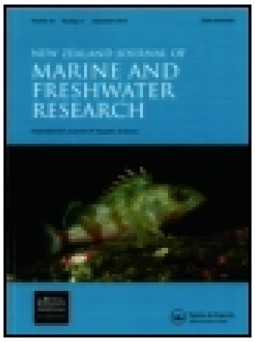

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Factors related to the distribution and abundance of brown and rainbow trout in New Zealand clear-water rivers

Ian G. Jowett

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Factors related to the distribution and abundance of brown and rainbow trout in New Zealand clear-water rivers

IAN G. JOWETT
Freshwater Fisheries Centre
Ministry of Agriculture and Fisheries
P. O. Box 8324, Riccarton
Christchurch, New Zealand

Abstract Brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) populations at 157 riverine sites throughout New Zealand were divided into groups based on species, size, and abundance. The groups were examined to determine significant differences in hydrological, water quality, water temperature, biological, in-stream habitat, and catchment variables between groups. A discriminant model was developed with nine environmental factors which correctly classified 72% of a subset of 65 sites. Fish species distribution was related to climatic (water temperature), geographical, and hydrological factors, whereas fish abundance was determined by factors relating to flow variability, river gradient, in-stream habitat, and the presence of lakes in the catchment.

Keywords brown trout; rainbow trout; distribution; abundance; discriminant analysis; classification; in-stream habitat; water quality; hydrology; geography

INTRODUCTION

Of the fish introduced to New Zealand, brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*, formerly *Salmo gairdneri*) are the most widespread. Because of their importance to anglers, there is a need to provide water managers with information which will assist them in evaluating the impact of land and water resource changes on trout populations. Numerous studies have attempted to model trout populations using many different environmental factors. Fausch et al. (1988) reviewed 99 models, most of which were multiple regression models with a variety of logarithmic, exponential, or polynomial transformations, although a few researchers used multivariate techniques (factor and principal components analysis) to select linear combinations of the variables investigated. By comparing the precision of models based on large datasets with that of models based on small datasets, Fausch et al. (1988) concluded that:

(1) the most precise models stem from small datasets collected over a relatively short period, a relatively small area, or both;

(2) a useful model must include variables that can be affected by management; and

(3) the geographical region to which the model applies must be accurately known.

Allen & Cunningham (1957) used angler catch data from a diary scheme (1947–52) to determine the distribution of brown and rainbow trout throughout New Zealand and defined regions according to the relative proportions of the two species in the catch. Their study attempted, in a qualitative way, to determine factors which might influence trout distribution and abundance. They concluded that the distribution of the two species was a result of ecological rather than historical factors, but that there was little evidence as to the nature of the ecological factors.

Discriminant models have been used to demonstrate the link between benthic aquatic invertebrate communities and various water quality variables (Wright et al. 1984), and fish assemblages with habitat variables (Tonn et al. 1983), catchment characteristics (Larsen et al. 1986), or both (Hayes et al. 1989). Bowlby & Roff (1986) classified 30 stream sites in Ontario according to trout biomass and derived discriminant functions using five variables selected from a set of 27 physical variables and six biotic variables. Their model correctly classified 27 of the 30 sites.

The present study uses classification and discriminant analysis to investigate relationships between hydrological, water quality, biological, in-

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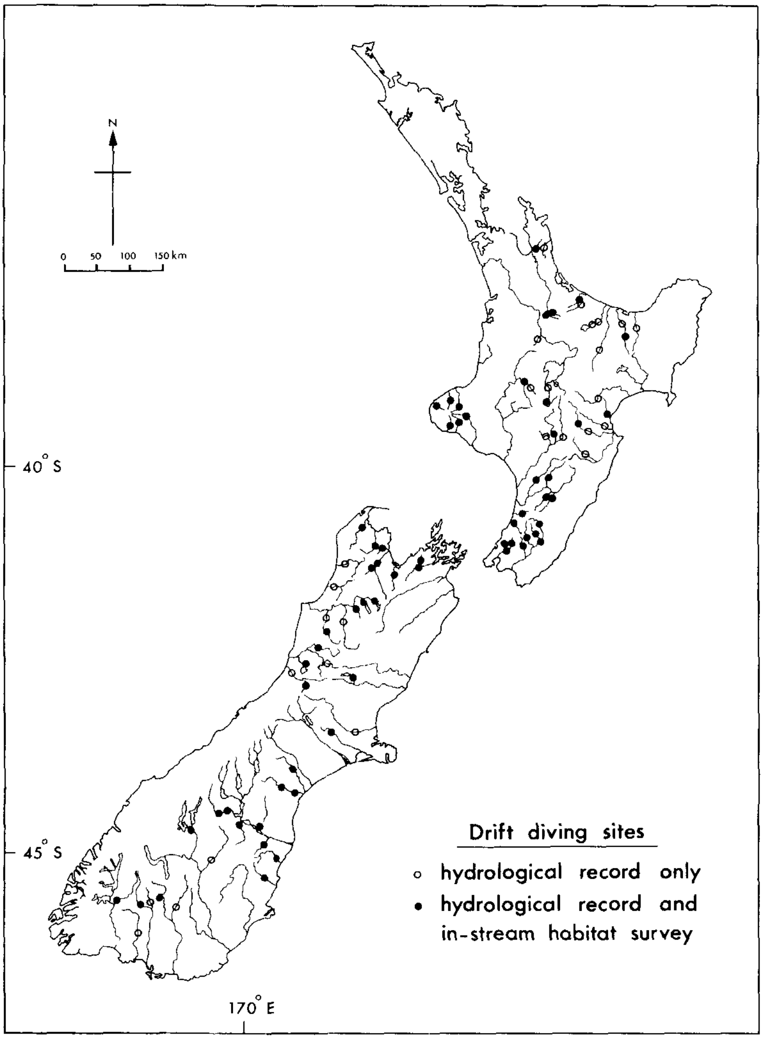


Fig. 1 Location of drift-diving sites, denoting those with hydrological records and those at which in-stream habitat surveys were made.

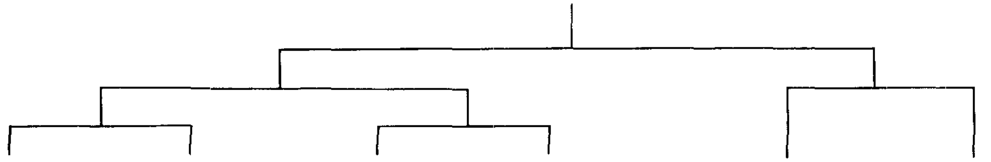
stream habitat, and catchment characteristics (Table 1), and the distribution and abundance of brown and rainbow trout in New Zealand clear-water rivers.

METHODS

Trout biomass data

Trout abundance was assessed by drift diving, a method that required a team of divers (2–10 depending on river width) in snorkelling gear to swim down stream in a line equally spaced across the river, and search for and count all visible trout. The team comprised experienced drift divers who used consistent techniques to survey the 157 sites in this study (Fig. 1). At least 1 km of river was surveyed at each site; minimum underwater visibility was 3 m for slower-flowing rivers containing only brown trout and 4 m for swifter rivers or those containing rainbow trout. All rivers surveyed had suitable underwater visibility and water depth (more than about 0.3 m) and rivers with good hydrological records were preferred, although some additional rivers were surveyed to provide a more extensive database. All drift diving was carried out in the summer months so that summer "resident" populations of fish were surveyed and problems with any spawning movement were avoided.

The species (brown or rainbow trout) and size class of every trout seen were recorded. The total fish



Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
*Ahuriri R. 1	*Akatarawa R.	*Arnold R. 1	Ahaura R.	*Clutha R.	*Kauaeranga R.
*Aorere R.	Aparima R.	Buller R. 1	*Ahuriri R. 2,3	*Mararoa R.	Makaroro R.
Hurunui R. 4	Arnold R. 2	*Gowan R. 1	*Esk R.	*Rai R.	Mangorewa R.
Hutt R. 2,5	*Baton R.	*Gowan R. 2	*Hakataramea R.	Rangitaiki R.	Tairua R.
*Inangahua R. 1	*Buller R. 2,3	Haupiri R.	*Maerewhenua R.	Rangitikei R. 10	Tarawera R. 1
Kakanui R. 1	*Grey R.	*Hurunui R. 1	Manganuioteao R. 1,2,3	Taruarau R. 1	Tarawera R. 2
Karamea R. 3	Hautapu R.	*Hutt R. 1	Manganuioteao R. 4,5,6	*Tauranga-Taupo R.	*Tongariro R. 1
*Kaupokonui Stm	Hurunui R. 2,3	*Mangles R.	Manganuioteao R. 7,8	Tekapo R. 3,6	*Tutaekuri R.
*Mangahao R.	Hutt R. 3,4	Mohaka R. 1	Mohaka R. 2	Tongariro R. 2	*Waiari Stm
*Manganui R.	Inangahua R. 2	*Motueka R.	Ngaruroro R. 1,3		*Waihou R.
*Ohau R.	Irthing Stm	*Riwaka R. 1,2	*Ngaruroro R. 2		*Waimakariri Stm
*Opihi R. 1	*Kakanui R. 2	*Shag R.	*Otematata R.		Waioeka R.
*Orari R.	Karamea R. 1,2	Spring Ck 1,2	*Pelorus R.		Waipapa R.
*Oroua R.	*Mangatainoka R.	*Waingongoro R.	Rangitikei R. 1,2,4		Whakapapa R. 1
*Otaki R.	Manuherikia R.		*Rangitikei R. 3,6,7		
Patea R. 1	Maruia R.		Rangitikei R. 5,11		
*Pohangina R.	*Mataura R.		Rangitikei R. 8,9,12		
Pomahaka R.	*Moawhango R.		*Stony R.		
*Ruamahanga R. 1	Mokihinui R. 1,2,3		Taramakau R.		
*Taipo R.	*Opihi R. 2		Taruarau R. 2,3		
*Takaka R. 1,2	*Oreti R.		Tekapo R. 1,2,4,5		
*Tauherenikau R.	*Patea R. 2		*Waimana R. 1		
Waikaia R.	*Ruamahanga R. 2		Waipawa R.		
Waikanae R.	*Selwyn R. 1,2		Waitaki R. 3,5		
Waimakariri R.	*Wairoa R.		Wanganui R. 1		
Waimana R. 2	Waitaki R. 4		*Wanganui R. 2		
*Waingawa R.			Whakapapa R. 2,4		
*Waiohine R.			Whakapapa R. 3,5,6		
Waitaki R. 1,2					
*Waiwakaiho R.					
*Whakatiki Stm					

Fig. 2 Dendrogram showing 157 drift-diving sites classified into six groups depending on trout species present, size, and abundance. Different reaches are identified in order down stream by the number after the river name. *sites with in-stream habitat surveys.

lengths used for the three size classes were small (100–200 mm), medium (200–400 mm), and large (> 400 mm). Underwater observations of medium and large trout lying in bedrock fissures, pressed against undercut banks, curled under boulders or in-stream debris, and amongst bankside willow roots, confirmed that such cover types were often used by fish when disturbed.

At each drift-diving site, the types of in-stream cover (bedrock, boulder, bank, and in-stream debris) were recorded, as was the association of trout with each of the cover types. In-stream debris was usually up-rooted vegetation, often willow; bankside cover was formed by steep banks, often undercut and held in place by a mass of roots. The amount of in-stream cover available (but not necessarily used) was assessed on a ten-point scale (0–9). Low ratings (2–3) were given to open channels with no distinct banks and fine uniform substrate. Rivers with high ratings (7–9) had continuous cover either because of their bank type or bouldery substrate. The results and techniques used are detailed in Teirney & Jowett (in press), who also reviewed the accuracy of fish abundance estimates derived by drift diving. They concluded that drift diving, in assessing adult trout abundance in larger rivers, is as good a method or better than other fisheries methods, provided appropriate techniques are used and visibility conditions are suitable. Counts of small fish were not considered as reliable as those of larger fish, as the small fish tend to school in large numbers in deep water or to occupy shallow boulder areas of the river which were difficult to survey by drift diving.

Table 1 Definition of the 120 variables used in the river-trout analyses.

Hydrological (flow in $m^3 s^{-1}$)	
CVFLOW	Coefficient of variation of flow
CVMAF	Coefficient of variation of mean annual maximum flow
CVMALF	Coefficient of variation of mean annual minimum flow
ELEV_S	Elevation of site above msl (m)
MAF	Mean of annual maximum flows
MALF	Mean of annual minimum flows
MEANF	Mean annual flow
MEDIANF	Median flow (exceeded 50% of time)
RUNOFF	Mean annual flow/catchment area expressed in metres
Catchment (% over catchment)	
ALLUVIUM	% alluvium
DEVEL	% developed pasture, crop, or horticulture
FLAT	% flat slope (< 4°)
FOREST	% native or exotic forest cover
EROSIONSB1	% streambank erosion
EROSION1	% severe and very severe erosion
HARDSED	% hard sedimentary rock
IGNEOUS	% igneous rock
LAKE	% lake area
LIME	% limestone
LOESS	% loess soil
ROLL	% rolling slope (8–20°)
SCHIST	% schist
SCRUB	% native scrub, gorse, or broom cover
SOFTSED	% soft sedimentary rock
STEEP	% steep slope (> 20°)
TUSSOCK	% undeveloped grassland or tussock
VOLCANIC	% volcanic ash
Temperature (°C)	
MAXTEMP	Maximum annual sinusoidal temperature (maximum annual)
MINTEMP	Minimum annual sinusoidal temperature (minimum annual)
RANGTEMP	Mean annual temperature amplitude
TEMP	Mean annual temperature
In-stream habitat	
BEDROCK	% bedrock substrate
BOULDER	% boulder (> 264 mm) substrate
COARSEGRAVEL	% gravel (10–64 mm) substrate
COBBLE	% cobble (64–264 mm) substrate
COVER	In-stream trout cover grade (1–9)
FINEGRAVEL	% fine gravel (2–10 mm) substrate
MANNING	Mean Manning's *n* (friction coefficient) for reach
SAND	% sand (0.06–2 mm) substrate
SILT	% silt (< 0.06 mm) substrate
SLOPE_S	River gradient
SQRSLOPE	Square root of river gradient
SUBSTRATE	Mean substrate size (mm) calculated from percentage compositions
VEGETATION	% in-stream vegetation/debris including aquatic macrophytes and root mats

(*continued*)

Table 1 *(continued)*

For the following 12 in-stream habitat parameters, five suffixes were used in the analysis to denote either the flow or variation between flows for which the particular variable is derived: (1) at MALF, (2) at MEDIANF, (3) at MEANF, (2–1) the percentage change from value at MEDIANF to value at MALF, and (2–3) the percentage change from value at MEDIANF to value at MEANF.

DEPTH	Mean depth (m)
RBS	Relative bed stability (ratio of water velocity to velocity which will just move substrate, calculated for each measurement point and averaged for reach)
VDEPTH	Standard deviation of mean cross-section depths
VEL	Mean velocity (m s^{-1})
VVEL	Standard deviation of mean cross-section velocities
WUABTA	Weighted usable area % for adult brown trout (Bovee 1978)
WUABTF	Weighted usable area % for brown trout feeding (Shirvell & Dungey 1983)
WUABTJ	Weighted usable area % for juvenile brown trout (Bovee 1978)
WUABTS	Weighted usable area % for brown trout spawning (Shirvell & Dungey 1983)
WUAFP	Weighted usable area % for food production (Waters 1976)
WUARTA	Weighted usable area % for adult rainbow trout (Bovee 1978)
WUARTJ	Weighted usable area % for juvenile rainbow trout (Bovee 1978)
Water quality (mean of three values taken at low to median flow)	
COND25	Total conductivity at 25°C (mS m^{-1})
DRP	Dissolved reactive phosphorus (mg m^{-3})
pH	pH
TKN	Total Kjedahl nitrogen (mg m^{-3})
TIN	Total inorganic nitrogen (mg m^{-3})
Biological (biomass g m^{-2})	
ALGAE	% cover of brown and green filamentous algae
CADDIS(F)	Biomass of filter feeding caddisflies
CADDIS(P)	Biomass of predatory caddisflies
CADDIS(T)	Total caddisfly biomass
DIATOM	% cover of brown and green films
INVERT	Total benthic invertebrate biomass
MAYFLY(F)	Biomass of filter feeding mayflies
MAYFLY(T)	Total mayfly biomass
MOLLUSC	Biomass of molluscs (snails)
STFLY(P)	Biomass of predatory stoneflies
STFLY(T)	Total stonefly biomass

Biomass was estimated for each fish species by size class, by multiplying the number of fish counted by the average weight of a fish in the size class, and dividing by the area of the river reach surveyed. The average weight of fish per size class was determined, using average condition factor (k) values of 111 and 126 for brown and rainbow trout respectively (E. Graynoth, MAF Fisheries unpubl. data), in the relationship:

Weight=k × Length^3/10^7 (Carlander 1969),

where weight is in g and length in mm. This conversion gave more emphasis to large trout than to medium or small trait, which was consistent with observational accuracy, but was only an approximate estimate of total biomass as there was no way of estimating lengths or weights of individual fish.

In-stream habitat data

In-stream measurements of water depth, velocity, and substrate were made within the drift-diving reaches following the general in-stream flow incremental methodology (IFIM) (Bovee 1982) and using survey and hydraulic modelling procedures detailed by Jowett (1989). The modified Wentworth particle size scale (Bovee & Milhous 1978) was used for substrate, except that gravel was subdivided into fine gravel (2–10 mm) and gravel (10–64 mm).

In-stream habitat data were collected from 65 of the drift-diving locations (Fig. 1 and 2). The amount of work, and in some instances the difficulty, involved in these surveys limited the number of sites that could be surveyed. Survey sites were selected so that they represented the habitat within the drift-diving reach and included pool-run-riffle habitat sequences, if possible. An average of 24 cross-sections (range 8–47), spaced at between 7 and 35 m (average 18 m) intervals, were surveyed at each site. Water depth, velocity, and substrate composition were recorded at an average of 486 points for each site and were at an average interval of 1.13 m. The surveyed reaches were modelled hydraulically and in-stream habitat and hydraulic parameters were predicted for mean annual low flow, median flow, and mean flow using the computer programme RHYHABSIM (Jowett 1989). Weighted usable areas (WUA) for brown and rainbow trout and for food production at mean annual low flow, median flow, and mean flow were computed using habitat preference curves described by Waters (1976), Bovee (1978), and Shirvell & Dungey (1983). Although other unpublished preference curves were investigated, the set selected described a wide range of habitat. Water's food production and Bovee's adult rainbow trout preference curves matched data on feeding locations of New Zealand brown trout in clear-water rivers (unpubl. data) and correlated with the logarithms of brown-trout biomass ($P = 0.056$ and $P = 0.022$, respectively).

The substrate categories, bedrock, boulder, and in-stream vegetation (Table 1) provided, and were related to, in-stream cover. The cover grade was correlated with the sum of bedrock, boulder, and in-stream vegetation percentages ($r = 0.58$, $P < 0.001$). However, the cover grade provided an overall estimate for the site, taking into account the quality of the cover—that is the ability of the cover to provide a hiding place from divers – and any cover provided by the banks.

Other data

Procedures for the collection and analysis of hydrological data are described by Jowett & Duncan (1990), water quality data by Close & Davies-Colley (1990), periphyton data by Biggs (1990), and invertebrate data by Quinn & Hickey (1990). Water temperature data were either obtained from Mosley (1982) or from more recent measurements using the same method (sine curves fitted to water temperatures sampled throughout the year). Mean annual temperature, amplitude, and extremes were calculated from the average annual sinusoidal water temperature variation.

Analysis

Two-way indicator species analysis, TWINSPAN (Hill 1979), was used to classify, into six groups, the 157 drift-diving sites by trout species, size class, and biomass. Three levels of trout biomass were used for each size class; low (0–0.5 g m^{-2}), moderate (0.5–2.0 g m^{-2}), and high (> 2.0 g m^{-2}). The division between low and moderate biomass was arbitrarily set so that the number of sites in each group was similar. The division between moderate and high biomass categories was more robust with little variation in group membership when different levels of abundance were set.

Data for the 120 environmental variables (Table 1) were compiled for each site. The following series of analyses were then carried out to identify and select variables which were the best predictors of trout species composition and abundance:

(1) A non-parametric analysis of variance (Kruskal-Wallis) was used to select variables which varied significantly between groups.

(2) A multiple comparison test (Tukey test) was used to select variables which showed differences between groups based on brown trout biomass and between groups based on species composition.

(3) Using this subset of environmental variables, a stepwise discriminant analysis (Klecka 1980) was used to eliminate weak or redundant variables. Discriminant models were formed from subsets of hydrological, catchment, in-stream habitat, temperature, and biological variables to determine the relative discriminating ability of the different environmental factors. The effectiveness of the discriminating functions was judged by comparing the original and predicted site classifications.

RESULTS

Classification of sites

All 157 sites were classified into six groups based on the fish species present and their relative biomass (Fig. 2). Examination of the indicator species (Hill 1979) and the groups themselves indicated that there was a primary division between brown and rainbow trout rivers with further subdivisions based on biomass of large trout (Fig. 2 and 3). Although trout biomass in rivers containing only rainbow trout varied, there were too few rivers in this category to subdivide into groups based on biomass. The six groups can be described as:

1. Brown trout—low biomass
2. Brown trout—moderate biomass
3. Brown trout—high biomass
4. Mixed brown/rainbow trout—low biomass
5. Mixed brown/rainbow trout—high biomass
6. Rainbow trout only

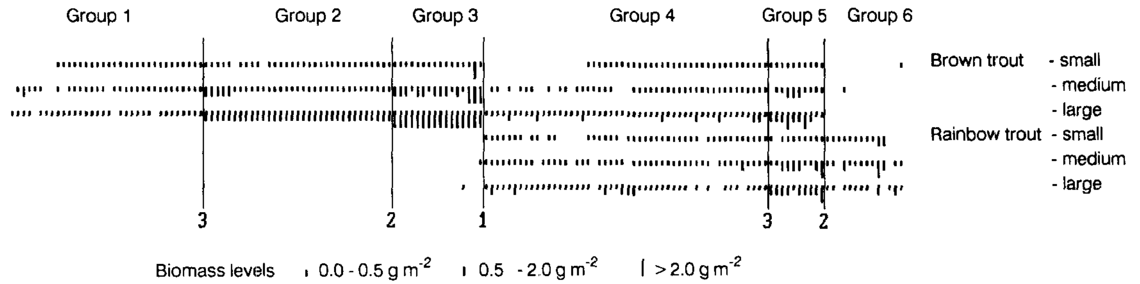


Fig. 3 TWINSPAN classification of 157 drift-diving sites by trout species, size, and biomass, showing biomass levels and classification division orders (1–3) and with sites and groups plotted in Fig. 2.

A geographical pattern is evident in this classification, with all sites in Group 6 being in the North Island, and with a North Island predominance in Groups 4 and 5. Brown trout sites (Groups 1–3) were predominantly in the south of the North Island or in the South Island. This reflects the known distribution of brown and rainbow trout (Allen & Cunningham 1957). Sites within the same river or river system were usually in the same group, with exceptions where there were differences in fish species present or in biomass for headwater and downstream reaches. Of the 22 different rivers with high trout biomass (Groups 3 and 5), five were lake outlets, four were up stream of a lake, and two were stable spring-fed rivers.

Univariate analysis of variance between groups

Only 91 of the 157 sites used in the fish-group classification were included in this analysis, as flow records and measurements of other environmental variables were not available for the remaining 66 sites. Significant differences between groups (Kruskal-Wallis $P < 0.05$) were found for 17 variables (Table 2). Mean annual temperature amplitude is excluded from Table 2 because it is a linear combination of two other variables (minimum annual and mean annual temperature). The square root of river gradient was a more significant variable than the untransformed gradient. Jowett & Richardson (1989) found that the effect of floods on trout populations depended upon the square root of river gradient which in turn is proportional to water velocity by Manning's equation (Henderson 1966). Of the water quality parameters, total conductivity and dissolved reactive phosphorus showed the most potential as indicators, although their between-group differences were not significant ($F = 2.05$ and $F = 1.96$ respectively). The more significant ($P < 0.01$) differences between groups were for temperature (mean annual and minimum annual temperature), catchment lithology (percentage of lake, percentage volcanic ash, and percentage alluvium), hydrological indices (ratio of mean to median flow), in-stream habitat (percentage in-stream vegetation), and total aquatic invertebrate biomass.

Several variables appeared to be related to brown trout abundance in that their values were linearly related to the group numbers based on brown trout biomass. Significant differences between the three "brown-trout-only" groups (Tukey test $P < 0.05$) were found between Groups 1 and 2 for only one variable (percentage silt substrate), and between Groups 1 and 3 for six variables (square root of river gradient, percentage in-stream vegetation, percentage lake area, standard deviation of mean cross-section depths at mean annual low flow, total aquatic invertebrate biomass, and variation in adult rainbow trout habitat between median and mean annual low flow). Between Groups 2 and 3 there were significant differences (Tukey test $P < 0.05$) for six variables (in-stream cover, percentage gravel substrate, adult rainbow trout habitat at mean annual low flow, percentage lake area, percentage undeveloped grassland, and substrate size).

Drift-diving observations showed that brown trout were usually associated with in-stream cover but that rainbow trout were not. Brown trout were associated with in-stream cover at 127 of 132 sites where brown trout were present, whereas rainbow trout were associated with cover at six of 17 sites, and at only three of the six sites were large or medium fish associated with cover. Not all cover types were utilised to the same extent. Brown trout were seen associated with bedrock at 82% of the sites where bedrock was present, with boulders at 71% of the sites with boulder cover, with bank cover at 62% of the sites, and with in-stream debris at 60% of the sites with that form of cover.

Table 2 Group means and standard deviations for independent environmental variables which show significant (P<0.05) difference between groups (abbreviations listed in Table 1). **P < 0.01.

Group	ALGAE	ALLUVIUM**	COVER	INVERT**	LAKE**	MALF/MEDIANF	MEANF/MEDIANF**	MINTEMP**
1	11.00 ± 15.17	10.40 ± 11.01	4.68 ± 1.37	0.56 ± 0.47	0.80 ± 0.40	0.30 ± 0.11	1.74 ± 0.28	6.54 ± 1.82
2	12.90 ± 16.12	19.00 ± 14.81	4.45 ± 1.02	1.35 ± 1.07	0.25 ± 1.12	0.29 ± 0.08	1.66 ± 0.22	5.90 ± 1.18
3	22.59 ± 13.67	10.90 ± 10.92	5.70 ± 1.48	1.88 ± 1.20	2.60 ± 3.50	0.32 ± 0.11	1.59 ± 0.49	6.78 ± 1.47
4	3.92 ± 6.71	8.89 ± 14.99	4.11 ± 0.98	0.67 ± 0.83	0.00 ± 0.00	0.37 ± 0.13	1.52 ± 0.28	6.37 ± 1.80
5	–0.60 ± 0.55	12.33 ± 18.48	4.67 ± 0.98	0.54 ± 0.61	1.33 ± 2.81	0.46 ± 0.22	1.31 ± 0.30	7.50 ± 1.38
6	12.86 ± 15.18	0.42 ± 1.16	4.92 ± 1.28	0.36 ± 0.26	1.83 ± 4.28	0.59 ± 0.29	1.39 ± 0.46	10.44 ± 1.94

Group	ROLL	SQRSLOPE	TEMP**	TUSSOCK	VEGETATION**	VOLCANIC**	WUABTS(2–3)	WUAFP(2)
1	11.20 ± 12.68	0.074 ± 0.026	12.09 ± 1.78	24.04 ± 24.11	1.21 ± 1.86	16.52 ± 33.91	35.75 ± 19.79	0.33 ± 0.08
2	15.75 ± 13.15	0.057 ± 0.014	11.39 ± 1.15	39.95 ± 24.99	1.98 ± 2.24	4.40 ± 18.10	37.69 ± 16.96	0.35 ± 0.10
3	13.40 ± 11.48	0.055 ± 0.016	12.21 ± 0.95	20.10 ± 24.40	3.64 ± 3.73	8.90 ± 28.14	29.44 ± 22.60	0.34 ± 0.12
4	17.61 ± 11.30	0.072 ± 0.022	11.61 ± 1.66	40.94 ± 34.33	0.38 ± 0.32	39.72 ± 37.33	17.69 ± 19.53	0.37 ± 0.08
5	17.00 ± 9.01	0.051 ± 0.028	11.50 ± 1.03	24.83 ± 25.73	2.18 ± 1.57	37.50 ± 41.08	17.12 ± 33.77	0.26 ± 0.09
6	28.58 ± 17.57	0.062 ± 0.019	14.39 ± 2.11	12.08 ± 8.27	9.32 ± 11.25	62.92 ± 33.82	6.51 ± 24.24	0.22 ± 0.09

Other variables separated both the mixed trout species and rainbow trout rivers from brown trout rivers. Percentage volcanic ash, ratios of both mean annual low and mean flow to median flow, minimum annual water temperature, variation in brown trout spawning habitat between median and mean flow, percentage scrub, and annual temperature range all showed significant (P < 0.005) differences between brown trout rivers and mixed species/rainbow-trout-only rivers.

Discriminant modelling with environmental variables

Water temperature, catchment, and hydrological variables were available for 91 sites, but the number available for analysis was reduced to 65 sites when in-stream habitat, water quality, and periphyton variables were included, and to 43 sites when the aquatic invertebrate data were incorporated in the analysis.

Stepwise discriminant analysis (SAS 1982) was used to form two discriminant models, the first from temperature, hydrological, and catchment variables, and the second from the above set plus in-stream habitat variables. The first model can be applied using data easily obtained from maps and hydrological record, whereas the second model requires more extensive on-site field measurements.

The first model used one temperature, one hydrological, and six catchment variables (Table 3) to form discriminant functions which correctly classified 57% or 52 of the 91 sites. Using the same set of discriminant functions on the 65 sites, for which there were in-stream habitat data, gave a similar result, correctly classifying 55%, or 36 of the 65 sites (Table 4).

When variables were selected from the pool of temperature, catchment, hydrological, and in-stream habitat variables, 11 were included (one temperature, one hydrological, two catchment, and seven in-stream habitat) (Table 3) and the new set of discriminant functions correctly classified 47 of the 65 sites or 72% (Table 4).

In both cases, first and second discriminant functions were highly significant (P < 0.001) and, when in-stream habitat variables were included, the third function was significant (P = 0.020). Higher functions were not significant (P > 0.10). The improvement in predictive ability was in Groups 2–5 which suggests that in-stream habitat variables were better able to discriminate between groups that were based on trout biomass. Further evidence of this is shown by the group centroids when plotted against the two principal discriminant functions (Fig. 4). Function 1, in Model 1 using temperature, catchment, and hydrological variables, gave good separation of the brown trout sites (Groups 1–3) from the mixed species/rainbow trout only sites (Groups 4–6) but neither Function 1 nor 2 was related to trout biomass. When in-stream habitat variables were included in the second model, Function 1 related to biomass, in that its value increased from Groups 1 to 3 and from Groups 4 to 5 (Fig. 4), as well as providing some separation between brown and mixed species/rainbow trout only sites. Function 2 was inversely related to trout biomass.

Correlations between variables and the discriminant function (structure coefficients) reveal how closely the variables and function are related (Table 4). In the first model, minimum annual water temperature, percentage volcanic ash, and ratio of mean annual low flow to median flow were most closely related to Function 1, which discriminated between brown trout sites and mixed species/rainbow trout only sites. In the second model, these variables were less dominant and other variables—square root of river gradient, percentage lake area, and variation in adult rainbow trout WUA between median and low flow—were also related to Functions 1 and 2. Function 3 was related to a number of in-stream habitat variables but was not obviously related to either trout species or biomass.

Of the 18 sites incorrectly classified by the second model, four had lower brown trout biomass than predicted and three had higher than the predicted level of biomass. Four of the six sites were misclassified between Groups 1 and 2. This can be explained by the arbitrary nature of the biomass level division between Groups 1 and 2 and the variation in biomass estimates. Four brown trout sites were predicted as mixed species and five mixed species sites predicted as brown-trout-only sites. Of the five sites predicted as brown-trout-only, two were in the Waitaki, two in Nelson/Marlborough district, and the other in Taranaki. Of the remaining two mis-classified sites, one contained a higher mixed species biomass than predicted, possibly because of a lake situated down stream of this site, and at the other there is a barrier to upstream movement of trout and no record of any release of brown trout into that section of the river (T. Stephens, Dept. of Conservation pers. comm.).

DISCUSSION

Rainbow trout in this study predominated north of a line between southern Hawke's Bay and northern Taranaki as was first described by Allen & Cunningham (1957). Using catch rate as an index of trout abundance, Allen & Cunningham (1957) suspected that climatic factors, especially temperature, were important, and also speculated that trout populations were related to physical features of the terrain but that the relationships were different for the two trout species. In the present study, some catchment characteristics, such as the amount of rolling and undeveloped grassland catchment, were related to the distribution of brown and rainbow trout but these were not the most important factors.

Table 3 Correlations between variables and discriminant functions (structure coefficients) for significant functions ($P < 0.001$) of discriminant models with and without in-stream habitat variables (abbreviations listed in Table 1). Model 1 includes temperature, hydrological, and catchment variables; Model 2 includes temperature, hydrological, catchment, and in-stream habitat variables.

	Model 1			Model 2		
Variable	Function 1	Function 2	Variable	Function 1	Function 2	Function 3
MINTEMP	0.795	–0.188	MINTEMP	–0.387	–0.275	0.302
VOLCANIC	0.509	0.439	VOLCANIC	–0.335	–0.048	–0.025
MALF/MEDIANF	0.592	0.170	MALF/MEDIANF	–0.392	–0.219	0.036
LAKE	0.238	–0.325	LAKE	0.186	–0.433	–0.066
TUSSOCK	–0.257	0.389	COVER	0.069	–0.202	0.294
ALLUVIUM	–0.345	–0.076	DEPTH(2)	0.032	–0.218	–0.464
ROLL	0.347	0.142	WUABTS(2–3)	0.255	0.173	0.272
SCRUB	0.156	0.429	SQRSLOPE	0.020	0.402	0.367
			SUBSTRATE	0.120	–0.158	0.425
			WUARTA(2–1)	–0.028	0.309	0.405
			WUAFP(2)	0.190	0.156	0.003

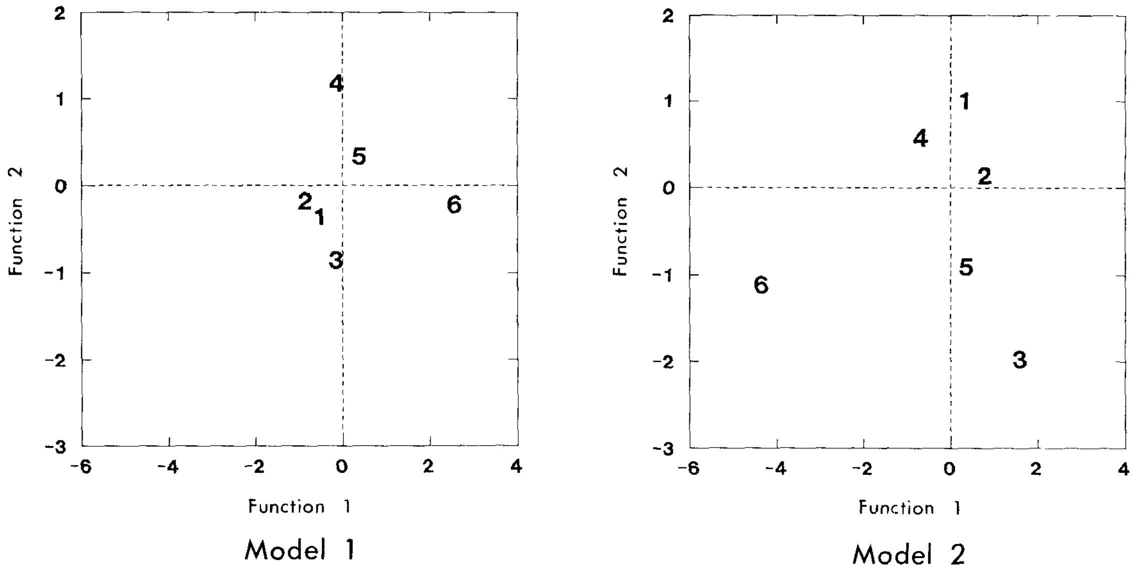


Fig. 4 Group centroids (Groups 1–6 inclusive) for the first and second discriminant functions for Model 1 with temperature, hydrological, and catchment variables and for Model 2 with the above variables and addition of in-stream habitat variables.

The factors which explained the geographical distribution of trout were minimum annual water temperature and the percentage of volcanic ash in the catchment. Although the temperature factor may be biologically linked to trout distribution, it is probable that the ash factor reflects either the influence of geography or hydrology rather than direct effects on species distribution.

Hydrological factors, the ratios of mean flow and mean annual minimum flow to median flow, were important. These factors identified lake- and spring-fed rivers with stable flow regimes as likely sites for rainbow trout. Similar stable flow regimes are also found in the central North Island pumice ash catchments, and this may partially explain the significance of ash catchments in trout distribution.

The minimum annual water temperature was a more significant factor than either the mean annual or the maximum annual water temperature, and has some connection with lake- and spring-fed rivers in which the seasonal temperature fluctuations are less than in rain-fed rivers. The ratio of mean to median flow and the variation in spawning habitat between median and mean flow also distinguished between brown trout and mixed-species/rainbow-trout-only rivers, and both these factors were correlated with the ratio of mean annual minimum flow to median flow ($r = 0.59$ and 0.40, respectively). Examination of mis-classified sites suggested that lakes situated down stream of the sites, or connected to lakes via other rivers, may affect species distribution and abundance.

Hall & Knight (1981), in a review of the literature on the variability of salmonid populations, classified factors affecting fish abundance as streamflow, physical habitat, food abundance, predation and

Table 4 Proportion of correctly predicted site classifications using discriminant functions derived with and without in-stream habitat variables. Model 1 includes temperature, hydrological, and catchment variables; Model 2 includes temperature, hydrological, catchment, and in-stream habitat variables. ccc, canonical correlation coefficient.

	Model 1		Model 2
Group	n=91	n=65	n=65
1	18/25	16/21	17/21
2	10/20	4/12	7/12
3	4/10	4/10	8/10
4	10/18	8/12	8/12
5	0/6	0/4	2/4
6	10/12	4/6	5/6
Overall	52/91	36/65	47/65
	57%	55%	72%
ccc	0.74		0.85

movement, and migration. They found that physical habitat was most closely related to salmonid abundance. Fausch et al. (1988) classified models of fish abundance according to environmental variables used in the model, and found that the best models used a combination of habitat, biological, physical, water quality, channel morphology, flow, and catchment characteristics. Fausch et al. found that the variables most commonly identified as significant were measures of in-stream and overhead cover, alkalinity/hardness/conductivity, mean streamflow, width, surface area, and dissolved oxygen—but they warned that this group was likely to be biased by the ease of data collection.

Allen & Cunningham (1957) suggested that catchments containing schist had low brown trout abundance, as measured by catch per unit effort. In this study, however, there was no such relationship. Brown trout abundance increased with increasing percentage of schist, although not significantly. Brown trout biomass was related to a large number of in-stream habitat variables; these were square root of river gradient, in-stream cover, standard deviation of mean cross-section velocities, percentage in-stream vegetation, substrate size, percentage gravel and silt substrates, and percentage change in WUA of adult rainbow trout habitat from median to mean annual low flow. However, it was related to only two catchment variables, percentage lake area and percentage undeveloped grassland. Water quality and biological indicators, except for total aquatic invertebrate biomass, were not related to trout abundance, although this may be because the sites were all in clear water with correspondingly good water quality. Brown trout were often observed associated with in-stream cover and exhibited a preference for the two forms of cover (bedrock and boulders) which are more stable in floods than the other two types of cover (banksides and in-stream debris).

Although some environmental variables were related to brown trout biomass, other variables were common to both trout species. Low gradients and stable flows were common features of rivers with high brown and rainbow trout abundance, as indicated by the values of the ratio of mean annual low flow to median flow, percentage change in WUA between mean annual low, median, and mean flow, percentage lake area, and square root of river gradient.

WUA is often considered to be specific to the microhabitat of a particular life-stage and species, with an implicit assumption that the amount of suitable microhabitat relates to abundance (Bovee 1982; Orth 1987). WUA, calculated at median flow using the preference criteria described by Waters (1976) for "food production", was an important discriminating variable. These criteria also agree with MAF Fisheries unpublished data on water column velocities and depths at New Zealand brown trout feeding locations. Although WUA calculated for adult rainbow trout at mean annual low flow was significantly correlated with brown trout biomass ($P = 0.022$), its variation was more important in the discriminant model. Percentage changes in WUA between mean annual low, median, and mean flow for brown trout spawning habitat and for adult rainbow habitat were important discriminators. Trout biomass increased with decreasing variation in adult rainbow trout WUA, reflecting the tendency for stable flow rivers to contain higher trout numbers. Brown trout spawning habitat variation discriminated between brown and rainbow trout rivers because the latter tended to lack suitable spawning gravels.

Overall, the factors identified in this study as related to the distribution of trout species were largely climatic whereas factors determining abundance were related primarily to in-stream habitat, some of which are determined by river morphology and others by the magnitude of river flow and flow variation.

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REFERENCES

Allen, K. R.; Cunningham, B. T. 1957: New Zealand angling 1947–1952: results of the diary scheme. New Zealand Marine Department, *Fisheries bulletin 12*. 153 p.

Biggs, B. J. 1990: Periphyton communities and their environments in New Zealand rivers. *New Zealand journal of marine and freshwater research 24*: this issue.

Biggs, B. J. F.; Duncan, M. J.; Jowett, I. G.; Quinn, J. M.; Hickey, C. W.; Davies-Colley, R. J.; Close, M. E. 1990: Ecological characterisation, classification, and modelling of New Zealand rivers: an introduction and synthesis. *New Zealand journal of marine and freshwater research 24*: this issue.

Bovee, K. D. 1978: Probability of use criteria for the family Salmonidae. United States Fish and Wildlife Service, Cooperative Instream Flow Group, *Instream flow information paper 4*. 80 p.

———1982: A guide to stream habitat analysis using the instream flow incremental methodology. United States Fish and Wildlife Service, Cooperative Instream Flow Group, *Instream flow information paper 12*. 248 p.

Bovee, K. D.; Milhous, R. 1978: Hydraulic simulation in instream flow studies: theory and techniques. United States Fish and Wildlife Service, Cooperative Instream Flow Group, *Instream flow information paper 5*. 131 p.

Bowlby, J. N.; Roff, J. C. 1986: Trout biomass and habitat relationships in southern Ontario streams. *Transactions of the American Fisheries Society 115*: 503–514.

Carlander, K. D. 1969: Handbook of freshwater fishery biology, volume 1. Ames, Iowa, Iowa State University Press. 752 p.

Close, M. E.; Davies-Colley, R. J. 1990: Baseflow water chemistry in New Zealand rivers. 1. Characterisation. *New Zealand journal of marine and freshwater research 24*: this issue.

Fausch, D. F.; Hawkes, C. L.; Parsons, M. G. 1988: Models that predict standing crop of stream fish from habitat variables: 1950–85. General technical report PNW-GTR-213. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 62 p.

Hall, J. D.; Knight, N. J. 1981: Natural variation in abundance of salmonid populations in streams and its implications for design of impact studies. EPA-600/S3-81-021, Corvallis, OR: U.S. Environmental Protection Agency. 85 p.

Hayes, J. W.; Leathwick, J.R.; Hanchet, S. M. 1989: Fish distribution patterns and their association with environmental factors in the Mokau River catchment, New Zealand. *New Zealand journal of marine and freshwater research 23*: 171–180.

Henderson, F. M. 1966: Open channel flow. New York, Macmillan. 522 p.

Hill, M. O. 1979: TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and systematics, Cornell University, Ithica, New York. 90 p.

Jowett, I. G. 1989: River hydraulic and habitat simulation, RHYHABSIM computer manual. *New Zealand fisheries miscellaneous report 49. Ministry of Agriculture and Fisheries*, Christchurch. 39 p.

Jowett, I. G.; Duncan, M. J. 1990: Flow variability in New Zealand rivers and its relationship to in-stream habitat and biota. *New Zealand journal of marine and freshwater research 24*: this issue.

Jowett, I. G.; Richardson, J. 1989: Effects of a severe flood on instream habitat and trout populations in seven New Zealand rivers. *New Zealand journal of marine and freshwater research 23*: 11–17.

Klecka, W. R. 1980: Discriminant analysis. Sage University paper series on quantitative applications in the social sciences, 07-019. Beverly Hills and London, Sage Publications. 73 p.

Larsen, D. P.; Omernik, J. M.; Hughes, M. M.; Rohm, C. M.; Whittier, T. R.; Kinney, A. J.; Gallant, A. L.; Dudley, D. R. 1986: Correspondence between spatial patterns in fish assemblages in Ohio streams and aquatic ecoregions. *Environmental management 10*: 815–828.

Mosley, M. P. 1982: New Zealand river temperature regimes. *Water and soil miscellaneous publication 36*, Ministry of Works and Development, Wellington. 87 p.

Orth, D. J. 1987: Ecological considerations in the development and application of instream flow-habitat models. *Regulated rivers: research and management 1*: 171–181.

Quinn, J. M.; Hickey, C. W. 1990: Characterisation and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. *New Zealand journal of marine and freshwater research 24*: this issue.

SAS 1982: SAS User's Guide: Statistics SAS Institute Inc., Cary, North Carolina. 584 p.

Shirvell, C. S.; Dungey, R. G. 1983: Microhabitats chosen by brown trout for feeding and spawning in rivers. *Transactions of the American Fisheries Society 112*: 355–367.

Teirney, L. D.; Jowett, I. G. in press: Trout abundance in New Zealand rivers: an assessment by drift diving. *Freshwater fisheries report 118*. Freshwater Fisheries Centre, Ministry of Agriculture and Fisheries, Christchurch. 47 p.

Tonn, W. M.; Magnuson, J. J.; Forbes, A. M. 1983: Community analysis in fishery management: an application with northern Winsconsin lakes. *Transactions of the American Fisheries Society 112*: 368–377.

Waters, B. F. 1976: A methodology for evaluating the effects of different streamflows on salmonid habitat. *In*: Orsborn, J. F.; Allman, C. H. *ed*., Proceedings of the symposium and speciality conference on instream flow needs II. Bethesda, Maryland, American Fisheries Society. Pp. 224–234.

Wright, J. F.; Moss, D.; Armitage, P. D.; Furse, M. T. 1984: A preliminary classification of running-water sites in Great Britain based on macro-invertebrate species and the prediction of community type using environmental data. *Freshwater biology 14*: 221–256.