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# Environmental variability and population dynamics of juvenile brown trout (*Salmo trutta*) in an upstream and downstream reach of a small New Zealand river

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**Abstract** Population densities, size and condition factor of juvenile brown trout and variation in environmental factors (discharge, temperature, and food availability) were examined over 2.5 years (28 months) in an upstream and downstream reach of Silverstream, a lowland river in New Zealand. Population densities of juvenile brown trout varied between the upstream and downstream reach, with the latter showing considerably higher temporal variation in fish density than the upstream reach. Juvenile brown trout from the downstream reach were larger and had higher condition factors than those from the upstream reach over the study period. Discharge had a negative effect on fish densities in 1 year in the downstream reach, and high water temperatures were recorded in one summer, with possible negative effects on fish densities. However, the different effects of environmental variables on populations between the two reaches could not explain the higher temporal variation in fish densities in the downstream reach as spatial variation in population densities also occurred in years without high discharge events or high summer water temperatures. Variability in food availability over time was higher in the upstream reach, but differences between the two reaches were small. These results suggest that factors other than condition of the local environment are important

in controlling brown trout population dynamics in Silverstream.

**Keywords** temperature; discharge; food availability; spatial variation

## INTRODUCTION

Determining causes of variation in population size and identifying factors responsible for fluctuations in abundance are crucial issues both in theoretical and applied ecology (Begon et al. 2005). Populations of stream salmonids can exhibit pronounced temporal and spatial variation in abundance (Elliott 1994; Klemetsen et al. 2003). Understanding the reasons for this variation is crucial for several reasons, including fisheries management and the design and interpretation of impact studies (Milner et al. 1993). Spatiotemporal variation in abundance of stream salmonids has been reported for a range of populations in Europe (Milner et al. 1993; Elliott 1994), North America (Newman & Waters 1989), and New Zealand (Allen 1951; Hayes 1995) and has been the focus of intensive research. Studies on juvenile life-history stages are essential for understanding the variation in these salmonid populations since they are typically influenced by various abiotic and biotic factors during the early stages of life (Allen 1951; Elliott 1989; Heland 1999).

Abiotic factors that often affect densities and population dynamics (spatiotemporal variation in population abundance) of salmonids include stream temperature and discharge (Jackson et al. 2001; Lobon-Cervia & Rincon 2004). Floods can cause large losses during the incubation period by washing eggs out of the gravel (McNeil 1966; Elliott 1976) or impairing the survival of emergent fry through downstream displacement or direct mortality (Heggenes & Traaen 1988). Water temperature influences the growth rate and distribution of aquatic organisms (Elliott & Hurley 1997; Ebersole et al. 2001). Most species have a specific range of temperature that they can tolerate and the optimum

temperature range for most salmonid species is 14–17°C with high mortality above 24–25°C (Elliott 1994). An increase in temperature towards the critical level may therefore result in displacement of the fish to a more suitable habitat or eliminate the population (Closs & Lake 1996).

In addition, both inter- and intraspecific competition have been reported to influence densities and population dynamics of juvenile salmonids (e.g., Franco & Budy 2005) and the impact has been linked to several biotic factors, such as food availability (Armstrong et al. 2003). Given the territorial nature of most salmonids (Chapman 1966), competition for food is often linked to the availability of space. Juvenile salmonids defend a feeding territory in a stream, the size of which is regulated by food availability and food demand (Grant et al. 1998). Density is therefore expected to decrease as fish grow bigger and increase their demands for space and food, assuming the availability of food and space stays constant over time. This decrease in density as fish grow bigger can be moderated by variation in food availability over time. Evidence from experimental studies has shown that a decrease in food availability can cause increased mortality, higher emigration rates and lower growth rates of salmonids, whereas an increase in food availability results in lower mortality, lower emigration rates, and higher growth rates (Keeley 2001; Imre et al. 2004).

Few published studies exist on the spatial and temporal variation of juvenile brown trout, *Salmo trutta* (Linné 1758) abundance in New Zealand and how this variation is related to abiotic and biotic factors. Studies that do exist show that temporal variation in densities is high and that floods are a dominant feature driving this variation (Allen 1951; Jowett & Richardson 1989; Hayes 1995). Only one study has examined within-river spatial variability of juvenile brown trout (Hayes 1995) and it did not document the role of food availability on population dynamics. Furthermore, no study to date has investigated effects of temperature on population dynamics of juvenile salmonids in New Zealand. The aim of this study was therefore to investigate the effects of abiotic (discharge and summer temperature) and biotic (food availability) factors on population dynamics of juvenile brown trout in Silverstream, a small lowland river in Otago, New Zealand. Silverstream is an important spawning habitat for migratory brown trout from the lower Taieri River (Kristensen 2006). Fisheries managers and local government bodies have therefore initiated

a habitat enhancement project in this area to improve brown trout habitat (N. McGrouther, Otago Regional Council pers. comm.), but the effects of environmental variability on densities and population dynamics have not previously been investigated in Silverstream. Effects of discharge, water temperature and food availability on population dynamics were therefore investigated in both an upstream reach (limited human land use) and a downstream reach (intensive human land use) of Silverstream.

## MATERIALS AND METHODS

### Study area

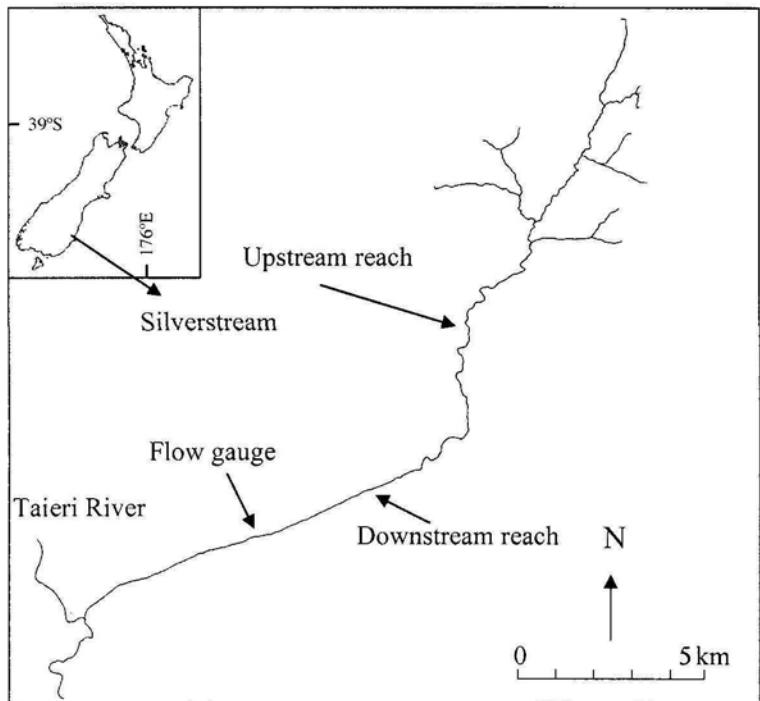
Silverstream, a third order tributary of the Taieri River, is located in eastern Otago, New Zealand (Fig. 1). It is c. 30 km long with its headwater flowing through dense native forest and the lower reaches through a mixture of farmland and urban areas. The lower 10 km of this stream have been heavily impacted by agriculture, and have been channelled for flood mitigation.

For the purpose of this study, an upstream and a downstream reach were selected, which were separated by 8 km (Fig. 1) and approximately 20 and 5 m a.s.l., respectively. Each reach was 600 m long, and for estimating fish density it was divided into 20–30-m subsections, containing both pool and riffle habitats. The reaches were chosen so that differences in riparian vegetation were minimal (both upstream and downstream reaches were partly grass/agriculture and partly lined with willows). Furthermore, the substrate was dominated by gravel at both reaches and mean stream width ( $\pm$  SD) was 7.1 m ( $\pm$  3.3) in the upstream and 7.5 m ( $\pm$  2.8) in the downstream reach (E. A. Kristensen unpubl. data).

### Fish variables

To investigate spatial and temporal variation in population densities, estimates of juvenile brown trout densities were obtained monthly from December 2003 to March 2006, with the exception of June and August in both 2004 and 2005 owing to high water levels. On most sampling occasions, six 30-m subsections were randomly chosen in each reach for density estimates. During periods with very high numbers of juvenile brown trout (October – December), 18 smaller 10-m subsections were chosen in each reach to account for the sometimes patchy distribution of the fish immediately after emergence. Density estimates were obtained by spotlighting (Hickey & Closs 2006) with surveys

**Fig. 1** Location of Silverstream, South Island, New Zealand, the upstream and downstream reaches and location of the flow gauge.



starting 1 hour after sunset, and completed between 19:00 and 04:00 h. Counts were conducted by walking upstream with the light moved slowly from side to side. Any fish observed was recorded and assigned to one of two year classes (0+ and 1+) based on size. Only these two age classes were generally present, and a clear difference in size between the age classes was evident. 0+ fish were dominant during the study period, with the proportion of 1+ fish ranging from 0% to 13% in the upstream reach and between 0% and 4% in the downstream one. Only data for 0+ fish are presented in this study. The six or 18 density estimates from each reach were combined to provide a monthly average juvenile brown trout density for the upstream and downstream reach each (fish per m<sup>2</sup>).

Spotlighting has been shown to be an effective method for obtaining density estimates of brown trout in small streams and the method can be superior to electro-fishing under low flow conditions (Hickey & Closs 2006). To ensure estimates obtained by spotlighting represented actual densities, three-pass depletion electro-fishing was completed in a total of 21 subsections (in both reaches) at seven different dates throughout the study period and the density estimates from this method were compared with those from spotlighting. Electro-fishing was

completed the day after spotlighting and densities were estimated using Zippin's maximum likelihood method (Zippin 1958). No difference in density estimates was found between the two methods ( $t$  test,  $t = -0.128$ ,  $n = 21$ ,  $P = 0.669$ ).

To compare size and calculate condition factors of juvenile brown trout, 10 fish (a random subsample of a larger catch) were collected from each reach on each sampling occasion. On a few sampling occasions (June and July 2004 and 2005) fewer than 10 fish ( $n = 5$ ) were collected owing to low fish densities at that particular time. Fish were collected either by dip netting following spotlight counts or by electro-fishing the following day. Fish were anaesthetised and weights ( $\pm 0.1$  g) and standard lengths ( $\pm 1$  mm) were recorded. Fulton's condition factors (Weatherly 1972) were calculated and combined into an average condition factor for the upstream and downstream reach for each month between December 2003 and March 2006. Condition factors are an indirect but useful indicator of differences in growth rates among populations (Wootton 1998).

#### Abiotic variables

To analyse the relationship between discharge and juvenile brown trout population densities, discharge data from December 2003 to March 2006 and daily

instantaneous loss rates of juvenile brown trout from each reach per month were compared. Daily instantaneous loss rates were calculated separately for the upstream and downstream reach in each month as:

$$M = -\frac{N_1 - N_0}{t_1 - t_0}$$

where  $N_0$  and  $N_1$  are the average number of juvenile brown trout at time  $t_0$  (beginning of month) and  $t_1$  (end of month), respectively. Discharge (litre/s) was measured automatically every day by a flow gauge located in the lower section of the river (Fig. 1). Measurements by this gauge were considered representative of the flow conditions in both the upstream and downstream reach. Both mean monthly and maximum monthly discharge were calculated to investigate the effect of a single high discharge event (maximum monthly) on population densities.

To compare water temperatures between the two reaches, water temperatures ( $\pm 0.1^\circ\text{C}$ ) were recorded at both reaches from December 2003 to March 2006 at 1-h intervals using TidBit Stowaway temperature loggers placed at the downstream end of each reach. The loggers were placed in well-mixed water. Owing to failure and disappearances of temperature loggers, temperature was not recorded between March 2005 and October 2005. Minimum, maximum and mean monthly temperature were calculated for each reach.

### Biotic variables

To compare food availability between the upstream and downstream reach, benthic and drifting invertebrate biomass were assessed on eight occasions during the first year of study (December 2003 to January 2005). Two days after estimation of fish densities, a sample of benthic invertebrates was collected from a riffle located in each of the six randomly selected 30-m subsections per reach using a Surber sampler ( $0.0625 \text{ m}^2$ , mesh size 250  $\mu\text{m}$ ). Samples were preserved in 70% ethanol. All invertebrates were examined under a microscope and identified using Winterbourn et al. (2000). Total biomass of benthic invertebrates was calculated using length-dry mass models previously developed for Silverstream and expressed as mg dry mass/ $\text{m}^2$  (Appendix 1) (Kristensen 2006).

Invertebrate drift was assessed the night before fish density estimation, as most invertebrate drift in streams with drift-feeding fish occurs at night (McIntosh et al. 2002) and trout had been observed to actively feed at night in Silverstream (E. A.

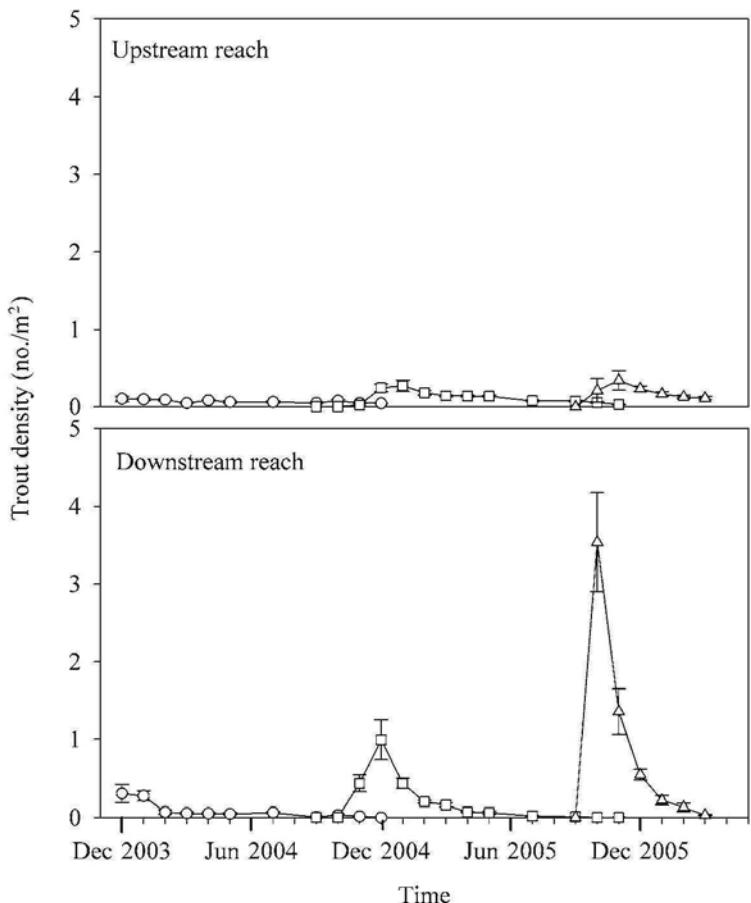
Kristensen pers. obs.). Drift nets (250  $\mu\text{m}$  mesh, 25 cm mouth diam.) were placed at the downstream end of six riffles per reach. Nets reached the bottom of the stream and extended above the water surface (to ensure collection of surface-drifting invertebrates). Samples were collected between 19:00 and 04:00 h depending on season. Upon collection, the retrieval time was noted and water velocity (m/s) and depth (to nearest cm) were measured at the mouth of each net using a portable flow meter and a ruler, respectively. Collected items were preserved in 70% ethanol. All invertebrates (benthic and terrestrial) were identified (Winterbourn et al. 2000). Drift was expressed as mg dry weight/ $\text{m}^3$  of water by calculating the volume of water ( $\text{m}^3$ ) passing through each drift net during a sampling period (using water depth and velocity) and using length-dry mass models (Appendix 1) for calculation of benthic invertebrate biomass.

Diet of juvenile brown trout was investigated on three occasions: December 2003, May 2004, and October 2004. On each occasion, the stomach contents of 10 fish from each reach were removed and examined under a microscope, and prey items were identified using Winterbourn et al. (2000). To assess the dietary importance of particular prey categories, diet composition (the relative abundance of all prey categories found in fish stomachs) was calculated (Bonnett et al. 1989). Dietary analysis showed that many invertebrate species in the benthic fauna were under-represented in the diet of juvenile brown trout. Estimation of the biomass of prey items observed to be consumed would therefore give a better assessment of the invertebrates important to the fish. Benthic invertebrate data was therefore divided into two variables: total benthic invertebrate biomass and biomass of invertebrates important as food items. Invertebrate species that had a relative frequency in the diet of more than 4% on any occasion were considered important as prey.

### Data analysis

Differences in standard length and condition factor between fish from the upstream and downstream reach and over time were examined in separate three-factor ANOVAs using the categorical variables reach, year, and month (Quinn & Keough 2002). Before applying ANOVA to condition factor data, data were assessed using scatter plots for a negative relationship between condition factor and fish length. As no relationship was found, ANOVA was performed without fish length as a covariate. Residual plots of the data indicated Poisson distributions (right skewness), and square root transformations

**Fig. 2** Mean ( $\pm$  SE) densities of juvenile brown trout *Salmo trutta* in 2003–04 (circles), 2004–05 (squares) and 2005–06 (triangles) in the upstream and downstream reach of Silverstream, New Zealand. Each data point represents the mean of 6 or 18 (October to December) density measurements for each reach in each month.



were used to normalise distributions and control for heteroscedasticity. Only months when fish were present in both reaches were included in ANOVAs, which were followed by Tukey *post hoc* tests (Quinn & Keough 2002).

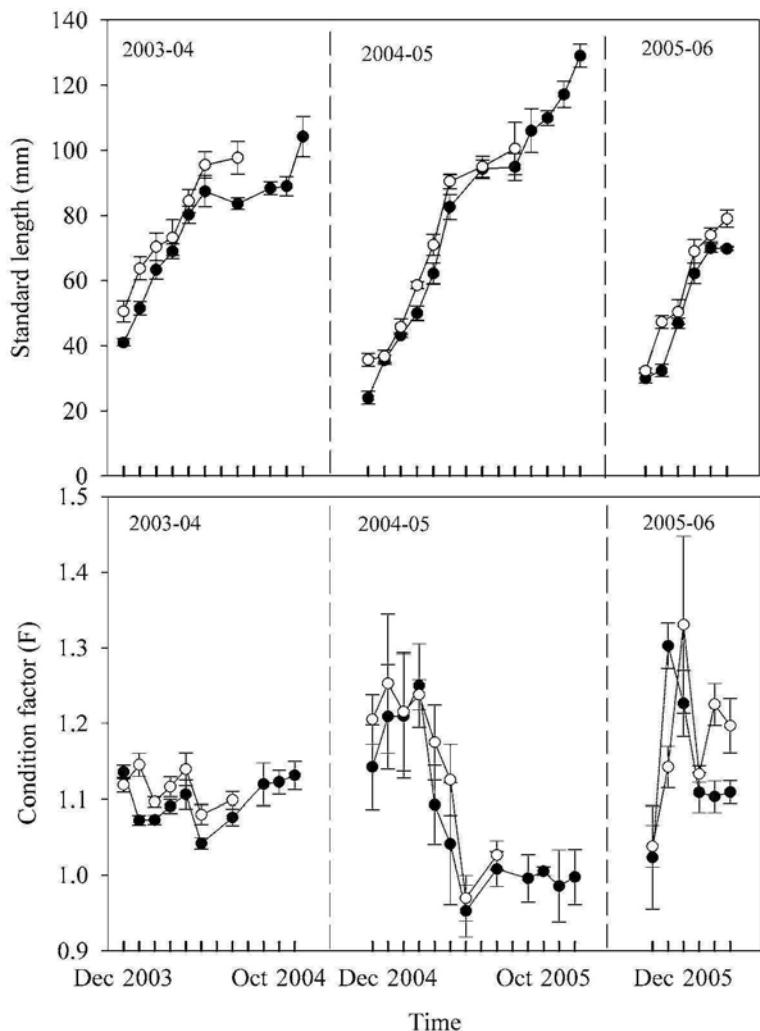
To investigate relationships between discharge and daily instantaneous loss rate of juvenile brown trout, Pearson's product-moment correlations were used (Quinn & Keough 2002). Correlations were performed separately for the up- and downstream reach and for each year. Differences in water temperature (mean monthly, monthly maximum, and minimum) were examined by one-way ANOVA. Multivariate Analysis of Variance (MANOVA) was used to investigate differences in biotic variables between the two reaches and over time, by using a two-factor design (reach and months) with total biomass of benthic invertebrates, biomass of benthic invertebrates important as food items and biomass of drifting invertebrates as the three dependent

variables. All biotic variables were square root-transformed before analysis and all statistical analyses were conducted using SPSS 10.1.

## RESULTS

### Fish variables

Densities of juvenile brown trout showed considerable spatial and temporal variation in Silverstream. Densities were generally highest in the downstream reach and there was an increase in densities throughout the study period in both reaches (Fig. 2). Temporal variation was relatively higher in the downstream than in the upstream reach and densities also changed over a shorter period (Fig. 2). Furthermore, densities each year declined to zero in the downstream reach each year. In the upstream reach, fish from the previous year remained when the new cohort emerged from the gravel.

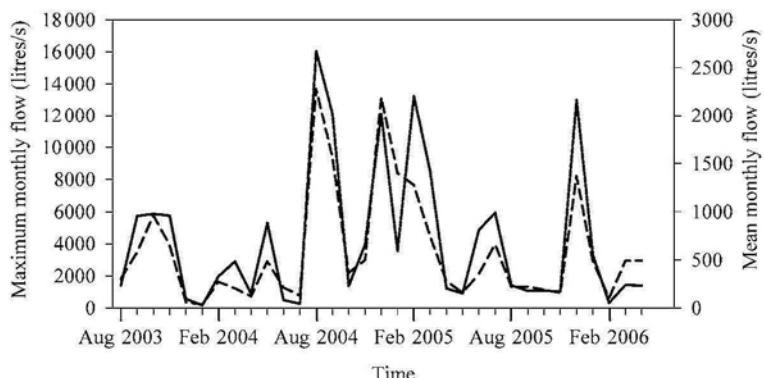


**Fig. 3** Mean ( $\pm$ SE) standard length and condition factor (Fulton's F) of juvenile brown trout *Salmo trutta* from the upstream (filled circles) and the downstream (empty circles) reach of Silverstream, New Zealand for the 28 months of study. Each data point represents the mean of up to 10 fish ( $n = 5-10$ ).

Standard length and condition factors of juvenile brown trout from the downstream reach were significantly higher than for the upstream reach in all years (Fig. 3, Table 1). Overall, standard length and condition factors varied between years, with length decreasing over time (Tukey test,  $P < 0.001$ ) whereas condition factors were lowest in the first year of study. There was also a significant effect of month (Table 1) with length increasing over time and lowest condition factors during winter or early spring (July to September, Tukey test,  $P < 0.001$ , Fig. 3). Juvenile brown trout caught during summer (December to February) generally had the highest condition factor (Tukey test,  $P < 0.001$ , Fig. 3).

There was no significant interaction between reach and year (Table 1), indicating that juvenile brown trout from the downstream reach were longer and had significantly higher condition factors than juvenile brown trout from the upstream reach in all years. Furthermore, no significant interaction between reach and month was found (Table 1). There was a significant interaction between year and month in both comparisons (Table 1), indicating that juvenile brown trout with the overall highest or lowest condition factors or lengths were not caught in the same month each year. There was also a significant interaction between reach, year, and month for length but not for condition factor (Table 1).

**Fig. 4** Mean (dashed line) and maximum (solid line) monthly discharge (litres/s) from August 2003 to March 2006 in Silverstream, New Zealand. Note different scale on y axes.



**Table 1** ANOVA comparisons of standard length and condition factors between juvenile brown trout (*Salmo trutta*) in the upstream and downstream reach during the study period.

Comparison	Length			Condition factor		
	F	(d.f.)	P	F	(d.f.)	P
Reach	50.46	1, 219	<0.001	6.79	1, 219	0.010
Year	87.52	2, 219	<0.001	9.57	2, 219	<0.001
Month	234.49	7, 219	<0.001	24.36	7, 219	<0.001
Reach × Year	0.13	2, 219	0.876	0.36	2, 219	0.697
Reach × Month	1.09	7, 219	0.271	0.84	7, 219	0.555
Year × Month	7.74	11, 219	<0.001	13.61	11, 219	<0.001
Reach × Year × Month	2.23	11, 219	0.014	1.28	11, 219	0.239

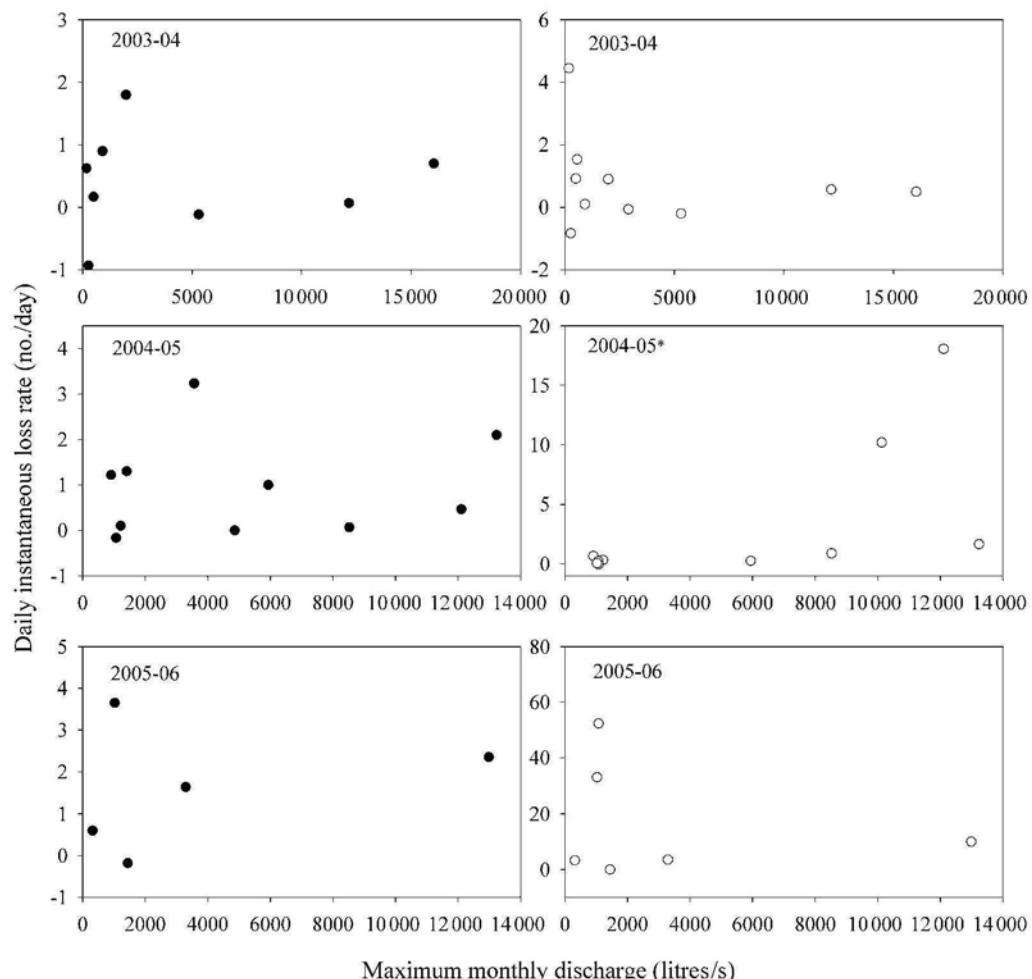
### Abiotic variables

Mean and maximum monthly discharge in Silverstream varied considerably during the study period (Fig. 4). The highest discharge was recorded in August 2004 (16 038 litres/s) and December 2004 (12 102 litres/s) when the mean monthly discharge was above 2000 litres/s but summer 2005–06 also had relatively high discharge. In general, only one high discharge event occurred per month during the study period, as reflected in the similar patterns of mean and maximum monthly discharge values (Fig. 4). Therefore, only maximum monthly discharge values were used in subsequent analysis.

There were no significant relationships between maximum monthly discharge and instantaneous loss rate of fish in 2003–04, 2004–05 and 2005–06 ( $r = 0.080, P = 0.837$ ;  $r = 0.114, P = 0.755$ ; and  $r = 0.283, P = 0.645$ , respectively) in the upstream reach (Fig. 5). In the downstream reach, there was a non-significant negative relationship between maximum monthly discharge and loss rates in 2003–04 and 2005–06 ( $r = -0.201, P = 0.577$  and  $r = -0.217, P = 0.680$ ). In 2004–05, high loss rates in December and January coincided with high discharge and a

significant positive relationship was found ( $r = 0.634, P = 0.049$ , Fig. 5).

Variation in temperature throughout the study period was similar in the upstream and downstream reaches (Fig. 6). Mean monthly temperature was between 10 and 15°C during summer 2003–04 and 2004–05, and mean temperature in winter 2004 was just below 5°C. No significant difference in mean monthly temperatures was found between the upstream and downstream reaches (one-way ANOVA,  $F_{1,38} = 0.332, P = 0.568$ ). The highest temperature recorded during the study period was 24.9°C and occurred in the downstream reach on 28 January 2004. This temperature was recorded at the end of a 10-day period (19–28 January 2004) when water temperatures were high, with readings on 19 and 22 January also above 24°C. The maximum temperature recorded in the upstream reach during the study period was 23.9°C on 19 January 2004. Maximum temperatures during summer 2004–05 in the up- and downstream reaches were recorded in February 2005 and were 21.5°C and 22.6°C, respectively. In summer 2005–06, temperatures reached 20.5°C in the upstream and 22.4°C in



**Fig. 5** Daily instantaneous loss rate of juvenile brown trout *Salmo trutta* (calculated per month) plotted against maximum monthly discharge. Data are plotted separately for the upstream (filled circles) and downstream (open circles) reach for each year of study. Note different scale on y axes. Asterix indicates significant correlation ( $P < 0.05$ ).

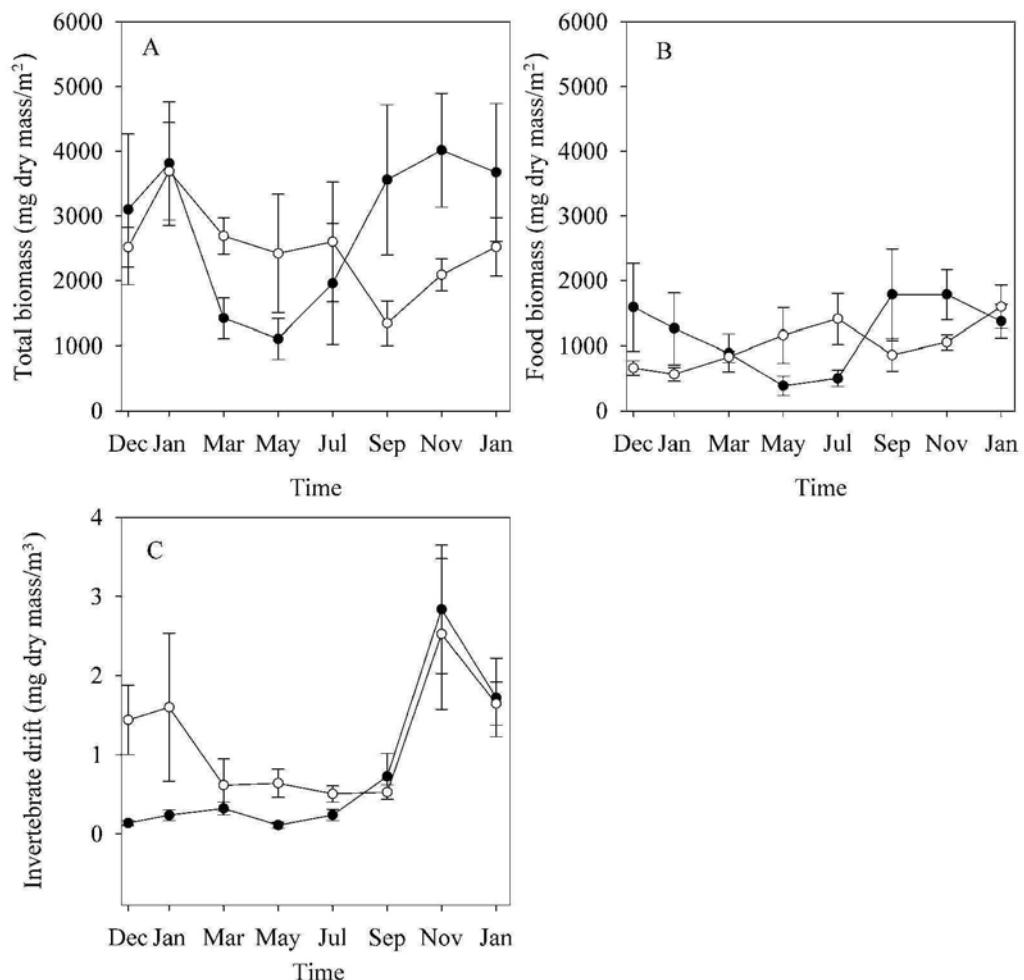
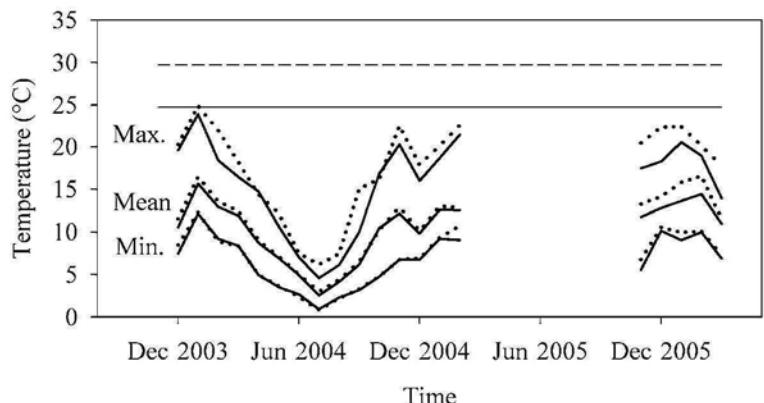
the downstream reach, both recorded in January 2006. No significant difference was found between monthly maximum temperature in the upstream and downstream reaches (one-way ANOVA,  $F_{1,38} = 1.123$ ,  $P = 0.296$ ). The lowest temperature ( $0.8^\circ\text{C}$ ) was recorded during July 2005 in the downstream reach, but overall minimum temperature did not differ between the two reaches (one-way ANOVA,  $F_{1,38} = 0.076$ ,  $P = 0.784$ ).

#### Biotic variables

There was a seasonal trend in total biomass of benthic invertebrates, with higher biomass values in summer than winter (Fig. 7). This difference was

primarily caused by a large increase in invertebrates not represented in trout diet in summer months, especially the snail *Potamopyrgus antipodarum* and *Pycnocentrodes* sp. caddis larva. MANOVA revealed a significant interaction between reach and month (Wilk's Lambda = 0.626, d.f. = 21, 224,  $P = 0.012$ ), indicating that time of year (month) influenced which reach had the highest biomass of invertebrates. Biomass of benthic invertebrates important as food items was generally higher in the upstream reach, except during winter (May 2004 – July 2004, Fig. 7) and biomass of drifting invertebrates was lowest in the upstream reach in the first part of the study period (December 2003 – July

**Fig. 6** Mean monthly, monthly maximum and monthly minimum temperature for upstream (solid lines) and downstream (dotted lines) reaches. Solid line represents incipient lethal temperature ( $24.7^{\circ}\text{C}$ ) and dashed line represents the ultimate lethal temperature ( $29.7^{\circ}\text{C}$ ) for brown trout *Salmo trutta* (Elliott 1981). No data was recorded from March 2005 to October 2005.



**Fig. 7** A, total benthic invertebrate biomass; B, biomass of benthic invertebrates important as food items; C, biomass of drifting invertebrates from December 2003 to January 2005 in the upstream (filled circles) and downstream (empty circles) reach of Silverstream, New Zealand.

2004) but values for this biotic variable were similar in the two reaches in the last part of this period (September 2004 – January 2005, Fig. 7).

## DISCUSSION

The results from the present study document great spatial variation in the population densities of juvenile brown trout in Silverstream, and that this pattern of variation repeats annually. These findings are consistent with previous studies of juvenile salmonids, which have shown substantial variation in densities and population dynamics over time and space (e.g., Allen 1951; Hayes 1995; Petty et al. 2005). The abundance of juvenile brown trout in Silverstream was to some extent determined by abiotic factors. Discharge was significantly positively correlated with loss rate of juvenile brown trout from the downstream reach in 2004–05, which indicates a negative effect of high discharge on fish numbers. This result is consistent with previous studies of brown trout population dynamics in New Zealand (Hayes 1995) and in the native range of the species (Elliott et al. 1997; Lobon-Cervia & Rincon 2004). Many of the studies that document negative effects of increased discharge on trout abundance highlight the importance of timing of high discharge events. The period during or just after emergence is critical and a flood in this period can substantially decrease growth and survival (Lobon-Cervia & Rincon 2004). The 2004–05 cohort of juvenile brown trout in Silverstream experienced two high discharge events in the first 4 months of free swimming life; the first event was in August, during or just before emergence, and the second one was in December. It is possible that these events caused a faster emptying of the downstream reach than in a year without high discharge events. The 2003–04 and 2005–06 cohorts were not influenced by high discharge events and the relationships between discharge and loss rates were negative (but not significantly so), indicating that most juvenile brown trout disappeared from the downstream reach during periods of low discharge. The high discharge events occurring during the study period were of a magnitude regularly occurring in Silverstream and nearby streams (annually or biannually) but bigger floods occur with larger time intervals (Otago Regional Council unpubl. data). These extremely high discharge events (approaching flow of 100 000 litres/s) probably have a more severe effect on the brown trout population than those observed during the study period. However,

high discharge alone does not explain the spatial difference in population dynamics of juvenile brown trout in Silverstream observed in the present study.

The maximum temperature recorded in Silverstream during the study period (24.9°C) was above the incipient lethal temperature for brown trout of 24.7°C (Elliott 1981). The incipient lethal temperature is defined as the temperature which fish can tolerate for a long period of time (usually 7 days) but beyond which fish cannot survive for an indefinite period (Elliott 1994). The maximum temperature in Silverstream was recorded at the end of a warm period and temperatures 6 and 10 days before the maximum reading were close to the incipient lethal temperature. Juvenile brown trout in the downstream reach were therefore likely experiencing thermal stress with possible alterations of population dynamics through mortality or displacements. However, each of the three occasions with temperatures close to or above the incipient lethal temperature had 2–5 days inbetween when maximum temperatures stayed below 21°C. Furthermore, the maximum temperatures were only recorded for 1–2 h during mid-afternoon with the remainder of the day having lower temperatures. The measured temperatures were also well below the ultimate lethal temperature for brown trout of 29.7°C (Elliott 1981) that fish cannot tolerate even for a short period (10 min; Elliott 1994). Finally, water temperature in summer 2004–05 and summer 2005–06 did not exceed 22.6°C when the same temporal variation in juvenile brown trout densities was observed as in the previous warmer summer, suggesting high summer temperature was not solely responsible for the rapid late summer decline in abundance in the downstream reach.

This study documents that variation in food availability over time was similar in the upstream and downstream reach. In populations of stream-dwelling salmonids, where individuals compete for feeding territories, density-dependent competition is thought to occur whenever a habitat becomes saturated with territories of a given size (Grant & Kramer 1990; Keeley 2001). Owing to the higher initial density of juvenile brown trout in the downstream reach, this habitat was likely to become saturated soon after trout started emerging, with intense competition over food and space as a likely consequence. As juvenile brown trout in the downstream reach increased in size, their demands for food and space increased as well (Grant et al. 1998). If the demand was greater than the available space and food, it might have resulted in downstream dispersal or mortality.

Densities in the downstream reach were relatively high just after emergence and density-dependent factors probably caused some reduction in fish number during this period. However, mid-summer densities in the downstream reach were relatively low (0.07 fish m<sup>-2</sup> in February 2004, 0.20 fish m<sup>-2</sup> in February 2005, and 0.13 m<sup>-2</sup> in February 2006) compared with other studies of salmonids: juvenile rainbow trout in a New Zealand stream in February had densities of 1.0–4.5 fish m<sup>-2</sup> (Hayes 1988), juvenile brown trout density was recorded to be 2.0 fish m<sup>-2</sup> in a British stream (Elliott 1987), 0.8 fish m<sup>-2</sup> in an Irish stream (Kelly & Dick 2005), and 1.18 fish m<sup>-2</sup> in a Swedish stream (Bohlin et al. 2001). Space limitation is thought to occur at much higher densities (Grant & Kramer 1990). For example, at a population density of 0.07 fish m<sup>-2</sup> (February 2004, downstream reach) each juvenile brown trout would have had between 5.3 and 14.6 m<sup>-2</sup> of available habitat. Despite the high availability of food and space, densities in the downstream reach decreased throughout summer and reached zero before the new cohort emerged in all years of study.

It is possible that the amount of available food was relatively low or high in Silverstream, which might affect the relationship between fish numbers and food availability in both the upstream and downstream reach. The average biomass of benthic invertebrates during summer 2003–04 in the upstream and downstream reach was 2589 mg dry weight (DW)/m<sup>2</sup> and 2960 mg DW/m<sup>2</sup>, respectively. This biomass is generally higher than has been found in other New Zealand rivers (Glova & Sagar 1994; Harding & Winterbourn 1995; Nystrom et al. 2003). The average biomass of drifting invertebrates during summer was 0.24 mg DW/m<sup>3</sup> in the upstream reach and 1.06 mg DW/m<sup>3</sup> in the downstream one. Summer biomass of drifting invertebrates in other New Zealand rivers has been reported to range from 0.41 to 0.58 mg DW/m<sup>3</sup> (Sagar & Glova 1992, 1995), higher than in the upstream reach but lower than values recorded in the downstream reach in this study. The amount of available food was therefore above average in Silverstream, especially in the downstream reach and thus food limitation seems unlikely. Population densities were higher in 2004–05 and 2005–06 than in 2003–04 when food availability was investigated. It is possible that juvenile brown trout from the downstream reach were experiencing food limitation in these 2 later years, resulting in the high loss rate from this reach. However, juvenile brown trout from this reach were consistently larger and had higher condition factors,

indicating favourable growth conditions (Wootton 1998). If the high loss rate of juvenile brown trout from the downstream reach was caused by food or space limitation, higher condition factors (and higher growth) would be very unlikely there. A trap placed in the two reaches catching up and downstream moving fish also showed that condition factors were similar among moving fish and stationary fish in the downstream reach (Kristensen 2006), providing further evidence for the hypothesis that growth conditions in the downstream reach were not primarily responsible for the high loss rates.

The results from the present study document that population dynamics of juvenile brown trout in two reaches of Silverstream are different and that variation persists over time. Discharge and temperature had possible negative effects on population densities of juvenile brown trout, but the overall pattern in the spatiotemporal difference in population densities could not entirely be explained by variation in these two factors or in availability of food. Given that juvenile brown trout from the downstream reach had higher condition factors than those from the upstream reach and that habitats were similar in the two reaches, it seems counter-intuitive that trout abundance declined annually along the downstream reach. Previous studies have documented that within a population, the decision to leave a habitat is under both genetic and environmental control (Northcote 1992). Olsson & Greenberg (2004) showed that average growth rates along stream reaches dominated by resident fish were higher than average growth rates from stream sections dominated by migratory behaviour. High individual growth rate is believed to promote residency by obviating any energetic benefits of migration (Jonsson & Jonsson 1993). However, despite the higher average growth rates, juvenile brown trout abundance still declined from the downstream reach at a much higher rate than from the upstream reach, and trout were absent from the downstream reach less than a year after emergence. This paradoxical pattern occurred annually in Silverstream and suggests that mechanisms other than the proximate environmental cues are influencing the decision to leave the downstream reach. This pattern is inconsistent with what has anecdotally been considered to be the most likely factors regulating the brown trout population in this reach. Analysis of trace element signatures in brown trout eggs has previously documented spatial separation of spawning by resident and migratory brown trout in Silverstream with spawning by both resident and migratory fish in the upstream reach, but only

migratory fish in the downstream reach (Kristensen 2006). It is possible that predisposed migratory behaviour affects the population dynamics in the two reaches and caused the observed spatial variability. This hypothesis is supported by the finding of high loss rates and rapid decline in juvenile brown trout densities in lower reaches of several tributaries to the Taieri River (Kristensen 2006), suggesting the observed pattern is generally occurring throughout the river catchment. Although the planned habitat enhancement project might improve in-stream habitat in the downstream reaches of Silverstream, it may not result in changes to the overall pattern of population dynamics of juvenile brown trout if external processes to Silverstream (specifically migratory trout spawning) are controlling abundance and population dynamics.

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## Appendix 1

Biomass of benthic invertebrates was calculated by length-mass equations, based on benthic invertebrates that were collected in Silverstream, New Zealand and for which length (to nearest 0.1 mm) and dry mass (to nearest 0.001 mg) were determined (Kristensen 2006). All measurements (length and mass) were  $\log_{10}$ -transformed before regression to meet the assumptions of normality and heterogeneity (Bird & Prairie 1985; Stoffels et al. 2003). A linearised power function was fitted to the data to establish length-mass equations:

$$\log_{10} M = \log_{10} a + b \log_{10} L + e$$

where  $M$  = dry mass/ash free dry mass (mg),  $L$  = the length (mm),  $a$  and  $b$  are the estimated parameters from the regression, and  $e$  is the normally distributed error term with mean 0 and a variance equal to the residual mean square (RMS) of the regression (Bird & Prairie 1985) where RMS equals the variance unexplained by the regression line (observed Y from estimated Y; Sokal & Rolff 1995).

**Table A1** Length- mass equation parameters for Silverstream, New Zealand benthic invertebrates ( $a$  and  $b \pm$  SE), including  $r^2$  values and residual mean square (RMS) to correct mass estimates, range of length A (mm) and mean dry mass  $y$  (mg)  $\pm$  95% CI.

Taxa	$\log_{10} a$	$b$	$r^2$	$n$	RMS	Range A	$y \pm 95\% \text{ CI}$
<b>Megaloptera</b>							
<i>Archichauliodes diversus</i>	$-2.778 \pm 0.148$	$2.929 \pm 0.136$	0.956	23	0.032	5.2–32.5	$9.436 \pm 0.210$
<b>Diptera</b>							
<i>Chironomidae</i>	$-2.414 \pm 0.173$	$1.973 \pm 0.251$	0.511	61	0.099	2.3–10.2	$0.134 \pm 0.001$
<i>Austrosimilium</i>	$-2.516 \pm 0.110$	$2.531 \pm 0.183$	0.881	28	0.012	2.2–5.7	$0.122 \pm 0.001$
<i>Aphrophila</i>	$-2.686 \pm 0.218$	$2.408 \pm 0.199$	0.790	41	0.036	6.7–21.9	$1.273 \pm 0.012$
<b>Trichoptera</b>							
<i>Aoteapsyche</i> sp.	$-3.570 \pm 0.294$	$3.785 \pm 0.264$	0.903	25	0.061	2.3–22.3	$7.446 \pm 0.091$
<i>Oxyethira albiceps</i>	$-2.736 \pm 0.215$	$3.084 \pm 0.467$	0.601	31	0.042	1.7–4.0	$0.057 \pm 0.004$
<i>Psilochorema</i>	$-3.396 \pm 0.237$	$3.153 \pm 0.229$	0.841	38	0.085	3.6–17.9	$1.488 \pm 0.016$
<i>Costachorema</i>	$-3.168 \pm 0.327$	$2.947 \pm 0.345$	0.829	17	0.093	3.2–22.4	$1.091 \pm 0.026$
<i>Hydrobiosis</i>	$-2.797 \pm 0.160$	$2.612 \pm 0.186$	0.892	26	0.057	2.0–22.6	$0.871 \pm 0.023$
<i>Polycentropodidae</i>	$-3.452 \pm 0.288$	$3.229 \pm 0.260$	0.928	14	0.035	5.5–21.7	$2.654 \pm 0.048$
<i>Hudsonema</i>							
<i>amabilis</i>	$-3.411 \pm 0.249$	$3.559 \pm 0.285$	0.848	30	0.057	3.7–12.6	$1.024 \pm 0.015$
<i>Pycnocentrodes</i> sp.	$-2.409 \pm 0.157$	$2.908 \pm 0.271$	0.816	28	0.035	2.1–7.0	$0.247 \pm 0.003$
<i>Olinga feredayi</i>	$-2.717 \pm 0.126$	$3.157 \pm 0.190$	0.891	36	0.046	2.1–10.2	$0.512 \pm 0.008$
<b>Ephemeroptera</b>							
<i>Deleatidium</i> spp.	$-2.791 \pm 0.100$	$3.134 \pm 0.132$	0.923	49	0.031	2.5–10.3	$0.649 \pm 0.008$
<b>Coleoptera</b>							
<i>Hydora</i>	$-2.836 \pm 0.134$	$3.207 \pm 0.187$	0.904	33	0.022	2.7–7.7	$0.416 \pm 0.004$
<i>Oligochaeta</i>	$-3.751 \pm 0.304$	$2.844 \pm 0.208$	0.912	20	0.029	12.7–45.3	$4.052 \pm 0.047$
<b>Crustacea</b>							
<i>Paracalliope</i> sp.	$-2.038 \pm 0.080$	$2.243 \pm 0.160$	0.880	29	0.008	1.6–4.6	$0.135 \pm 0.001$
<b>Gastropoda</b>							
<i>Potamopyrgus antipodarum</i>	$-1.254 \pm 0.050$	$1.903 \pm 0.107$	0.851	57	0.021	0.59–5.2	$0.511 \pm 0.004$
<i>Physella acuta</i>	$-1.790 \pm 0.063$	$2.861 \pm 0.111$	0.968	24	0.007	1.8–6.7	$1.047 \pm 0.013$
<i>Gyraulus</i>	$-1.671 \pm 0.078$	$2.778 \pm 0.167$	0.926	24	0.004	2.0–3.7	$0.435 \pm 0.003$