, with turf vegetation evident and fine substrates (silts and sands). The sheltered beach sites tended to have a higher slope and sparse vegetation amongst a matrix of cobbles and pebbles. The exposed shores were typified by larger substrate sizes (cobbles to boulders) and steeper slopes, with sparse grasses predominant.

Table 1 Overview of the location and physical characteristics of lakes Hawea and Wanaka, New Zealand (from Livingston et al. 1986).

	Lake Hawea	Lake Wanaka
Origin	Glacial	Glacial
Trophic status	Oligotrophic	Oligotrophic
Underlying geology	Schist	Schist
Altitude (m a.s.l.)	347	277
Orientation (longest axis)	NNW	NNE
Maximum depth (m)	384	311
Lake area (km^2)	137.60	180.10
Dominant catchment land uses (%)		
Tussock	52.5	55.7
Native forest	17.1	14.3
Scrub	14.6	13.3
Pasture	2.4	4.6
Average clarity (Secchi depth, m)	18.8	17.0

Table 2 Location and general description of the transects sampled.

	Habitat type	Shore slope (%)	NZMS map and grid reference	Transect bearing
Lake Hawea				
Terrace Creek	Sheltered delta	2.9	G39 183361	70
Kidds Bush	Sheltered beach	3.5	G39 136336	64
Timaru Creek	Exposed beach	5.0	G39 164262	249
Lake Wanaka				
Paddock Bay	Sheltered delta	3.0	F40 925095	169
Bishops Bay	Sheltered beach	5.0	F40 959119	168
Camp Creek	Exposed beach	7.0	F39 064387	249

Macrophyte and macroinvertebrate sampling

Sections of each transect which were under water at the time of sampling were surveyed using SCUBA divers operating from a boat. Samples were taken at 1, 3, 5, 7, and 12 m below the surface. The sampling depth was determined using sonar, and a weighted line was dropped attached to a marker buoy. Divers swam along the transect line sampling at each location.

Three quadrats (area 0.06 m^2) were randomly placed within a 2 m radius around each depth marker and the identity and relative cover of any macrophyte species assessed. At immediately adjacent locations to each quadrat, Surber samplers (0.06 m^2, 100 μm mesh) were used to sample the sediment and macrophytes to a depth of 5 cm. Substrate was scooped into the sample net by hand and water current generated to wash fine sediment and invertebrates into the sample net. The net was then detached, tied off to the dive line, and hauled to the surface, where the contents were sieved through a 250 μm sieve and stored in 5% formaldehyde for subsequent analysis. Between stations, the divers took note of changes in slope, macrophyte cover, and sediment type.

Laboratory processing

In the laboratory, each Surber sample was rinsed through a 250 μm sieve to remove formalin residue, and inspected at 10× magnification for macroinvertebrates. All complete invertebrates (defined as any invertebrate where the head was present) in the samples were identified to the lowest taxonomic level possible using Winterbourn et al. (2000). For chironomids, difficulties in identifying smaller specimens meant that they were separated into three main groups: *Chironomus zelandicus*, tanypode (predatory) chironomids, and others. Each invertebrate was counted and measured for length (to the nearest 0.5 mm). Lengths were converted to biomass (in mg) using length/mass regressions published in Towers et al. (1994).

All macrophytes were removed from the samples, washed and divided into different species based on the keys of Coffey & Clayton (1988) and Johnson & Brooke (1989). Samples were then weighed (to the nearest g) to provide a measure of wet weight of each macrophyte species.

Statistical analysis

Aquatic communities at the different transects were compared in terms of species biomass and community composition. Patterns of biomass of invertebrates and macrophytes were analysed using ANOVA for effects of lake, habitat, and depth nested as a continuous variable within habitat (Lawton & Jackson 1969). Linear regression (Galton 1886) was used to test for a relationship between macroinvertebrate biomass and macrophyte biomass. All data were tested for normality and homogeneity of variance and analysed in SYSTAT (2002).

RESULTS

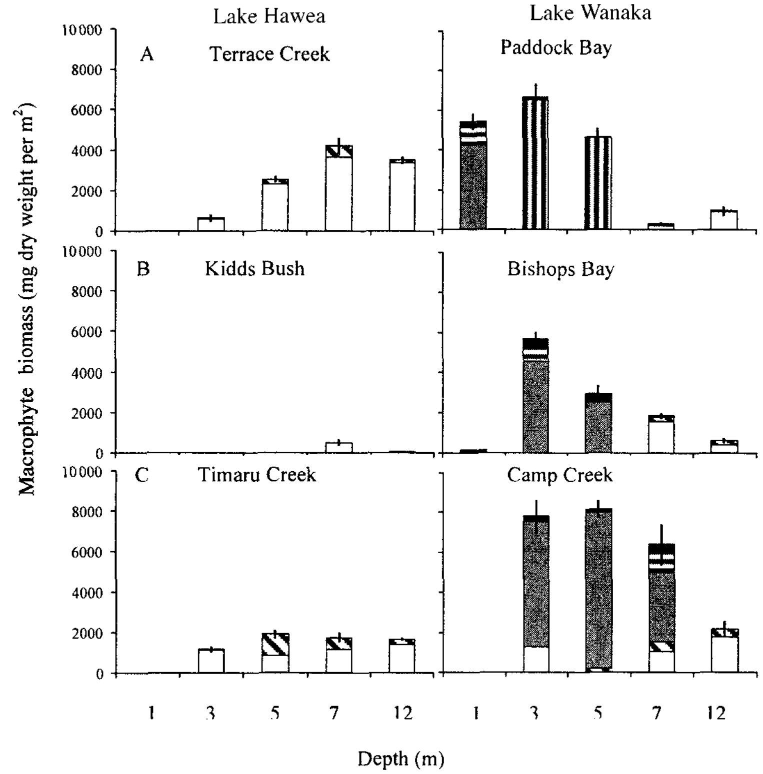
Aquatic vegetation patterns

A range of primary producers were present in the lakes (Table 3). Mats of green filamentous algae were observed at all depths where there was exposed rocky substrate and, less commonly, as a mat on top of silts. There were significant differences in biomass between lakes ($F_{1,6} = 26.71$, $P < 0.01$) with lower biomass in Lake Hawea (Fig. 2), and between habitats ($F_{1,6} = 6.96$, $P = 0.01$). In both lakes, the sheltered delta sites had the highest biomass, followed by exposed and then sheltered beach habitats. Between the two lakes, there was no significant difference in biomass with depth (within habitats) ($F_{2,6} = 0.47$, $P = 0.70$), but there was evidence of a significant interaction between lake and depth ($F_{2,5} = 6.36$, $P < 0.01$). In Lake Hawea, highest biomass values occurred in deeper water, particularly at the sheltered delta site (Fig. 2). In contrast, highest biomass in Lake Wanaka occurred in the mid water zone. In both lakes, charophyte species (*Chara corallina,*

Table 3 Depth ranges (metres below water surface) of macrophyte species observed in three dive transects each at lakes Hawea and Wanaka, New Zealand.

Species/group	Lake Hawea	Lake Wanaka
Isoetes kirkii	Absent	1.0–7.0
Lilaeopsis ruthiana	Absent	0.0–7.00
Myriophyllum triphyllum	0.0–1.0	1.0–7.0
Myriophyllum aquaticum	7.0	1.0–5.0
Green filamentous algae	0.0–12.0	1.0–5.0
Glossostigma elatinoides	Absent	1.0
Potamageton cheesmanni	1.0–3.0	5.0–7.0
Elodea canadensis	3.0–5.0	1.0–5.0
Turf-forming bryophytes	Absent	3.0
Lagarosiphon major	Absent	3.0
Chara corallina	3.0–12.0+	5.0–12.0+
Nitella hookeri	3.0–7.0	3.0–12.0+
Nitella hyalina	3.0–7.0	7.0–12.0+
Nitella pseudoflabellata	3.0–12.0+	3.0–12.0+

Fig. 2 Distribution of macrophyte biomass with depth at three transects each in lakes Hawea and Wanaka. **A**, sheltered delta; **B**, sheltered beach; **C**, exposed beach. Values for each depth are means of three samples with standard error for the average of the total biomass.



Nitella hookeri, N. hyaline, N. pseudoflabellata) dominated at depth (>7 m), a distinctive midwater flora (*Myriophyllum triphyllum, M. aquaticum, Potamageton cheesmanni, Elodea canadensis, Isoetes kirkii, Lilaeopsis ruthiana, Lagarosiphon major)* at depths of 3–5 m, and a shallow water community (green filamentous algae, *Glossostigma elatinoides*, turf-forming bryophytes) close to the lake edge (Table 3). The midwater floras of the two lakes were distinct. Whereas in Lake Wanaka the macrophytes *Myriophyllum* spp. and *I. kirkii* achieved near continuous cover and very high biomass at intermediate depths, these taxa were nearly absent from Lake Hawea. Instead, at comparable depths to macrophyte beds in Lake Wanaka, Lake Hawea exhibited a shallow water extension of charophytes (Table 3) or extensive cover by low biomass green filamentous algae. In shallow water (<3.0 m), Lake Wanaka transects were dominated by the exotic species *M. aquaticum, E. canadensis, L. major*, and by turf-forming bryophytes (Table 3).

Macroinvertebrate patterns

The two lakes were characterised by broadly similar macroinvertebrate communities, dominated by the grazing mollusc *Potamopyrgus antipodarum* and the chironomid *C. zelandicus*, with predatory tanypode chironomids, sphaerid bivalves, and other molluscs (*Gyraulus, Physa*) also contributing to the biomass (Appendix 1, Fig. 3). There were no significant differences in macroinvertebrate biomass between lakes ($F_{1,6} = 2.06$, $P = 0.16$), but there was a significant difference between habitats ($F_{2,6} = 14.91$, $P < 0.01$) and a significant interaction between those factors ($F_{2,6} = 5.59$, $P < 0.01$). In both lakes, biomass was highest in the sheltered delta transects, but differences in the other habitats were not consistent between lakes (Fig. 3). In both lakes, the shallowest locations had the lowest biomass, and there was a statistically significant effect of depth (within habitats) ($F_{2,6} = 6.54$, $P < 0.01$) which was consistent between lakes (lake × depth(habitat); $F_{2,5} = 1.71$, $P = 0.17$). Most taxa were present across a broad range of depths. *Potamopyrgus* and other grazing molluscs tended to be associated with coarse substrates, whereas *Sphaerium, Chironomus*, other chironomids and the freshwater mussel *Hydriella menziesii* were associated with fine silts.

Macroinvertebrate biomass was strongly positively related to macrophyte biomass in Lake Hawea (n =

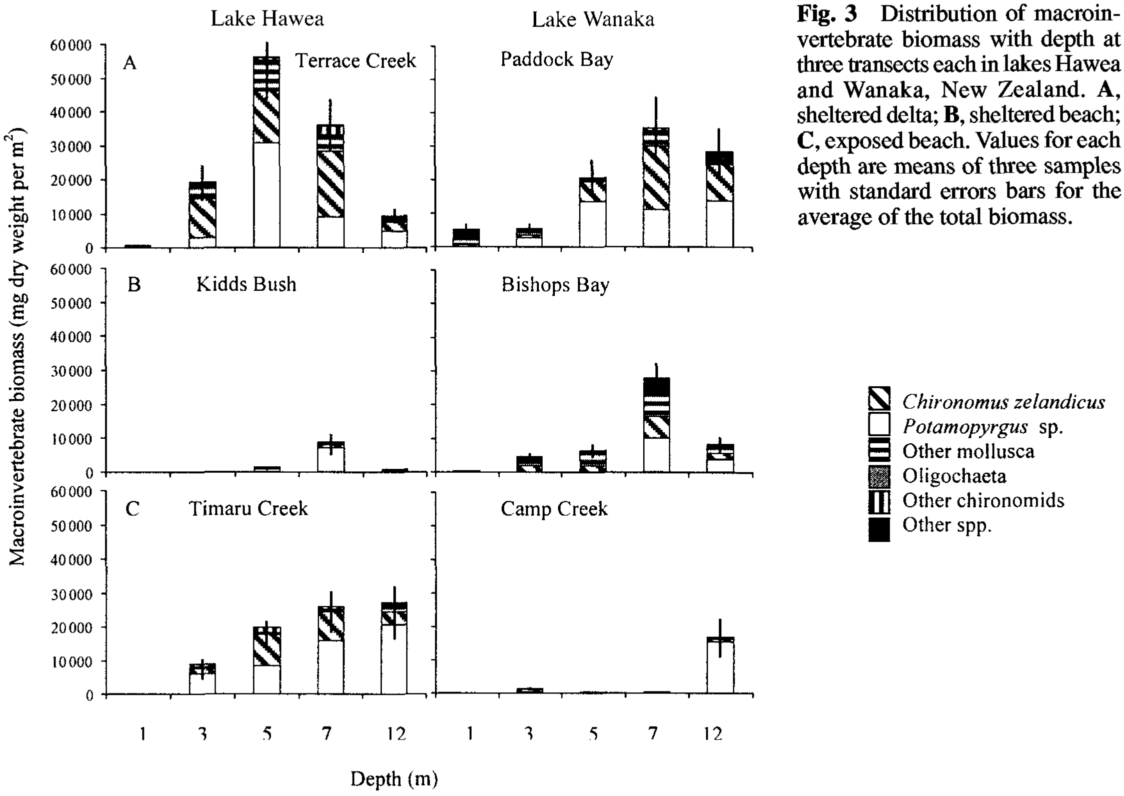


Fig. 3 Distribution of macroinvertebrate biomass with depth at three transects each in lakes Hawea and Wanaka, New Zealand. **A**, sheltered delta; **B**, sheltered beach; **C**, exposed beach. Values for each depth are means of three samples with standard errors bars for the average of the total biomass.

45, $y = 7.55x + 4786.59$, $r^2 = 0.48$, $P < 0.001$), but the low biomass of macroinvertebrates associated with intermediate depth macrophyte beds in Lake Wanaka produced a weak negative relationship between macrophyte and macroinvertebrate biomass ($n = 45$, $y = -1.54x+16314.73$, $r^2 = 0.15$, $P < 0.001$).

DISCUSSION

Lakes Hawea and Wanaka present an opportunity to appraise the effects of lake level fluctuations on the littoral communities of two lakes remarkably similar in all other physical aspects. Macroinvertebrate communities were typical of similar New Zealand lakes (e.g., Stark 1993; James et al. 1998; Kelly & Hawes 2005; Stoffels et al. 2005) with an assemblage dominated by *P. antipodarum* and *C. zelandicus*. Although biomass patterns with depth were similar to those observed in a similar New Zealand lake (Lake Coleridge, James et al. 1998), total biomass in these lakes was high, particularly in Lake Hawea. The invertebrate biomass in Lake Hawea can be considered high whether the results are considered in a national (James et al. 1998) or an international (Popp & Hoaglund 1995) context. Our samples generally ranged from 10 000–50 000 mg dry weight per m^2, compared with <0.1 mg/m^2 for Lake Pukaki, 2.1–8.3 mg/m^2 for Lake Alexandrina and 0.07–5.7 mg/m^2 for Lake Coleridge (James et al. 1998).

We found clear differences in macrophyte communities between the two lakes. Most notably, the extensive *I. kirkii* and *Myriophyllum* spp. beds evident in shallow water in Lake Wanaka were absent from Lake Hawea. A similar community dominates shallow waters at nearby lakes Te Anau, Manapouri (Johnson 1972; Stoffels et al. 2005) and, to a lesser extent, Monowai (Johnson 1991). *Isoetes kirkii* has been shown to be reduced in extent in response to lake level fluctuations (Johnson 1991), and this genus showed similar effects in a Scandinavian study (Rørslett & Johansen 1995). The absence of *Isoetes* beds from Lake Hawea allows the development of dense layers of filamentous algae on cobbles in shallow water. Whether this change results from the direct effects of disturbance through alteration in substrate (*sensu* Weatherhead & James 2001) or via some other mechanism can not be fully determined from this study. Given the general similarities in other aspects between lakes Wanaka and Hawea, the differences in macrophyte communities may result from the effects of fluctuating lake levels.

Strong associations between macrophyte communities and macroinvertebrates in lakes have been widely described (Elder 1965; Hunt & Jones 1972; Palomäki 1994, James et al. 1995; Kelly & Hawes 2005; Stoffels et al. 2005). Elder (1965) predicted that where lake level fluctuations are large, there will be a loss of macrophyte-associated species (e.g., larger insect larvae, crustaceans) and an increase in species associated with sediments (e.g., chironomids, oligochaetes, nematodes). Both lakes had low densities of invertebrates in the shallowest water, but in Lake Hawea the densities increased rapidly in deeper water. Previous studies have shown that the structural complexity, resources and refugia of macrophyte beds result in high biomass and diversity of macroinvertebrates (e.g., Elder 1965, Palomäki 1994, James et al. 1995; Stoffels et al. 2005), as was observed in Lake Hawea in the current study. In contrast, in Lake Wanaka, there was low biomass of macroinverterbates at intermediate depths, associated with *Isoetes* and *Myriophyllum*. Of particular note is that at similar depths in Lake Hawea, *Isoetes* beds were absent, and instead algal mats were present. Despite their low biomass, the algal mats present in Lake Hawea appear to support a much higher biomass of invertebrates than the macrophyte beds at comparable depths in Lake Wanaka. Diatoms and algae are capable of extremely fast generation times, and are highly palatable to invertebrates (Weatherhead & James 2001). In addition, the action of waves on the biofilm may act to slough off dead cells, maintaining the biofilm in a productive "new growth" state (Biggs & Close 1989). Recent research using stable isotope techniques is providing increasing evidence that algae (rather than macrophytes) underpin much of the productivity in lakes of this type (James et al. 2000; Kelly & Hawes 2005).

Studies of the effects of water level fluctuations on large lakes are usually hindered by the lack of suitable controls and of pre-fluctuation data. This study is a significant advance in that there was a suitable control lake for comparison. Nonetheless our inference is limited because we had no replicates of the fluctuated and unfluctuated treatments. Studies at this scale often suffer from this constraint and, in this instance, suitable replicate lakes do not exist. There is evidence to support our results from other fluctuated lakes in New Zealand that also show reduced macrophyte communities, but maintain high invertebrate productivity (Rowe et al. 2003). We were also unable to incorporate either within-habitat spatial variation or seasonal variation in our study. Earlier research (Chisholm et al. 2000) found relatively little variability within broad habitat types in Lake Hawea, with sediment type and macrophytes having a predominant effect on invertebrate communities. The same study sampled the same three transects in Lake Hawea as were sampled here, but in April (autumn) rather than November (spring). Patterns of macrophyte and macroinvertebrate distribution and biomass were very similar in the two studies, providing some evidence that seasonal variation may also be relatively muted.

Our results represent one of few studies of the direct effects of lake level fluctuations on benthic communities where there was a suitable control system for comparison. Of key importance in this study is the presence of higher invertebrate biomass in parts of the benthic zone which are disturbed by lake level fluctuations, than at similar depths in a comparable unfluctuated lake. There is the potential that benthic productivity may be higher in these areas owing to the growth of disturbance tolerant, but palatable, biofilms.

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Appendix 1 overleaf

Appendix 1 Macroinvertebrate biomass (mg dry weight per m^2) from lakes Hawea and Wanaka, New Zealand at different habitats and depths. Biomass was derived from published length/mass relationships (Towers et al. 1994).

	Lake Hawea					Lake Wanaka				
Taxa Depth (m):	1	3	5	7	12	1	3	5	7	12
Sheltered delta										
Chironomus zelandicus	99.91	2897.44	30772.80	9191.88	4695.85		2797.53	13587.99	11190.11	13887.73
Tanypodinae	49.78	298.70	746.75	2812.76	224.03		124.46	124.46	647.18	497.83
Other chironomids	74.34		8.26	8.26	16.52		8.26	528.64	8.26	
Hudsonema amabilis		24.80		24.80	24.80				74.39	322.37
Oecetis iti		88.58	167.32	187.01	9.84				19.68	19.68
Procodulia smithi						1927.30				1284.87
Potamopyrgus antipodarum	404.09	11583.86	15490.05	18992.15	2794.94	673.48	808.18	5758.26	18722.76	10607.32
Gyraulus spp.		2929.64	8351.16	2895.97	1178.59			639.81	2020.44	134.70
Physa spp.		370.41	269.39	1818.40	370.41	841.85		33.67	1751.05	1481.66
Lymnaea spp.						1718.09	1718.09		859.05	
Sphaeridae		922.04	390.62	131.72					152.16	102.20
Oligochaeta	3.00	2.46	3.00	4.37	1.09	13.92	0.27	0.82	0.55	4.64
Exposed beach										
Chironomus zelandicus		5794.88	8292.67	15786.05	20581.81		199.82			15486.31
Tanypodinae		696.97	1418.83	622.29	547.62					273.81
Other chironomids		8.26	24.78	66.08	33.04				16.52	57.82
Hudsonema amabilis		99.19	49.59	123.99						
Oecetis iti		9.84	108.27	39.37						
Potamopyrgus antipodarum		1582.68	9226.68	8485.85	3569.45	101.02	875.52	67.35	67.35	707.15
Gyraulus spp.		33.67	336.74	606.13	2121.46					
Physa spp.			168.37		67.35		101.02	67.35	33.67	134.70
Lymnaea spp.										
Sphaeridae			147.62	227.10		2.27				
Oligochaeta	19.11	644.12	1.64	1.09	1.36	10.10	151.21	30.30	52.13	16.92
Sheltered cobbly beach										
Chironomus zelandicus			799.29	7193.64	199.82				10190.99	3696.73
Tanypodinae			298.70	572.51	124.46				199.13	49.78
Other chironomids				8.26			8.26		24.78	33.04
Oecetis iti										9.84
Procodulia smithi							642.43		3854.61	
Potamopyrgus antipodarum			67.35	875.52	404.09	134.70	1852.07	1919.42	6499.09	1852.07
Gyraulus spp.										
Physa spp.							269.39	134.70	134.70	
Lymnaea spp.							1718.09	4295.23	6872.36	2577.14
Sphaeridae									31.79	
Oligochaeta	0.27	0.27	43.12	48.31	4.64	23.47	4.09	1.64	9.83	36.57