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# Does natural acidity mediate interactions between introduced brown trout, native fish, crayfish and other invertebrates in West Coast New Zealand streams?

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## ARTICLE INFO

### Article history:

Received 7 October 2005

Received in revised form

16 December 2005

Accepted 19 December 2005

Available online 10 February 2006

### Keywords:

Introduced trout

Native crayfish

Macroinvertebrates

Naturally acidic streams

New Zealand

## ABSTRACT

The presence of introduced brown trout (*Salmo trutta*) on the distribution of native crayfish (*Paranephrops planifrons*), native galaxiid fishes (*Galaxias* spp.) and invertebrate fauna was investigated in 18 West Coast New Zealand streams (8 with trout and 10 without trout) differing in chemical characteristics. Gut contents of trout, crayfish and eels were also examined to evaluate whether competition or predation could be linked to the patterns found. Abundances of crayfish and galaxiids were significantly lower in streams with trout, but in streams without trout, substrate size was one of the most important factors determining crayfish abundance. In contrast to crayfish, other macroinvertebrates were more abundant in trout streams than streams without trout and significantly more taxa were found in streams with trout. Macroinvertebrate abundance was related to environmental factors, such as pH, substrate, depth and total nitrogen. Gut content analysis showed an overlap in diet (mostly invertebrates) between trout and eels. Crayfish, however, had a more omnivorous diet where detritus was the most frequently occurring food material. Differences in chemical characteristics marked the streams with and without trout. Thus, trout were not present in streams with pH < 6.0. Crayfish and galaxiids were present in streams with pH ranging from 4.1 to 7.9, and those with pH < 6.0 may function as trout-free refuges where larger populations of these species may persist. However, other macroinvertebrate taxa may be more negatively affected by acidification than by trout. By protecting naturally acidic, brown water streams, New Zealand crayfish and galaxiid fish populations can be conserved within geographic areas where trout are present.

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## 1. Introduction

Management of non-indigenous (exotic) species is an important factor in maintaining native species and ecosystem functioning (Byers et al., 2002). Understanding the impact of exotic species on native ecosystem functioning and structure is

therefore one of the most important challenges in conservation biology today (Parker et al., 1999; Mack et al., 2000; Kolar and Lodge, 2001; Gido et al., 2004). The introduction of exotic species by humans (accidentally or deliberately) into an ecosystem often has effects at several trophic levels (Coblentz, 1990; Lodge, 1993; Allan, 1995; Nyström et al., 2001; Townsend,

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doi:10.1016/j.biocon.2005.12.019

2003). The level of impact of introduced species on interactions within native communities may be influenced by abiotic factors, and they may determine also whether key organisms in the food web are affected or not (Nyström and McIntosh, 2003). It is therefore important to study food webs under a range of environmental conditions. If appropriate conservation measures are to be taken in order to maintain native ecosystem functioning and diversity, it is necessary not only to identify the key interactions in complex food webs, but also the habitats and environmental conditions that influence the impact of the invader.

Trout are some of the most widely distributed exotic species in aquatic ecosystems (Allan, 1995), and their presence in simple food chains often results in cascading, “top-down” effects (Bechara et al., 1992; McIntosh and Townsend, 1996; Nyström et al., 2003). Brown trout (*Salmo trutta*) were introduced to New Zealand in 1867 to benefit recreational fishing and from the time of their first introduction until 1921 more than 60 million brown trout had been raised and released into New Zealand streams (Townsend, 1996). Today they are found throughout much of the country (Townsend, 1996). The introduction of brown trout into New Zealand streams has affected other stream fauna, notably native galaxiid fish, through predation and competition for food and space, and has led to the fragmented distribution of many galaxiid populations (Townsend and Crowl, 1991; McIntosh et al., 1992; McIntosh, 2000a). The presence of trout has also affected invertebrate grazer behaviour, indirectly leading to higher standing stocks of periphyton in some trout streams (Townsend and Crowl, 1991; McIntosh et al., 1992; McIntosh and Townsend, 1995; Townsend, 1996; Nyström et al., 2003). Trout may also influence the species composition and size distribution of invertebrates in streams, and some large invertebrates with long life cycles, and no protective cases or shells (e.g. many predatory species), may be particularly vulnerable to trout predation (Huryn, 1998; Townsend, 2003; Nyström et al., 2003). Consequently, the abundance of less vulnerable invertebrate species (e.g. small grazing caddisflies and snails with cases or shells) may be higher in streams with trout than in streams without fish, or with native galaxiid fish only (Nyström et al., 2003).

Most studies on the impact of exotic trout in New Zealand have focussed on simple food chains that include native fish species and invertebrate grazers, however, many ecosystems including streams on the West Coast of New Zealand also contain large bodied omnivorous freshwater crayfish, whose distribution may have been affected negatively by the introduction of brown trout (Townsend, 1996, 2003). The two endemic crayfish species (*Paraneohpops planifrons* and *Paraneohpops zealandicus*) can be regarded as keystone species in New Zealand freshwater communities, as they can play important roles as both predators and detritivores (Usio, 2000). In particular, they may be major processors of leaves in streams (Usio, 2000; Usio and Townsend, 2002), because large, shredding insects are often lacking. Hence, any negative impact on crayfish by trout will likely affect the functioning of an invaded community (Townsend, 2003).

In addition to predation and competitive interactions, abiotic factors can have strong effects on the species composition and abundance of invertebrates and fish in New

Zealand streams. For example, physical disturbance, acidification and associated water chemistry, have all been shown to influence stream biota (Winterbourn and Collier, 1987; Collier et al., 1990; Winterbourn and McDuffett, 1996; McIntosh, 2000a). On the West Coast of the South Island many brown water streams with naturally low pH support populations of galaxiid fish and crayfish, but brown trout have not been recorded in waters with pH below 5.0 (Collier et al., 1990). It is therefore possible that brown water streams act as refuges for native species that are tolerant of moderately low pH.

In the present study multiple streams with and without trout and with varying chemical characteristics, including pH were investigated. In each stream the relative importance of abiotic factors (e.g. pH) and trout in determining the composition of food webs was assessed. Additionally, gut contents of trout, eels and crayfish were used to evaluate whether competition for food or predation could be linked to the community patterns found.

## 2. Materials and methods

Fieldwork was conducted between 22 and 30 January 2003 in 18 streams on the West Coast, South Island, New Zealand (Fig. 1). Eight of the sites were on open streams surrounded by pasture, tussock grassland or shrub/forest, whereas ten sites were in native or exotic forest. Based on data from New Zealand freshwater fish database (<http://fwdb.niwa.cri.nz>) and observations, it was known that all streams contained a native crayfish species (*P. planifrons*) and that eight were expected to contain the introduced brown trout (*S. trutta*). No physical barriers (e.g. waterfalls) to colonisation by

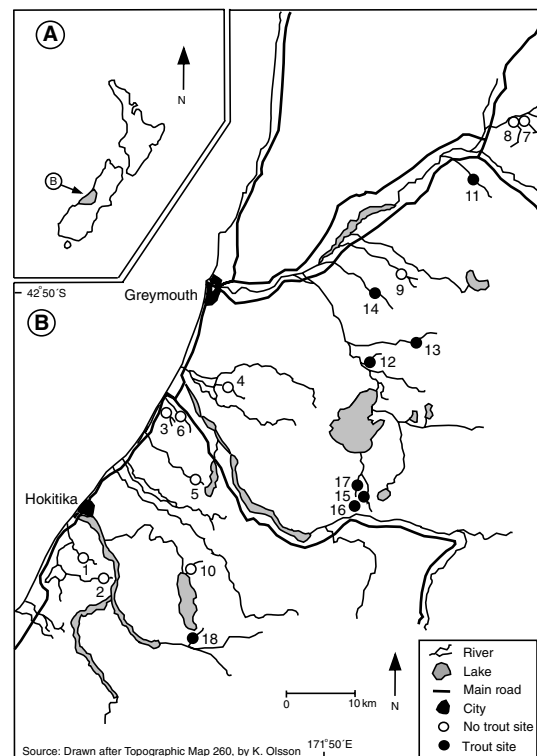


Fig. 1 – Map of New Zealand (A) and Westland showing the study sites (B). Site numbers as in Table 1.

trout, crayfish or most other fishes were present in any of the study streams.

### 2.1. Physical factors and water chemistry

At each site a study reach 9.5–28.5 m long, depending on width and availability, (area 17–128 m<sup>2</sup>) was established. Water temperature, current velocity, average depth, stream width, substrate size and bed stability (Pfankuch bottom score; a subjective index of streambed stability, as described by McIntosh, 2000b) were measured at each site. Current velocity was estimated by measuring the time taken for fluorescein dye to travel through the study reach. Average depth was estimated from nine measurements (three on each of three cross-stream transects) and average width from three measurements at each site. Average substrate size was estimated by measuring the longest axis of 30 randomly chosen substrate particles within the study reach. Canopy cover (% streambed covered), macrophyte cover (% streambed covered) and undercut banks (% of stream bank length undercut) were estimated visually for each study reach. A water sample, kept frozen until analysis was performed, was used to determine pH, conductivity (at 25 °C), total nitrogen, total phosphorus, calcium and dissolved organic carbon. Except for pH and conductivity, which were measured at the University of Canterbury, all samples were analysed in the Environment Canterbury laboratory (Christchurch, New Zealand), using the APHA 3111 B (20th Ed) acid soluble method for calcium, NI APHA 5310 C (20th Ed) uv-persulphate method for dissolved organic carbon, APHA 4500-N C (20 Ed) – modified method for total nitrogen and APHA 4500-P B5 (20 Ed) – auto-analyser method for total phosphorus.

### 2.2. Particulate organic matter

Coarse particulate organic matter was collected with a Surber sampler (0.0625 m<sup>2</sup>, 250 µm mesh). Five randomly located samples were taken at each site, and preserved in 80% ethanol. Invertebrates, macrophytes, twigs and pieces of wood were removed and the remaining organic matter (>1 mm) was dried for 24 h at 65 °C. Coarse particulate organic matter was weighed to the nearest milligram and a subsample (~1 g) was taken to estimate ash-free dry weight. The subsample was ashed in a muffle furnace at 450 °C for one hour and reweighed.

### 2.3. Epilithic algae

Five stones were selected randomly at each site for the determination of epilithic algal biomass. An 18.7 cm<sup>2</sup> or 8.55 cm<sup>2</sup> circle of epilithon was removed from the upper surface of each stone with a wire brush, filtered on to a glass fibre filter and frozen for later analysis. Chlorophyll *a* was extracted with 95% ethanol (12 h in the dark at 20 °C) and estimated spectrophotometrically according to Jespersen and Christoffersen (1987).

### 2.4. Fish, crayfish and invertebrates

Fish and crayfish were sampled at all sites by electrofishing (Kainga EFM 300 backpack machine). Three downstream runs

were made at all sites (9.5–28.5 m), which were delineated by stop nets (5 mm mesh). Captured crayfish were measured to the nearest millimetre (total length, TL) and weighed to the nearest milligram. Fish were anaesthetized, and identified to species level following McDowall (2000), measured and weighed as above. The abundance (per m<sup>2</sup>) of crayfish, galaxiids, eels and trout was estimated from the absolute number captured. Thirty-eight trout, 59 crayfish and 24 longfin eels (*Anguilla dieffenbachii*) from various sites were sacrificed for analyses of gut contents. Sixteen eels and four of the larger trout were examined in the field, whereas smaller trout, eight eels and all crayfish were frozen for later identification. Organic matter was separated into fine detritus and plant fragments, and invertebrates were identified to generic level in most cases following Winterbourn et al. (2000). Frequency of food items in trout, eel and crayfish guts was calculated from the data. Only eels larger than 17.3 cm (the smallest eel containing crayfish in this study) were included as earlier studies indicate that smaller eels are not able to eat crayfish (Jellyman, 1989; Schulze et al., 2004). Invertebrates present in the Surber samples (see above) were preserved in 80% ethanol and identified and counted at up to 10× magnification.

### 2.5. Statistical analysis

All statistical analyses were conducted using the software SPSS 11.0 for Windows, except for the canonical correspondence analysis that was conducted in CANOCO 4.5 for Windows. To test whether there were physico-chemical differences between trout and no-trout streams a principal component analysis was performed. It included the following variables: water temperature, depth, width, conductivity, velocity, substrate size, pH, disturbance score (bed stability), total nitrogen, total phosphorus, coarse particulate organic matter, chlorophyll *a*, calcium, dissolved organic carbon, canopy cover, macrophyte cover and bank undercutting. A correlation matrix with varimax rotation was used (Aronsson, 1999). All axes with eigenvalues > 1 were retained, and variables with an absolute loading of 0.606 (1% significance level, *n* = 17) were considered to be important (Watt, 1993; Aronsson, 1999; McGarigal et al., 2000). Principal component analysis scores were compared between trout and no-trout streams with independent sample *t*-tests.

To compare the abundance of crayfish, galaxiids, eels and invertebrates in streams with and without trout, independent sample *t*-tests were used. A two-sample Kolmogorov–Smirnov test (Aronsson, 1999) was used to compare the size frequency distribution of crayfish between streams with and without trout. Previous experimental and field studies in New Zealand streams have shown that multiple factors including the presence of crayfish (Usio, 2000), periphyton biomass (Biggs et al., 2000), canopy cover (Nyström et al., 2003), coarse particulate organic matter (Nyström et al., 2003), pH (Harding et al., 2000) and physical disturbance (Death and Winterbourn, 1995) may affect the abundance of invertebrates. Consequently, it was tested whether the abundances of the 72 identified macroinvertebrate taxa (excluding all *Paranehrops*) were related to any of the measured environmental factors in a canonical correspondence analysis by multivariate constrained ordination and a Monte Carlo

permutation test (McGarigal et al., 2000; Leps and Smilauer, 2003). Invertebrate taxa with an absolute loading of 0.302 (1% significance level,  $n = 72$ ) and environmental variables with an absolute loading of 0.606 (1% significance level,  $n = 17$ ) were considered to be important. To test whether the presence of crayfish influenced invertebrate abundance linear regressions were performed on abundances in streams with and without trout, respectively.

To ensure variables were normally distributed, environmental- and abundance data were transformed prior to analysis. For percentage data (canopy cover, macrophytic cover and undercut banks) arc-sin  $\sqrt{x}$  was used and for all other variables  $\ln(x + 1)$ . Temperature, pH, substrate (median) and disturbance (index score) values were not transformed.

### 3. Results

Streams with and without trout varied considerably in chemical factors, including pH, conductivity, calcium and dissolved organic carbon, but not in physical factors, such as substrate size, depth and disturbance index (Table 1).

Five principal component axes with eigenvalues greater than one, collectively explained 77% of the variation in physico-chemical factors in the streams (Table 2). Scores on the first axis differed between streams with and without trout ( $t = 4.195$ ,  $df = 3.864$ ,  $p = 0.001$ ). Trout streams had high pH (6.4–7.9), whereas streams without trout had lower pH (4.1–6.6). Other measured physico-chemical variables varied among sites and overlapped considerably between the two kinds of streams (Table 1). Crayfish, galaxiids and eels were found across the whole pH spectrum (4.1–7.9). A total of 258 trout was caught with an average abundance in the trout streams of 0.54 trout/m<sup>2</sup> (range 0.01–2.10 per m<sup>2</sup>). The largest trout captured was 50 cm long and weighed 1.2 kg, but most were small (median length 5.1 cm, median weight 1.4 g). Crayfish were found in 17 of the streams, 281 at sites without trout and 41 at trout sites. The largest crayfish was 10.4 cm long and weighed 30.7 g (median length 4.3 cm, median weight 2.0 g). The size distribution of crayfish (Fig. 2) differed between streams with trout (median length 54 mm) and without trout (median length 41 mm) (two-sample Kolmogorov–Smirnov test,  $Z = 2.2$ ,  $p < 0.0001$ ). In streams with trout no juvenile crayfish (<20 mm) were caught, while some juveniles were caught in streams without trout (Fig. 2). Crayfish abundance was also significantly lower at sites with trout ( $t = 2.845$ ,  $df = 9.593$ ,  $p = 0.018$ ), but was highly variable at sites without trout. At the latter, crayfish abundance was highest where median substrate size was about 9 cm and lower on both coarser and finer substrates (Fig. 3).

Two species of eel, longfin eel (*Anguilla dieffenbachii*) and shortfin eel (*Anguilla australis*), were caught in 16 of the streams, and 233 galaxiids (belonging to four species, *Galaxias fasciatus*, *Galaxias postvectis*, *Galaxias brevipinnis* and *Galaxias divergens*) were captured at sites without trout and 19 at sites with trout. Four other native fish species were also caught. Galaxiid abundance was lower at sites with trout ( $t = 2.406$ ,  $df = 9.472$ ,  $p = 0.038$ ), but the abundance of eels did not differ ( $t = -0.284$ ,  $df = 15.214$ ,  $p = 0.780$ ) between sites with and without trout. Numbers of fish and crayfish caught at each site are given in Appendix 1.

Gut content analysis showed that trout had consumed a wide variety of food items. Nymphs of *Deleatidium* (Leptophlebiidae) and other mayflies were the most frequently found prey, and the largest trout caught contained a crayfish of about 5 cm total length (Fig. 4). However, none of the smaller trout had consumed crayfish. Of the 12 longfin eels from streams with trout, 25% contained crayfish in addition to other macroinvertebrates (Fig. 4). Of the 12 longfin eels from streams without trout, 50% contained crayfish in addition to other macroinvertebrates (Fig. 4). Crayfish had consumed a variety of food items (Fig. 4), of which detritus was found most frequently. However, fresh plant fragments, and several invertebrate taxa, including trichopteran larvae, nymphs of the mayfly *Deleatidium* and other crayfish, were also found in guts.

In all, 72 macroinvertebrate taxa (excluding *P. planifrons*) were identified in samples from the 18 streams. Collector/grazers dominated numerically in all streams and only three shredder taxa were found. Nineteen of the 72 taxa were present only in trout streams and 14 were present only in streams without trout (Appendix 2). The mean number of taxa differed between streams with and without trout ( $t = 2.735$ ,  $p = 0.015$ ), with more being present in trout streams. Furthermore, the mean abundance of invertebrates was more than three times higher in trout streams than streams without trout ( $t = 2.944$ ,  $p = 0.019$ ). The abundance of shredders did not differ between streams with and without trout, but there were more predatory invertebrates in streams with trout ( $t$ -tests, shredders,  $p = 0.670$ , predators,  $p = 0.056$ ). However, significantly more collector/grazers and filterfeeders were found in streams with trout ( $t$ -tests, collector/grazers  $p = 0.022$ , filterfeeders  $p = 0.045$ ). Invertebrate taxa with cases or shells (16 taxa, see Appendices 1 and 2) were also more abundant in streams with trout ( $t$ -test  $t = -2.783$ ,  $df = 7.013$ ,  $p = 0.027$ ). The two most common invertebrate taxa in the “cased” category were the snail *Potamopyrgus* (mean abundance of 510 individuals/m<sup>2</sup> in trout streams and 0.64 individuals/m<sup>2</sup> in streams without trout) and the caddisfly *Pycnocentroides* (mean abundance of 564.6 individuals/m<sup>2</sup> in trout streams and 0.64 individuals/m<sup>2</sup> in streams without trout). *Deleatidium* was the only invertebrate present at high densities in all streams (trout vs. no-trout streams  $t = -1.406$ ,  $df = 15.937$ ,  $p = 0.179$ ).

Canonical correspondence analysis showed that invertebrate abundance patterns were related to environmental variables (Fig. 5). The first axis explained 31.8% of the variation in abundance and was correlated with pH, conductivity (–) and canopy cover (+). The second axis explained 23.5% and was correlated with disturbance score, substrate (–), macrophytic cover and depth (+). A Monte Carlo permutation test with 999 permutations showed that pH ( $F = 2.56$ ,  $p = 0.002$ ), substrate ( $F = 1.80$ ,  $p = 0.006$ ), depth ( $F = 1.51$ ,  $p = 0.022$ ) and total nitrogen ( $F = 1.49$ ,  $p = 0.04$ ) had a significant effect on invertebrate abundance patterns. *Deleatidium* and Chironomidae, the two most common invertebrate taxa, were positively correlated with canopy cover and dissolved organic carbon, respectively (Fig. 5). Of the more common predatory invertebrates, *Stenoperla* was associated with large substrates. However, the abundance of *Neppia*, which was present only in trout streams, was correlated with conductivity and epilithon

**Table 1 – Physico-chemical and other environmental factors of the 18 study sites on the West Coast, South Island**

Sites	River name	Map coordinates East/North	Site area (m <sup>2</sup> )	Width (m)	pH	Cond. (µS/cm)	Ca (mg/l)	DOC (mg/l)	Total nitrogen (mg/l)	Total phosphorus (mg/l)	Substrate (cm)	Depth (cm)	Temp. (°C)	Disturb. score	Velocity (m/s)	Macrophyte cover (%)	Canopy cover (%)	Undercut banks (%)	CPOM (g/m <sup>2</sup> )	Chl.a (µg/cm <sup>2</sup> )
1	Duskes Creek	23440/58231	63.9	3.0	4.5	41	25.0	41	0.33	<0.008	17.3	27.3	14.4	22	1.0	5	75	5	3.3	0.5
2	Frosty Creek	23462/58205	29.6	2.9	4.4	36	0.5	4	0.23	<0.008	5.5	45.2	13.2	15	0.4	70	65	0	11.1	0.4
3	Kapitea Creek trib.	25348/58438	40.8	2.3	4.7	58	1.3	46	0.33	0.014	12.5	17.1	13.3	25	0.8	5	10	5	21.1	0.1
4	Nemona Creek	23639/58472	62.3	3.7	6.6	50	2.7	36	0.15	0.011	12.3	11.0	12.8	20	0.4	0	95	20	12.7	0.8
5	Kapitea Creek swamp	23598/58340	42.2	2.3	5.3	27	0.6	45	0.18	<0.008	9.8	23.0	12.2	25	0.3	10	50	80	27.1	0.4
6	Serpentine Creek trib.	23578/58430	29.3	3.1	4.4	46	0.6	46	0.27	0.011	10.3	15.6	14.5	16	0.4	15	70	80	6.5	0.1
7	Red Jack Creek trib.	24064/58840	19.7	1.2	5.1	43	13.0	54	0.38	0.023	8.9	8.6	11.4	26	0.6	5	70	40	51.4	0.3
8	Red Jack Creek trib.	24062/58839	52.1	2.2	5.2	40	24.0	51	0.37	0.020	11.4	13.7	12.2	23	0.5	5	5	50	32.2	0.2
9	Graham Creek	23891/58623	48.8	2.4	4.4	41	0.9	52	0.43	0.020	11.0	21.8	11.6	26	0.3	30	75	30	33.3	0.9
10	Lake Kaniere trib.	23585/58213	16.9	0.9	4.1	40	0.3	44	0.27	<0.008	3.4	14.7	12.5	17	0.2	40	90	40	31.7	0.2
11	Duffers Creek	23993/58754	76.7	4.6	6.8	36	17.0	32	0.18	0.021	8.8	17.2	12.7	24	0.8	5	5	10	6.0	0.7
12	Molly Creek trib.	23846/58502	46.2	4.9	7.9	129	7.0	0.9	0.11	<0.008	13.8	21.6	11.7	24	0.7	5	30	5	25.2	6.9
13	Deep Creek	23914/58522	66.7	8.8	6.6	31	1.4	34	0.21	0.010	16.0	19.6	12.8	25	0.7	5	5	5	7.1	0.9
14	Red Jacks Creek	23854/58598	127.9	6.7	6.5	48	12.2	35	0.29	0.023	12.1	19.2	12.8	31	0.7	5	40	15	1.3	0.8
15	Orangipuku River trib.	23836/58302	76.2	2.7	7.4	71	8.6	<0.2	0.30	<0.008	9.3	16.3	12.7	21	0.3	10	5	70	11.5	0.3
16	Orangipuku River	23832/58298	36.8	3.0	7.4	72	8.9	0.4	0.16	0.025	6.3	18.3	13.7	21	0.2	30	60	50	30.3	1.4
17	Bruce Creek trib.	23836/58352	47.6	3.1	6.4	89	11.0	38	0.46	0.013	4.1	33.8	13.7	21	0.3	70	5	70	2.7	0.5
18	Styx River trib.	23596/58123	45.9	3.2	6.9	91	9.9	1	0.17	0.016	9.7	14.6	10.8	29	0.6	50	95	5	7.4	1.0

Map coordinates are for New Zealand Map Series 260. Site numbers are those used in Fig. 1 (sites 1–10 are streams without trout and 11–18 are streams with trout). Cond. is conductivity at 25 °C, Ca is the calcium concentration, DOC is dissolved organic carbon, Substrate is median substrate size, Disturb. Score is the Pfankuch bottom score index (see methods), CPOM is coarse particulate organic matter and Chl. a is chlorophyll a concentration.

**Table 2 – Component loadings of abiotic factors for the 18 streams and percentage of variance explained by the five retained principal component axes**

Source	PC1	PC2	PC3	PC4	PC5
Variance explained (%)	25.05	17.92	14.78	11.02	8.0
Eigenvalues	4.26	3.05	2.51	1.87	1.36
pH	<b>0.882</b>	0.199	0.227	0.241	–0.030
Dissolved organic carbon (mg/l)	– <b>0.848</b>	0.276	0.051	0.057	0.013
Chlorophyll a ( $\mu\text{g}/\text{cm}^2$ )	<b>0.796</b>	0.089	–0.094	0.021	0.333
Conductivity ( $\mu\text{S}/\text{cm}$ )	<b>0.750</b>	–0.225	0.052	0.234	–0.078
Total nitrogen (mg/l)	– <b>0.647</b>	–0.275	0.175	0.445	–0.234
Macrophytic cover (%)	0.030	– <b>0.961</b>	–0.026	–0.064	–0.014
Substrate median size (cm)	–0.069	<b>0.858</b>	0.094	0.093	0.249
Depth (cm)	0.060	–0.587	0.487	–0.309	0.323
Coarse particulate organic matter ( $\text{g}/\text{m}^2$ )	0.073	0.096	– <b>0.782</b>	–0.037	–0.331
Temperature ( $^{\circ}\text{C}$ )	–0.252	–0.080	<b>0.698</b>	–0.394	–0.192
Canopy cover (%)	–0.081	–0.177	– <b>0.624</b>	–0.258	0.173
Width (m)	0.386	0.314	0.575	–0.018	0.468
Total phosphorus (mg/l)	–0.041	0.023	–0.133	<b>0.790</b>	–0.061
Calcium (mg/l)	0.240	0.121	0.320	<b>0.723</b>	0.013
Disturbance (Pfankuch bottom score index)	0.109	0.346	–0.090	<b>0.701</b>	0.388
Undercut banks (%)	–0.115	0.067	0.035	0.028	– <b>0.908</b>
Velocity (m/s)	–0.081	0.475	0.291	0.253	<b>0.656</b>
t-test ( <i>p</i> value)	<b>0.001</b>	0.833	0.086	0.188	0.765

Important loadings are shown in bold face. *p*-values refer to Independent Sample *t*-tests, testing the differences in scores between streams with and without trout.

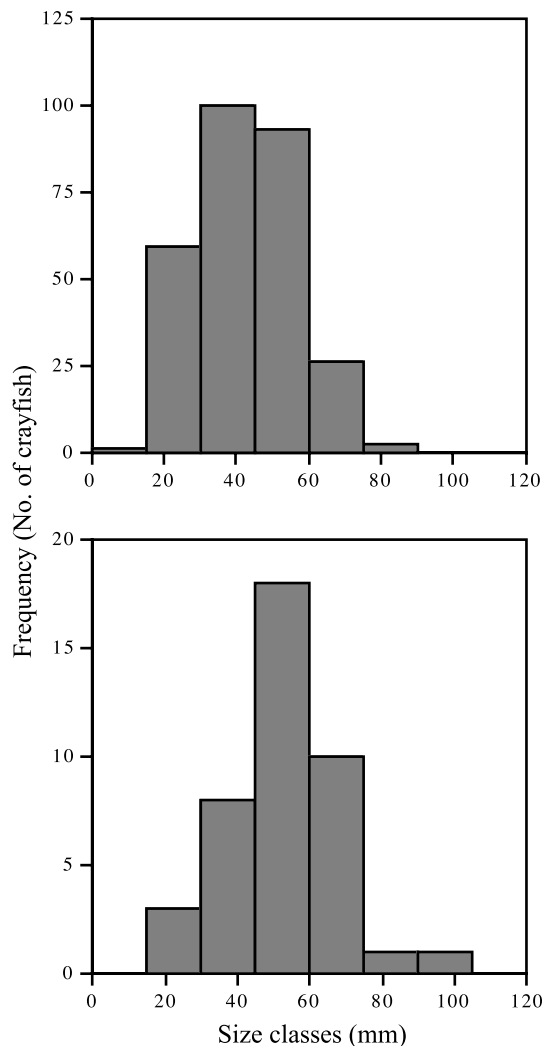
biomass (Fig. 5). The cased or shelled collector–grazers, *Potamopyrgus*, *Pycnocentria*, *Pycnocentroides* and *Olinga*, were present only in trout streams and were negatively correlated with axis 1 and positively correlated with axis 2 (Fig. 5). In contrast, *Polyplectropus*, *Psilochorema*, Tanypodinae, Oligochaeta and *Zephlebia* (the first three are predators and the last two are collector–grazers), were found only in streams without trout and were positively correlated with both axes (Fig. 5). Overall, the canonical correspondence analysis showed that a majority of invertebrate taxa were negatively correlated with axis 1, indicating they were most common in the more circumneutral streams. Several taxa, such as *Aoteapsyche*, Elmidae, Chironomidae and *Hydrobiosis*, were also negatively correlated with axis 2, suggesting they are adapted to living in streams with a high level of physical disturbance. The linear regressions showed that crayfish abundance was not related to invertebrate abundance in either stream type (trout streams:  $r^2 = 0.044$ ,  $F = 0.277$ ,  $p = 0.618$ ; no-trout streams:  $r^2 = 0.001$ ,  $F = 0.006$ ,  $p = 0.943$ ).

#### 4. Discussion

Previous experimental and field studies in New Zealand have shown that exotic brown trout affect the functioning of New Zealand stream ecosystems at the population, community and ecosystem levels, by modifying the behaviour of organisms (summarized in Townsend, 2003). For example, the presence of trout can lead to strong top-down control of community structure and ecosystem functioning by fragmenting the distribution and reducing the abundance of galaxiid fish species, probably through predation and competition (Crowl et al., 1992; McIntosh, 2000a, 2003). Moreover, trout have been shown to affect the structure of the

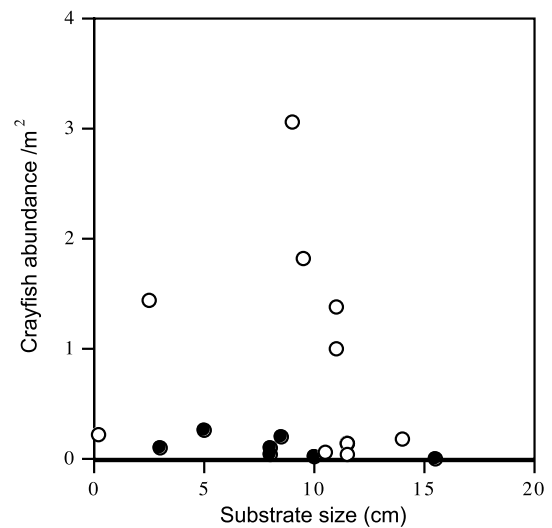
macroinvertebrate community and the abundance of periphytic algae through effects on grazer biomass and behaviour (Flecker and Townsend, 1994; McIntosh and Townsend, 1995, 1996; Nyström et al., 2003; Zhang et al., 2004). The impact of trout on food webs dominated by large omnivores, such as crayfish, is less well known. However, the results of the present study indicate that the abundance of native galaxiid fish, endemic crayfish and other macroinvertebrates differs between streams with and without trout and that naturally acidic, brown water streams on the West Coast of New Zealand can act as refuge areas for native crayfish and galaxiid species. Although numerous New Zealand stream invertebrate species tolerate low pH and moderately elevated concentrations of metals (Winterbourn and McDiffett, 1996), others do not, and overall brown water streams have less species-rich benthic faunas than circumneutral pH streams. The negative effects of acidity seem to have a stronger effect on macroinvertebrate community structure than any indirect effects associated with a reduction in crayfish density in circumneutral streams due to the presence of trout.

The results of the present study indicate that the native crayfish (*P. planifrons*) could be affected negatively by introduced brown trout in West Coast streams. Usio and Townsend (2000) came to a similar conclusion with respect to the second native crayfish (*P. zealandicus*) in a study on the east of the South Island. They showed that crayfish abundance was negatively associated with trout abundance and positively with wood cover, which provided habitat and refuge from predators. The vulnerability of crayfish to predation by trout may in part reflect their inability to respond to chemical cues released by trout (Shave et al., 1994). Because trout have replaced native fishes in many New Zea-



**Fig. 2 – Size frequency of crayfish from streams with trout (lower,  $n = 41$ ) and without trout (upper,  $n = 281$ ). Note the different scales on the y-axes.**

land streams (McIntosh et al., 1992; McIntosh and Townsend, 1995), predation pressure on crayfish has probably increased since their introduction. Even though only one trout, the largest one, had consumed crayfish in the present study, it is likely that predation by large trout affects crayfish abundance. Small trout may compete with crayfish for shelter and may exclude juveniles that become more exposed to the risk of predation by larger trout. Most native fishes in New Zealand are small and not major predators of crayfish, although eels eat crayfish (Jellyman, 1989; Schulze et al., 2004; present study) despite crayfish exhibiting antipredatory behaviour towards them (Shave et al., 1994). Although eels were present in most of the West Coast study streams, their abundance, unlike that of trout did not explain the variation in crayfish abundance. This is consistent with a study by Hicks and McCaughan (1997) on the North Island where the abundance and biomass of eels did not affect the abundance and biomass of *P. planifrons*. Instead, both the abundance and biomass of eels and crayfish seemed to be related to environmental conditions in that study. In the

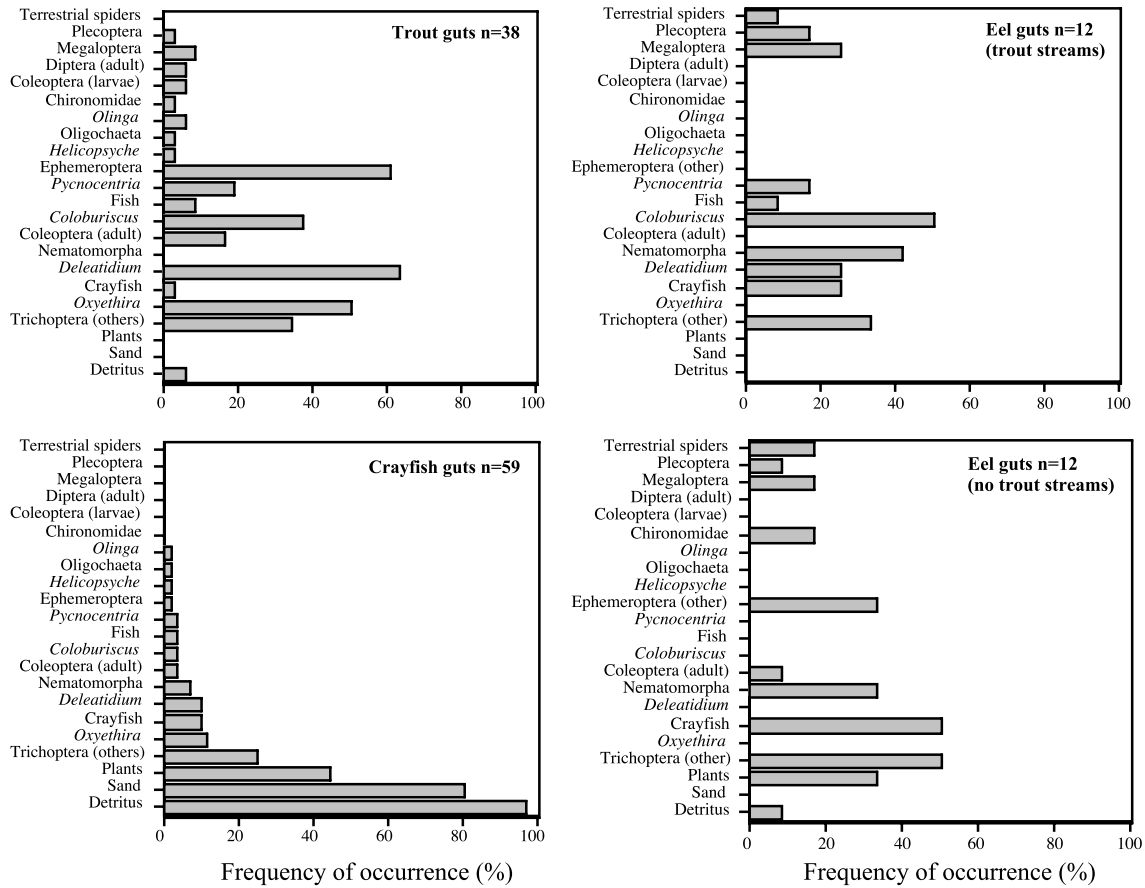


**Fig. 3 – Mean crayfish abundance in relation to median substrate size for streams with trout ( $n = 8$ , black circles) and without trout ( $n = 10$ , open circles).**

present study the gut content analysis also showed that eels and trout had some overlap in diet but little overlap with crayfish diet. This suggests that crayfish are not affected by competition for food from eels or trout.

In addition to trout affecting their abundance, the size distribution of crayfish differed between sites with and without trout, with fewer small individuals being caught in trout streams. Englund and Krupa (2000) also found that fish had a negative effect on small (25–30 mm body length) crayfish (*Cambarus bartonii* and *Orconectes putnami*), but that large crayfish were not eaten even by the largest fishes (120–190 mm body length). Similarly, Usio and Townsend (2000) found a lower percentage of small (15–25 mm) crayfish (*P. zealandicus*) and a higher percentage of large (>35 mm) crayfish in trout pools than no-trout pools in a New Zealand stream. These findings suggest that trout prey selectively on small crayfish. Whitmore and Huryn (1999) showed that *P. zealandicus* was amongst the most long-lived and slowest-growing crayfish species known, therefore small, slow-growing, juvenile crayfish are likely to be particularly vulnerable to trout predation for a relatively long time. In the absence of trout, crayfish abundance seemed to be related to substrate size with more crayfish associating with sites dominated by cobbles (about 9 cm) than with sites dominated by sand or large boulders. In the West Coast streams, which lack trout and primarily terrestrial predators that might feed on crayfish, cobbles provided refuges for crayfish, perhaps mainly from each other during moulting, since *P. planifrons* is cannibalistic like many other crayfish species (Nyström, 2002).

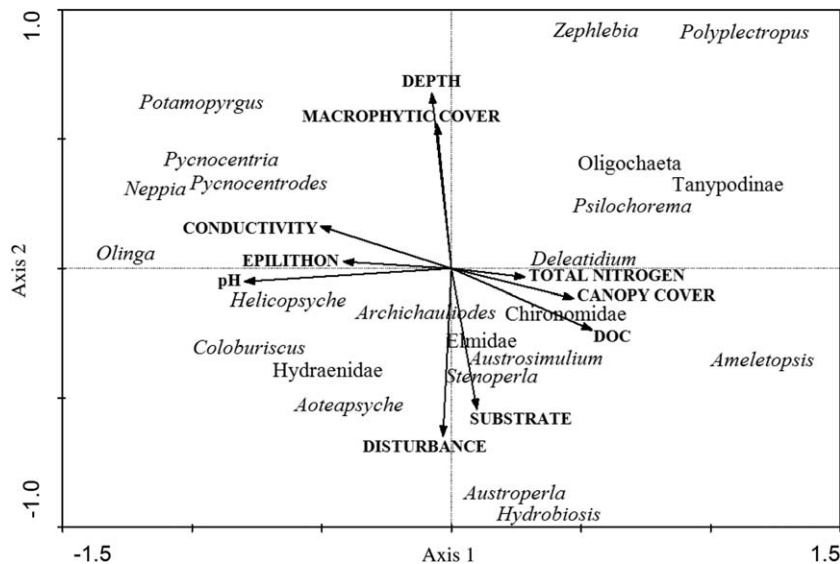
Trout also appeared to have a negative effect on galaxiid species consistent with the results of previous studies (McIntosh, 2000a; Townsend, 2003), but whether crayfish also influence galaxiid distributions is unknown. Some crayfish species potentially have negative effects on the distribution of small benthic fishes through predation, competition for food and shelter (Guan and Wiles, 1997; Dorn and



**Fig. 4 – Frequency of occurrence (%) of food items in trout, crayfish and eel guts. The crayfish analysed were taken from streams both with and without trout. The eels are divided into eel guts from streams with trout (upper right) and streams without trout (lower right).**

Mittelbach, 1999), but in the West Coast streams *P. planifrons* appeared to have few if any negative effects on the abundance of galaxiids.

Tolerance to low pH varies a great deal among crayfish species within the Cambaridae (France, 1993; Seiler and Turner, 2004), whereas species of Astacidae are usually



**Fig. 5 – Simple correlation plot of the most common invertebrate taxa to axes 1 and 2 from the Canonical correspondence analysis with the environmental factors that explained most of the variation, also shown.**

considered to be intolerant of acid water with pH < 5.5 (Nyström, 2002) and low calcium concentrations < 2.0 mg/l (Naura and Robinson, 1998). However, in Tasmania *Parastacoides tasmanicus* and other species of Parastacidae live in highly acidic water (Williams, 1974; Newcombe, 1975). *P. planifrons* was found in streams with pH down to 4.1 in the present study and at sites where calcium concentration was as low as 0.9 mg/l. Most brown water streams in New Zealand have a naturally low pH because of high concentrations of organic acids in the water, and also have high concentrations of dissolved aluminium, which is rendered non-toxic through complexation with dissolved organic matter (Collier et al., 1990). Both native crayfish and some native fish species in New Zealand are well adapted to life in this stream environment (Collier et al., 1990) and also occur in circumneutral waters. Seiler and Turner (2004) found that the cambarid crayfish (*C. bartonii*) grew more slowly in acid water (pH around 4) than at more circumneutral sites, but crayfish were less abundant at the circumneutral sites where fish biomass (brook trout, creek shub and mottled sculpin) was significantly higher. It is unlikely that pH, in itself, accounts for the low abundance of *P. planifrons* in the less acidic West Coast streams; instead trout are implicated by the result of the present study. McIntosh (2000a) argued that trout do not affect native New Zealand fishes in some streams, because the physical conditions prevailing do not suit them. Similarly, brown water streams with low pH and low calcium concentrations can act as “safe” havens for native crayfish as well.

The macroinvertebrate fauna of many New Zealand streams is dominated numerically by species that can be categorized as collector–grazers (Death, 1995) and of these a higher proportion had cases (caddis) or shells (molluscs) in trout streams than no-trout streams on the eastern slopes of the South Island mountains (Nyström et al., 2003). Results of the present study are consistent with these patterns as collector–grazers predominated in all streams and species with

cases or shells were more common in trout streams. The higher abundance of invertebrates in streams with trout (including consumers with cases or shells) could potentially be an indirect effect brought about by reduced predation by crayfish. However, the variation in invertebrate abundance observed was not related to crayfish abundance. Furthermore, the gut content analyses suggested that few crayfish had consumed invertebrates, although even in low numbers they can make a disproportionately large contribution to the energy required for tissue growth in *P. planifrons* (Parkyn et al., 2001). Instead, variation in invertebrate abundance appeared to be related most strongly to differences in abiotic factors such as pH, conductivity, depth, substrate and disturbance. *Potamopyrgus* requires calcium for shell formation and may be absent from naturally acidic brown water streams for that reason (Winterbourn and Collier, 1987), whereas other physiological constraints and/or low food quantity or quality may limit the distribution and abundance of other taxa (Collier et al., 1990). An increase in the production and/or biomass of algae can have positive effects on the local abundance of grazers, through a bottom-up effect (Forrester et al., 1999) and might help explain why the abundance of many invertebrates (insects and snails) was higher in West Coast streams with trout. In contrast, crayfish and galaxiid abundances were greater where trout were absent, suggesting that interactions with trout have brought about their retreat to trout-free refuges.

**Acknowledgement**

We thank landowners, the Department of Conservation, Timberlands West Coast Limited and Fish and Game New Zealand for permission to sample and for valuable information. This research was conducted under permit 2002:39R from the University of Canterbury Animal Ethics Committee. The study was supported by grants from FORMAS to Per Nyström and Wilhelm Granéli.

**Appendix 1**

Number of crayfish and fish caught by electrofishing at the different sites

Species	Site no.																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Paranephrops planifrons</i>	11	6	5	2	2	53	60	71	48	24	2	6	0	1	15	9	4	4
<i>Salmo trutta</i>	0	0	0	0	0	0	0	0	0	0	1	8	7	11	160	62	6	3
<i>Anguilla dieffenbachii</i>	8	3	10	4	5	1	1	0	3	0	2	7	8	2	5	3	1	11
<i>Anguilla australis</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Galaxias fasciatus</i>	22	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>Galaxias postvectis</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Galaxias brevipinnis</i>	0	0	26	1	8	0	12	94	20 <sup>a</sup>	1	0	0	0	0	0	0	0	1
<i>Galaxias divergens</i>	0	0	0	0	0	0	0	0	0	0	1 <sup>a</sup>	0	0	9 <sup>a</sup>	0	0	8	0
<i>Cheimarrichthys fosteri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
<i>Gobiomorphus huttoni</i>	0	0	0	0	5	0	0	0	0	0	19	0	3	6	0	0	0	6
<i>Gobiomorphus cotidianus</i>	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	17	0
<i>Gobiomorphus hubbsi</i>	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0

a Identification uncertain.

## Appendix 2

All invertebrate taxa found in the Surber samples. Total number of individuals caught at each site is presented as absolute numbers. Sites 1–10 are the streams without trout and 11–18 are the ones with trout

Species	Functional group	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11	Site 12	Site 13	Site 14	Site 15	Site 16	Site 17	Site 18
<b>Ephemeroptera</b>																			
<i>Deleatidium</i>	G	77	5	288	73	224	18	226	79	75	14	165	38	312	104	376	113	238	37
<i>Zephlebia</i>	G	1	8	2	0	8	8	0	0	1	0	0	5	0	0	0	36	0	1
<i>Neozephlebia</i>	G	0	3	0	9	1	0	0	0	1	0	0	0	0	0	0	98	9	0
<i>Austroclima</i>	G	0	0	0	0	0	0	8	0	0	0	0	0	0	0	4	39	0	4
<i>Mauiulus</i>	G	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coloburiscus</i>	F	0	0	0	1	0	2	2	9	0	0	14	51	38	5	114	194	0	2
<i>Nesameletus</i>	G	0	3	0	0	0	0	0	0	0	0	8	0	21	16	0	0	0	0
<i>Ameletopsis</i>	P	7	0	1	1	2	1	2	0	12	0	0	0	0	0	0	0	0	0
<i>Ichthybotus</i>	G	0	0	0	2	0	0	0	0	0	0	0	2	0	1	0	0	0	0
<b>Plecoptera</b>																			
<i>Stenoperla</i>	P	0	0	2	3	2	0	6	7	4	0	0	8	2	5	5	6	0	7
<i>Austroperla</i>	S	0	0	0	1	0	0	10	3	6	0	1	0	3	1	0	2	0	6
<i>Spaniocerca</i>	G	0	0	1	3	0	0	3	7	0	0	1	0	0	0	0	0	0	1
<i>Cristaperla</i>	G	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
<i>Zelandobius</i>	G	3	0	3	0	0	3	3	0	34	0	0	0	0	1	0	0	0	1
<i>Acroperla</i>	G	10	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Taraperla</i>	G	1	0	1	1	18	0	0	0	0	1	0	0	0	1	0	0	0	0
<i>Spanioceroides</i>	G	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
<i>Megaleptoperla</i>	P	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	11	0	0
<b>Trichoptera</b>																			
<i>Aoteapsyche</i>	F	0	0	13	3	0	0	1	0	0	0	1	2	8	3	13	2	0	1
<i>Hydrobiosella</i>	F	0	0	26	0	0	0	2	3	1	0	0	0	0	3	0	2	0	1
<i>Hydrobiosis</i>	P	0	0	9	2	8	0	4	7	4	0	23	0	23	29	15	5	15	1
<i>Psilochorema</i>	P	10	2	9	2	15	1	3	5	15	1	1	0	4	0	18	15	14	2
<i>Costachorema</i>	P	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Neurochorema</i>	P	0	0	0	0	0	0	0	0	0	0	3	0	1	1	0	0	0	0
<i>Hydrochorema</i>	P	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Polyplectropus</i>	P	2	2	1	0	2	0	0	3	1	3	0	0	0	0	0	0	1	0
<i>Zelolessica<sup>a</sup></i>	G	3	0	0	1	3	2	0	0	8	0	0	0	0	1	0	0	0	1
<i>Zelandoptila</i>	G	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Triplectides<sup>a</sup></i>	S	0	0	2	5	3	0	2	2	0	2	0	0	0	0	0	18	0	0
<i>Hudsonema<sup>a</sup></i>	G	0	0	2	0	0	0	0	0	0	0	0	0	3	0	0	1	4	0
<i>Oxyethira<sup>a</sup></i>	G	0	0	2	0	0	0	0	1	0	0	1	0	0	0	0	0	6	0
<i>Pycnocentroides<sup>a</sup></i>	G	0	0	0	0	0	2	0	0	0	0	34	3	26	0	322	56	553	6
<i>Pycnocentria<sup>a</sup></i>	G	0	0	0	0	1	0	0	0	0	0	0	7	23	0	3	64	24	1
<i>Olinga<sup>a</sup></i>	G	0	0	0	0	0	0	0	0	0	0	0	72	24	4	15	41	2	0
<i>Beraeoptera<sup>a</sup></i>	G	0	0	0	0	0	0	0	0	0	0	0	0	61	0	0	0	0	0
<i>Pycnocentrella<sup>a</sup></i>	G	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oeconesus<sup>a</sup></i>	S	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	6	6	0
<i>Helicopsyche<sup>a</sup></i>	G	0	0	42	3	1	0	0	0	1	0	0	4	29	3	60	217	3	1
<i>Rakiura<sup>a</sup></i>	G	0	12	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
<i>Philorheithrus</i>	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	20	5	0
<b>Megaloptera</b>																			
<i>Archichauliodes</i>	P	3	0	2	1	1	1	3	8	14	0	6	39	25	11	18	40	3	0
<b>Coleoptera</b>																			
Elmidae	G	21	0	13	42	72	2	163	28	60	2	245	66	320	141	167	46	175	8
Hydraenidae	G	1	0	0	11	0	0	1	1	0	0	1	1	21	1	3	2	3	0
Ptilodactylidae	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	11	0	0

Appendix 2 – continued

Species	Functional group	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11	Site 12	Site 13	Site 14	Site 15	Site 16	Site 17	Site 18
Hydrophilidae	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Liodessus</i>	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0
Scirtidae	G	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Diptera																			
Chironomidae	G	2	0	14	16	131	16	22	9	29	14	36	41	9	31	19	25	33	4
Tanypodinae	P	11	9	4	40	28	0	28	2	1	7	2	0	4	0	0	4	3	0
<i>Paradixa</i>	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
<i>Aphrophila</i>	G	2	0	0	0	3	1	0	0	0	0	0	9	3	1	3	2	0	0
Hexatomini	G	0	0	5	1	0	0	0	0	0	0	1	0	0	0	3	0	6	0
<i>Austrosimulium</i>	F	0	0	8	1	2	1	18	11	12	0	64	0	6	11	12	7	3	1
Eriopterini	G	0	0	0	0	0	1	0	2	0	0	1	0	1	2	0	0	2	2
<i>Mischoderus</i>	G	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Empididae	G	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0
Ephydriidae	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Muscidae	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0
Tabanidae	P	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ceratopogonidae	P	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Crustacea																			
<i>Paraleptamphopus</i>	G	0	3	0	1	0	0	0	0	0	50	0	0	0	0	0	0	0	0
" <i>P. caeruleus</i> "	G	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0	0	0	0
<i>Paranephrops</i>	O	0	2	0	1	0	5	0	1	0	0	0	0	0	0	0	0	0	0
Ostracoda	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Arachnida																			
Acari	P	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1
Mollusca																			
<i>Potamopyrgus</i> <sup>a</sup>	G	0	1	1	0	0	0	0	0	0	0	20	96	1	0	234	576	348	0
<i>Sphaerium</i> <sup>a</sup>	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Austropeplea</i> <sup>a</sup>	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Physella</i> <sup>a</sup>	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Annelida																			
Oligochaeta	G	7	10	3	4	38	7	3	20	16	40	30	9	1	0	20	6	250	8
<i>Alboglossiphonia</i>	P	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Tricladida																			
<i>Neppia</i>	P	0	0	0	0	0	0	0	0	0	0	11	11	4	0	8	16	4	0
Porifera	F	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Functional groups: G = collector/grazer, F = filterfeeder, S = shredder, P = predator and O = omnivore.  
a Invertebrates with cases or shells.

REFERENCES

Allan, J.D., 1995. Stream Ecology: Structure and Function of Running Waters. Chapman and Hall, London, Great Britain.

Aronsson, Å., 1999. SPSS En introduktion till basmodulen. Studentlitteratur, Lund, Sweden.

Bechara, J.A., Moreau, G., Planas, D., 1992. Top-down effect of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. Canadian Journal of Fisheries and Aquatic Sciences 49, 2093–2103.

Biggs, B.J.F., Francoeur, S.N., Huryn, A.D., Young, R., Ar Buckley, C.J., Townsend, C.R., 2000. Trophic cascades in streams: effects of nutrient enrichment on autotrophic and consumer benthic communities under two different fish predation regimes. Canadian Journal of Fisheries and Aquatic Sciences 57, 1380–1394.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E., Hayes, D., 2002. Directing research to reduce the impacts of nonindigenous species. Conservation Biology 16, 630–640.

Coblentz, B.E., 1990. Exotic organisms: a dilemma for conservation biology. Conservation Biology 4, 261–265.

Collier, K.J., Ball, O.J., Graesser, A.K., Main, M.R., Winterbourn, M.J., 1990. Do organic and anthropogenic acidity have similar effects on aquatic fauna? Oikos 59, 33–38.

- Crowl, T.A., Townsend, C.R., McIntosh, A.R., 1992. The impact of introduced brown trout and rainbow trout on native fish: the case of Australia. *Reviews in Fish Biology and Fisheries* 2, 217–241.
- Death, R.G., 1995. Spatial patterns in benthic invertebrate communities: products of habitat stability or are they habitat specific? *Freshwater Biology* 33, 455–467.
- Death, R.G., Winterbourn, M.J., 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* 76, 1446–1460.
- Dorn, N.J., Mittelbach, G.G., 1999. More than predator and prey: a review of interactions between fish and crayfish. *Vie et Milieu* 49, 229–237.
- Englund, G., Krupa, J.J., 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. *Freshwater Biology* 43, 75–83.
- Flecker, A.S., Townsend, C.R., 1994. Community wide consequences of trout introduction in New Zealand streams. *Ecological Applications* 4, 798–807.
- Forrester, G.E., Dudley, T.L., Grimm, N.B., 1999. Trophic interactions in open systems: effects of predators and nutrients on stream food chains. *Limnology and Oceanography* 44, 1187–1197.
- France, R.L., 1993. Effect of experimental lake acidification on crayfish *Orconectes virilis* population recruitment and age composition in north-western Ontario, Canada. *Biological Conservation* 63, 53–59.
- Gido, K.B., Schaefer, J.F., Pigg, J., 2004. Patterns of fish invasions in the Great Plains of North America. *Biological Conservation* 118, 121–131.
- Guan, R.-Z., Wiles, P.R., 1997. Ecological impact of introduced crayfish on benthic fishes in a British lowland river. *Conservation Biology* 11, 641–647.
- Harding, J.S., Quinn, J.M., Hickey, C.W., 2000. Effects of mining and production forestry. In: Collier, K.J., Winterbourn, M.J. (Eds.), *New Zealand Stream Invertebrates: Ecology and Implications for Management*. New Zealand Limnological Society, Christchurch, New Zealand, pp. 230–259.
- Hicks, B.J., McCaughan, H.M.C., 1997. Land use, associated eel production, and abundance of fish and crayfish in streams in Waikato, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31, 635–650.
- Hurny, A.D., 1998. Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. *Oecologia* 115, 173–183.
- Jellyman, D.J., 1989. Diet of two species of freshwater eel (*Anguilla* spp.) in Lake Pounui, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 23, 1–10.
- Jespersen, A.-M., Christoffersen, K., 1987. Measurements of chlorophyll-*a* from phytoplankton using ethanol as extraction solvent. *Archiv für Hydrobiologie* 109, 445–454.
- Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16, 199–204.
- Leps, J., Smilauer, P., 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. University Press, Cambridge, UK.
- Lodge, D.M., 1993. Biological invasions: lessons for ecology. *Trends in Evolution and Ecology* 8, 133–137.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10, 689–710.
- McDowall, R.M., 2000. *New Zealand Freshwater Fishes*. Reed Publishing (NZ) Ltd., Auckland, New Zealand.
- McDowall, R.M., 2003. Impact of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. *Transactions of the American Fisheries Society* 132, 229–238.
- McGarigal, K., Cushman, S., Stafford, S., 2000. *Multivariate Statistics for Wildlife and Ecology Research*. Springer-Verlag, New York.
- McIntosh, A.R., 2000a. Habitat- and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 2140–2151.
- McIntosh, A.R., 2000b. Aquatic predator–prey interactions. In: Collier, K.J., Winterbourn, M.J. (Eds.), *New Zealand Stream Invertebrates: Ecology and Implications for Management*. New Zealand Limnological Society, Christchurch, New Zealand, pp. 125–156.
- McIntosh, A.R., Townsend, C.R., 1995. Contrasting predation risks presented by introduced brown trout and native common river galaxias in New Zealand streams. *Canadian Journal of Fisheries and Aquatic Sciences* 52, 1821–1833.
- McIntosh, A.R., Townsend, C.R., 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? *Oecologia* 108, 174–181.
- McIntosh, A.R., Townsend, C.R., Crowl, T.A., 1992. Competition for space between introduced brown trout (*Salmo trutta*, L) and a native galaxiid (*Galaxias vulgaris* Stokell) in a New Zealand stream. *Journal of Fish Biology* 41, 63–81.
- Naura, M., Robinson, M., 1998. Principles of using river habitat surveys to predict the distribution of aquatic species: an example applied to the native white-clawed crayfish *Austropotamobius pallipes*. *Aquatic Conservation: Marine and Freshwater Ecosystems* 8, 515–527.
- Newcombe, K., 1975. The pH tolerance of the crayfish *Parastacoides tasmanicus* (Erichson) (Decapoda, Parastacidae). *Crustaceana* 29, 231–234.
- Nyström, P., 2002. Ecology. In: Holdich, D.M. (Ed.), *Biology of Freshwater Crayfish*. MPG Books Ltd., Bodmin, Cornwall, Great Britain, pp. 192–235.
- Nyström, P., McIntosh, A.R., 2003. Are impacts of an exotic predator on a stream food web influenced by disturbance history? *Oecologia* 136, 279–288.
- Nyström, P., Svensson, O., Lardner, B., Brönmark, C., Granéli, W., 2001. The influence of multiple introduced predators on a littoral pond community. *Ecology* 82, 1023–1039.
- Nyström, P., McIntosh, A.R., Winterbourn, M.J., 2003. Top-down and bottom-up processes in grassland and forested streams. *Oecologia* 163, 569–608.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1, 3–19.
- Parkyn, S.M., Collier, K.J., Hicks, B.J., 2001. New Zealand stream crayfish: functional omnivores but trophic predators? *Freshwater Biology* 46, 641–652.
- Schulze, T., Kahl, U., Radke, R.J., Benndorf, J., 2004. Consumption, abundance and habitat use of *Anguilla anguilla* in a mesotrophic reservoir. *Journal of Fish Biology* 65, 1543–1562.
- Seiler, S.M., Turner, A.M., 2004. Growth and population size of crayfish in headwater streams: individual- and higher-level consequences of acidification. *Freshwater Biology* 49, 870–881.
- Shave, C.R., Townsend, C.R., Crowl, T.A., 1994. Anti-predator behaviours of a freshwater crayfish (*Paranephrops zealandicus*) to a native and an introduced predator. *New Zealand Journal of Ecology* 18, 1–10.
- Townsend, C.R., 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. *Biological Conservation* 78, 13–22.

- Townsend, C.R., 2003. Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams. *Conservation Biology* 17, 38–47.
- Townsend, C.R., Crowl, T.A., 1991. Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout? *Oikos* 61, 347–354.
- Usio, N., 2000. Effects of crayfish on leaf processing and invertebrate colonisation of leaves in a headwater stream: decoupling of a trophic cascade. *Oecologia* 124, 608–614.
- Usio, N., Townsend, C.R., 2000. Distribution of the New Zealand crayfish *Paranephrops zealandicus* in relation to stream physico-chemistry, predatory fish, and invertebrate prey. *New Zealand Journal of Marine and Freshwater Research* 34, 557–567.
- Usio, N., Townsend, C.R., 2002. Functional significance of crayfish in stream food webs: roles of omnivory, substrate heterogeneity and sex. *Oikos* 98, 512–522.
- Watt, T.A., 1993. *Introductory Statistics for Biology Students*. Chapman and Hall, London, Great Britain.
- Whitmore, N., Hury, A.D., 1999. Life history and production of *Paranephrops zealandicus* in a forest stream, with comments about the sustainable harvest of a freshwater crayfish. *Freshwater Biology* 42, 467–478.
- Williams, W.D., 1974. Freshwater Crustacea. In: Williams, W.D. (Ed.), *Biogeography and Ecology in Tasmania*. W. Junk, The Hague, pp. 63–112.
- Winterbourn, M.J., Collier, K.J., 1987. Distribution of benthic invertebrates in acid, brown water streams in the South Island of New Zealand. *Hydrobiologia* 153, 277–286.
- Winterbourn, M.J., McDiffett, W.F., 1996. Benthic faunas of streams of low pH but contrasting water chemistry in New Zealand. *Hydrobiologia* 341, 101–111.
- Winterbourn, M.J., Gregson, K.L.D., Dolphin, C.H., 2000. Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand*, 13.
- Zhang, Y., Richardson, J.S., Negishi, J.N., 2004. Detritus processing, ecosystem engineering and benthic diversity: a test of predator–omnivore interference. *Journal of Animal Ecology* 73, 756–766.