

## The influence of juvenile brown trout (*Salmo trutta*) on habitat use of inanga (*Galaxias maculatus*) in a stream simulator

Martin L. Bonnett<sup>1</sup> and Angus R. McIntosh<sup>2</sup>

**Abstract** Introduced salmonid fishes may have affected native galaxiid fishes in New Zealand by forcing alterations in their use of spatial resources. A stream simulator was used to test the effects of juvenile brown trout (*Salmo trutta*) (fork length range 66–115 mm) on habitat use of inanga (*Galaxias maculatus*) (fork length range 51–100 mm) during autumn. The stream simulator consisted of a single run-riffle-pool sequence lined with gravel and cobble substrates, and c. 8 m<sup>3</sup> of untreated artesian water was recirculated through the stream simulator at a rate of 3 litres s<sup>-1</sup>. Stream invertebrates were introduced into the stream simulator to provide food for the fish. Four experiments were run, each consisting of three 1-day trials using either 10 inanga, 20 inanga, or 10 inanga and brown trout. Counts of inanga visible in each of 12 designated habitat zones were made throughout the day, and proportions of visible inanga were used in repeated measure ANOVAs to test whether the proportion of fish visible varied according to the time of day, the density of inanga, or the presence of trout. Our experiments showed that neither the presence of juvenile brown trout nor the density of inanga had significant influence on inanga habitat use in the stream simulator. We conclude that in New Zealand streams any influence of brown trout on inanga is more likely to result from predation and/or competition for food by larger brown trout.

**Keywords** *Galaxias maculatus*; *Salmo trutta*; introduced species; interaction; artificial stream; intra- and inter-specific competition

### INTRODUCTION

New Zealand's sparse indigenous freshwater fish fauna is dominated by galaxiids, which comprise 22 of about 38 species (McIntosh & McDowall 2004). A very large proportion of these galaxiids (>15 species) are classified by the New Zealand Department of Conservation as threatened (Hitchmough 2002). A perceived decline in the stocks of some of these galaxiid fishes has coincided with the introduction of trout, and the subsequent, highly successful, establishment of sports fisheries (McDowall 2003). With increasing concern for the conservation of New Zealand's indigenous fish, there have been suggestions that the presence of exotic salmonid fishes, particularly brown trout (*Salmo trutta*), has had a deleterious impact on the galaxiids (McDowall 1968a, 1984, 1987; Crowl et al. 1992).

---

<sup>1</sup>National Institute of Water and Atmospheric Research Ltd, P. O. Box 8602, Christchurch, New Zealand.  
Email: m.bonnett@niwa.co.nz

<sup>2</sup>School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand.

Brown and rainbow trout were introduced into New Zealand during the late 19th century, but their impact on the indigenous fauna is hard to assess, especially as the latter was poorly studied before the 1950s (McDowall 2003). Furthermore, galaxiid populations may have declined in response to habitat modification and degradation associated with the substantial land-use changes that have occurred throughout most of New Zealand since European colonisation (Allen 1961; Hanchet 1990; McDowall 1990; Crowl et al. 1992).

Predation by large introduced trout has been suggested as an important mechanism leading to declines in native galaxiid populations in New Zealand and Australia (Crowl et al. 1992; McIntosh 2000). However, interspecific competition for habitat may also result in trout displacing galaxiids from their preferred microhabitat. Edge et al. (1993) observed that the presence of brown trout changed the behaviour of three Otago galaxiids, and the proportion of galaxiids feeding was reduced in the presence of trout. Cadwallader (1975) suggested that the presence of juvenile brown trout explained declines in *G. vulgaris* populations in Canterbury, and McIntosh et al. (1992) concluded that interspecific competition for space, perhaps combined with competition for food and predation by trout, could explain declines in Otago galaxiid populations. Both Crowl et al. (1992) and McDowall (2003) discussed the roles of predation and competition between trout and galaxiids, and suggested that clarification of the processes responsible for negative interactions should form the basis for informed conservation protocols.

There are more than 10 species of small, stream-dwelling galaxiids in New Zealand that are potentially vulnerable to competitive interactions with trout for spatial resources. Of these, inanga (*G. maculatus*) is probably the most likely to directly compete with brown trout where the two species co-occur. Sagar (1993, p.7) described inanga as “a gregarious, pelagic species (that is, they usually live in shoals in mid-water and move about a lot)”, and McDowall (2000) reported that inanga’s open, pool-living and shoaling habits mean it is more often seen than other (galaxiid) species. Inanga are known to feed on a wide range of bottom, mid-water, and surface/terrestrial organisms, especially aquatic larval insects and crustaceans (McDowall 1968b, 2000), and Jowett (2002) reported that they fed at locations where the current concentrated food, and in water velocities similar to those of trout of the same size. Overall, inanga have “lifestyles” (diets, feeding habitats, habits, and habitat requirements) similar to juvenile brown trout. By contrast, general descriptions of the other small stream galaxiids indicate they are predominantly bottom dwelling, cryptic, secretive, and/or nocturnal (McDowall 2000). Thus, interactions between inanga and trout are particularly important to investigate.

Although inanga are not ranked as threatened, and juvenile inanga comprise a significant component of the annual whitebait harvest, there is concern that inanga stocks have been impacted by the introduction of trout and that whitebait catches are declining (McDowall 1984). Because inanga and brown trout do co-occur in many lowland streams and rivers around New Zealand, and have similar “lifestyles” and diets, there is potential for interspecific competition for spatial resources. The aim of this study was to determine if juvenile brown trout displaced inanga from preferred habitat in a simulated stream environment.

## METHODS

### Stream simulator

To control environmental conditions and fish densities we undertook our studies in a stream simulator. A series of experiments was completed in an outdoor artificial stream located on the campus of the National Institute of Water and Atmospheric Research (NIWA) in Christchurch, New Zealand. The stream simulator was constructed of fibreglass and mounted above ground level. It was lined with a mixture of gravel and cobbles, and windows on the true left (TL) side allowed a clear view of most of the c. 8.5 m length of simulated stream. The stream simulator

contained c. 8 m<sup>3</sup> of water, and a submersible electric pump was used to recirculate water from a separate sump below the outlet of the simulator to a header tank. Water was then gravity fed from the header tank back into the simulator. Flow through the stream simulator could be manipulated with an adjustable gate valve on the header tank outlet. Flow was measured by timing the filling of the sump, and for all the experiments in this study was maintained at 3 litres s<sup>-1</sup>. Both the inlet to, and the outlet from, the stream simulator were screened with 3.5 mm stainless steel mesh to contain the fish. To prevent the intrusion of litter and predators, the simulator was covered overhead with 10 mm mesh fabric netting mounted on wooden frames c. 0.3 m above the water surface. Water used in the simulator was from the Christchurch City supply, which is of artesian origin and not subjected to any treatment. It therefore contains no additives or chemical substances from other fishes. The water in the simulator was continuously circulated through the header tank, and oxygen concentrations were typically >9 mg ml<sup>-1</sup> and close to 100% saturation.

The stream simulator comprised three sections. At the upstream end, a run (3 m long, and from c. 0.4–0.8 m wide) contained gravel substrates (10–20 mm) and moderate water velocities (0–0.21 m s<sup>-1</sup>). Overhanging and partly submerged native grasses (*Carex* spp.) along c. 80% of the true right (TR) side of the run provided cover for fish. Downstream of the run was a riffle (2 m long × 0.25 m wide), with gravel and cobble substrate (10–200 mm). The slope of the riffle section was c. 4%, and water velocities were relatively high (0.05–0.51 m s<sup>-1</sup>). Downstream of the riffle was a pool (3.5 m long, and 0.6–1.5 m wide). Substrate in the pool consisted of gravel (10–20 mm) on the bottom, plus cobbles and boulders (up to c. 200 mm) sloping up to the tail of the riffle in a “boulder bank”. Water velocities were generally low in the pool section (0–0.15 m s<sup>-1</sup>). Branches of broom (*Cytisus scoparius*) were placed in and above the upstream end of the pool (near the boulder bank) and also above the windows on the TL side of the pool to provide cover for fish. Overhead movement easily disturbed both fish species, and a shade-cloth barrier was erected above the windows on the TL side to minimise any potential disturbance during observation periods. Fish did not appear to be disturbed by observers approaching the viewing windows, or by movement near the window under most light conditions. However, observers had to be cautious when strong sunlight struck the observation windows during the late afternoon, when sudden movement or changes in light intensity did disturb the fish.

Twelve distinct zones of water habitat available to fish within the simulator were designated. The area of each zone was measured, and a minimum of five water depth and velocity measurements using a current meter were made in each zone (Table 1).

### Density of fish in the stream simulator

To imitate conditions in a stream, we stocked the simulator with a natural density of inanga for each trial. Information from the New Zealand freshwater fisheries database (McDowall & Richardson 1983) indicated inanga densities in waterways around Christchurch were variable up to a maximum of c. 0.5 m<sup>-2</sup>. Inanga density in a small North Island stream during autumn averaged 1–2 m<sup>-2</sup> over several years (I. Jowett pers. comm.). Thus, for this study, we assumed that 10 inanga in an area of c. 6.4 m<sup>2</sup> (i.e., 1.6 m<sup>-2</sup>) of simulated stream was an appropriate base density.

### Study design

Before commencing experiments, we conducted preliminary trials using various densities of inanga and brown trout. These took place during April 2003, to establish the time it took for fish to acclimatise and begin feeding on stocked invertebrates, to determine if fish habitat use changed appreciably during trials up to 6 days in length, to observe if fish were able to

**Table 1** Description, dimensions, and water velocities of designated zones in the stream simulator during Apr–May 2003. Zones are listed in order downstream from the inlet. Note that zones 2 and 3 were side-by-side in the run, and zones 8, 10, and 12 were below the water surface under zones 7, 9, and 11, respectively.

Zone	Description	Mean surface			Depth (m)			Velocity (m s <sup>-1</sup> )			
		Length (m)	Width (m)	Area (m <sup>2</sup> )	Mean	Min.	Max.	Mean	Min.	Max.	SD
1	Upstream section of run immediately below inlet	0.47	0.83	0.39	0.09	0.00	0.11	0.04	0.04	0.04	0.00
2	True right side of run only, with vegetation cover	1.95	0.28	0.55	0.07	0.00	0.11	0.02	0.01	0.03	0.01
3	True left side of run only, against windows	1.95	0.53	1.02	0.11	0.09	0.14	0.01	0.00	0.02	0.01
4	Tail of run	0.55	0.39	0.21	0.08	0.00	0.09	0.07	0.02	0.21	0.07
5	Riffle, upstream section	1	0.21	0.21	0.09	0.08	0.10	0.36	0.29	0.51	0.09
6	Riffle, downstream section	0.95	0.25	0.23	0.09	0.07	0.11	0.26	0.05	0.41	0.10
7	Head of pool immediately below riffle	0.75	0.85	0.64	0.44	0.20	0.60	0.02	0.00	0.03	0.01
8	Boulder bank in head of pool (below zone 7)	0.75	0.75	0.53	0.53	0.30	0.70	0.03	0.00	0.15	0.06
9	Middle of pool, near surface	2.1	1.22	2.56	0.40	0.40	0.40	0.02	0.01	0.03	0.01
10	Middle of pool, near bottom (below zone 9)	2.1	1.15	0.79	0.79	0.74	0.84	0.00	0.00	0.00	0.00
11	Tail of pool, near surface	0.7	0.78	0.54	0.40	0.40	0.40	0.01	0.01	0.02	0.01
12	Tail of pool, near bottom (below zone 11)	0.7	0.65	0.79	0.79	0.75	0.80	0.01	0.00	0.02	0.01

utilise the range of habitats available, and to determine if there were distinct periods of activity.

Since changes in fish density as well as the presence of brown trout could influence inanga behaviour, we compared inanga habitat use at two inanga densities and in the presence and absence of brown trout. Four replicates each of three experimental treatments were completed within 1 month (Table 2). The treatments were a density of 10 inanga, a density of 20 inanga, and a density of 10 inanga with 5–10 brown trout in the simulator. For the latter treatment we varied the number of trout in an attempt to maintain a total fish biomass equivalent to that in the treatment using 20 inanga; this was imprecise, as in order to avoid anaesthetising and measuring fish before the experiments, we relied on a brief visual estimate of each fish's weight. In each replicate, a 1-day trial of each treatment was conducted in random sequence (Table 2).

### Experimental procedure

Inanga, brown trout, and invertebrates for the experiments were collected from various streams in or close to Christchurch. Trout and invertebrates were collected using a backpack electrofishing machine and hand-held nets. Inanga were mostly collected using small seine nets, although electrofishing was used for the collection of inanga for the fourth replicate (20–24 May), as the area of the stream sampled was unsuitable for netting. Brown trout were known to be present in all the catchments sampled for inanga.

All of the fish used in experiments were introduced into the run and pool of the simulator during the afternoon preceding each observation period, and allowed to acclimate to the simulator overnight. Live stream invertebrates (predominantly larval mayflies, with some stoneflies and caddisflies) were also introduced to the stream simulator before and during each day of the experiment to provide natural

**Table 2** Treatments, water temperatures, fish lengths, and biomass in experiments conducted in the stream simulator, Apr–May 2003.

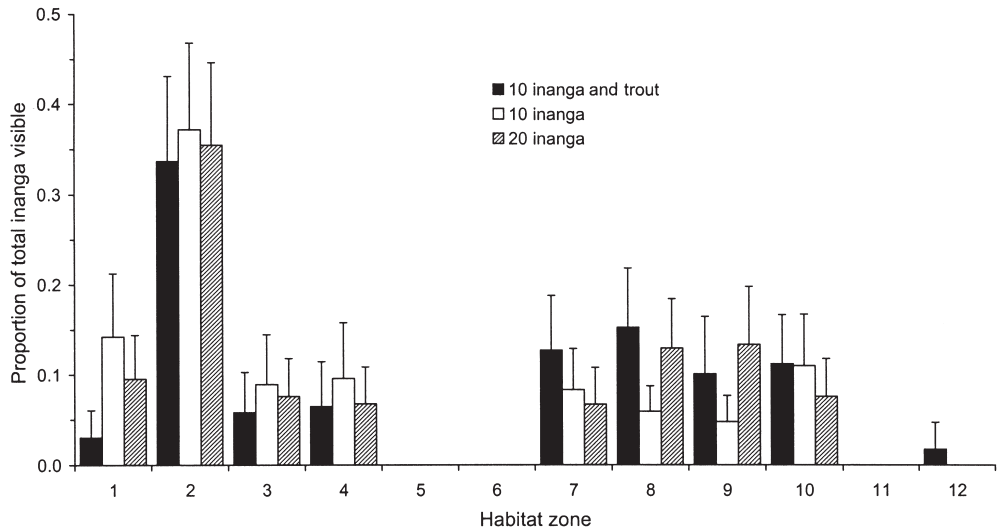
Replicate	Treatment	Trial date	Temperature (°C)			Inanga				Brown trout				
			Min.	Max.	n	Length (mm)			n	Length (mm)				
						Mean	Min.	Max.		Mean	Min.	Max.		
1	10 inanga and trout	30 Apr	14	15	10	64.6	53	94	34.3	10	96.5	77	115	109.6
1	10 inanga	2 May	14	15	10	63.8	54	77	9.6					
1	20 inanga	4 May	13	13	20	64.6	53	94	26.3					
2	10 inanga	6 May	11	14	10	69.8	50	94	17.8					
2	10 inanga and trout	8 May	13	15	10	78.6	69	100	23.8	5	91.4	70	108	50.1
2	20 inanga	10 May	12	15	20	77.6	57	95	44.1					
3	20 inanga	13 May	11	15	20	66.2	54	88	30.0					
3	10 inanga and trout	15 May	12	14	10	59.4	52	92	9.3	5	77.0	66	87	30.4
3	10 inanga	17 May	12	14	10	64.1	51	90	13.9					
4	10 inanga and trout	20 May	13	17	10	76.9	62	93	22.5	5	92.0	86	97	45.7
4	10 inanga	22 May	14	15	10	81.9	74	87	27.4					
4	20 inanga	24 May	11	12	20	63.5	52	82	26.8					

food for the fish. At the time fish were introduced, c. 15 g (wet weight) of stream invertebrates were added; a further c. 3 g were added just before the trial, and c. 1.5 g were added immediately after each observation period. To minimise disturbance, invertebrates were gradually introduced via submerged plastic tubes at the head of the run and at the head of the riffle.

During each experimental day, five sets of observations were made through side windows. Every 2 hours, three observations of fish positions were made at 5-min intervals, starting at 08:30 NZST and finishing at 16:30 NZST, i.e., observations were made at 08:30, 08:35, 08:40, 10:30, 10:35 and so on until the final observation at 16:40. Observations entailed scanning all 12 habitat zones of the simulated stream, and counting and recording the number of fish (inanga and brown trout) in each zone. The three observations made within the 10-min set were then averaged to give five sets of observations per trial.

At the completion of each experimental day, fish were removed for measurement, and the stream simulator was drained and allowed to dry to remove any residual fish chemical cues.

We used repeated measures ANOVA to test whether the proportion of fish visible (and by implication active) varied according to the time of day, the density of conspecifics or the presence of trout. The analysis was conducted on the arcsine-square root transformed proportion of inanga visible. The five time periods through the day were used as the repeated measure in an ANOVA with the three treatments (10 inanga, 10 inanga plus trout, and 20 inanga) used as three levels of a single factor in the ANOVA.



**Fig. 1** The mean proportional use (+SE) of 12 habitat zones in the stream simulator by inanga in trials with either 10 inanga, 20 inanga, or 10 inanga and trout. The 12 habitat zones are described in Table 1.

To test whether inanga habitat use varied according to inanga density or the presence of trout, multivariate and univariate analysis of variance was conducted on arcsine-square root transformed proportional use of eight habitat zones in the stream simulator. During observation periods inanga were never observed in the riffle (zones 5 and 6), and only once was an inanga observed near the downstream end of the pool (zones 11 and 12). Consequently, these four zones were excluded from the analysis.

## RESULTS

Preliminary trials, using various densities of inanga and trout in the stream simulator, established that both trout and inanga were quite capable of moving between the pool and run (i.e., up or down the riffle) and had access to all of the habitat, although neither species appeared to utilise riffle habitat for feeding or as cover. Furthermore, there was no tendency for fish to congregate near either the inlet or the outlet of the stream simulator. Both inanga and brown trout appeared to adapt to the simulator environment within a few hours of introduction, and in trials lasting up to 6 days, there was no apparent change in habitat use by either species.

Neither inanga nor trout were active in the simulator during darkness; night observations using a hand-held spotlight with a cherry-red filter revealed little fish movement and fish were not seen foraging or attempting to feed on drifting invertebrates at night. Trout were active at dawn and dusk, whereas inanga appeared to be active only during full daylight.

Both inanga and brown trout readily fed on stream invertebrates that were introduced into the simulator, and were frequently observed feeding on invertebrates drifting in the water column. Both species were also seen to forage amongst the cobbles in the boulder bank, presumably for invertebrates that had settled amongst the substrate.

Inanga congregated in shoals that mostly moved slowly through the run and pool habitats, and at times were almost stationary within, or close to, cover in low velocity areas. At times, some inanga within a shoal would be observed taking food from the water column in areas of faster-flowing water. Trout were most frequently observed individually foraging or moving

around the pool or run habitats. Occasionally, trout congregated in a small shoal, and on several occasions one or two brown trout were seen moving with a shoal of inanga. We observed very little agonistic behaviour between the two species or amongst either species.

During any one observation, from 0 to 95% of the inanga were seen (means 39, 40, 54% for low inanga density, high inanga density, and inanga with trout treatments, respectively). Those fish not counted in any observation period were presumably hidden amongst the instream cover provided by the boulder bank in zone 8 (both inanga and brown trout were at times lost to view while foraging amongst the boulders), or under and amongst overhanging vegetation in zone 2 (where fish were very difficult to observe). It was not possible to determine whether those fish visible and active in the water column were the same fish observed during each observation period, or whether the identity of “active” fish changed during each observation period.

The proportion of inanga visible can be regarded as an index of activity, because those inanga visible were not in deep cover, frequently moved around the simulator, and sometimes attempted to capture prey from the water column. Although those inanga not visible may have been attempting to forage, it is unlikely they could have done so repeatedly without being detected. Therefore, it is likely that those not visible were inactive and under cover.

Repeated measures ANOVA indicated there was no significant temporal change in the number of inanga visible at any one time period ( $F = 1.161$ ,  $P = 0.34$ ), nor were there any significant effects associated with the presence of trout or a higher density of inanga ( $F = 0.768$ ,  $P = 0.63$ ). Thus, neither the presence of trout nor an increase in density had any significant effect on the proportion of inanga that were active in the simulator.

Inanga were quite selective in their habitat use (Fig. 1). Although they passed through the riffle to move between the pool and run sections, they were never recorded in the riffle during any of the observation periods. Furthermore, only one inanga was ever recorded in the tail of the pool. The tail of the pool presented a large expanse of water with little overhead or substratum cover. Thus, the inanga did not occupy fast velocity areas or deep pool areas with little cover, and divided their time between the run and the head to middle sections of the pool. These habitats offered slow to medium water velocities (Table 1) adjacent to cover. The overhead cover provided by the overhanging vegetation associated with zone 2 of the run was particularly important, and this was the most heavily used habitat. Fish were also frequently associated with the boulder bank at the head of the pool (zone 8), which was also close to the other pool habitats used.

The proportional use of habitats by inanga changed relatively little when 20 inanga were present compared to 10. The presence of brown trout also had relatively little effect on inanga use of habitats. These conclusions are supported by the MANOVA ( $F = 0.540$ ,  $P = 0.83$ ), and univariate ANOVAs ( $0.31 < P < 0.98$ ), that indicated there were no significant differences between inanga habitat use at different densities of inanga or in the presence and absence of brown trout.

## DISCUSSION

Our experiments indicated juvenile brown trout had no influence on the habitat use of inanga in the stream simulator. Also, the patterns of inanga habitat use did not alter significantly when their density was doubled. These two results indicate that inanga were unresponsive to changes in the abundance of potential competitors in their habitat. This result was unexpected given the previous history of trout effects on the behaviour of other small New Zealand galaxiids (McIntosh et al. 1992; Edge et al. 1993). However, the lack of changes in inanga spatial resource use despite increasing competitor densities is likely to reflect both the gregarious behaviour of inanga and the size of the fish used in the experiments.

### **Inanga responses to competitors**

As has been frequently observed in the wild (McDowall 1990; Sagar 1993; Jowett 2002) inanga commonly formed schools in the stream simulator. Inanga, like other schooling fish, presumably gain some benefit from this social behaviour, probably in the form of protection from predators (Morgan & Godin 1985; Magurran 1990) or enhanced foraging (Morgan 1988; Ranta & Kaitala 1991). Such behaviour may explain the lack of response observed when low versus high inanga densities were compared.

The lack of any influence by trout on inanga may be because we used relatively small trout (mean fork lengths: 77–97 mm) in our experiments. In comparison, most deleterious influences of trout in New Zealand have been associated with trout >150 mm long. In their experiments demonstrating trout-induced changes in the behaviour of Otago galaxiids, Edge et al. (1993) and McIntosh et al. (1992) both used trout in the 110–150 mm range. Trout >150 mm long start to become piscivorous (Mittelbach & Persson 1998), and are capable of predation on galaxiids up to 120 mm long (McIntosh 2000). Moreover, the outcome of behavioural interactions for space among fish is usually controlled by size (Taniguchi et al. 2002). Thus, it is likely that the trout did not displace inanga in our experiments because they were not large enough to present a predation risk or to competitively displace inanga from their preferred habitats.

We used inanga that had probably resided in freshwater for several months. Consequently, they were mostly large (mean length >70 mm) and close to maturity. It is possible that juvenile inanga (fresh-run whitebait or post-whitebait stages) have different habitat requirements, and because of their smaller size might consequently be more vulnerable to displacement by trout.

The purpose of our experiments was to determine if small trout have the potential to influence adult inanga habitat use. Our experiments indicate they do not. However, trout >150 mm have the potential to deleteriously impact inanga populations and circumstantial evidence indicates this is likely. An analysis of the patterns of distribution and associations of New Zealand freshwater fish by Minns (1990) found a significant negative association between the presence of brown trout and inanga, and Sagar (1993) reported that maturing inanga tended to be more abundant in the absence of large brown trout. Jowett & Richardson (2003) also found a relatively low rate of co-occurrence between trout and inanga in a nationwide analysis of fish communities.

Large trout are presumably able to prey on all sizes of inanga, as well as many of the other stream galaxiids, which may at least partly explain why small galaxiids are generally uncommon or absent from streams containing larger trout (McIntosh 2000; Crowl et al. 1992). Sagar (1993) found remains of inanga whitebait in the gut of adult brown trout in a small stream. Glova (2003) reported up to 40% mortality of inanga attributable to predation by large brown trout (fork lengths 255–390 mm) in stream simulator trials. While it is generally accepted that brown trout prey upon inanga, it is unclear how deleterious this is to inanga populations, and whether the impact is exacerbated by competition for space. Thus, efforts to determine the outcome of interactions between inanga should concentrate on the dual effects of predation and displacement by trout >150 mm.

There have been various reports of trout diet overlapping with that of galaxiids in New Zealand, and suggestions that competition for food may partly explain the incompatibility of some galaxiids and trout (Cadwallader 1975; Glova & Sagar 1991; Kusabs & Swales 1991). However, McDowall (2003) suggested that there might be complex interactions between stream dwelling galaxiids and trout, and that the intensity of trout predation on fish and invertebrates may result in galaxiid populations being food limited.

The nocturnal habits of some galaxiids may provide temporal separation, and thereby partly reduce competition with trout for food, as suggested by a number of authors (Glova 1989; Glova & Sagar 1991, 1993; Kusabs & Swales 1991; Glova et al. 1992). Such a situation seems unlikely for inanga populations, as our observations suggested that inanga were only active during daylight. Possibly they are more nocturnally active in some natural waters or in different situations (e.g., when water temperatures are higher). In addition, fresh-run whitebait and post-whitebait stages may be more active nocturnally than the older fish tested during these experiments.

### **Inanga habitat use**

Inanga in the stream simulator were regularly observed taking invertebrate food from the water column (i.e., drift-feeding), usually in zones 3 and 4 of the run, and zone 7 in the pool. The water velocities in these zones coincided with those reported by Jowett (2002), who outlined habitat suitability criteria for drift-feeding inanga. In the stream simulator inanga were also observed foraging amongst the substrates in the pool (zones 8 and 10) where water velocities were generally low, which is consistent with field observations by Jowett (2002). It appeared that inanga foraged for food even though invertebrates were available nearby in areas suitable for drift-feeding. Thus, drift-feeding requirements represent the facet of feeding habitat with the highest water velocity requirement, especially since inanga naturally occur in a wide range of water types, including still water habitats such as swamps, coastal lakes, and lagoons (McDowall 2000) where drift-feeding could not occur. However, our observation that inanga did not feed in the riffle zone matches the negative association between inanga and fast flowing habitats in the analysis by Jowett & Richardson (2003) of New Zealand fish communities.

Inanga demonstrated a strong preference for habitat zones that provided some overhead or instream cover, and we observed that, if disturbed when in other habitat zones, they quickly retreated into zones providing the most cover (zones 2 and 8). So, although inanga may well be the least cryptic of the galaxiid species, they are typical of New Zealand's native fish in being closely associated with overhead cover. Inanga did not, apparently, use the cobbles and boulders in the riffle zones of the stream simulator as cover, nor did the riffle provide suitable water depths and velocities for inanga drift-feeding described by Jowett (2002). It is possible they did utilise the riffle as cover and/or feeding, but without being observed. However, if this had occurred frequently we were confident of observing at least some of this behaviour, given that the riffle was narrow and our view into the riffle through the windows was good.

It is difficult to determine how pertinent our results are in understanding the impact of trout on inanga in New Zealand waters, as we studied an artificial situation by using a stream simulator, and controlled many variables such as fish density, fish size, the number of species, and duration of the trials. However, we conclude that interaction between juvenile brown trout and inanga seems unlikely to result in significant displacement of inanga in New Zealand stream habitats. Any influence of brown trout seems much more likely to be as a result of competition for food and/or direct predation by larger trout on inanga.

### **ACKNOWLEDGMENTS**

Thanks to Dave Rawlings and Alan Stokes for their efficiency in setting up the stream simulator, and Julian Sykes for field assistance with collecting fish and invertebrates. We also thank Bob McDowall and two anonymous referees for constructively reviewing the manuscript. The cooperation of the Department of Conservation is also acknowledged. This study was funded by the New Zealand Foundation for Research, Science and Technology Contract CO1X0022.

## REFERENCES

- Allen, K. R. 1961: Relations between Salmonidae and the native freshwater fauna in New Zealand. *Proceedings of the New Zealand Ecological Society* 8: 66–70.
- Cadwallader, P. L. 1975: Feeding relationships of galaxiids, bullies, eels and trout in a New Zealand river. *Australian Journal of Marine and Freshwater Research* 26: 299–316.
- Crowl, T. A.; Townsend, C. R.; McIntosh, A. R. 1992: The impact of introduced brown and rainbow trout on native fish: the case of Australasia. *Reviews in Fish Biology and Fisheries* 2: 217–241.
- Edge, K.-A.; Townsend, C. R.; McIntosh, A. R. 1993: Investigating anti-predator behaviour in three genetically differentiated populations of non-migratory galaxiid fishes in a New Zealand river. *New Zealand Journal of Marine and Freshwater Research* 27: 371–377.
- Glova, G. J. 1989: Native and salmonid fishes: are they compatible? *Freshwater Catch* 40: 12–13.
- Glova, G. J. 2003: A test for interaction between brown trout (*Salmo trutta*) and inanga (*Galaxias maculatus*) in an artificial stream. *Ecology of Freshwater Fish* 12: 247–253.
- Glova, G. J.; Sagar, P. M. 1991: Dietary and spatial overlap between stream populations of a native and two introduced fish species in New Zealand. *Australian Journal of Marine and Freshwater Research* 42: 423–433.
- Glova, G. J.; Sagar, P. M. 1993: A further assessment of trophic and spatial inter-relations of galaxiids and salmonids in New Zealand. *Ecology of Freshwater Fish* 2: 132–140.
- Glova, G. J.; Sagar, P. M.; Naslund, I. 1992: Interaction for food and space between populations of *Galaxias vulgaris* Stokell and *Salmo trutta* L. in a New Zealand stream. *Journal of Fish Biology* 41: 909–925.
- Hanchet, S. M. 1990: Effect of land use on the distribution and abundance of native fish in tributaries of the Waikato River in the Hakarimata Range, North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 24: 159–171.
- Hitchmough, R. 2002: New Zealand threat classification system lists, 2002. Wellington, Department of Conservation. 210 p.
- Jowett, I. G. 2002: In-stream habitat suitability criteria for feeding inanga (*Galaxias maculatus*). *New Zealand Journal of Marine and Freshwater Research* 36: 399–407.
- Jowett, I. G.; Richardson, J. 2003: Fish communities in New Zealand rivers and their relationship to environmental variables. *New Zealand Journal of Marine and Freshwater Research* 37: 347–366.
- Kusabs, I. A.; Swales, S. 1991: Diet and food resource partitioning in koaro, *Galaxias brevipinnis* (Günther), and juvenile rainbow trout, *Oncorhynchus mykiss* (Richardson), in two Taupo streams, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 25: 317–325.
- Magurran, A. E. 1990: The adaptive significance of schooling as an anti-predator defence in fish. *Annales Zoologici Fennici* 27: 51–66.
- McDowall, R. M. 1968a: Interactions of the native and alien faunas of New Zealand and the problems of fish introductions. *Transactions of the American Fisheries Society* 97: 1–11.
- McDowall, R. M. 1968b: *Galaxias maculatus* (Jenyns), the New Zealand whitebait. New Zealand Marine Department, Fisheries Research Bulletin 2. 84 p.
- McDowall, R. M. 1984: Trout in New Zealand waters – the biology and management of trout in New Zealand's lakes and rivers. Wellington, The Wetland Press. 120 p.
- McDowall, R. M. 1987: Impacts of exotic fishes on the native fauna. In: Viner, A. B. ed. Inland waters of New Zealand. New Zealand Department of Scientific and Industrial Research Bulletin 241. Pp. 291–306.
- McDowall, R. M. 1990: New Zealand freshwater fishes: a natural history and guide. Auckland, Heinemann Reed. 553 p.
- McDowall, R. M. 2000: The Reed field guide to New Zealand freshwater fishes. Auckland, Reed. 224 p.
- McDowall, R. M. 2003: Impacts of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. *Transactions of the American Fisheries Society* 132: 229–238.
- McDowall, R. M.; Richardson, J. 1983: New Zealand freshwater fish survey: a guide to input and output. New Zealand Ministry of Agriculture and Fisheries, Fisheries Information Leaflet 12. 15 p.
- McIntosh, A. R. 2000: Habitat- and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 2140–2151.
- McIntosh, A. R.; McDowall, R. M. 2004: Fish communities in streams and rivers. In: Harding, J. S.; Mosely, M. P.; Pearson, C. P.; Sorrell, B. K. ed. Freshwaters of New Zealand. Christchurch, New Zealand, New Zealand Hydrological Society Inc. and New Zealand Limnological Society Inc. 764 p.

- McIntosh, A. R.; Townsend, C. R.; Crowl, T. 1992: Competition for space between introduced brown trout (*Salmo trutta* L.) and common river galaxias (*Galaxias vulgaris* Stokell) in a New Zealand stream. *Journal of Fish Biology* 41: 63–81.
- Minns, C. K. 1990: Patterns of distribution and association of freshwater fish in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 24: 31–44.
- Mittelbach, G. G.; Persson, L. 1998: The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1454–1465.
- Morgan, M. J. 1988: The influence of hunger, shoal size and predator presence on foraging in bluntnose minnows. *Animal Behaviour* 36: 1317–1322.
- Morgan, M. J.; Godin, J-G. J. 1985: Antipredator benefits of schooling behaviour in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus*). *Zeitschrift fur Tierpsychologie* 70: 236–246.
- Ranta, E.; Kaitala, V. 1991: School size affects individual feeding success in three-spined sticklebacks (*Gasterosteus aculeatus* L.). *Journal of Fish Biology* 39: 733–737.
- Sagar, P. M. 1993: Habitat use and models of abundance of maturing inanga in South Island, New Zealand streams. Ministry of Agriculture and Fisheries, New Zealand Freshwater Miscellaneous Report No. 104.
- Tanuguchi, Y.; Fausch, K. D.; Nakano, S. 2002: Size-structured interactions between native and introduced species: can intraguild predation facilitate invasion by stream salmonids? *Biological Invasions* 4: 223–233.