

**EFFECTS OF TROUT ON GALAXIID GROWTH
AND ANTIPREDATOR BEHAVIOUR**

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Preface

This thesis investigates interactions between trout (brown trout, *Salmo trutta* and rainbow trout, *Oncorhynchus mykiss*) and non-migratory Canterbury galaxias (*Galaxias vulgaris*) and Alpine galaxias (*Galaxias paucispondylus*) in the Upper Waimakariri River catchment of the South Island, New Zealand. The thesis is arranged in two ‘stand alone’ chapters intended for publication, each dealing with a different aspect of the topic.

The first chapter concerns how varying degrees of trout and galaxiid co-occurrence may affect galaxiid antipredator responses. The first chapter necessarily introduces trout predation as an important factor explaining why co-occurrence does, or does not, occur between trout and galaxiids and an introduction on how past experience with predators can influence antipredator behaviour. The second chapter investigates the competitive effects of trout on galaxiid growth rate and examines the effects of food and space competition between trout and galaxiids.

Descriptions of the study region and some methods are similar between chapters and where necessary, references to findings between chapters are made in discussions. To avoid repetition in the thesis, where method descriptions are similar, they are included in the first chapter and referred to in the second chapter. General conclusions based on findings in each chapter are kept separate and are presented at the end of their respective discussions.

It is intended that publications resulting from this work will be multi-authored, reflecting the contributions of others to the work. Specifically Peter McHugh assisted with

the design and data collection for the field sampling for both chapters, Darragh Woodford assisted with the design and execution of the stream manipulation experiment, and my supervisor, Angus McIntosh, contributed to study design, analysis and the writing. Although these people made significant contributions, the work is primarily my own and I will be first author on both publications.

Abstract

The introduction of trout has been implicated in the declines in native fish fauna in New Zealand and worldwide. Since the introduction of brown (*Salmo trutta*) and rainbow (*Oncorhynchus mykiss*) trout to New Zealand in 1867, their distribution has spread and they have been implicated in the fragmentation of native fish distributions, particularly native non-migratory galaxiids. However, in the Upper Waimakariri basin the co-occurrence of trout and galaxiid populations is relatively common, even in streams where trout reach sizes known to be piscivorous. To investigate mechanisms that may regulate trout and galaxiid co-occurrence, I investigated differences in antipredator behaviour and growth rate between stream types with varying levels of trout presence. Using quantitative survey data collected between 1997 and 2006, I found that trout abundance was low and varied annually in frequently disturbed sites compared their high abundance in stable streams. This finding was used to classify streams into three population types, barrier (trout absent), disturbed (trout presence intermittent) and sympatric (constant trout presence). Using this classification, I tested the effects of trout chemical cues on galaxiid activity and refuge use in artificial channels. There were no differences in activity or refuge use between trout odour and there were no effects of population type or galaxiid size during both the day and the night. Using otolith weight-fish length relationships in galaxiids collected from each population type, I found that galaxiid growth rate was higher in disturbed streams than in stable streams either with or without trout. An experiment manipulating trout size and presence, over two months in a natural stream, found galaxiids from treatments without trout grew slower than those with trout. Slow growth rates in galaxiids above trout-migration barriers and in sympatry, combined with low growth rates in treatments without trout suggest that the mechanisms that regulate galaxiid growth are more complex than previously thought.

Chapter One: Effects of past trout experience on galaxiid antipredator responses

1.1 Introduction

Prey species can alter their vulnerability to predation via changes in phenotypic traits (Sih 1987, McIntosh & Townsend 1994, Harvell & Tollrian 1999, McIntosh & Peckarsky 2004, Bell et al. 2006). These traits can be changes in morphology, physiology, development or behaviour in prey organisms, that either, reduce encounter rates with predators, or increase escape success following predator encounters (Sih 1987, Lima & Dill 1990, Harvell & Tollrian 1999). Introduced species can have important negative impacts on native populations, via predation and competitive interactions (Townsend 1996). The development of adaptive antipredator responses may well determine the ability of native and introduced species to co-occur. Therefore it is important to identify where antipredator responses exist, how they operate, and their relative importance to interactions between native and introduced species.

Past experience with a predator can influence the expression of antipredator responses over different ecological scales. At an evolutionary scale, past history may influence the interactions between predators and prey via coevolved antipredator responses in prey (Thorp 1986, Cox & Lima 2006, Strauss et al. 2006, Salo et al. 2007). Conversely several studies attribute the detrimental impacts of introduced predators on native prey to a lack of evolutionary history with, and whence antipredator responses towards, introduced predators (Townsend & Crowl 1991, Townsend 1996, Short et al. 2002, McDowall 2003). There is some evidence for this in studies that show prey display a greater variety or intensity of

antipredator responses towards native predators than introduced predators (McIntosh & Townsend 1994, Shave et al. 1994, Pearl et al. 2003, Bosch et al. 2006, Anthony et al. 2007, McLean et al. 2007). At the population level, co-occurrence with predators can lead to differences in the display and effectiveness of antipredator responses. This is reflected in a large number of studies that show morphological (Moore et al. 2004, Fisk et al. 2007) and behavioural (Kiesecker & Blaustein 1997, Åbjörnsson et al. 2004, Kristensen & Closs 2004, Murray et al. 2004) antipredator responses in prey populations sympatric with introduced predators, but not in adjacent predator-free populations. In individuals, antipredator responses can be learned following exposure to either predators or predator cues (Mirza & Chivers 2002, 2003a, Darwish et al. 2005). Repeated exposures can enhance the display and effectiveness of learned antipredator behaviours and social learning between individuals can propagate learned behaviours (Mathis et al. 1996, Vilhunen et al. 2005). Several studies have shown increased survival in prey with past experience with introduced predators (Kiesecker & Blaustein 1997, Berejikian et al. 1999, Åbjörnsson et al. 2004, Darwish et al. 2005, Vilhunen 2006).

Galaxiids (Family: Galaxiidae) comprise around sixty percent of New Zealand's native fish species, and represent over sixty percent of all galaxiid species (McDowall 2006). Of New Zealand's ~ 22 described native galaxiids, five are in serious decline or worse, and eleven are in gradual decline (Hitchmough et al. 2005). This decline is often attributed to the introduction of salmonids. The introduction of brown trout (*Salmo trutta*) to New Zealand as sport fish in 1867 (MacCrimmon & Marshall 1968) means historical records of native fish distributions are few. Consequently much of the basis for the negative effects of salmonids comes from a convincing, although circumstantial, body of research (reviewed by McDowall 2006). Such evidence includes the historical decline, and eventual extinction of the New

Zealand grayling (*Prototroctes oxyrhynchus*) around 1870, the same time trout were introduced (McDowall 2006). However, the introduction of trout was concurrent with European settlement during which vast destruction and modification of habitat occurred (Taylor & Smith 1997). This has confounded the causes of declines in native fish, particularly in lowland species, where habitat modification has been, and continues to be, extensive .

The negative effects of introduced trout on galaxiids parallel the negative interactions between trout and native fish found elsewhere and a number of studies reporting disjunct distributions between galaxiids and trout suggest that trout may have negative effects on galaxiids (Minns 1990, Townsend & Crowl 1991, Crowl et al. 1992). Predation by trout, in particular has been suggested to have large effects on galaxiid populations, leading to the localised extirpations (Townsend & Crowl 1991, Townsend 2003). Trout are known to be piscivorous (Mittelbach & Persson 1998) and studies of trout diet (Kusabs & Swales 1991) and predation trials in artificial enclosures have found that all size classes of galaxiids, with the possible exception of adult large-bodied galaxiids such as kokopu (*Galaxias argentus*, *G. fasciatus* and *G. postvectis*), may be vulnerable to trout predation (Glova 1990, Crowl et al. 1992, McIntosh 2000, Jellyman 2004). In addition to the predatory impacts on galaxiids, competitive interactions between trout and galaxiids for food and space can also have negative impacts on galaxiids. These interactions may have negative long-term effects on galaxiids such as reductions in growth rate and are discussed in Chapter Two.

The galaxiid species used in this study, Canterbury galaxias (*G. vulgaris*), is a non-migratory native galaxiid that frequently co-occurs with brown (*S. trutta*) and rainbow trout (*Oncorhynchus mykiss*) in the Upper Waimakariri basin, New Zealand. Trout have been present in the Waimakariri basin for over one hundred years (McDowall 2000) and in this

region trout presently co-occur with *G. vulgaris* in many streams (McIntosh 2000). Given the relatively prolonged co-occurrence between trout and galaxiids in this region, sufficient time may have passed for the development of antipredator mechanisms in galaxiids. Additionally, because trout presence is variable in frequently disturbed streams and several trout-naïve galaxiid populations exist above trout migration barriers, this region provides an opportunity to investigate how past trout experience may affect galaxiid antipredator behaviour.

The aim of this study was to investigate two main questions 1) do galaxiids display antipredator behaviours capable of explaining their co-occurrence with trout? and 2) how are these antipredator behaviours affected by past trout experience? I use recent and past quantitative fish surveys to show that trout and galaxiid co-occurrence is common and that trout presence and abundance is affected by disturbance regime. I investigate antipredator behaviour in *G. vulgaris* sourced from streams with varying levels of past trout experience in artificial channels to evaluate differences in behavioural responses to trout odour cues.

1.2 Methods

Study region

All sites (except the Acheron River; Figure 1.0, site No. 14) used in the study were located in the Cass region between 42°59 and 43°20 latitude (Figure 1.0). The catchment itself lies on the eastern slopes of the Southern Alps of the South Island and drains east approximately 150 km, across the Canterbury Plains to the sea (Figure 1.0). The geology is dominated by greywacke (Reinfelds & Nanson 1993) and, although in the study region there are some limestone outcrops, conductivity in streams is remains low (Death 1995, McIntosh 2000). Rainfall varies from 8000 mm to 700 mm, travelling east from the main divide (Reinfelds & Nanson 1993) to the sea. At Cass Field Station (situated at the Grasmere Stream site; Figure 1.0 No. 24) the mean annual rain fall is around 1300 mm (Greenland 1977). In streams used in this study, riparian vegetation consisted mainly of short tussock grassland (*Festuca* spp. and *Poa* spp.) and mountain beech forests (*Nothofagus solandri* var. *cliffortioides*), although disturbed streams were often situated in wide river beds without substantial streamside vegetation.

Long-term variability in trout presence and abundance

Antipredator behaviours can be influenced by past experience with a predator. To evaluate how past trout experience may influence galaxiid antipredator behaviour, I first investigated how trout presence and abundance varied temporally across streams with different hydrological disturbance regimes. I used historic survey data collected between 1997 and 2004 and my own data collected in 2005 and 2006 to test for differences in trout

presence, and to compare trout and galaxiid biomass between disturbed and stable sites (Table 1.0). Two historical survey datasets were used, the first was published data (McIntosh 2000) collected between 1997 and 2000 (Table 1.0). The second set is unpublished data collected between 2000 and 2004 as part of various studies by Angus McIntosh and co-authors (Table 1.0).

In all surveys, the quantitative fishing methods were kept the same. Sites were delineated using stopnets and fished using three passes with a backpack electric fishing machine (Kainga 300, NIWA Instrument Systems, New Zealand). Fish caught in each pass were anaesthetised with 2-phenoxyethanol before being weighed and measured separately. Caught fish were retained for consecutive electric fishing passes, then released. Density estimates were calculated using the three pass depletion equations of Cowx (1983) and reach dimensions (reach length \times mean reach width). Where more fish were caught on the second than in the final run, violating the assumptions of the depletion equation and yielding negative results (Cowx 1983), the total number of fish caught was used. Reach biomass was calculated using density estimates multiplied by mean fish mass for each fish species in respective survey years. Fish biomass was grouped as galaxiid (*G. vulgaris*, *G. brevipinnis* and *G. paucispondylus*), salmonid (*S. trutta*, *O. mykiss* and *O. tshawytscha*) and total fish biomass (both galaxiid and salmonid biomass as above, plus longfinned eel, *Anguilla dieffenbachia* and upland bully *Gobiomorphus breviceps*).

Disturbance regime was assessed at each site using the stream bed component (hereafter Pfankuch bottom score) of the channel stability index of Pfankuch (1975). This method of assessing physical disturbance was chosen because sampling sites were numerous, distant and visited infrequently prohibiting the use of more extensive methods. The

assessment uses characteristics of the stream bed particles (angularity, brightness, consolidation and size distribution), bed scouring and deposition, and aquatic vegetation. Scores are assigned to one of four categories within each characteristic by an observer and summed to give a composite score. Scores are weighted according to relative importance and increase with bed instability (scouring and deposition and particle size distribution score highly) with high overall scores representing streams with high physical disturbance (Death & Winterbourn 1994). Each survey independently estimated the bottom score index for sampled sites and observers were kept constant within, but not between, surveys. In sites sampled over multiple occasions, a mean bed stability index was calculated from a maximum of three bed stability estimates (Table 1.0).

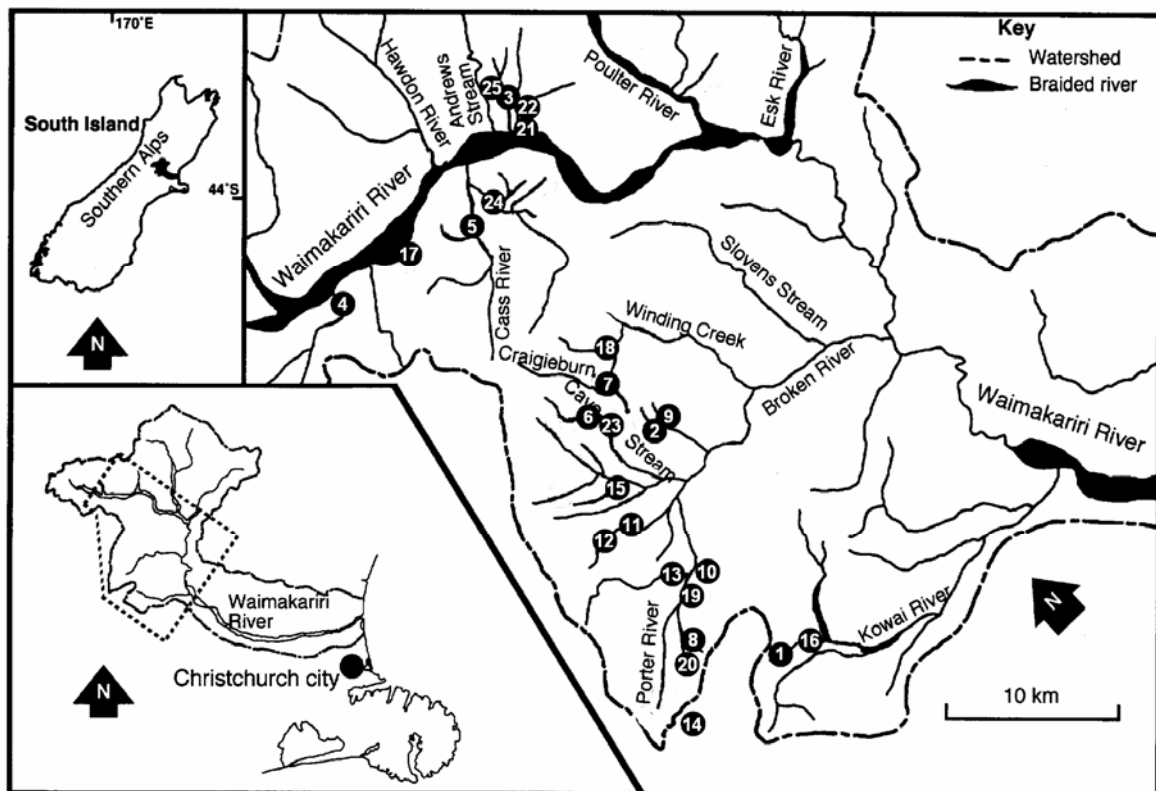


Figure 1.0 Distribution of sampling sites in the Upper Waimakariri basin. Filled circles represent the location of quantitative sampling sites. Numbers within filled circles correspond to stream names and characteristics given in Table 1.0.

Statistical analyses were performed using all study sites with two or more years of quantitative survey data. Individual sites were classified as one of four stream types according to the mechanisms determining trout presence or absence. Firstly sites were classified as containing either galaxiids only (barrier type sites) or trout only (trout type). Trout were absent from barrier sites by virtue of downstream trout migration barriers. These barriers were either shallow drying reaches, steep road culverts (Figure 1.1a) or natural velocity barriers (Figure 1.1b). Trout only sites had no previous records of galaxiids. The remaining two stream types, disturbed and sympatric type sites, both had past records of trout and galaxias presence and were separated according to flow disturbances using Pfankuch bottom score (see above). Sites with a mean Pfankuch bottom score between 40 - 55, were classified as disturbed type, and sites between 20 – 35 as sympatric type sites (Table 1.0).

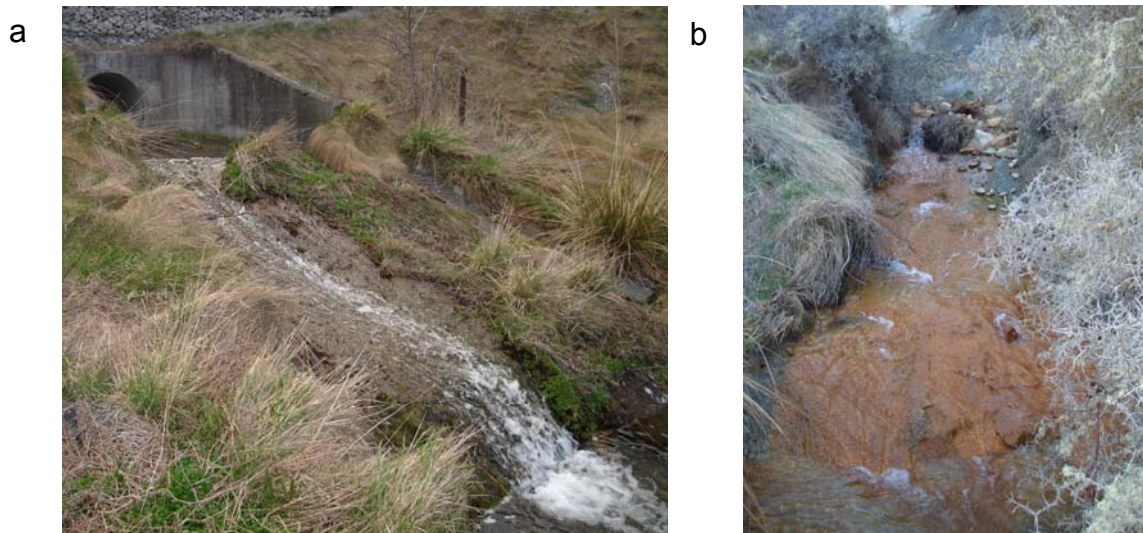


Figure 1.1 Examples man-made (a).and natural (b) velocity trout migration barriers.

Table 1.0 Locations, years and Pfankuch bed stability index of sites with more than two survey years.

No. in Fig. 1.0	Stream type	Stream name	Map location (NZMG)	Sampling summer						Times surveyed	Bottom score estimates			Mean bottom score		
				97/98 ^a	98/99 ^a	99/00 ^a	00/01 ^{ab}	04/05 ^b	05/06 ^c		06/07 ^c	2000 ^a	2004 ^b		2005 ^c	
1	Barrier	Coach Steam (upper)	K35 092 659	x		x	x		x	x	5	31	18	48	32	
2		Flock Hill Stream (trib)	K34 083 807		x				x		2		40		40	
3		Lower Farm Stream (upper)	L34 128 998				x		x	x	3		35	26	30	
		Barrier total									10	Mean bed stability			34.4	
4	Disturbed	Bruce Stream	K34 986 967	x			x				2	59	50		54	
5		Cass River	K34 079 970	x		x	x		x	x	5	59	53	44	52	
6		Cave Stream (upper)	K34 054 834	x		x					2	42			42	
7		Craigieburn	K34 085 846	x		x					2	41	45		43	
8		Dry Stream (lower)	K34 053 714					x		x	3		37	43	40	
9		Flock Hill Stream	K34 086 805		x				x		2	49		34	42	
10		Ghost Creek	K34 077 735						x	x	2			49	49	
11		Thomas River (lower)	K34 049 772						x	x	2			45.5	45	
12		Thomas River (upper)	K34 048 773	x		x				x	3	44			44	
13		Whitewater Stream	K34 064 728	x		x					2	45			45	
			Disturbed total									25	Mean bed stability			45.7
14		Sympatric	Acheron River	K39 019 639					x	x	2		31	23	27	
15			Bradley Stream (lower)	K34 054 788		x	x			x		3		22	22	
16	Coach Stream (lower)		L35 102 655						x	x	2		24	24		
17	Cora Lynn Spring*		K34 027 968	x			x				2	23	25		24	
18	Manson Creek (lower)		K34 027 968	x		x	x				3	36	26		31	
19	Roadmarker Spring *		K34 063 727	x					x	x	3	18		23	20	
20	Slip Spring		K34 052 708	x		x	x				3	28	19	16	21	
21	Waimakariri Spring *		L34 133 982		x		x		x	x	4		44	24	34	
			Sympatric total									23	Mean bed stability			25.3
22	Trout	Binser Saddle Stream	L34 129 996		x	x	x			3				NA		
23		Cave Stream (lower)	K34 067 833	x		x				2	25			25		
24		Grasmere Stream	K34 088 962	x		x	x			3	24		20	22		
25		Peacock Stream*	L33 117 099	x		x	x				3	31			31	
		Trout total									11	Mean bed stability			26.0	

^a Published survey data from McIntosh (2000)^b Unpublished survey data from Angus McIntosh^c Unpublished survey data obtained during this study

* Unofficial names

Annual variability in trout presence was tested using frequency of trout presence/absence, for all survey years, between disturbed and sympatric type sites in a Chi-squared test for independence. Differences in galaxiid biomass, salmonid biomass and bottom score index between population types were tested with ANOVA using sites as replicates. Mean biomass for individual sites was calculated using all survey years. Differences in galaxiid biomass were tested between barrier, disturbed and sympatric stream types only (trout types excluded), while differences in salmonid biomass were tested between disturbed, sympatric and trout stream types (barrier types excluded) because galaxiids and trout were absent from trout and barrier type streams, respectively. Galaxiid, salmonid and total fish biomass were log-transformed ($\log_e [x + 1]$) to normalise distributions. An ANOVA was used to test for stream type differences mean Pfankuch bottom scores (Table 1.0) using individual sites as replicates. Where significant differences were detected in ANOVA analyses, Tukey multiple comparison tests were used to evaluate pairwise differences.

Antipredator behaviour experiment

I used variability in trout presence and abundance from the long-term data above to test the effects of past trout experience on galaxiid antipredator behaviour. Antipredator behaviours can be fixed or flexible. Flexible responses are in response to a stimulus associated with the presence of a predator, whilst fixed responses are displayed independent of a stimulus. To investigate whether galaxiids display any fixed or flexible antipredator behaviour I tested galaxiid activity and refuge use both in the absence and in the presence of trout odour. Additionally, because predation threat may vary with galaxiid size I tested for antipredator behaviours in large and small galaxiids.

Observations were conducted in artificial channels at the University of Canterbury's Cass Field Station between 4 May and 27 October, 2006. Channels were constructed of two 1 m lengths of 125 mm wide kerbing channel (Everdrain[®], Everhard Industries, Australia) and corner fittings to create 31 L recirculating tanks (Figure 1.2). Each tank contained two refugia made from 10 cm lengths of round 50 mm diameter black PVC piping (Figure 1.2). Water used in the experiment was sourced from a fishless stream (Reservoir Bush Stream, NZMG: K34 093 964) at Cass Field Station and gravity-fed from around 800 m away to experimental tanks. Flow was maintained in channels using two flow inlets and depth was maintained at 9 cm using two tank outlets (Figure 1.2). Tank temperature and velocity were measured 0.85 m from tank jets at the end of trials. Differences in velocity and temperature between day and night trials were tested using paired t-tests. Tank temperatures were $8.6\text{ }^{\circ}\text{C} \pm 0.6$ (mean ± 1 SE) and $7.6\text{ }^{\circ}\text{C} \pm 0.3$ for day and night trials, respectively. There were no significant differences in tank temperature between the day and night ($t = 2.31$, $df = 4$, $P = 0.08$). Mean tank velocities for all trials were $5.2\text{ cm}\cdot\text{s}^{-1} \pm 0.2$ (mean ± 1 SE) and there were no significant differences in velocity between day and night trials ($t = 0.40$, $df = 4$, $P = 0.70$).

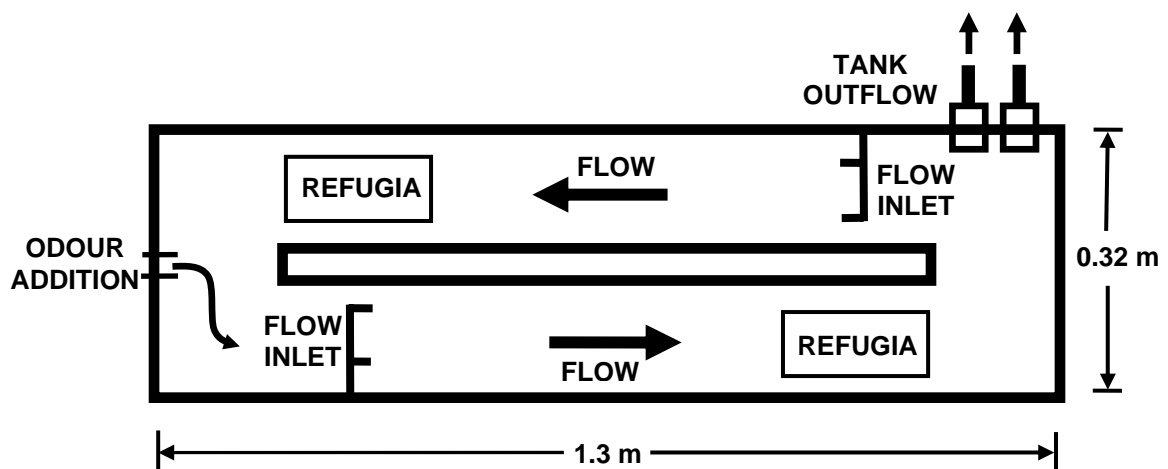


Figure 1.2 Schematic (not to scale) showing tank dimensions, flow direction and positions of flow inlets, outlets, odour addition and refugia within experimental channels.

Trials were conducted during the day and night between 2300 and 0200 and 1100 and 1400, for night and day trials, respectively. The experiment was replicated using different galaxiid source streams for each trial so galaxiid populations were used as replicates (Table 1.1). The first three trials were conducted between 4 and 28 May 2006. Initially the experiment was limited to three replicates due to a lack of trout-free galaxiid populations above trout migration barriers. However, after finding additional trout-free populations two more trials were conducted between 27 September and 27 October 2006.

Table 1.1 Population type classification, elevation and location of sites used in the behavioural experiment.

Population type	Stream name	Map sheet Grid reference (NZMG)
Barrier	Bradley Stream (upper)	K34 048 788
	Coach Stream (upper)	L35 092 659
	Kowai tributary *	L35 104 664
	Skifield *	K35 022 695
	Thunder Creek *	K34 058 782
Disturbed	Bruce Stream	K34 986 967
	Cass River	K34 079 970
	Dry Stream	K34 053 714
	Thomas River (lower)	K34 049 772
Sympatric	Bradley Stream (lower)	K34 054 788
	Cave Stream	K34 065 812
	Coach Stream (lower)	L35 102 655
	Roadmarker Spring *	K34 063 727
	Waimakariri Spring	L34 133 982

* Unofficial name

Experimental tanks were arranged in three pairs. Population type was randomly assigned to each tank pair and odour treatment randomly assigned to tanks within pairs. Trials were conducted during both the day and night, and replicated through time. Galaxiids were collected from streams (Table 1.1) using a backpack electric fishing machine (see above) between 24 and 48 hours before their use in trials. Galaxiids were then transferred to in 28 L holding tanks for 24 hours at a 12D:12L light regime and fed mayfly prey *ad libitum*, before

use in trials. Two galaxiids (1 large and 1 small) were placed in each tank, two hours prior to observations. Galaxiids were only used once in each replicate with separate fish for day and night. Trout odour cues were provided by two 28 L tanks (one with trout, one control without), suspended two metres above and to the side of the experimental channels. Trout were placed in tanks four hours before the start of the trial, to allow odour cues to accumulate. Water from cue tanks was gravity-fed into channels at a rate of $0.5 \text{ L}\cdot\text{min}^{-1}$ via a small tube (Figure 1.2). A single brown (*S. trutta*) and single rainbow trout (*O. mykiss*) were used to provide chemical cues. Both trout species were used because the two species co-occur with galaxiids in disturbed and sympatric streams. Trout were held separately in the same tank, with a plastic partition to prevent interspecific aggression. Trout used in the experiment were collected from local streams using the same methods as for galaxiid collection. Fork lengths of trout used were $116 \text{ mm} \pm 1.3$ and $122 \text{ mm} \pm 1.9$ (mean TL ± 1 SE) for brown and rainbow trout, respectively. Trout were held separately from galaxiids and fed mayfly prey 24 hours prior to their use in trials. The same trout were used as odour cues in both day and night trials but not between replicates. Water used in holding tanks was from the same source as that used in the experimental tanks. Separate holding tanks were used for each population type and following trials, fish were held in tanks separate from unused fish.

Trials were recorded using infrared sensitive video cameras (Panasonic WV-BP 550, Matsushita Electric Industrial Co. Ltd., Japan), connected to a sequential switcher (Panasonic WJ SQ 308, Matsushita Electric Industrial Co. Ltd., Japan) at 30 second intervals and recorded using a video recorder (Panasonic AG-TL 300, Matsushita Electric Industrial Co. Ltd., Japan). Cameras were mounted 1.2 m above the channel allowing the entire channel to be viewed. Day trials were performed under fluorescent light, provided by two fluorescent tubes. Night trials were performed under infrared light, which galaxiids are unlikely to detect

(McIntosh & Townsend 1994). Galaxiids were visually isolated from the observer and were left undisturbed during trials.

Response variables

Activity and refuge use were determined from two hours of observations of individual fish using video footage. Any movement of fish was recorded as time spent active. Fish did not move once in refugia so a single variable for refuge use, time spent in refugia, was used. Galaxiids were defined as in refugia if over half of the galaxiids body length was under cover. Time spent in refugia was determined for individual fish as the total time spent in refugia, and expressed as a proportion of the experiment duration. Time spent active was determined as the time spent active whilst out of refugia, and expressed as proportion of all time spent out of refugia. Percent time spent active and in refugia for odour absent treatments, used to test fixed effects were arcsin squareroot-transformed ($\arcsin \sqrt{x}$) to normalise distributions. Differences in percent time spent active and in refugia, used to test flexible behaviour in response to trout odour, were normally distributed and were not transformed. An ANOVA with time of day, population type and odour as factors was used to test for differences in galaxiid total length between treatments. Galaxiid total length was normally distributed and was untransformed. Time spent in refugia and time spent active, from odour absent treatments, were used to test for fixed antipredator responses in *G. vulgaris*. The two response variables were recorded from observations of the same fish and were unlikely to be independent, therefore a nested MANOVA was used to simultaneously test the effects of time of day, population type, galaxiid size and relevant interactions. A nested MANOVA was used to test for time of day, population type, galaxiid size and relevant interaction effects on percent time spent in refugia and percent time spent active. Differences between same sized fish in each odour treatment

pair (odour present – odour absent) for percent time spent in refugia and time spent active while out of refugia were used to test for flexible galaxiid antipredator behaviour in response to trout odour. Following the MANOVA tests for fixed and flexible antipredator responses, significant effects were further tested using univariate ANOVA. Following each of the MANOVA s above, activity and refuge use were analysed using separate univariate ANOVA for those effects found significant in the MANOVA.

1.3 Results

Long term variability in trout presence

Galaxiid and trout co-occurrence was relatively common in disturbed and sympatric population types used in this study (Figure 1.3). The frequency of trout presence and absence was not independent of population type ($\chi^2 = 7.56$, $df = 1$, $P = 0.006$). Trout were present in the majority of surveys conducted at sympatric sites but were only present in around half of surveys at disturbed sites (Figure 1.4).

There was no significant difference in mean galaxiid biomass for all years between barrier, disturbed and sympatric stream types ($F_{2,18} = 0.85$, $P = 0.445$; Figure 1.5a). There was a significant difference in mean salmonid biomass for all years, between disturbed, sympatric and trout only sites ($F_{2,19} = 4.81$, $P = 0.02$; Figure 1.5b). There was a significant difference in Pfankuch bottom score between stream types ($F_{3,20} = 30.14$, $P = 0.001$; Figure 1.6). Specifically, there were significant differences in Pfankuch bottom score between disturbed, and barrier (Tukey pairwise comparison, $P = 0.010$), sympatric ($P < 0.001$) and trout ($P < 0.001$), population types (Figure 1.6).

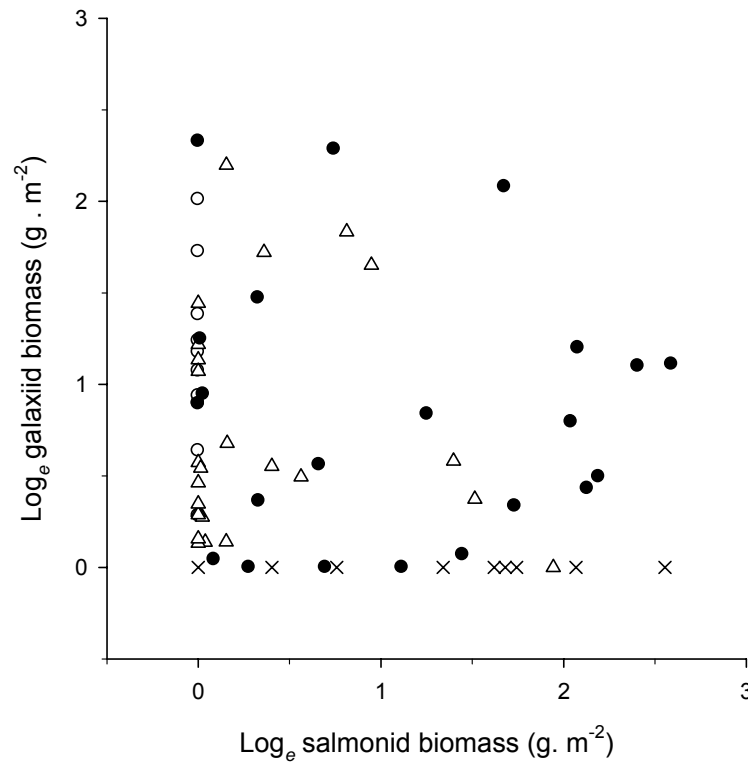


Figure 1.3 Relationship between salmonid and galaxiid biomass. Points represent individual streams and survey years for barrier (○), disturbed (Δ) sympatric (●) and trout (×) stream types. $N = 66$.

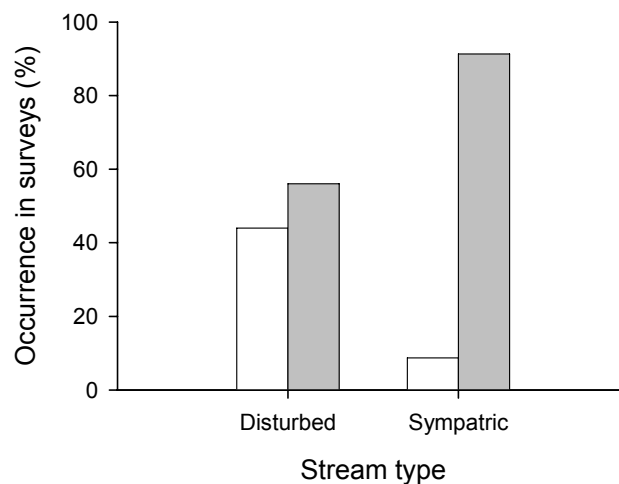


Figure 1.4 Percent of surveys conducted between the summers of 1997/1998 and 2006/2007, in which trout were either absent (open bars) or present (shaded bars).

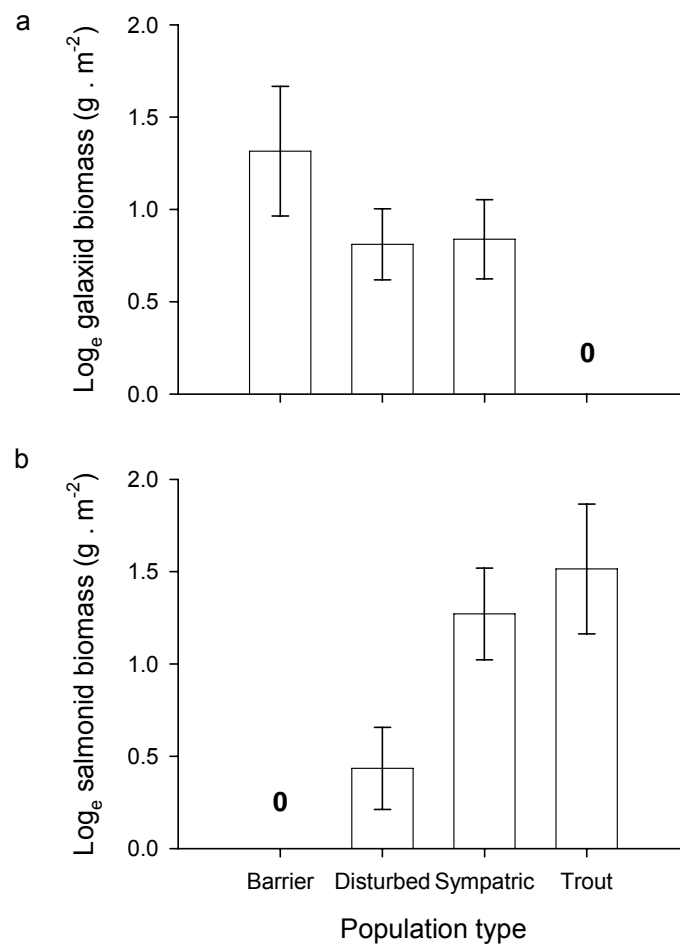


Figure 1.5 Stream type differences in mean (mean \pm 1 SE) galaxiid (a) and salmonid biomass (b) using stream means as replicates. Stream means were calculated using all survey years.

Tukey pairwise comparisons showed that there were, significant differences in salmonid biomass between disturbed and sympatric streams ($q = 3.67$, $P = 0.044$) and near significant differences between sympatric and disturbed streams ($q = 3.54$, $P = 0.053$), but no significant differences between trout and sympatric ($q = 0.79$, $P > 0.8$) streams.

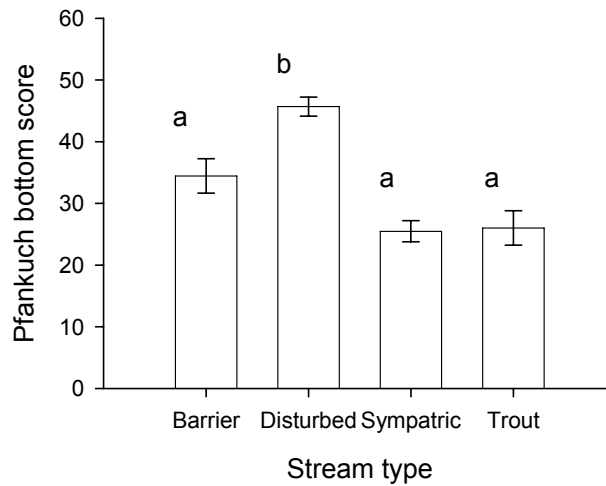


Figure 1.6 Pfankuch bottom score (mean \pm 1 SE) for stream types using streams as replicates. Letters denote groupings based on Tukey pairwise comparisons.

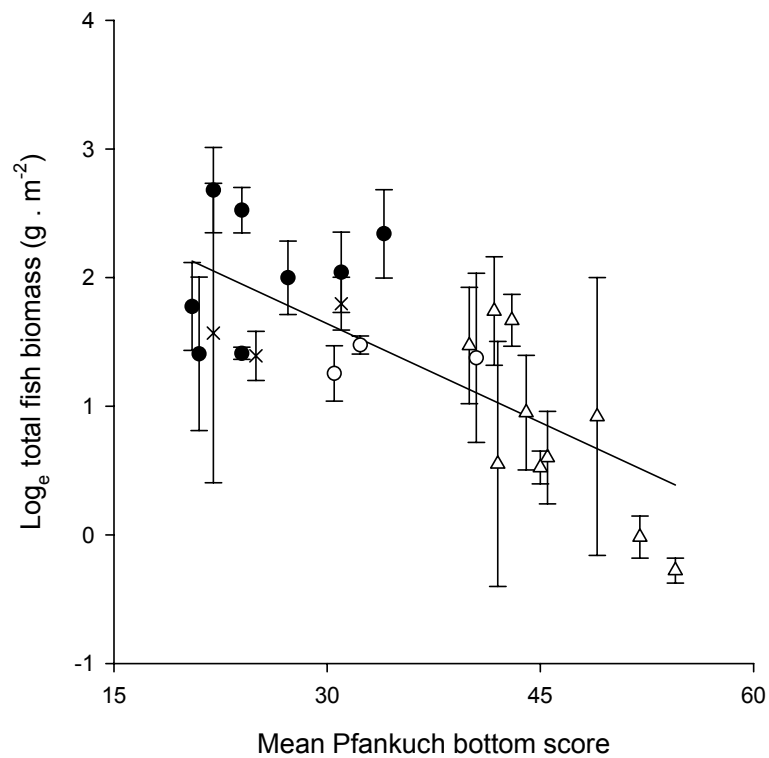


Figure 1.7 Relationship between total fish biomass and Pfankuch bottom score in barrier (○), disturbed (Δ) sympatric (●) and trout (×) stream types. Points represent individual stream means (mean \pm 1 SE) and Pfankuch bottom scores calculated using data from all survey years $R^2 = 0.55$, $N = 24$.

There was a significant relationship between total fish biomass and Pfankuch bottom score ($F_{1, 22} = 26.12$, $P = 0.001$). Mean total fish biomass for all years decreased with increasing Pfankuch bottom score in streams (Figure 1.7).

Antipredator behaviour experiment

Galaxiid total length (mean TL \pm 1 SE) was 106.5 mm \pm 1.7 and 76.4 mm \pm 1.5 for large and small galaxiid treatments, respectively. There were no significant differences in galaxiid total length between treatment combinations (Table 1.2).

Table 1.2 ANOVA summary of treatment effects on total length of fish in experiment.

Source	df	MS	F-ratio	P
Time	1	201.172	0.50	0.481
Type	2	41.629	0.10	0.902
Odour	1	4.831	0.01	0.913
Time x type	2	63.327	0.16	0.854
Time x odour	1	67.623	0.17	0.683
Type x odour	2	85.576	0.21	0.809
Time x type x odour	2	290.460	0.72	0.488
Error	95	401.769		

A MANOVA analysis using both response variables found that there were no significant population type, galaxiid size or interaction effects on time spent in refuge and time spent active in odour absent treatments (Table 1.3). There was a significant time of day effect (Table 1.3) and this was further tested using univariate ANOVA which indicated significant time of day effects on refugia use, but not on activity (Table 1.3; Figure 1.8). The time of day effect on refugia use was independent of population type and galaxiid size as shown by the absence of significant interactions (Table 1.3).

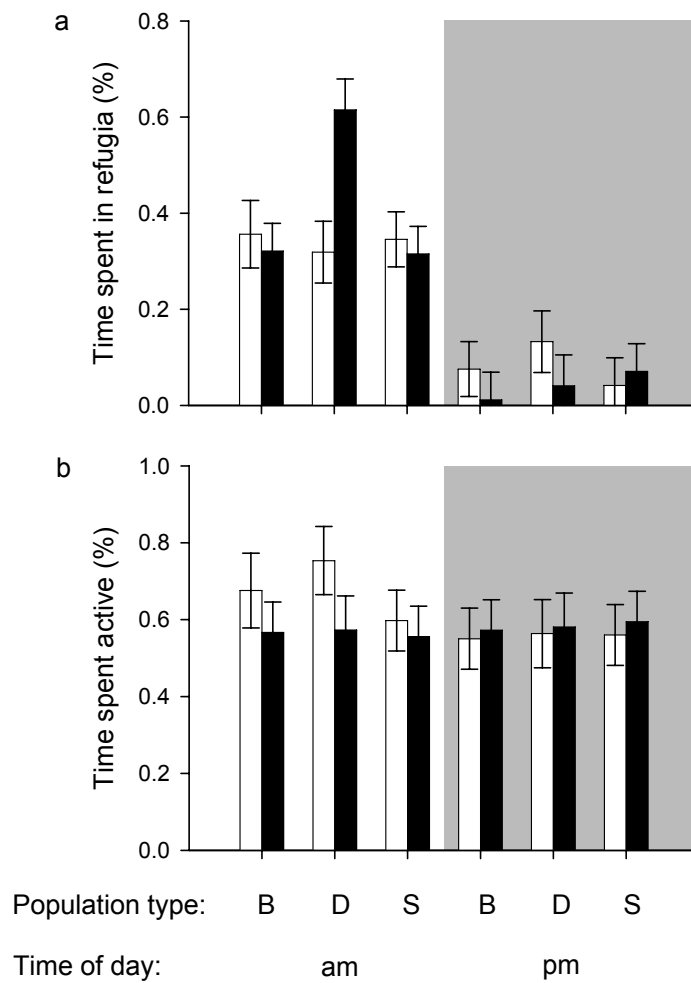


Figure 1.8 Galaxiid refuge use (a) and activity (b) in the absence of trout odour. Percent time spent in refugia and percent time spent active were arcsin squareroot-transformed. Galaxiid size is represented by bar shading (small, open bars; large, filled bars), population type on the x-axis (Barrier, B; Disturbed, D and Sympatric, S) and time of day is indicated by shading in the graph area (day, unshaded; night, shaded). Means and associated error (± 1 SE) are least squares from univariate ANOVA (Table 1.3).

Table 1.3 Nested MANOVA and univariate ANOVA for arcsin squareroot-transformed percent time spent in refugia and percent time spent in refugia in relation to time of day (day vs night; time), source stream type (barrier vs disturbed vs sympatric; type) galaxiid size (small vs large; size) and source streams (stream) for galaxiids used in the experiment. Streams were nested within stream type (stream[type]) and used as the denominator for the F-ratio tests between time of day and stream type. A time of day interaction with streams nested within stream type (time x stream[type]) was used as the denominator in the F-ratio test time of day and stream type. Nesting was the same for both MANOVA and ANOVA analyses. All remaining factors and interactions were tested using the error MS. $\alpha = 0.05$.

Response	Factors	SS	Df	F-ratio	P
MANOVA	Time	0.484*	2, 10	5.33	0.027
	Type	0.939*	4, 20	0.16	0.956
	Time x type	0.942*	4, 20	0.15	0.960
	Size	0.939*	2, 20	0.65	0.533
	Time x size	0.762*	2, 20	3.12	0.066
	Type x size	0.833*	4, 40	0.95	0.443
	Time x type x size	0.701*	4, 40	1.94	0.123
% time spent in refugia	Time	1.336	1	10.95	0.007
	Type	0.080	2	0.33	0.726
	Stream(type)	1.343	11		
	Time x type	0.027	2	0.11	0.897
	Time x stream(type)	1.349	11		
	Size	0.004	1	0.25	0.625
	Time x size	0.047	1	2.87	0.105
	Type x size	0.050	2	1.52	0.242
	Time x type x size	0.120	2	3.66	0.043
	Error	0.346	21		
% time spent active	Time	0.0334	1	0.53	0.482
	Type	0.0149	2	0.12	0.890
	Stream(type)	0.6946	11		
	Time x type	0.0198	2	0.30	0.748
	Time x stream(type)	0.3651	11		
	Size	0.0246	1	0.78	0.387
	Type x size	0.0136	2	0.22	0.807
	Time x size	0.0611	1	1.94	0.178
	Time x type x size	0.0081	2	0.13	0.879
	Error	0.6600	21		

* Wilks' lambda

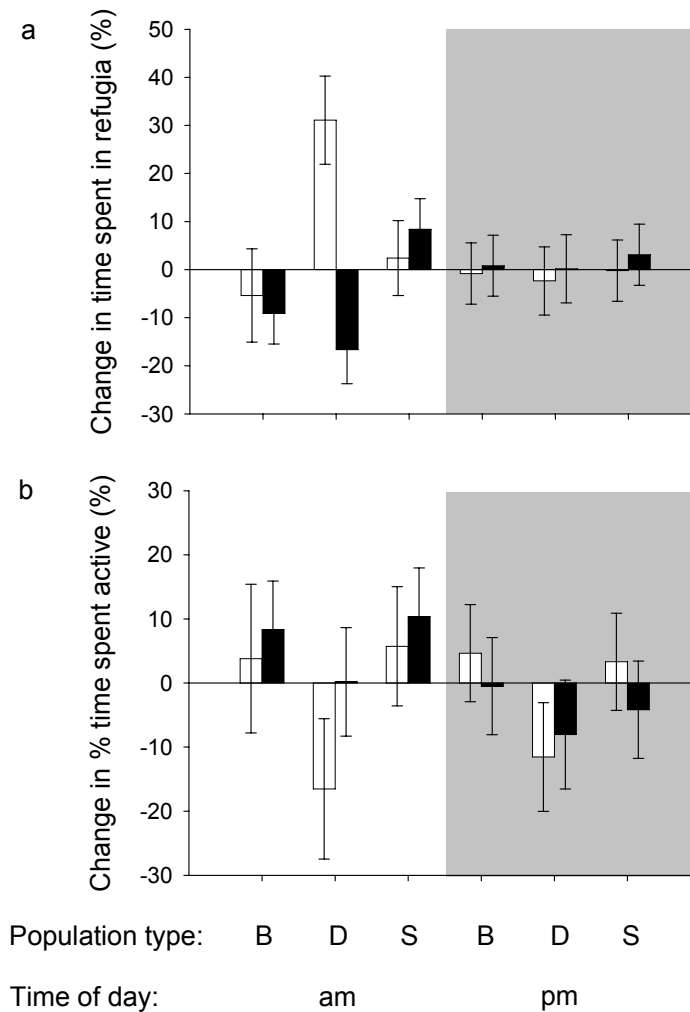


Figure 1.9 Mean changes in galaxiid refuge use (a) and activity (b) in the presence of trout odour. Changes in percent time spent in refugia and percent time spent active were calculated by subtracting odour present values from odour absent values for treatment combinations. Galaxiid size is represented by bar shading (small, open bars; large, filled bars), population type on the x-axis (Barrier, B; Disturbed, D and Sympatric, S) and time of day is indicated by shading in the graph area (day, unshaded; night, shaded). Means and error (mean \pm 1 SE) are least squares from univariate ANOVA (Table 1.4).

Table 1.4 Nested MANOVA and univariate ANOVA for change in time spent in refugia (s.min-1) and percent time spent in refugia in relation to time of day (day vs night; time), source stream type (barrier vs disturbed vs sympatric; type), and galaxiid size (small vs large; size) and source streams (stream) for galaxiids used in the experiment. Changes in each response variable were calculated by subtracting odour absent values from odour present values. Streams were nested within stream type (stream[type]) and used as the denominator for the F-ratio tests between time of day and stream type. A time of day interaction with streams nested within stream type (time x stream[type]) was used as the denominator in the F-ratio test time of day and stream type. Nesting was the same for both MANOVA and ANOVA analyses. All remaining factors and interactions were tested using the error MS. $\alpha = 0.05$.

Response	Factors	df	SS	F - ratio	P
MANOVA	Type	4, 20	0.504*	2.04	0.127
	Time	2, 10	0.917*	0.45	0.649
	Time x type	4, 20	0.878*	0.34	0.850
	Size	2, 17	0.881*	1.14	0.342
	Time x size	2, 17	0.774*	2.48	0.113
	Type x size	4, 34	0.691*	1.73	0.166
	Time x type x size	4, 34	0.706*	1.62	0.192
Change in % time spent in refugia	Time	1	11.60	0.04	0.844
	Type	2	87.04	0.33	0.723
	Stream(type)	11	260.99		
	Time x type	2	85.11	0.30	0.749
	Time x stream(type)	11	287.38		
	Size	1	165.72	2.28	0.148
	Time x size	1	321.55	4.42	0.050
	Type x size	2	275.94	3.80	0.042
	Time x type x size	2	269.79	3.71	0.045
	Error	18	72.69		
Change in % time spent active	Time	1	253.19	0.79	0.394
	Type	2	805.54	4.12	0.046
	Stream(type)	11	195.66		
	Time x type	2	48.37	0.15	0.862
	Time x stream(type)	11	322.35		
	Size	1	89.43	0.31	0.584
	Time x size	1	390.12	1.36	0.259
	Type x size	2	148.01	0.51	0.606
	Time x type x size	2	3.03	0.01	0.990
	Error	18	287.56		

* Wilks' lambda.

The MANOVA analysis found no significant factor or interaction effects in changes in time spent active and refugia use (Table 1.4). Univariate ANOVAs on each response variable found significant population type effects of time spent active (Table 1.4). This was caused by an overall decrease in time spent active in disturbed populations (Figure 1.9), an effect which did not significantly vary between day and night (Table 1.4). Univariate ANOVA of time spent in refugia revealed a significant three-way time of day, population type and galaxiid size interaction (Table 1.4). This was caused by increased diurnal refugia use in small galaxiids from disturbed populations (Figure 1.9). The failure of the MANOVA, however, to detect the effects found in the univariate ANOVA means that the experiment-wise power was insufficient to detect differences in the two response variables between my three factors.

1.4 Discussion

The behavioural responses of prey towards introduced predators or competitors may have a large influence on interactions between introduced and native species. Moreover, past experience with predators can affect the development and effectiveness of antipredator responses. In this study, disturbance regime had a large affect on trout presence and hence galaxiid experience of trout.

The co-occurrence between galaxiids and trout found in this study and others (Cadwallader 1975, Glova & Sagar 1991, Kusabs & Swales 1991, McIntosh 2000) is in contrast to other studies indicating that trout and galaxiids co-occur infrequently (reviewed by Crowl et al. 1992). In New Zealand (McIntosh 2000, Leprieur et al. 2006), and elsewhere (Meffe 1984, Strange et al. 1992, Closs & Lake 1996, Bernardo et al. 2003), the abiotic regulation of introduced fish populations influences the co-occurrence of introduced and native fish species. Most of the above studies (but see Strange et al. 1992) attribute the local extirpation of introduced, but not native fish, following hydrological disturbances to a lack of adaptations to local flow regime in introduced species. Conversely such adaptations appear common in native species (Meffe 1984, Jowett & Richardson 1994, McIntosh 2000), allowing native species to persist following hydrological disturbances.

In the Upper Waimakariri, the presence of trout-free galaxiid populations in small tributaries above trout migration barriers may assist the recolonisation of downstream reaches following hydrological disturbances that remove trout. Recolonisation from within reaches is common in native fish following the removal of introduced species by hydrological disturbances (Matthews 1986, Closs & Lake 1996) and there is evidence for this from studies

of the Upper Waimakariri region (Darragh Woodford, unpublished data). However, in streams with low frequencies of hydrological disturbances where trout proliferate, trout predation probably prevents the establishment of co-occurring populations. Hence, this study still found several stable trout-only sites where galaxiids are excluded. In stable sites where both galaxiids and trout did occur, galaxiid densities were relatively unaffected by co-occurrence with trout. I predicted that antipredator behaviour towards trout may allow the two species to occur in relatively high densities.

In this study I found there were no differences in fixed *G. vulgaris* behaviour associated with either past trout experience or *G. vulgaris* size. However, *G. vulgaris* did show a strong fixed preference for refuge use during the day, independent of past trout experience or fish size. There were no effects of past trout experience or galaxiid size on flexible behavioural changes in *G. vulgaris* behaviour in response to trout odour. Specifically behaviour in *G. vulgaris* from streams known to contain trout did not differ in behavioural response, to trout-naïve *G. vulgaris*. Moreover, *G. vulgaris* from sympatric streams were more similar in behavioural response to trout-naïve *G. vulgaris* than to trout-experienced *G. vulgaris* from disturbed streams.

Galaxiids were expected to have developed antipredator behaviours to trout for several reasons. Such behaviours, could develop either by the evolution of fixed or flexible behavioural responses towards trout, or via learning to associate trout as a predation threat in individual fish. Introduced predators can present a strong selection pressure for the evolution of antipredator responses in native prey populations, despite relatively short coevolutionary histories. As such, the short evolutionary history between galaxiids and trout is not necessarily prohibitive to the development of antipredator responses. In a review of evolved

antipredator responses by Strauss et al. (2006), fifteen of sixteen studies found evolved morphological or behavioural responses in native animal species in response to introduced species, over periods of less than 150 years. Furthermore, over the recent history with introduced predators several New Zealand species, including galaxiids (Edge et al. 1993), have developed antipredator behaviours towards introduced predators (McIntosh & Townsend 1994, Maloney & McLean 1995, Kristensen & Closs 2004). Learning in fishes is common and many fish species can learn to associate novel predators as a threat (Darwish et al. 2005, Ferrari et al. 2006). The evolution of certain antipredator responses can be limited by current physiology (Sih 1987). Galaxiids have well developed olfactory acuity and can use fish odours as migratory cues (Baker & Hicks 2003) and avoidance cues towards native predators (McLean et al. 2007). Although, if the role of olfaction in galaxiids is primarily migratory, then non-migratory species, *G. vulgaris* included, may have lost the ability to detect chemical cues entirely. Antipredator behaviours to chemical cues are common in other fish species and can lead to significant benefits in survival in the presence of predators (Berejikian et al. 1999, Mirza & Chivers 2000, Darwish et al. 2005, Vilhunen 2006). Given the lack of any overt morphological antipredator adaptations in galaxiids, antipredator behaviours, possibly towards predator chemical cues, seem the most likely to develop in galaxiids.

In the absence of physiological barriers to the development of antipredator behaviours in galaxiids and sufficient time frames for such development to occur, what other factors could influence the development of galaxiid antipredator behaviour, or lack thereof, in the galaxiids observed in this study? One possible reason *G. vulgaris* may have lacked antipredator behaviour in this study is because trout predation may be less important in structuring galaxiid populations in the Upper Waimakariri region. The common co-occurrence of galaxiids and trout in this study could suggest that trout predation may be less important

than in other studies where galaxiids and trout distributions seldom overlap and by extension trout predation is high. Although, given the ability of trout to prey on galaxiids of all size classes (Glova 1990, Crowl et al. 1992, McIntosh 2000), it seems likely that trout predation would be an important factor, when contact between galaxiids and trout occurs. Trout predation on galaxiids may be particularly high during periods of stable flow. If trout predation causes local reductions in galaxiid populations, then this may prevent the accumulation of genetic variation in trout-sympatric galaxiid populations. Frequent reductions in population size and gene flow from upstream trout-naïve galaxiid populations may prevent the accumulation of adaptations necessary for the evolution of antipredator responses in downstream galaxiid populations (Strauss et al. 2006).

Alternatively, the lack of difference in behaviour between populations with different levels of trout experience, may reflect a fixed response in galaxiids towards a predation threat unaffected by trout migration barriers. Candidates for such threats include native eel (*Anguilla dieffenbachii*) and avian predators. Eels were found in all stable streams, including sites above trout barriers, but were found in reduced densities or not at all in disturbed streams. Additionally, nocturnal refuge use in galaxiids in this study corresponds to the nocturnal activity of eels. Behaviour likely to increase, not reduce, vulnerability to eel predation. Piscivorous avian predators are typically visual predators. The current predation threat by avian predators streams in the Upper Waimakariri is probably by black shags (*Phalacrocorax carbo*). High post-capture mortality associated with avian predators may represent a strong selection pressure for refuge use during the day (Power 1987, Allouche & Gaudin 2001), possibly explaining the fixed nocturnicity in galaxiids I found in my behavioural experiment. Black shags, not uncommon in streams in the study region (personal observation), are known

to consume galaxiids (Heather & Robertson 1996) and historically (Falla & Stokell 1945) may have been a strong selective pressure for diurnal habitat use in galaxiids.

The relatively small size of trout that co-occur with galaxiids in the Upper Waimakariri may limit the effects of predation on galaxiids and the overall threat that trout may pose as predators. The onset of piscivory in trout is around 130 – 160 mm (Mittelbach & Persson 1998) and predation risk to galaxiids from trout below this size may be low. Specifically, even small galaxiids used in my behaviour experiment (~ 75 mm TL) may be relatively invulnerable to predation by trout < 150 mm FL. With the exception of larger rivers, trout approaching and occasionally exceeding 150 mm FL are rare in sites where trout and galaxiids co-occur in the Upper Waimakariri (McIntosh 2000). Therefore in my behaviour experiment galaxiids may not respond to trout odour because predation in streams where trout and galaxiids co-occur may be low. This does leave open the possibility that juvenile galaxiids vulnerable to predation by trout < 150 mm FL may display antipredator responses towards trout. The use of small trout (~ 120 mm FL) as odour cues may not be as problematic as the overall small size of trout in streams where galaxiids and trout co-occur. Several studies that have found anti-predator behaviour in New Zealand native fish have used predator and prey sizes comparable to this study (Edge et al. 1993, Kristensen & Closs 2004), although perch in the Kristensen and Closs (2004) study may have a larger gape size for given length than trout (Mittelbach & Persson 1998). Furthermore, notwithstanding the known effects of predator diet on antipredator behaviour (Mirza & Chivers 2003a, Vilhunen & Hirvonen 2003), prey responses to chemical cues may be relatively insensitive to predator size (Chivers et al. 2001). Therefore the small size of trout used as sources of odour may not be as important as small trout size in streams where trout and galaxiids co-occur, to the lack of antipredator behaviour found in my behavioural experiment.

Galaxiid antipredator behaviours could have arisen in response to trout via two mechanisms, either by rapid evolution of antipredator behaviour via strong selection for such responses or via learning in individuals. Fish can learn to associate novel predators as threats via simultaneous pairings of conspecific stress- or damage-induced alarm cues with predator cues (Mirza & Chivers 2002, Ferrari et al. 2006). Alarm cues in digested prey can label specific predators as active predators of conspecifics, regardless of predator species. Such responses to specific alarm cues may be more useful against a variety of predators as fish can learn to recognise many predators as a threat (Wisenden 2000).

Given the limited suite of native predators, galaxiids in New Zealand may display innate predator-specific responses to predators, such as responses to odours associated with predators (Vilhunen & Hirvonen 2003). The lack of response to conspecific alarm cues may restrict the ability of galaxiids to learn to recognise novel predators. However, some native New Zealand fish can learn to associate novel predators as threats. Common bullies (*Gobiomorphus cotidianus*) from populations sympatric with a novel predator, perch (*Perca fluviatilis*) show antipredator responses towards perch skin extract (Kristensen & Closs 2004). This response was probably learned via pairings of damage-induced cues with predator odour cues, as common bully exhibited behavioural changes, regardless of past experience to conspecific skin extract (Kristensen & Closs 2004). The presence of epidermal club cells in bullies suggests that bullies may possess such alarm substances (Kristensen & Closs 2004). The ability of bullies, but not to galaxiids to learn to recognise novel predators as a threat, suggests that a lack of alarm cues is not a general attribute of New Zealand fish. In bullies the ability to learn to recognise novel predators may be a pre-adaptation (Irving & Magurran 1997).

The evolutionary significance of such pre-adaptations may be different than current uses. Conspecific cues are also used in kin recognition (Sorensen & Stacey 2004) and may prevent the cannibalism of offspring in nesting fish (Neff 2003). Bullies maintain and defend nests, often containing several developmental stages of offspring and conspecific predation of offspring can be high (Hamilton 1998). Under these circumstances the recognition of offspring would be expected to increase individual fitness and may favour the maintenance of club cells and in bullies the ability to recognise conspecific alarm cues may be related to their nesting habit. A lack of behavioural response in galaxiids in this study may come from an inability to recognise damage-induced alarm cues, possibly related to the absence of pre-adaptations that may facilitate learning to associate novel predators as threats. My experiment however, did not explicitly investigate galaxiid responses to conspecific alarm cues, rather I assumed that galaxiids had either learnt to associate trout as a predation threat in wild populations, or that galaxiids had evolved antipredator behaviours because of strong selection by trout predation. My experiment shows that galaxiids do not display strong antipredator responses to trout odour, but did not test for the presence of alarm cues in galaxiids.

My experiment also assumed that trout odour provides an ecologically relevant cue for assessing predation threat in galaxiids. Most studies investigating antipredator responses are performed in relatively small experimental arenas. Under these conditions, low structural complexity, turbulence and flow have been suggested to overestimate the role of chemical cues in assessing predation threat. Responses to chemical cues may become increasingly redundant as structural complexity and turbulence increases in natural environments, especially in streams (Magurran et al. 1996, Irving & Magurran 1997). However, because

antipredator behaviours are costly (Houston et al. 1993) it is in the best interests of prey to use a variety of cues to assess predation threats.

Visual and chemical cues represent close and distant predation threats, respectively, and may be used in conjunction to provide more accurate assessments of predation threat (Chivers et al. 2001). Both visual and chemical cues can be used interchangeably depending on external factors such as turbidity (Hartman & Abrahams 2000) and time of day (Brown & Magnavacca 2003) and factors internal to fish, such as hunger (Brown & Cowan 2000). Some antipredator behaviours use combinations of both visual and chemical cues. Predator inspection behaviour is often mediated by chemical and visual cues. Odour cues, dependent of predator diet, can influence how prey species visually inspect predators to determine attack motivation (Brown & Godin 1999, Brown et al. 2000, Brown & Dreier 2002). In this case odour cues provide information about whether a predator's diet includes conspecifics, that visual cues alone cannot. Concentrations of chemical cues need not necessarily be large to be useful. The detection of chemical cues can occur at extremely low concentrations in fish (Mirza & Chivers 2003b), and a number of fish detect cues without overt behavioural responses (Brown & Smith 1996, Brown et al. 2004, Foam et al. 2005). In streams even low concentrations of predator odour can provide important information about the presence of predators and prey fish may use both chemical and visual cues to build more accurate assessments of predation threat.

The ecological implications of a lack of response in galaxiids found in this study depends on whether galaxiids cannot detect trout or whether galaxiid antipredator behaviour is dependent on other factors. I have shown that galaxiids from populations sympatric with trout do not show the kind of behaviours usually associated with survival benefits in prey fish,

such as increased refuge use (Mirza & Chivers 2000, Åbjörnsson et al. 2004) and reductions in activity (Berejikian et al. 1999), in response to trout odour. If galaxiids do not respond to trout as a predator then galaxiids may be particularly vulnerable to trout predation, especially given that trout predation on galaxiids may be high. If the inability to associate novel predators as predatory threats is a trait of all galaxiids, then threatened small-bodied galaxiid populations may be particularly vulnerable to introduced predators.

This research suggests that native species cannot be expected to develop antipredator responses to introduced predators, even where predation risk is high and evolutionary history with predators is relatively long. I suspect that antipredator responses in native organisms are either pre-adaptations that allow individuals to learn to associate introduced predators as threats, or that they occur in organisms with large population sizes under strong stabilising selection. If this is the case, then because pre-adaptations evolve for purposes entirely different than antipredator behaviour, the development of antipredator behaviour in response to introduced predators may be relatively unpredictable in large organisms with small population sizes. In this study I did not specifically investigate the existence of conspecific alarm cues in galaxiids. If galaxiids do lack conspecific alarm cues then this may seriously impair their ability to learn to recognise introduced predators as a threat. The consequences for such predator-naiveté may be important if it is a characteristic of all galaxiids. Further research into the ability of galaxiids, of lack thereof, to recognise introduced predators as threats may resolve some important questions about galaxiid declines and the role of trout predation in these declines.

Chapter Two: Trout effects on galaxiid growth rate

2.1 Introduction

Introduced organisms compete rigorously for resources (Moyle & Light 1996), causing reductions in food availability which may have negative consequences for growth in native species (Brett & Groves 1979, Mittelbach 1983). Reductions in growth may have long term consequences on fecundity and survival in native organisms.

Large body size, flexible life history, omnivorous diet and territorial aggression in salmonids makes them a particularly successful invasive group (Townsend 1996). Salmoniid invasion is often assisted by humans, typically for sport fisheries, however once established salmonids often compete with native fish fauna and can have detrimental effects on native fauna and even ecosystem function (Simon & Townsend 2003). Salmonids are known to be piscivorous (Mittelbach & Persson 1998) and predation by introduced piscivores can directly reduce native fish abundance (White & Harvey 2001, Museth et al. 2003). Space competition, is substituted for food competition in salmonids, as suitable foraging positions also increase food availability (Chapman 1966). Trout often compete aggressively for preferred foraging positions excluding native drift-feeding fish (Fausch & White 1981, Wang & White 1994). Exclusion from foraging positions may have detrimental effects on foraging efficiency in native fish, particularly where their diet overlaps with that of salmonids.

When faced with piscivorous predators or aggressive competitors, native fish may display a variety of antipredator responses (Dill 1983). This is the case in many native fish

responses to salmonids (Chivers et al. 2001), and other introduced piscivores (Werner et al. 1983) and can affect foraging efficiency. Competition for food and space with salmonids along with antipredator behaviour in native fish, all serve to deprive native fish of resources. Reductions in available resources and foraging efficiency associated with introduced fish can have negative long-term effects such as reductions in growth in native fish populations (Werner et al. 1983, Mills et al. 2004, McHugh & Budy 2006, Zimmerman & Vondracek 2006).

The previous chapter introduced the negative effects of introduced trout on New Zealand's native galaxiid fauna via predation. In addition to predatory effects, trout also affect galaxiids via competition for food and space. Some galaxiids are drift-feeding (Cadwallader 1975, Eldon 1975, Glova & Sagar 1989) and their diets (Cadwallader 1975, Glova & Sagar 1991) and habitat preferences (Cadwallader 1975, Glova et al. 1992) have been shown to overlap considerably with trout. Studies on space competition have found that in the presence of trout, galaxiids are excluded from preferred foraging positions in both artificial channels (McIntosh et al. 1992) and natural streams (McIntosh et al. 1994). Galaxiid antipredator responses to trout presence can negatively affect feeding behaviour and foraging success (Edge et al. 1993). The overall effect of trout competition on galaxiids is likely to be a reduction in foraging efficiency in galaxiids, which may be a tradeoff for reduced confrontations with introduced trout (Glova 1989, Edge et al. 1993).. Given the known effects of trout on galaxiid foraging reductions, several authors have suggested that trout may have negative effects on galaxiid growth (Crowl et al. 1992, McDowall 2003, Simon & Townsend 2003). Although other studies have found that trout can affect galaxiid behaviour, if galaxiids avoid confrontations with trout their growth may be largely unaffected. In the previous chapter I found that galaxiid behaviour was unaffected by the presence of trout odour. Thus,

whether the changes in galaxiid behaviour resulting from confrontations with trout mentioned above are sufficient to affect galaxiid growth remains unknown. Moreover, how the presence of conspecifics and intraspecific competition might affect growth relative to the influence of trout is also unknown.

The galaxiids used in this study are Canterbury galaxias (*Galaxias vulgaris*) and alpine galaxias (*G. paucispondylus*), both non-migratory galaxiids found in upland braided rivers throughout the East coast of the South Island and frequently co-occur with brown (*S. trutta*) and rainbow trout (*O. mykiss*). The aims of this chapter were to test 1) how long-term galaxiid growth rate differed across a gradient of trout biomass and presence, and 2) to determine if there were any negative effects of trout on short-term galaxiid growth rate. Based on the known negative effects of confrontation with trout on galaxiid foraging efficiency, I hypothesised that either, 1) galaxiid growth rate would decrease with increases in trout abundance, or 2) galaxiids with a history of trout co-occurrence may sacrifice reduced reproductive growth for increased somatic growth as a developmental response to escape size-dependent trout predation.

2.2 Methods

I examined galaxiid growth rates, in both wild populations and in experimental reaches to test how variable trout presence and biomass affected galaxiid growth rate. Differences in relative growth rate in wild populations were determined using otoliths collected during a survey of sites in the 2005/06 summer, across a disturbance gradient of sites and trout presence (see previous chapter). An experiment in which galaxiids were manipulated in natural stream enclosures with trout of varying size was used to determine how trout presence affected galaxiid growth over relatively short periods in natural conditions.

Study region

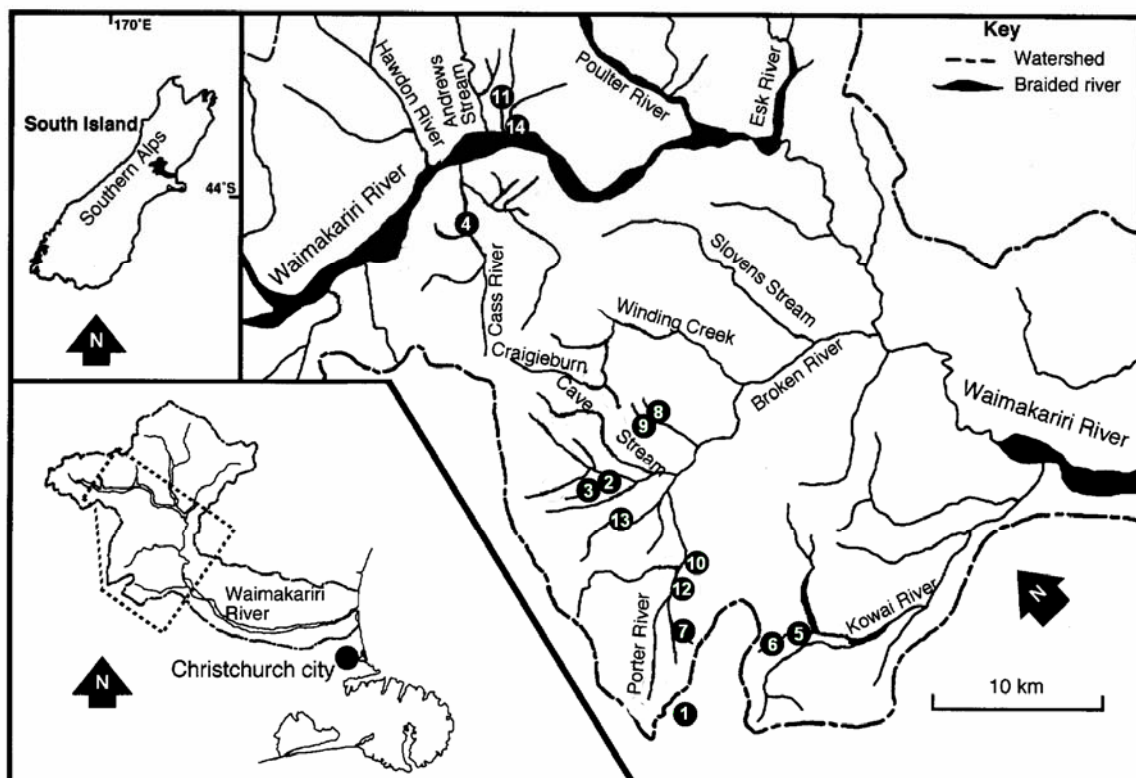


Figure 2.0 Distribution of galaxiid collection sites for long-term growth rate survey in the Upper Waimakariri basin. Filled circles represent collections sites and numbers correspond to site characteristics in Table 2.0.

Galaxiids were collected from fourteen streams (Figure 2.0; Table 2.0). All but one of the study sites, the Acheron River site (Figure 2.0, site No. 1), were located in the Upper Waimakariri basin (see Chapter One).

Table 2.0 Location, Pfankuch bottom score, elevation and stream type classification of collection streams for galaxiid growth survey. Letters in the *Galaxias* species column represent galaxiid species (Gp; *G. paucispondylus* and Gv; *G. vulgaris*). Stream types represent presence of trout and relative bed stability at sites (barrier = no trout; disturbed = trout present, Pfankuch score > 30; sympatric = trout present, Pfankuch bottom score < 30). Pfankuch bottom scores were derived during 2005 by a single observer (see text).

Stream name	Map location (NZMG)	No. in Fig. 1.	Pfankuch bottom score	Elevation (m a.s.l.)	<i>Galaxias</i> species present	Stream type
Acheron River	K39 019 639	1	23	820	Gp	Sympatric
Bradley Stream (lower)	K34 054 788	2	22	740	Gv	Sympatric
Bradley Stream (upper)	K34 048 788	3	22	780	Gv	Barrier
Cass River	K34 079 970	4	44	560	Gp + Gv	Disturbed
Coach Stream (lower)	L35 102 655	5	24	620	Gv	Sympatric
Coach Stream (upper)	K35 092 659	6	18	660	Gv	Barrier
Dry Stream (lower)	K34 053 714	7	43	750	Gp + Gv	Disturbed
Flock Hill Stream	K34 086 805	8	34	720	Gp + Gv	Disturbed
Flock Hill tributary	K34 083 807	9	40	740	Gv	Barrier
Ghost Creek	K34 077 735	10	49	710	Gp + Gv	Disturbed
Lower Farm Stream	L34 128 998	11	35	550	Gv	Barrier
Roadmarker Spring *	K34 063 727	12	23	700	Gv	Sympatric
Thomas River (lower)	K34 049 772	13	45	740	Gv	Disturbed
Waimak Spring *	L34 133 982	14	24	500	Gv	Sympatric

Long-term galaxiid growth rate

Differences in lifetime galaxiid growth rate associated with varying trout biomass and presence in streams (previous chapter) were estimated using differences in the relationship between otolith weight and fish total length. As in the previous chapter, individual sites were classified according to the mechanism determining trout presence or absence. Trout were absent from sites containing galaxiids only ('barrier' type sites) by virtue of downstream trout

migration barriers (see Chapter One). Remaining stream types, ‘disturbed’ and ‘sympatric’, had past records of trout presence and lacked any trout migration barriers. Disturbed and sympatric sites were separated according to Pfankuch bottom score (see Chapter One). Sites with a total Pfankuch bottom score > 30 were classified as disturbed sites and sites < 30 as sympatric sites. Differences in mean bottom score were tested using an ANOVA with individual streams as replicates. Pfankuch bottom score was normally distributed and was not transformed. Quantitative estimates of galaxiid (*G. paucispondylus* and *G. vulgaris*) and trout biomass (*S. trutta* and *O. mykiss*) collected during an October 2005 field survey (see Chapter One) were used to test for differences in biomass between stream types. Trout and galaxiid biomass were log-transformed ($\log_e [x + 1]$) to normalise distributions. Differences in trout biomass between disturbed and sympatric stream types were tested using a two-sample t-test. Differences in galaxiid biomass between barrier, disturbed and sympatric stream types were tested using an ANOVA.

Using otolith weights to estimate lifetime galaxiid growth rates depends on the relationship between otolith weight and fish length. Calcium deposition on the otolith surface occurs throughout the life of a fish (Francis & Campana 2004). Fish length and otolith size are positively correlated among fish of the same age, or conversely, fish age and otolith weight are positively correlated among fish of the same length (Francis & Campana 2004). If fish length and, either age or otolith size are known, then growth rate can be estimated using the Templeman-Squire relationship (Templeman & Squires 1956, Francis & Campana 2004), whereby, for a given fish length, older fish tend to have larger otoliths. Otolith size can be determined using length, width and weight of otoliths. I used otolith weight to measure otolith size because in older fish, growth in otolith length and width can become decoupled from fish

age (Secor & Dean 1989). Otolith weight, however, does not become decoupled from fish age as otolith thickness continues to increase with fish age (Boehlert 1984).

Galaxiids were collected during October 2005 using a backpack-mounted electric-fishing machine (Kainga EFM300, NIWA Instrument Systems) as part of a quantitative fish survey from four streams for each of the three stream types described above (Table 2.0, Figure 2.0). Captured fish were anaesthetised using 2-phenoxyethanol and total length was measured to the nearest mm using a measuring board and weighed to the nearest 0.1 g using an Ohaus Scout balance (Ohaus Corporation). Upon dissection the sex and presence or absence of body cavity parasites, predominantly on the liver, were noted. Otoliths were extracted in the laboratory by digesting fish heads in a 2.2 % solution of pancreatin enzyme buffered with KOH. Sagittae otoliths were then removed from the slurry under a dissecting microscope, rinsed using distilled water and dried in a dessicator for 24 hours. Otolith pairs were then weighed to the nearest 0.001 mg using a microbalance (Model UMX2, Mettler-Toledo). Stream type differences in *G. vulgaris* and *G. paucispondylus* otolith weight were tested using an ANCOVA model. Otolith weight and galaxiid total length were log-transformed ($\log_e [x]$) to normalise distributions, and an ANCOVA model using population type (barrier, disturbed and sympatric), galaxiid sex, parasite presence and source stream as factors, and galaxiid total length as a covariate, was used to test for differences in otolith weight. A backwards stepwise regression using all factors was used to remove non-significant effects from the final model. Only mature fish, (those with developed gonads), were included in analysis of sex effects. *G. vulgaris* < 65 mm and *G. paucispondylus* < 70 mm in natural total length were considered age 0 + fish (Cadwallader 1978, Bonnett 1990) and excluded from analysis on the basis that they had not experienced a full growing season.

Galaxiid condition

I assessed the condition of each fish captured, using the relative weight index, W_r :

$$W_r = W / W_s \times 100$$

where W is the observed mass of an individual fish at capture and W_s is the mass predicted using a fishes' total length and a standard length-weight relationship for the species. Using all fish captured during the 2005 survey, standard length equations (W_s) for *G. vulgaris* (equation 2.1) and *G. paucispondylus* (equation 2.2) were derived from the linear relationship between \log_e weight and \log_e total length based on 486 *G. vulgaris* (TL range = 39 – 126 mm) and 148 *G. paucispondylus* (TL range = 49 – 96 mm).

Equation 2.0 $W_s = 3.23 \times 10^{-6} \cdot TL^{3.190}$

Equation 2.1 $W_s = 1.64 \times 10^{-5} \cdot TL^{2.733}$

Mean relative weight was normally distributed and was not transformed. Differences in mean relative weight (W_r) were tested using an ANOVA with individual streams as replicates.

Short-term galaxiid growth rate experiment

A substitutive experiment whereby trout and galaxiid densities were manipulated in natural stream reaches was used to determine the relative effects of trout on short-term galaxiid growth rate. The experiment was set up during mid January 2007 in Binser Stream (NZMG: L34 126 996), a second order tributary of the Waimakariri River. Binser Stream originates in a forested catchment and the fish fauna is dominated by brown trout reaching

sizes > 170 mm, with extremely low densities of *G. vulgaris* (S. Howard, personal observation). In the experimental area the stream is low gradient and flows through low-intensity pasture grazed mainly by sheep. Riparian shrub cover was intermittent and dominated by matagouri (*Discaria tomatou*). Experimental reaches of twenty square metres were selected to contain pool, riffle and undercut bank habitat and were delineated using mesh fences perpendicular to the stream to prevent fish passage. Fences were constructed using three steel 'Waratah[®]' fence posts driven into the stream bed and stream margins were excavated 20-30 cm to provide protection against rising stream level and fish passage. A coarse (2 cm mesh) plastic backing netting was used to provide strength to the fence and a fine polyester netting (4 mm mesh) (Silver International Corporation, Taiwan purchased from T & L Netmaking, Victoria, Australia) was used to prevent fish passage while still allowing most invertebrate prey items to pass through. Netting was attached to waratahs and a 30 cm 'skirt' was folded downstream and excavated ~ 10 cm into the stream bed. Excavated areas were filled using boulders (~15 cm diameter) and fine gravel. Following fence construction, trout were removed using 5 – 6 downstream passes with a backpack-mounted electrofishing machine (described above) until no trout were captured on the final pass. There were two galaxiid only treatments and one trout + galaxiid treatment in each of five blocks arranged downstream. Treatments were designed so that the effects of trout could be separated from the effects of increased total fish biomass. Two galaxiid-only treatments called galaxiid low density (GLD) and galaxiid high density (GHD), respectively, were used. The GLD treatment was stocked with six, and the GHD treatment with twelve, individuals of each of the galaxiid species *G. vulgaris* and *G. paucispondylus* to produce final densities of 0.3 fish . m⁻² and 0.6 fish . m⁻², respectively. A third treatment called small trout (ST), tested the effects of added trout biomass on galaxiid growth. The ST treatment was stocked with the same density of galaxiids as the GLD treatment. Additionally, within each block for the ST treatment the

deficit in galaxiid biomass between GHD and GLD treatments was made up with small brown trout *S. trutta* (FL range = 85 – 100 mm; mean FL = 91.6 mm), making the total fish biomass for GHD and ST treatments equal to within 1 gram.

G. vulgaris used in the experiment were sourced from Waimakariri Spring (NZMG: L34 129 985) a low gradient spring-fed stream with a stable flow regime. The fish fauna consists of high densities of both *G. vulgaris* and longfinned eels and occasionally has low densities of medium sized trout (~ 150 mm) that probably swim upstream from the main stem of the Waimakariri River. *G. paucispondylus* were from Lower Farm Stream (NZMG: L34 126 996) an intermediate gradient stream originating in beech forest dominated by high densities of *G. paucispondylus* and very low densities of *G. vulgaris*. Surface flow in Lower Farm Stream is intermittent which, along with a cutting at its confluence with the Waimakariri River, has until recently (December 2006) prevented the upstream migration of trout. Both source streams were within 1 km of the experiment site. Brown trout used were either from Binser Stream or from Peacock Stream (NZMG: L33 117 008). All fish were captured from source populations using a backpack electric fishing machine (described above) and were allowed to recover and checked for injury before use in the experiment.

Prior to stocking all fish were tagged by injecting a non-toxic, water-resistant acrylic paint (Chromacryl © Student Acrylic, Cool Red, Chroma Australia Pty. Ltd) under the skin at three out of ten possible positions using a 25 gauge hypodermic needle (Terumo Corporation). The system used was similar to that of Dunn (2003) and allowed a total of 15 fish to be identified in each reach with separate tags in one of four positions to represent treatments. The total length of all galaxiids and fork length of trout were measured to the nearest 0.5 mm using a measuring board with 1 mm increments. Galaxiids were weighed to the nearest 0.001

g using an electronic balance (Model FX-320, A&D Company, Ltd.) and trout were weighed to the nearest 0.1 g using an electronic balance (Model Scout, Ohaus Corporation). Galaxiids were stocked in reaches between 17 and 19 January and trout were added to reaches between 22 and 23 January. During the experiment fences were regularly cleared of debris and every 2 – 3 days. The experiment ran for 20 full days and all fish were recovered from reaches, using the same methods as for removing trout (see above), between 13 and 14 February. All fish captured at the end of the experiment were then weighed, measured and released in source streams. The growth index used in this experiment was instantaneous (specific) growth rate (Ricker 1979), calculated using the equation:

$$G_w = [(ln W_{final} - ln W_{initial}) / t] \cdot 100$$

where G_w is the specific growth rate of individual fish each day, W_{final} and $W_{initial}$ are the mass of individual fish at the end and start of the experiment and t is the elapsed time in days.

Due to some movement of galaxiids between reaches and variable trout removal success, *post-hoc* tests were performed based on reclassification of reaches using maximum trout size and were classified as ‘medium’ (trout FL range: 95.5 – 111.0 mm; mean = 102.0 mm), ‘small’ (trout FL range = 48 – 56 mm; mean = 52.6 mm) and ‘no trout’ treatments, subject to three main assumptions: 1) galaxiids that were released into and recovered from the same treatment reach, had remained in the treatment for the duration of the experiment, 2) due to their larger size and poor burrowing ability, trout were unable to move between treatment reaches, and 3) all immigrant galaxiids moved early on in the experiment and interacted with resident populations throughout. Growth rates were calculated from tagged fish re-captured in the same reach they were released into. The total reach biomass of both galaxiids and trout were calculated using the sum of the weights of all fish captured, both initially stocked fish and immigrant fish from other reaches, at the end of the

experiment. Galaxiid, trout and total biomass were log-transformed ($\log_e [x + 1]$) to normalise distributions. Instantaneous growth rate was normally distributed and was not transformed. Differences in mean trout size and final trout biomass between small and medium trout treatments were tested using a t-test assuming equal variances. Differences in final galaxiid biomass between all treatments were tested using an ANOVA. The effects of trout size on mean galaxiid instantaneous growth rate for individual reaches were tested using a GLM with treatment and block factors and total fish biomass as a covariate.

2.3 Results

Stream characteristics

There was a significant difference in Pfankuch bottom score ($F_{2, 11} = 12.56$, $P = 0.001$; Figure 2.1a) but not trout ($t = 1.67$ $df = 5$ $P = 0.133$; Figure 2.1b) and galaxiid ($F_{2, 11} = 0.48$, $P > 0.6$; Figure 2.1c) biomass between the three stream types used.

Long-term galaxiid growth rate

Of the 66 *Galaxias vulgaris* otolith pairs recovered from sacrificed fish, ten *G. vulgaris* pairs were excluded from analysis as they were from fish < 65 mm TL. Otolith pairs were collected from 3-6 fish for each stream representing three barrier (14 otolith pairs), five disturbed (23 pairs) and four sympatric (19 otolith pairs) type streams. During processing single otoliths were lost from five otolith pairs. In these cases the weight of the remaining otolith was doubled for use in the analysis (Templeman & Squires 1956). One barrier type stream, Flock Hill Stream main stem, was reclassified as a disturbed site following the discovery of a small (90 mm) trout. Only 23 *G. paucispondylus* otolith pairs were collected, of these, seven pairs were from fish < 70 mm TL and excluded from analysis. Only 16 otolith pairs from four stream types were available for analysis and because streams were used as replicates, this was insufficient to test stream type effects.

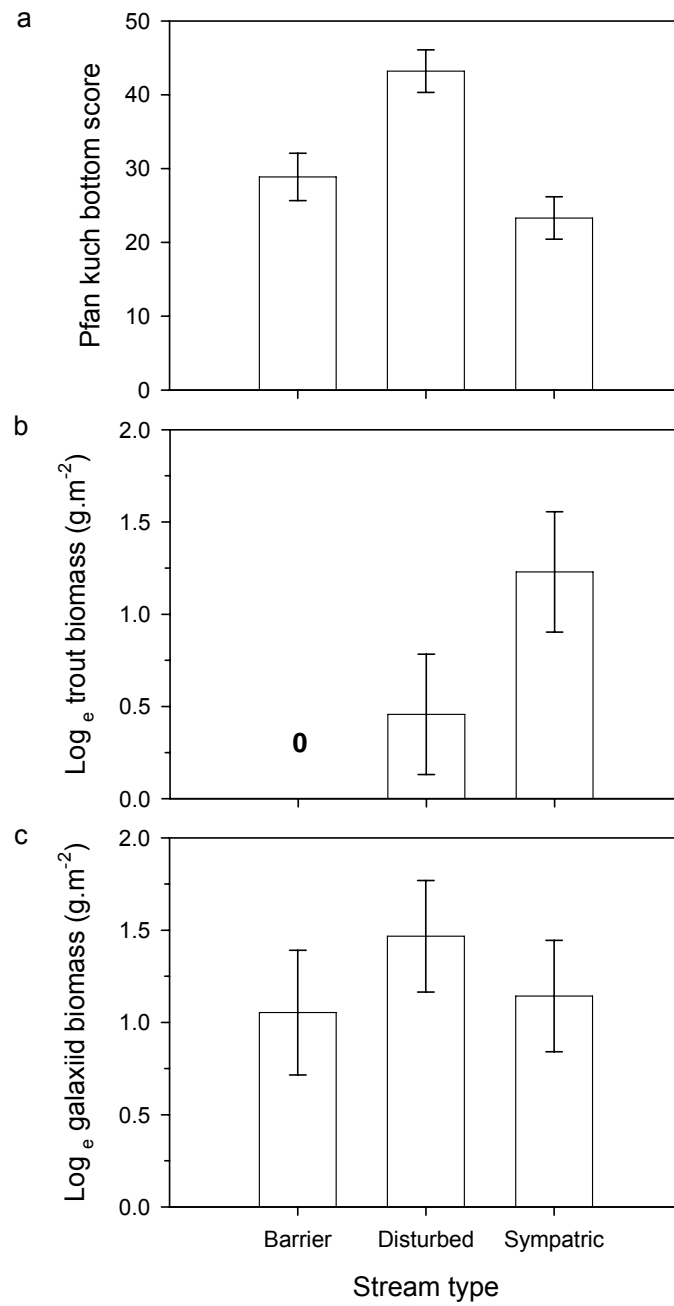


Figure 2.1 Mean (mean \pm 1 SE) Pfankuch bottom score (a) \log_e -transformed trout biomass (b) and galaxiid biomass (c) for each population type using individual streams as replicates.

The effects of parasite presence ($F_{1,30} = 0.04, P > 0.8$), individual streams ($F_{7,35} = 1.15, P = 0.357$) and galaxiid sex ($F_{2,42} = 1.64, P = 0.206$) on *G. vulgaris* growth rate were not significant and were successively excluded from the final model following a backwards stepwise regression. The final model included stream type as a factor and fish total length as a covariate. There was a significant effect of both source stream type ($F_{2,52} = 6.62; P = 0.002$) and the covariate, fish total length ($F_{1,52} = 789.76; P < 0.001$) on otolith weight (Figure 2.2).

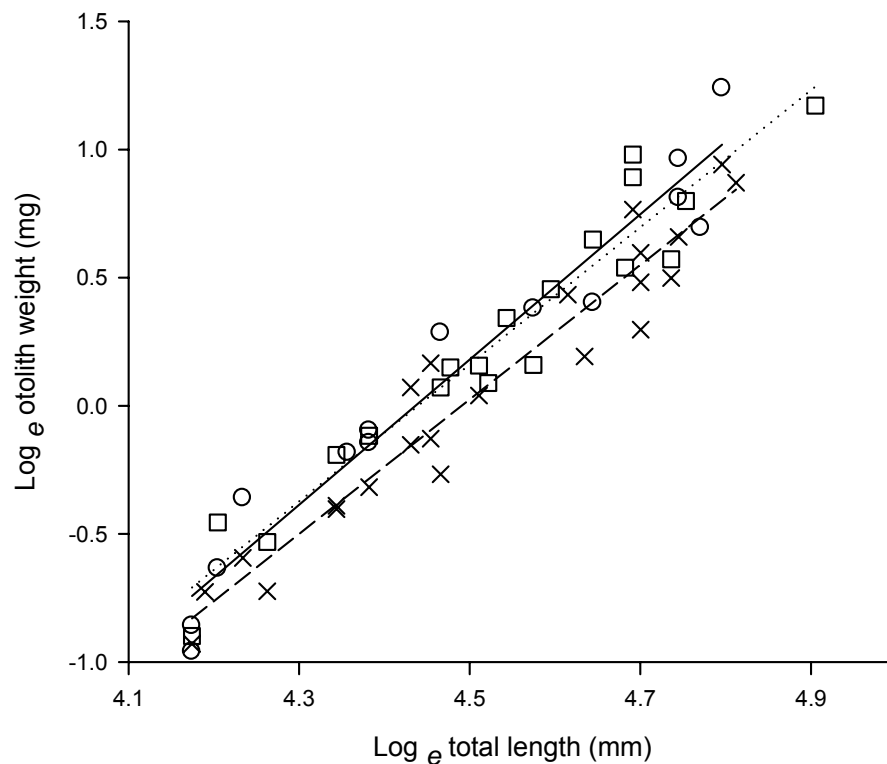


Figure 2.2 Source population effects on relationship of \ln otolith weight (mg) and \ln total length (mm). Each point represents an individual fish and lines are best fit regressions for fish from either barrier (— O —), disturbed (- - x - -) or sympatric (•••□•••) population types.

A homogeneity of slopes test confirmed there was no interaction between total length and source population ($F_{2,50} = 0.423, P = 0.657$). This allowed Tukey pairwise comparison

tests to be performed to evaluate differences in mean otolith weight among source population types using least square means and error MS from the ANCOVA model (Figure 2.3). Least square means are determined by holding the covariate effect constant allowing comparisons between fixed factors. The least-square means indicated there was a significant difference in otolith weight between disturbed and both barrier ($q_{52,3} = 4.38$; $P < 0.01$) and sympatric ($q_{52,3} = 4.264$; $P < 0.025$) populations (Figure 2.3), but no significant difference between barrier and sympatric populations ($q_{52,3} = 0.47$; $P > 0.50$; Figure 2.3). When the effects of total length were held constant *G. vulgaris* from disturbed populations had lighter otoliths than fish from either barrier or sympatric populations (Figure 2.3), suggesting that galaxiids from disturbed populations have higher growth rates.

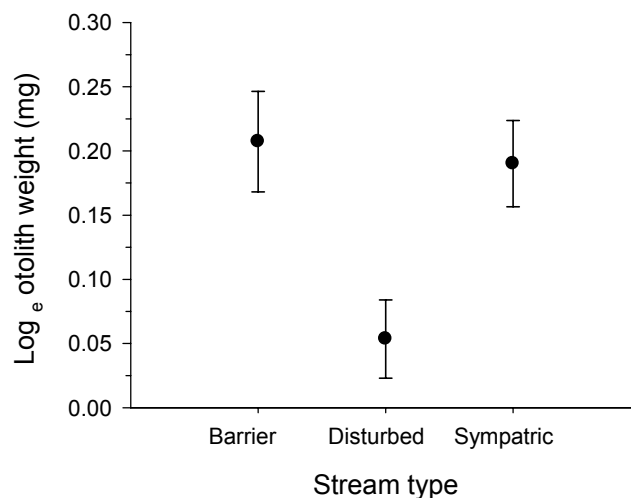


Figure 2.3 Population type effects on otolith weight standardised for fish length from barrier, disturbed and sympatric streams, using streams as replicates. Means (± 1 SE) were calculated from the least square means from ANCOVA using population type as a factor and fish total length as a covariate.

Galaxiid condition

There was no significant effect of stream type on mean relative weight (W_r) of *G. vulgaris* ($F_{2, 10} = 0.76$, $P = 0.490$). There was insufficient replication to test population type effects on *G. paucispondylus*, with barrier and sympatric sites each having only a single replicate. *G. paucispondylus* at all sites had similar mean relative weight (range: 97.6 % – 105.5 %).

Short-term galaxiid growth rate experiment

The reach manipulation experiment ran from 23 January to 14 February 2007. Recaptures were higher for *G. vulgaris* than for *G. paucispondylus* (Table 2.1), probably due to the smaller size and thin body shape of the latter allowing greater movement between fences. Only mean instantaneous growth rate calculated from *G. vulgaris* was tested as insufficient *G. paucispondylus* were recovered from experimental reaches (Table 2.1). A single *G. vulgaris* was excluded from analysis on the basis of tail discolouration combined with negligible growth, indicating a spinal injury probably sustained during collection.

Table 2.1 Total number of reaches and number of galaxiids released and recaptured from trout size treatments.

Species	Trout size	Number of reaches	Captured (total no.)	Released (total no.)	Recaptured (%)
<i>Galaxias vulgaris</i>	No trout	2	4	11	36.4
	Small	3	16	30	53.3
	Medium	6	11	42	26.2
<i>Galaxias paucispondylus</i>	No trout	1	1	13	7.7
	Small	3	5	30	16.7
	Medium	4	9	42	21.4

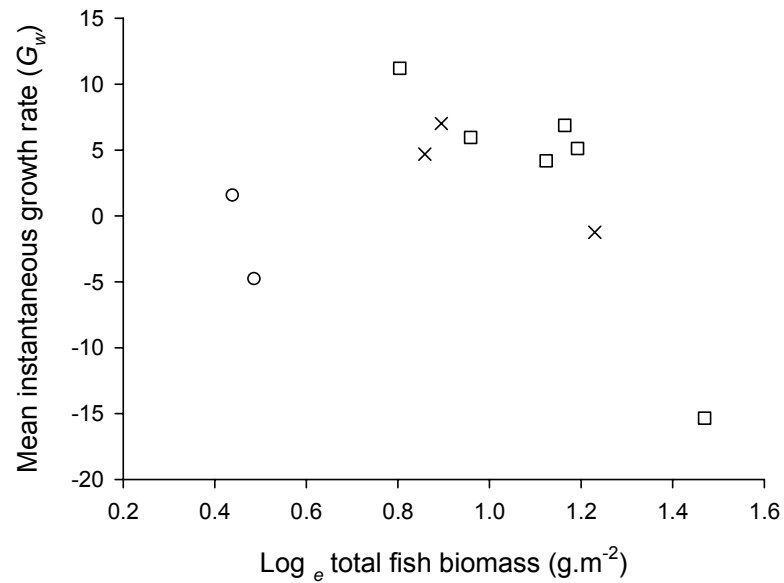


Figure 2.4 Mean instantaneous growth rate of *G. vulgaris* in relation to log-final fish biomass in reaches without trout (O), with small trout (\square) and with medium trout (x). Points represent standardised mean growth rates for reaches following removal of block effects (see text).

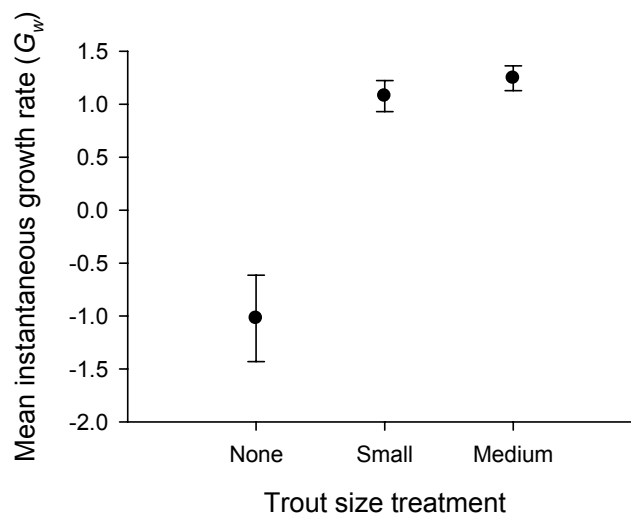


Figure 2.5 Trout size effects on instantaneous growth rate (LS mean \pm 1 SE) standardised for block and total biomass. Means and standard errors used are least mean squares from a GLM using treatment and block as a factor and log-total fish biomass as a covariate.

There was a significant difference in trout size (mean FL \pm 1 SE) between small, 48 ± 0.2 mm, trout and medium, 79 ± 2.7 mm, trout treatments ($t = 4.52$, $df = 5$, $P = 0.006$). There was a significant difference in final trout biomass ($t = 4.56$, $df = 5$, $P = 0.006$) but not final galaxiid biomass ($F_{2,8} = 2.83$, $P = 0.11$) between trout-size treatments. There was a significant effect of block ($F_{3,4} = 13.20$, $P = 0.015$), trout size ($F_{2,4} = 10.49$, $P = 0.026$) and total fish biomass ($F_{1,4} = 23.86$, $P = 0.008$) on mean instantaneous growth rate in *G. vulgaris*. A homogeneity of slopes test confirmed there was no significant interaction between either treatment ($F_{2,5} = 0.722$, $P > 0.5$) or block ($F_{3,6} = 0.43$, $P > 0.60$) with total biomass.

The effects of trout size and total fish biomass on growth rate varied among blocks. Residual deviations around block means (standardised using block standard deviations) were calculated for individual reaches to separate block effects from further analysis. Following the removal of block effects there was a negative relationship between final fish biomass and galaxiid growth rate in reaches with small and medium sized trout (Figure 2.4). *G. vulgaris* growth rate in reaches without trout, however, did not conform to the negative relationship with total fish biomass found in trout treatments (Figure 2.4). There was no difference in growth rate between reaches with small and medium sized trout (Figure 2.5). The significant treatment effect was, surprisingly, driven by reduced growth in treatments lacking trout where galaxiid growth was slower (Figure 2.5).

2.4. Discussion

It has been suggested by a variety of authors that reduced foraging efficiency in galaxiids via food competition (McDowall 2003), space competition (McIntosh et al. 1992) and behavioural changes (Simon & Townsend 2003) when in the presence of trout may ultimately reduce growth rates in native galaxiids. In New Zealand a number of studies have shown that trout can affect galaxiid foraging efficiency via changes in habitat use and behaviour (McIntosh et al. 1992, Edge et al. 1993). Also consumption of invertebrate production by trout can be high in New Zealand streams (Flecker & Townsend 1994, Huryn 1996, 1998), leading to suggestions that galaxiids may be severely food limited (McDowall 2003). Additionally, diet overlap between trout and galaxiids is well documented (Cadwallader 1975, Glova & Sagar 1991, Glova et al. 1992) suggesting that galaxiids and trout may compete for food. However, this is the first time an attempt has been made to quantify the presumably negative effects of trout on galaxiid growth.

In this study, using an index of fish growth, I found that galaxiid growth rate was higher in disturbed streams, and that among streams with similar disturbance regimes, there were no differences in growth rate between streams with and without trout. In my short-term manipulation experiment I found that galaxiids in treatments without trout grew more slowly than in treatments containing both galaxiids and trout. This pattern is opposite to studies in other parts of the world indicating that native fish sympatric with introduced trout suffer reduced growth rates (McHugh & Budy 2006, Zimmerman & Vondracek 2006). The differences in growth rate between disturbed and stable trout-sympatric galaxiid populations in this study, are unlikely to be explained by the negative effects of food and space competition with trout predicted in previous studies. Increased galaxiid growth in disturbed

streams is consistent with the infrequent presence and reduced abundance of trout in disturbed populations found in Chapter One. However the effects of trout presence cannot explain 1) the differences in growth rates observed between trout-allopatric galaxiid populations and disturbed trout-sympatric populations, 2) the lack of differences in growth between trout-sympatric and trout-allopatric galaxiid populations, nor 3) the reduced growth rates in trout-free treatments compared to trout-present treatments found in my stream manipulation experiment. In both the otolith survey and stream manipulation experiment, growth rates were tested in natural streams. While otolith weight-fish length relationships are an indirect measure of growth rate, and the stream manipulation experiment was short-term, both types of study are useful measures of fish growth rate (Reznick et al. 1989, Secor & Dean 1989, Nilsson & Persson 2005, McHugh & Budy 2006). Although it is useful to identify where negative interactions between introduced and native species may occur, it is also important to test the ecological relevance of interactions between species in natural settings rather than to suggest, *a priori* that effects might be important.

Galaxiids in disturbed streams had higher growth rates than galaxiids from stable streams, both with and without trout. One explanation may be that higher growth rates are a characteristic of disturbed streams and the effects of trout described above may be secondary to these effects. Growth rate is related to foraging efficiency and temperature (Brett & Groves 1979). In disturbed streams, differences in faunal composition and the abundance of galaxiids, trout and their prey may result in increased foraging efficiency and growth.

The composition of invertebrate fauna in disturbed streams may increase galaxiid foraging efficiency. In frequently disturbed streams the instability of the substrate, excludes the settlement of sedentary species and increased patchiness of suitable habitat types favours

highly mobile ‘weedy’ invertebrate communities (Death 1993, Scarsbrook & Townsend 1993). *G. vulgaris* detects prey items, with equal efficiency between day and night via mechanical cues (McIntosh & Townsend 1995). The overall trend towards increases in abundance of mobile invertebrates in unstable streams (Death 1993, Scarsbrook & Townsend 1993) may favour increased galaxiid foraging efficiency as mobile prey are easily located by galaxiids like *G. vulgaris*, effectively increasing availability of prey to galaxiids in disturbed streams.

Reduced galaxiid density following high flows would also be expected to reduce intraspecific competition as prey density increases relative to galaxiid density. However from the analysis of multi-year (Chapter One) and single year galaxiid biomass (this chapter) there were no differences in galaxiid biomass between disturbed and stable streams, a result probably related to morphological and behavioural adaptations allowing galaxiids to withstand hydrological disturbances (Jowett & Richardson 1994, McIntosh 2000, Dunn 2003). However, whilst galaxiid biomass was not reduced in frequently disturbed streams, trout biomass was (Chapter One), and total fish biomass declined with increasing disturbance across all streams. Furthermore, in my stream manipulation experiment, growth rates in *G. vulgaris* were strongly related to total fish biomass despite differences in final trout biomass between treatments. Therefore increased growth rate may be related to reductions in overall competition for resources in galaxiids, regardless of whether competitors are conspecifics or trout.

Streams in the Upper Waimakairi basin frequently disturbed by high flows are also susceptible to drying periods. Low flows can concentrate mobile prey in drying channels as stream width contracts (Extence 1981, Stanley et al. 1997, Suren & Jowett 2006) and despite

the physiological stresses associated with drying streams (Magoulick & Kobza 2003), growth rates in fish from drying streams may be higher than in fish from perennial streams (Spranza & Stanley 2000). In galaxiids, increased temperatures and foraging efficiency during low flows, may be associated with reductions in energy expenditure whilst foraging on high densities of prey. Additionally, a shift to benthic foraging in galaxiids as stream velocities slow may increase foraging efficiency as drift feeding may be energetically expensive in negatively buoyant galaxiids (Hayes 1996, McIntosh 2000). Low flows, rather than high flows, are more likely to produce the increased growth rates observed in galaxiids from disturbed streams found in this study. This may be enhanced by the ability of galaxiids to aestivate (Dunn 2003) in drying streams. Aestivation may be particularly important for escaping physiological stresses such as emersion and reduced dissolved oxygen that develop during prolonged dry periods (Magoulick & Kobza 2003). Low flows associated with disturbed streams, may explain differences in growth rate patterns from my survey of long-term growth rates. However, trout biomass is also reduced in disturbed streams and trout migration barriers are often absent in disturbed streams making the separation of disturbance and trout effects difficult.

Trout may also increase the availability of prey to galaxiids via changes in prey behaviour. Typical responses of mayfly prey to fish predators, involve behaviours that reduce their availability to the predator species. In mayflies this typically involves changes in drift rate (McIntosh & Peckarsky 2004), periodicity (Flecker 1992, Miyasaka & Nakano 2001), and foraging times (Muotka et al. 1999). When in the presence of multiple predators, appropriate responses of prey to one predator may increase vulnerability to another predator, representing a trade off for prey. Facilitation between predators can occur when prey exhibit a behavioural response to one predator that results in increased vulnerability to other predators

(Soluk & Collins 1988, Sih et al. 1998). Predation threats to invertebrate prey may not vary with trout size, as small and large trout would be able to prey on most invertebrates. Positive effects of trout presence, but not trout size on galaxiid growth in my manipulation experiment, suggest that the effects of trout may be indirect and associated with changes in prey availability to galaxiids rather than through direct interactions between trout and galaxiids. Nilsson et al. (2006) in a New Zealand study on facilitation between koaro (*G. brevipinnis*), a stonefly (*Stenoperla* sp.) and brown trout (*S. trutta*) found that during the night in the presence of galaxiids, stoneflies and trout the consumption of mayflies (*Deleatidium* sp.) was higher than expected from single predator treatments. While prey consumption in the Nilsson et al. (2006) study was contingent on predator combinations, the study indicates facilitation between trout and galaxiids is possible. Thus, suppression of mayfly antipredator behaviour towards galaxiids when in the presence of trout may explain the reduced growth rates of galaxiids in treatments without trout from my reach manipulation experiment but not differences between stream types.

Although my results reveal no effects of trout on galaxiid growth, they do not elucidate what mechanisms may affect galaxiid growth in direct interactions with trout. Galaxiids have been shown to alter their habitat use in response to trout, potentially reducing their food consumption and hence growth rate (McIntosh et al. 1992, McIntosh et al. 1994). However if the effects of trout are mainly predatory, then it may be advantageous for galaxiids to avoid trout, especially if the effects of such avoidance are relatively benign compared to the effects of predation as shown in my stream manipulation experiment. McIntosh and Townsend (1995) found that whilst under cover during the day galaxiids can consume similar amounts of prey as when they are active at night. The benthic foraging of galaxiids may have allowed them to co-occur with small trout despite considerable overlap in

diet (Cadwallader 1975, Glova & Sagar 1991). Thus, although there are strong interactions between trout and galaxiids when they meet, galaxiids may reduce the impact of trout by avoiding confrontations with trout and any negative effects of altered habitat selection may be offset by trout facilitation of galaxiid feeding. This could explain the neutral effect of trout on galaxiids observed in the otolith data and the positive effect of trout in my stream manipulation experiment.

Conclusions

This study is the first to test the effects of trout-sympatry on galaxiid growth rates. The finding that trout do not affect galaxiid growth rate in this study suggests that the reductions in galaxiid foraging efficiency found in other studies may have negligible effects on growth. Instead this study suggests that galaxiids are affected by increases in biomass of all competitors, regardless of species. If the negligible impacts of trout on galaxiid growth are common to most small-bodied galaxiid species then the negative effects of competition may be less important than trout predation on smaller galaxiid size classes (Crowl et al. 1992, McIntosh 2000, McDowall 2003, Jellyman 2004). My research also does not support suggestions that galaxiid distributions are restricted to sub-optimal streams by trout (McIntosh et al. 1992, McDowall 2006). In this study the kinds of streams suggested to be sub-optimal, in fact produced faster growing galaxiids than other habitats, including trout-free streams. However, the contention that these streams may be sub-optimal (McDowall 2006) was based on findings in McIntosh (2000) that low galaxiid densities were found in disturbed streams. Disturbed streams are dynamic environments and whilst fluctuations in abundances may be great in disturbed streams, and as shown in the previous chapter over time galaxiid biomass may be similar between stable disturbed streams. My assessment of growth rate is based on

otolith weight which accumulates over the lifetime of a fish. The maximum age in *G. vulgaris* is four to six years (McDowall 2000). Therefore the growth rate used in this study probably reflects the conditions over several years. Given that conditions in disturbed streams may vary greatly between years it seems likely that during particularly stable years when trout may be abundant, disturbed streams may be less profitable than observed in this study. Although, in the period leading up to this study conditions in disturbed streams were unusually benign (S. Howard, personal observation). Disturbed streams are unlikely to be any less profitable than stable streams which always contain trout.

This study has important implications for future study of interactions between galaxiids and trout and future management of galaxiid populations. If trout have negligible effects on galaxiid growth rate, the negative effects of trout on galaxiid distributions may be more attributable to trout predation. However, in this study the conditions under which galaxiids and trout co-occur are probably related to small trout size and abiotic regulation of trout densities (McIntosh 2000), conditions which may be relatively uncommon in other catchments. Factors such as galaxiid size and the availability of alternative foraging areas may influence the outcomes of trout competition in other galaxiid species. In large-bodied drift-feeding galaxiids, competitive interactions with trout may be particularly important while the effects of predation may be less important. Whilst in small-bodied galaxiids, the outcomes of direct interactions with trout may well depend on the availability of alternative foraging areas and possibly trout facilitation of galaxiid foraging.

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