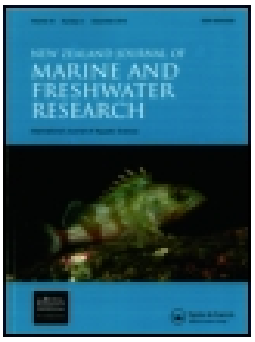

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Influence of fluctuating lake levels and water clarity on trout populations in littoral zones of New Zealand alpine lakes

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Abstract Brown trout (*Salmo trutta* Linnaeus 1758) and rainbow trout (*Oncorhynchus mykiss* Richardson 1836) populations in littoral zones of eight South Island, New Zealand alpine lakes were compared using gill and seine net sampling during summer. Lakes were selected to provide a matrix of lake level and water clarity variations and to assess how these variables influenced trout abundance (as reflected by catch rate), depth distribution, and size. Brown trout were small and in poor condition in three turbid lakes with shallow littoral zones and were scarce in one of these with a 14 m fluctuation. Although brown trout condition was generally higher in clear lakes, Lake Wanaka fish were an exception. Trout depth distribution was positively related to depth of the littoral zone. Brown trout were caught at most depths whereas rainbow trout showed variable depth preferences in different lakes. Rainbow trout catch rate, weight, and condition factor were unrelated to differences in depth of the littoral zone or lake level fluctuations, and it was concluded that spawning success and limnetic food supplies may be more important for this species. Spawning interactions may account for the different species composition between the stable clear Lake Wanaka, and the adjacent fluctuating clear Lake Hawea. Moderate and slow lake level fluctuations appear to have limited effects on trout in clear lakes, probably because trout are able to use deep littoral habitat and food supplies.

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Keywords rainbow trout; *Oncorhynchus mykiss*; brown trout; *Salmo trutta*; abundance; CPUE; size; condition factor; water clarity; lake level fluctuations

INTRODUCTION

Littoral zones of unmodified oligotrophic lakes can be more productive per unit area than deep limnetic zones and typically support a diverse and abundant flora and fauna (Graynoth et al. 1993a; James et al. 1998; Graynoth 1999). However, primary productivity in the littoral depends upon water clarity and the extent and duration of water level fluctuations (Schwarz & Hawes 1997; Schwarz et al. 2000).

In the South Island of New Zealand some oligotrophic alpine lakes have low water clarity as a result of inputs of glacially-derived suspended sediment whereas others have brown heavily humic stained water from surrounding native forest. Many lakes also have water levels artificially manipulated for hydro-electric power (HEP). These changes can reduce diversity, biomass, and production of periphyton, macrophytes, and macroinvertebrates (James & Graynoth 1995; James et al. 1998) and reduce trout food supplies. In particular, snails, chironomid, and other insect larvae associated with macrophyte beds may decline (Graynoth et al. 1993a; James et al. 1998).

Little is known of the combined effects of changes in water clarity and fluctuating lake levels on trout populations. Although some research has been carried out on brown trout (*Salmo trutta* Linnaeus 1758) in Europe (e.g., Nilsson 1961; Garnaas & Hesthagen 1982; Borgstrom et al. 1992) and Australia (Sanger 1992, 1994), and on rainbow trout (*Oncorhynchus mykiss* Richardson 1836) in the North Island of New Zealand, results are not applicable to South Island lakes, primarily because of differences in fish and invertebrate species present and habitats occupied by trout. For example, rainbow trout in the North Island live in the limnetic zone of clear lakes and eat smelt (*Retropinna retropinna*), whereas in turbid lakes they feed near the lake bed on common bullies

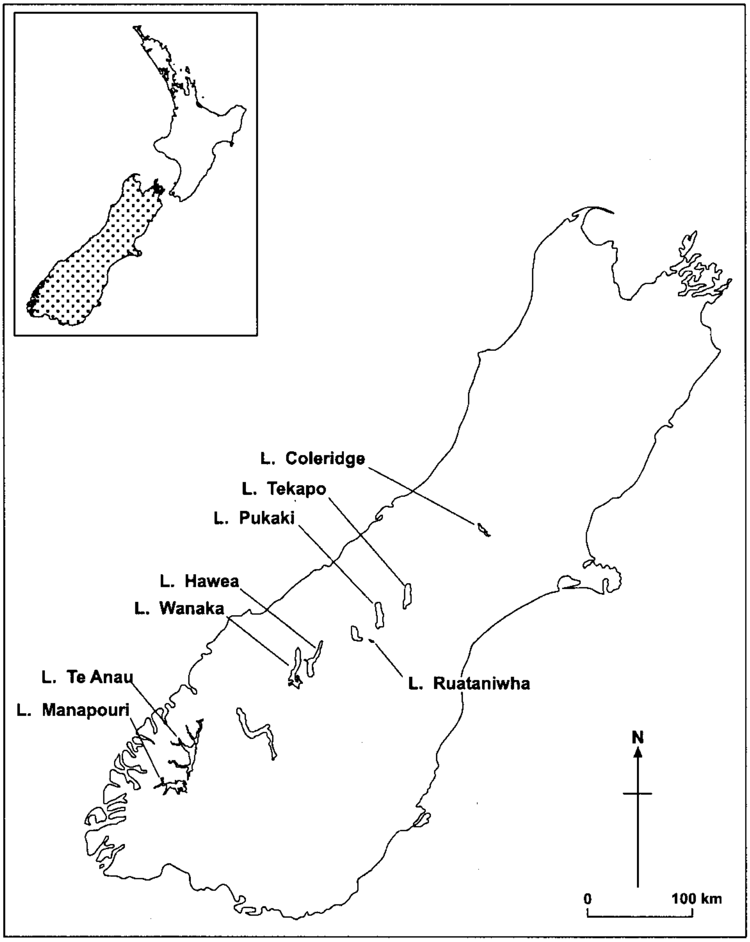

Fig. 1 South Island of New Zealand, showing lakes investigated during this study.

(*Gobiomorphus cotidianus*) (Smith 1959; Rowe 1984). In addition, growth rates are slower in the turbid lakes (Fish 1968) and few large specimen trout were caught. Mylechreest (1978) concluded that water level fluctuations in a North Island hydro-electric lake reduced trout carrying capacity and that rainbow trout appeared to be affected more than brown trout.

The situation is different in South Island lakes because smelt are generally absent and it has been concluded that most trout live in the littoral zone and feed on benthic invertebrates (Graynoth et al. 1986, 1993a; Graynoth 1999). There were indications that trout abundance and condition were relatively low in turbid South Island lakes with high glacial silt loads and extensive annual fluctuations in water level (James 1992; James & Kelso 1992; Bloomberg & James 1993). However, moderate increases in turbidity resulting from diversion of silt-laden river water into formerly clear Lake Coleridge, had no measurable effects on growth, size, and condition of trout and landlocked chinook salmon (*Oncorhynchus tshawytscha*) (Graynoth et al. 1993a; NIWA unpubl. data). Although light levels and turbidity influence visual foraging and reaction distances in salmonids (Bruton 1985; Vogel & Beauchamp 1999), recent experimental studies indicate turbid water has little effect on juvenile rainbow trout feeding rates (NIWA unpubl. data).

Therefore we hypothesised that trout abundance (as reflected by catch per unit effort (CPUE)), depth distribution, size, and condition would be directly related to littoral zone depth, and hence food supplies available, in these South Island lakes and designed a study to investigate this hypothesis using a matrix of lakes with different water clarities and level variations.

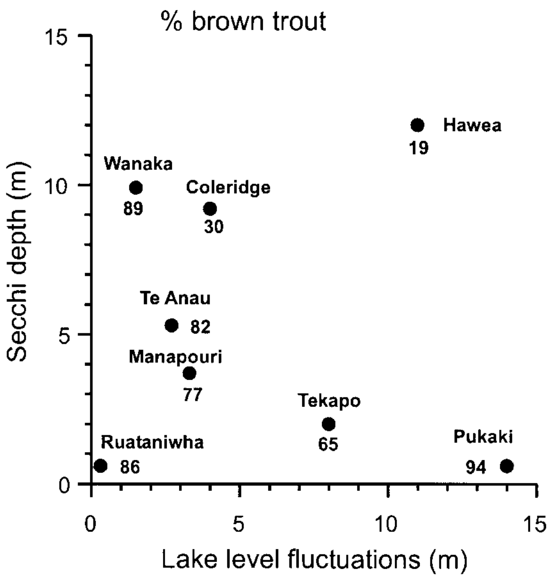

Fig. 2 Variation in water clarity (Secchi depth during survey), mean annual lake level fluctuations, and relative species composition of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) in eight study lakes. Data values are for % brown trout caught in gill nets.

METHODS

Study lakes

Eight contrasting South Island alpine lakes and reservoirs were selected (Fig. 1) for this study based on differences in littoral zone depth, caused by variations in water clarity and levels (Fig. 2). All are oligotrophic or ultra-oligotrophic with relatively productive littoral zones (James et al. 1998) and unproductive limnetic zones (Graynoth 1999; Taylor et al. 2000). With the exception of Lake Ruataniwha, which is a small artificial reservoir, these lakes are glacially derived, and moderately to relatively deep. They are all alpine lakes regularly exposed to strong winds, and consequently have cool summer surface temperatures (<20°C) and deep, oxygenated, thermoclines. They range in size from Te Anau (347.5 km^2) to Ruataniwha (3.4 km^2) and in altitude from 708 to 179 m a.s.l. (Table 1). Littoral habitats vary between lakes and Table 2 contains subjective visual assessments of the percentage composition of the substrates and macrophyte cover in the locations studied.

All these lakes (except Lake Wanaka) are controlled for HEP, with consequent increased fluctuations in lake levels. Water levels usually rise to a peak after spring snow melt, remain high over summer, and are drawn down for power generation in winter. Levels fluctuate to varying degrees between lakes (Fig. 2) and years (Table 1). Lakes which fluctuated most (Pukaki, Tekapo, and Hawea) were more stable than normal before our surveys (Table 1), and were exceptionally constant in the previous winter, fluctuating <4 m. Lake Coleridge was also more stable than usual whereas Lake Wanaka showed small changes in lake level from 1998 to early 2000, except for a "100-year flood" in mid November 1999 that increased levels by up to 3.7 m for a few weeks, and discoloured water throughout much of the lake for several months.

Secchi disc records were the only historical data available to describe water clarity, which also varied between and within lakes depending on flood events and water sources (Fig. 2). Lakes Wanaka and Hawea are typically clear. Lakes Te Anau and Manapouri have low Secchi values as a result of humic substances, whereas four lakes (Pukaki, Tekapo, Coleridge, and Ruataniwha) contain varying amounts of fine particles of glacial silt (Table 1). However, suspended sediment concentrations are low, with maximum mean values recorded in Lake Pukaki of 12 g m^{-3}, at 0.41 m Secchi (Maslin 1994). Turbidity (NTU) caused by glacial flour in these lakes is related to Secchi depth (m) (Sm) using the following equation (Maslin 1994):

$$NTU = 5.305 \times Sm^{-1.273}$$

Therefore suspended glacial flour is unlikely to have any direct deleterious effects on fish or invertebrates in these lakes.

Depth of the littoral zone in these lakes depends on both water clarity and lake level fluctuations (Fig. 3). For example, a narrow littoral fringe exists in Lake Ruataniwha, despite its low water clarity, because it has stable water levels. Lake Pukaki is also turbid, but has no littoral plants because levels fluctuate 14 m. Maximum recorded depth of aquatic plants below mean lake level (Z_c) (Schwarz et al. 2000) were strongly correlated with Secchi disc records ($n = 8$, $r = 0.969$). Littoral zone depth was estimated using Z_c because lake levels usually change slowly and bare substrates are colonised by periphyton and macrophytes.

Fish species diversity in these lakes is low, with only five widespread species. Two are introduced salmonids—brown and rainbow trout, which co-occur in all eight lakes. The remaining three are native species: common bully, koaro (*Galaxias brevipinnis*), and longfinned eel (*Anguilla dieffenbachii*). In addition, smelt and upland bully

Table 1 Characteristics of the study lakes, arranged in order from north to south. All lakes are of glacial origin, except for Lake Ruataniwha which is an artificial reservoir. All lakes, except Lake Wanaka, are controlled to varying extents for hydro-electric power generation. (Lake areas, altitude, maximum depth, mean Secchi, from Livingstone et al. (1986) except Lake Ruataniwha. Values of Z_c (maximum recorded depth of aquatic plants below mean lake level) are from Schwarz et al. (2000), except Lake Ruataniwha (from NIWA records), and Tekapo (from Stark 1993) who recorded macrophytes down to at least 8 m below maximum level, i.e., 4 m below mean lake level. Secchi depths during surveys, maximum Secchi range, and all Lake Ruataniwha data are from NIWA records. Survey periods: Lake Coleridge, February 1988; Lakes Manapouri and Te Anau, February 1998; other lakes, February 1999.

	Lake							
	Coleridge	Tekapo	Pukaki	Ruataniwha	Hawea	Wanaka	Te Anau	Manapouri
Area (km^2)	32.9	86.8	98.9	3.4	137.6	180.1	347.5	143.3
Altitude (m a.s.l.)	507	708	494	460	347	277	203	179
Max. depth (m)	200	120	70	28	384	311	417	444
Mean annual water level fluctuations (m)	4	8*	14*	0.3	11	1.5	2.7†	3.3†
Range of Secchi depths recorded (m)	4.0–18.5	1.2–7.0	0.2–1.0	0.2–5.0	8.9–21.5	9.5–19.0	5.3–11.3	3.7–10.0
Mean Secchi depth recorded (m)	13.0	4.1	0.6	0.6	18.8	17.0	10.0	6.5
Secchi depth during survey period (m)	9.2	2.0	0.6	0.6	12.0	9.9	5.3	3.7
Max. depth of aquatic plants or Z_c (m)	33.0	c. 4	0	2.5	34.4	23.6	13.7	12.6

*Data from 1975 to date (following regulation). †Data courtesy of Meridian Energy.

Table 2 Substrate features of the littoral locations studied. (Substrate composition: for Lake Coleridge is from the shore to 30 m offshore; for other lakes records are of the exposed shoreline and shallow littoral.)

	Lake							
	Coleridge	Tekapo	Pukaki	Ruataniwha	Hawea	Wanaka	Te Anau	Manapouri
No. of substrate observations	90	33	45	18	40	42	44	41
% boulders (>300 mm)	1	12	24	2	6	8	0	6
% cobbles (>60 mm)	10	65	54	22	24	33	41	15
% gravel (>3 mm)	44	8	21	51	35	22	20	15
% mud and sand	37	15	1	25	35	37	39	64
Macrophyte abundance	Common	Sparse	Nil	Common	Common	Abundant	Abundant	Abundant

(*Gobiomorphus breviceps*) are present in several lakes, and significant introduced landlocked populations of chinook salmon (*Oncorhynchus tshawytscha*) occur in Lakes Coleridge, Hawea, and Wanaka.

Trout recruitment is from natural spawning in tributaries; stocking is not practised and there is no known lake shore spawning. There are no quantitative data on the extent and suitability of spawning and rearing habitats. Five lakes contain important salmonid recreational fisheries. A nationwide angling survey in the mid 1990s (M. Unwin, NIWA pers. comm.) indicated Lakes Wanaka and Hawea had highest effort (18 000–25 000 fishing days per annum), whereas Lakes Te Anau, Coleridge, and Manapouri had moderate levels of effort (5000–10 000 days). Only minimal harvest data exist for these lakes, and angling pressure is generally considered to have only limited effects on fish abundance and size. Limited angling is undertaken in Lakes Tekapo and Ruataniwha, whereas the most turbid lake, Lake Pukaki, is only fished around stream mouths (Bloomberg & James 1993).

Field sampling

To determine differences in trout stocks between lakes, field studies were undertaken in late summer (late January and February) from 1997 to 2000 (Table 3). This season was chosen to optimise sampling for juvenile trout, which migrate down stream from tributaries in spring and early summer and take several months to disperse around the shoreline (Graynoth 1999). However, it is possible that our methods may underestimate adult rainbow trout numbers as telemetry studies in Lake Coleridge suggested some fish moved offshore in summer

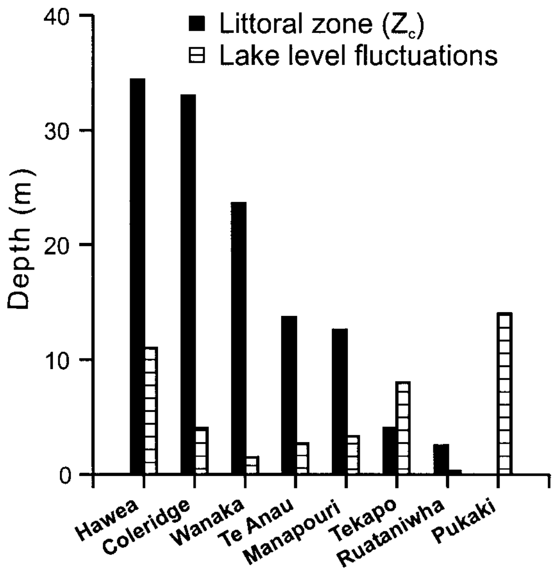

Fig. 3 Variability in depth of the littoral zone in study lakes, as represented by maximum depth at which macrophytes were found (Z_c), and mean annual lake level fluctuations (Table 1).

Table 3 Species composition and catch rate (CPUE, catch per unit effort) of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) taken by gill net in the eight study lakes. (Bt, brown trout; Rt, rainbow trout; CPUE, mean number of fish/100 m of net/h.)

Lake	Date	No. of sets	Total trout	% Bt	CPUE Bt	CPUE Rt	CPUE total trout
Coleridge	Feb 1988	7	213	30	0.26	0.62	0.88
Tekapo	Feb 1999	17	97	65	1.64	1.07	2.71
Pukaki	Feb 1999	19	31	94	0.03	0.00	0.03
Ruataniwha	Feb 1997	5	29	86	3.01	0.40	–
	Feb 1999	12	52	81	1.44	0.33	–
	Total	17	81	83	1.90	0.35	2.25
Hawea	Feb 1999	14	91	19	1.00	3.25	–
	Sep 1999	8	79	11	0.59	4.74	–
	Nov 1999	8	79	19	1.10	4.59	–
	Total	30	249	16	0.92	4.01	4.93
Wanaka	Feb 1999	16	54	89	2.52	0.32	–
	Sep 1999	8	14	79	0.89	0.23	–
	Nov 1999	8	61	74	2.62	0.90	–
	Feb 2000	17	40	65	1.28	0.14	–
	Total	49	169	77	1.97	0.38	2.35
Te Anau	Feb 1998	30	71	82	1.45	0.38	1.83
Manapouri	Feb 1998	30	90	77	1.24	0.35	1.59

(James & Kelso 1995). Other comparable data from Lake Coleridge have been incorporated: gill net data from 1988 (Graynoth et al. 1993a) and seine net data from 1993 (Graynoth 1999).

In an attempt to link changes in fish populations to an anticipated winter lake level draw-down in Lake Hawea, seasonal gill net sampling was undertaken from February 1999 to February 2000. As water levels in the similar adjacent Lake Wanaka vary naturally, it was also sampled seasonally as a control.

Fish capture methods

Gill netting

To determine relative abundance of adult salmonids by depth in the littoral zone, 100 m long sinking gill nets were set at right angles from the shore at randomly selected locations. Similar depth ranges were fished in each lake (typically 0 to c. 30 m), with maximum depths fished ranging from 21 m in Lake Ruataniwha to 40 m in Lakes Wanaka and Pukaki. At each location, four nets were usually set, at least 100 m apart, totalling 17–49 sets per lake, except for Lake Coleridge with only seven overnight sets (Table 3). Nets were set during the day for 1–3 h, except for Lakes Coleridge and Pukaki, where daytime catches were low and additional overnight sets were needed. Each net was 100 m long by 3 m deep, with stretched mesh (knot to opposite knot) either 63 or 83 mm, and with monofilament nylon diameter of 0.3 mm. Gill nets used in Lake Coleridge were of similar size, but comprised four panels, each 25 m long and with a slightly wider range of mesh sizes (57, 63, 83, and 101 mm) (Graynoth et al. 1993a). This was the first occasion that Lakes Tekapo, Hawea, Wanaka, Te Anau, and Manapouri have been gill or seine netted.

All trout caught were identified, counted, and measured. Stomach, scale, and otolith samples were collected and stored but, to date, have not been examined. The bottom depth at which each fish was caught by gill net was recorded, except for Lakes Manapouri, Te Anau, and Coleridge.

Seine netting

Relative abundance of juvenile salmonids in the littoral zone was assessed using a seine net 27 m long by 3.3 m deep with 8 mm stretched mesh (Graynoth 1999). Usually five hauls were made in close proximity at up to five different, randomly selected, beaches in each lake during the day, making a total of 14–45 hauls per lake (Table 4). Beaches close to lake tributaries (<1 km) were not fished. The seine was set on the lake bed 30 m offshore and parallel to the beach, before it was hauled ashore slowly. A few hauls (<5%) were abandoned, and data excluded, because the seine rolled on weeds or snagged on boulders or wood. Depths sampled ranged down to 20 m, and mean maximums ranged from 3.4 m in Lake Hawea to 9.3 m in Lake Wanaka.

Data analysis

Fish and habitat data collected were stored in an ACCESS database, and analysed using EXCEL and SYSTAT. Fish population status was assessed using both percentage composition and gill net CPUE indices. CPUE was calculated as the number of fish caught per hour per 100-m-long gill net (James & Kelso 1992; Bloomberg & James 1993). Percentage composition is a useful index, especially when CPUE levels in different lakes are influenced by external factors such as poor weather conditions. Fish size and condition were used as an index of the adequacy of food supplies and growth rates. Fulton

Table 4 Species composition and catch rate (CPUE, catch per unit effort) of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) caught by seine net in the study lakes in late January or February. (Bt, brown trout; Rt, rainbow trout; CPUE, mean number of trout per seine net haul; ±, 95% confidence intervals.) Forty-three juvenile (0+) chinook salmon were also caught in Lake Coleridge.

Lake	No. of sets	No. of trout	Species % Bt	CPUE Bt	CPUE Rt
Coleridge	45	109	16	0.4 ± 0.2	2.0 ± 0.7
Tekapo	19	34	35	1.0 ± 0.6	1.3 ± 0.7
Pukaki	14	2	100	0.1 ± 0.3	0.0
Ruataniwha	19	16	62	1.6 ± 1.2	0.5 ± 0.4
Hawea	20	50	2	0.1 ± 0.1	2.8 ± 2.5
Wanaka	23	19	57	0.5 ± 0.6	0.4 ± 0.4
Te Anau	29	16	12	0.1 ± 0.1	0.6 ± 0.7
Manapouri	25	33	64	0.9 ± 1.0	0.6 ± 0.4

condition factor was adjusted for differences in trout length between lakes using ANCOVA.

Effects of mean annual lake level fluctuations and Secchi disc depth on arithmetic CPUE, mean trout weight, and length adjusted condition factor was tested using Pearson correlation analysis. Probability (P) values were not adjusted for multiple tests and therefore the significance of individual tests is slightly overestimated.

It was assumed gill net CPUE was proportional to population density (Hubert 1996) but no adjustments were made to compensate for reduced CPUE in clear water, or increased fish activity at dusk and dawn (Fujimori et al. 1994) leading to increased catch rates in gill nets set overnight. No relevant studies have been carried out in New Zealand and low catch rates occurred in both clear and turbid lakes. Gear saturation is unlikely to have occurred because nets were only set for a few hours and catches were low, although nets set overnight in Lakes Pukaki and Coleridge may have depleted adjacent populations.

To compare gill net CPUE between lakes and species, we estimated ANOVA models with C = $\log_{10}(1 + \text{CPUE})$ as the dependent variable, lake (L) and site (T) nested within lakes as random factors, and species (S) as a fixed factor. We restricted this analysis to samples collected in summer from all eight study lakes. The most general model used was:

$$C_{ijkl} = \mu + L_i + T_{j(i)} + S_k + L_i \times S_k + \varepsilon_{ijkl}$$

where μ and ε are mean and error terms, respectively. This model showed a strong interaction between lake and species, so we re-analysed the data independently for each species using only lake and site as factors. Residuals from these models tended to increase with CPUE, but were otherwise normally distributed. For models showing a significant lake effect, we conducted pairwise post-hoc Scheffe tests to compare marginal means for individual lakes. All significance tests were performed at $\alpha = 0.05$.

RESULTS

Catch rates in gill nets

Catch rates in gill nets for both species combined (Table 3) were exceptionally low (0.03 trout h^{-1}) in Lake Pukaki which is a turbid, fluctuating lake with no littoral zone (Table 1). By contrast, catch rates were unexpectedly high in Lakes Ruataniwha (2.25 trout h^{-1}) and Tekapo (2.71 trout h^{-1}) which are also turbid with shallow littoral zones (Z_c, 2.5 m and 4 m respectively). The highest CPUE occurred in clear lakes with deep littoral zones (Lake Hawea, 4.93 trout h^{-1}, Lake Wanaka, 2.35 trout h^{-1}), although Lake Coleridge appears to be an outlier with unexpectedly low CPUE (0.88 trout h^{-1}), possibly caused by low catch rates in gill nets set overnight.

For brown trout, mean log transformed CPUE were not linearly related to water clarity or the depth of the littoral zone (Table 5). However, brown trout comprised 65–94% of all trout caught in six lakes which, except for Lake Wanaka, were of lower clarity with littoral zones of moderate depth (<14 m, Table 1). Log transformed CPUE did not differ between Lakes Wanaka, Ruataniwha, Tekapo, Te Anau, and Manapouri, but was higher for all five lakes than for either Lake Hawea or Lake Pukaki (Table 6).

For rainbow trout, CPUE was highest in Lake Hawea, and higher in Lake Tekapo than in Lake Pukaki, but did not differ between any other pairs of lakes (Table 6). There was some evidence of site-specific effects (P = 0.01) for rainbow trout, particularly in Lakes Hawea and Manapouri, but for brown trout CPUE did not vary between sampling sites

Table 5 Pearson correlation coefficients between features of the eight study lakes and brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) caught in gill nets in summer. (CPUE, catch per unit effort; Bt, brown trout; Rt, rainbow trout; P values are for a single test; –, not relevant.)

Feature	Trout species	Percentage Bt	Log CPUE	Mean weight (g)	Mean condition factor
Max. depth aquatic plants or Z_c (m)	Bt	–0.77 $P < 0.05$	–0.22	0.73 $P < 0.05$	0.82 $P < 0.05$
	Rt	–	0.58	0.44	0.25
Secchi disc during survey period (m)	Bt	–0.66	–0.10	0.66	0.67
	Rt	–	0.58	0.29	0.05
Mean annual water level fluctuations (m)	Bt	–0.23	–0.72 $P < 0.05$	–0.17	–0.22
	Rt	–	0.31	–0.54	0.05

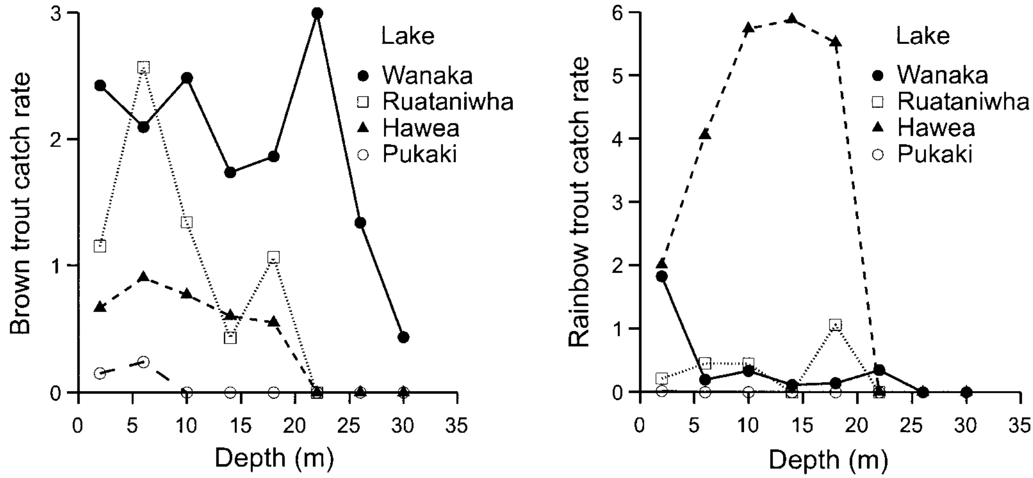

Fig. 4 Depth distribution of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) (species combined) in four study lakes, as determined by catch rate (trout/100 m of net/h) at different depths.

Table 6 Comparison of mean logarithmic CPUE (catch per unit effort) (±1 SE) between study lakes for brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) taken by gill net, based on ANOVA with post-hoc pairwise contrasts (see text). Vertical bars denote means which do not differ at $\alpha = 0.05$. Sample sizes are as given in Table 3.

Brown trout		Rainbow trout	
Lake	Log(1 + CPUE)	Lake	Log(1 + CPUE)
Wanaka	0.44 ± 0.04	Hawea	0.51 ± 0.05
Ruataniwha	0.37 ± 0.05	Tekapo	0.23 ± 0.04
Tekapo	0.36 ± 0.05	Coleridge	0.16 ± 0.06
Te Anau	0.33 ± 0.04	Ruataniwha	0.11 ± 0.04
Manapouri	0.30 ± 0.04	Manapouri	0.10 ± 0.03
Coleridge	0.10 ± 0.08	Te Anau	0.09 ± 0.03
Hawea	0.14 ± 0.06	Wanaka	0.08 ± 0.03
Pukaki	0.04 ± 0.05	Pukaki	0.00 ± 0.04

($P = 0.33$). Mean log-transformed CPUE for rainbow trout were not linearly related to water clarity (Table 5). However, rainbow trout dominated in two of the three lakes with clear water and deep littoral zones, forming 81 and 70% of gill net catches in summer in Lakes Hawea and Coleridge respectively (Tables 1 and 3, Fig. 2). Also rainbow trout percentages in Lake Wanaka were surprisingly different in two successive summers at 11 and 35% (Table 3).

Lake level variability appeared to have little direct or additional influence on trout CPUE, especially in clear lakes. It did not influence species composition or log transformed CPUE for rainbow trout (Fig. 2, Table 5). Although log-transformed CPUE for brown trout appeared to decline in fluctuating lakes ($P = 0.04$ for a single test), this may be because brown trout were relatively scarce for other reasons in Lake Hawea.

Species composition of brown and rainbow trout was broadly similar throughout the seasonal sampling periods in Lakes Wanaka and Hawea (Table 3), although there was some suggestion of a downward trend in the percentage of brown trout in Lake Wanaka over time. We hypothesised that rainbow trout would be less abundant in these lakes during spring when this species spawns in tributaries. This was only apparent when fish of spawning size (>400 mm) were considered, producing a trend from 77% rainbows in February through 67% in September to 52% in November.

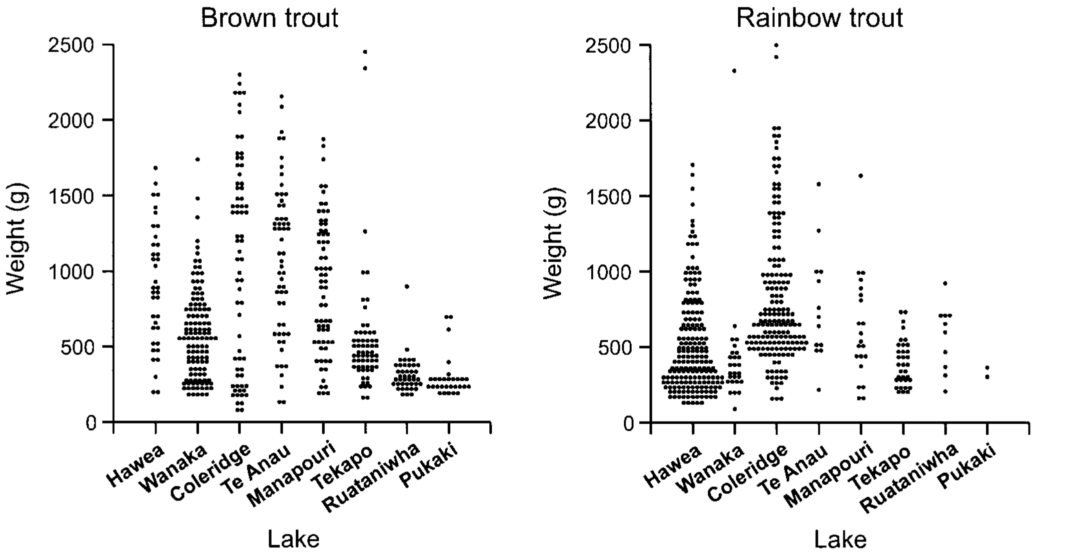

Fig. 5 Weight-frequency distribution of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) caught by gill net in eight study lakes, in order of decreasing Secchi depth.

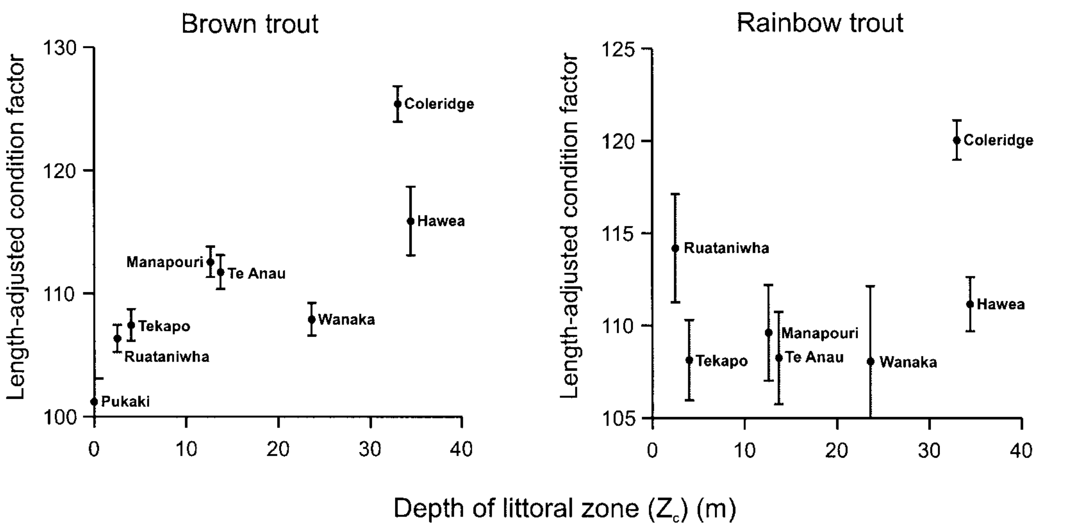

Fig. 6 Condition factor (± SE) of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) by depth of littoral zone (Z_c) in eight study lakes.

Depth distribution in gill nets

All brown trout were caught in shallow water (<7 m deep) in Lake Pukaki even though nets were set in water 40 m deep (Fig. 4). In Lake Ruataniwha, brown trout were found in deeper water but were most abundant in water 4–8 m deep, just below the shallow littoral zone. In the clear Lakes Hawea and Wanaka, brown trout were caught throughout most of the littoral zone, down to depths of 20–30 m.

Rainbow trout showed a strong preference for water 6–18 m deep in Lake Hawea but by contrast they were mainly caught in shallow water, <4 m deep, in Lake Wanaka (Fig. 4).

Size and condition of trout in gill nets

Brown trout from turbid Lakes Tekapo, Ruataniwha, and Pukaki were generally less than 1 kg in weight, and were smaller and in poorer condition than those

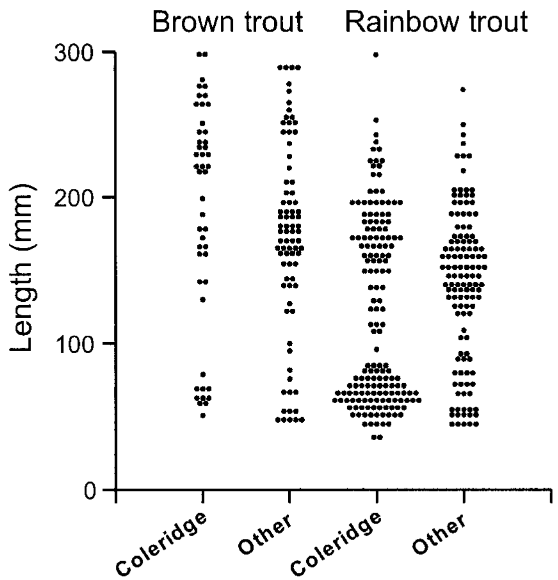

Fig. 7 Length-frequency distribution of juvenile brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) seined in the eight study lakes, "Other", compared with that reported from Lake Coleridge, New Zealand (Graynoth 1999).

caught in clear lakes with deep littoral zones (Fig. 5 and 6, Table 5). Lake Wanaka was atypical and contained brown trout which were smaller and in poorer condition than those in other clear water lakes.

Large rainbow trout (>1 kg) were also scarce in turbid lakes, and in Lake Wanaka (Fig. 5), but weights and condition factors were unrelated to water clarity and depth of the littoral zone (Table 5). This was because a small number (14) of rainbow trout caught in Lake Ruataniwha were larger and in better condition than expected (Fig. 5 and 6). Rainbow trout weights and condition factors were also unrelated to mean annual lake level variations (Table 5).

Juvenile trout

A higher proportion of juvenile rainbow trout were caught in seine nets (Table 4) than adults in gill nets (Table 3); with the exception of Lake Pukaki. Whereas juvenile (<200 mm) chinook salmon were caught in Lake Coleridge (28% of juvenile salmonids), they were not caught in Lakes Wanaka and Hawea, possibly because numbers fluctuate annually.

Catch rates were highly variable within lakes with wide confidence intervals (Table 4). Rainbow trout catches appeared to be highest in clear lakes with deep littoral zones (Lakes Hawea and Coleridge) (Z_c; $r = 0.75$, $P = 0.03$) but no other significant relationships were identified.

Two size groups of juvenile trout were caught (Fig. 7). Fry and 0+ fingerlings averaged 60 mm (range 36–100 mm), whereas 1+ and possibly a few small 2+ averaged 158 mm (see also Graynoth 1999). There was a higher proportion of 0+ fish (51%) in the rainbow trout catch than 0+ fish (31%) in the brown trout catch.

DISCUSSION

Trout species composition and abundance in the littoral zones of these lakes varies and depends upon a variety of ecological factors and biological processes (Percival & Burnet 1963; Hayes 1987; Elliott 1994; Graynoth et al. 1993a,b, 1999). These include reproduction and survival rates in tributary streams and trout survival rates and behaviour in the littoral. It was impractical to determine life histories and movements between the littoral and limnetic zones, or model population dynamics of trout in this study, and therefore regression methods were used to assess whether water clarity and level fluctuations influenced stocks in the littoral zone.

Of particular interest is that statistically significant differences were found in this study, considering only eight lakes were sampled over limited periods. Ideally, it would have been preferable to have sampled a larger number of lakes (perhaps 15–50 as can be achieved in Europe (Garnaas & Hesthagen 1982; Vehanen 1995, 1997), with repeated long-term observations to take into account temporal changes, fluctuations, and oscillations in trout year class strength (Percival & Burnet 1963; Aass 1986; Borgstrom et al. 1993; Elliott et al. 1996).

Brown trout

In general, results supported the original hypotheses that brown trout abundance, distribution, size, and condition are directly related to depth of the littoral euphotic zone (Z_c) and hence food supplies. Brown trout were small and in poor condition in all three turbid lakes and there was also some evidence that trout were growing slowly and maturing at small sizes (NIWA unpubl. data). They were also closely associated with the littoral zone and found in shallower water than in clear lakes. Similar results were found in earlier studies in Lake Benmore (McCarter 1986, 1987); a turbid hydro-electric lake situated downstream of Lake Ruataniwha.

Small size, poor condition, and scarcity of trout in Lake Pukaki was probably caused by lack of food, as the benthic macroinvertebrate fauna is virtually non-existent (Timms 1982, NIWA unpubl. data). There are also no large zooplankters present in these lakes which could act as alternative foods. Mysids and zooplankton, such as *Daphnia longispina*, *Bythotrephes longimanus*, and *Holopedium gibberum* support brown trout stocks in turbid European lakes with barren littoral zones (Hegge et al. 1993), especially where Arctic char (*Salvelinus alpinus*) are absent (L'Abee-Lund et al. 1992).

The high CPUE of trout in Lakes Tekapo and Ruataniwha was unexpected considering the limited littoral zones in these lakes. Preliminary studies showed that trout in Lake Tekapo eat relatively few benthic macroinvertebrates and have a restricted diet of terrestrial insects, whereas trout in Lake Ruataniwha were mainly caught in, and just below, the littoral and consumed a variety of snails and other macroinvertebrates associated with littoral macrophytes (NIWA unpubl. data). The lack of large trout (>1 kg) in these three turbid lakes is probably related to reduced availability of large food items, such as dragonfly larvae and forage fish.

Brown trout were larger and in better condition in two clear lakes (Lakes Hawea and Coleridge), but not in the third (Lake Wanaka). This is probably because they are abundant and compete for food.

In contrast to angler observations and studies in Lake Waikaremoana (Mylechreest 1978), we found good numbers of brown trout throughout most of the littoral zone during the day and fish were not markedly more abundant in shallow water. Dietary studies (Graynoth et al. 1993a; NIWA unpubl. data) show that they eat a variety of benthic macroinvertebrates and small fish, but it is not known precisely where they feed because recent telemetry studies (NIWA unpubl. data) show adults move inshore at night in these lakes, sometimes into very shallow water.

The low CPUE values in late winter in Lakes Hawea and Wanaka may be associated with fish movements, notably winter spawning migrations into tributaries, or perhaps lowered vulnerability to netting during periods of cooler temperatures.

The results obtained provide a best case scenario of the effects of fluctuating lake levels on trout stocks in clear lakes, because of the atypically high winter lake levels that preceded our sampling, and the record flooding in Lake Wanaka. Rapid and extreme draw-downs erode shorelines, increase water turbidity, and reduce trout stocks in European lakes (Kaatra & Simola 1985; Mutenia 1985; Aass 1986, 1991), and therefore typical winter draw-downs may have more impact in New Zealand lakes than we observed. Ideally, draw-downs should be annual and occur slowly, so that invertebrates, macrophytes, and sediments have time to adjust.

Rainbow trout

We were surprised to find that littoral zone depth, water clarity, and lake level fluctuations had no statistically significant effects on rainbow trout CPUE, mean weights, or condition factor in these lakes. For example, although large rainbow trout (>1 kg) appeared scarce in turbid lakes, as in the North Island (Rowe 1984), they were also rare in a clear lake (Lake Wanaka). Rainbow trout condition factor was also lower in clear Lake Wanaka and higher in turbid Lake Ruataniwha than expected. Although the latter situation could have arisen from fish recently migrating downstream from the clearer Lake Ohau, this is considered unlikely. Rather, it appears rainbow trout may be utilising a food source in Lake Ruataniwha that is little exploited by the more numerous brown trout. Rainbow trout are known to consume large quantities of snails, especially *Potamopyrgus antipodum*, in Lake Ruataniwha and other turbid lakes (McCarter 1986; NIWA unpubl. data). McCarter also found that rainbow trout can digest this food source more efficiently; in nearby Lake Benmore they extracted almost 20% of the available energy from unbroken *P. antipodum* shells, whereas brown trout extracted less than 2%. The lack of a relationship between the CPUE and condition of rainbow trout and water clarity was surprising, and deserves further investigation.

Rainbow and brown trout are much more abundant in littoral than limnetic zones in these alpine lakes and reservoirs based on gill net CPUE and telemetry (Graynoth et al. 1986, 1993a,b; McCarter 1987; James & Kelso 1995; NIWA unpubl. data). However, whereas brown trout are always found inshore, some rainbow trout enter the limnetic zone in summer and feed on fish and terrestrial insects (James & Kelso 1995; Taylor et al. 2000). The data indicate rainbow trout are less associated with the substrates and weed beds than brown trout and generally live in the deep littoral, as in Lake Hawea. Water level regulation in Norway alters bottom fauna/zooplankton ratios favouring plankton feeding fish species such as Arctic char and impairing bottom feeders like brown trout (Aass 1991). Rainbow trout are better adapted to feed on plankton and other limnetic foods than brown trout (Graynoth et al.

1986; McCarter 1986) and similar changes may occur in New Zealand lakes.

It is not known why rainbow trout preferred shallow water in Lake Wanaka. Highest catches occurred after the November 1999 floods and may have been caused by fish moving inshore from the limnetic zone to feed on drowned terrestrial invertebrates.

Dominance of rainbow trout in two of three clear lakes (Lakes Hawea and Coleridge) could also be related to food supplies and the deep littoral zone in these lakes. However, trout spawn in only a few small tributaries (Flain 1986; Graynoth 1999; C. Halford, Otago Fish and Game Council pers. comm.), and rainbow trout may be more successful because they superimpose their redds on those of brown trout (Hayes 1987). Scarcity and variable numbers of rainbow trout in Lake Wanaka might also be explained by a lack of suitable spawning streams. Detailed information is not available yet on trout diets and spawning grounds so these hypotheses remain untested.

Juvenile trout

Seine net catch rates were too variable within lakes to determine whether level fluctuations and water clarity influenced juvenile trout. Differences in life history probably explain why relatively higher numbers of 0+ and 1+ rainbow trout than brown trout were seined. Juvenile rainbow trout usually migrate from tributaries into Lake Coleridge within a few months of emergence, whereas most juvenile brown trout remain and rear in tributary streams for 1–2 years (Graynoth 1999).

Management implications

Major reductions in the depth of littoral zones in South Island alpine lakes, resulting from fluctuating water levels and increased turbidity, are likely to reduce trout food supplies and brown trout size and condition. Where the littoral zone is absent, as in Lake Pukaki, brown trout abundance will also decline. Controlled, but usually stable turbid lakes, such as Lakes Ruataniwha and Benmore, although capable of supporting adequate trout stocks and recreational fisheries, are particularly vulnerable to draw-downs.

Moderate and slow fluctuations in water levels in clear lakes such as Lakes Hawea and Coleridge, appear to have relatively minor effects on trout populations. Rainbow trout also appear to be more tolerant of these changes than brown trout, and populations may be restricted by other factors such as quality of spawning grounds and limnetic food supplies.

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