CHAPMAN
TRIPP

3 March 2010

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The Chairperson
Water Hearing Panel
Horizons One Plan
C/- Robyn Harrison, Hearings Administrator

by email

REQUEST FOR FURTHER INFORMATION - FONTERRA CO-OPERATIVE GROUP LIMITED

Introduction

1 On Friday 19 February, Fonterra Co-Operative Group Limited (*Fonterra*) presented submissions and evidence to the Water Hearing Panel (*the Panel*) on the Water Chapters of the Proposed One Plan (*One Plan*).

2 At the hearing, the Panel requested that Fonterra provide the following further information:

2.1 Submissions on the relationship between sections 30(1)(fa) and 30(4) of the Resource Management Act 1991 (*RMA*);

2.2 A list of catchments in the Region which were considered to be sensitive for the purposes of the Primary Sector Water Partnership (*PSWP*);

2.3 Comments from Fonterra's witness, Dr Mike Scarsbrook, on the latest version of the water quality targets listed in Schedule D of the One Plan;

2.4 References for studies regarding the effects of trout on stream ecosystems;

2.5 Data about average Nitrogen-loss (*N-loss*) rates in other regions; and

2.6 Clarification as to which sentence was being referred to in Footnote 22 of Dr Terry Parminter's evidence (Dr Parminter appeared as a witness on behalf of Fonterra).

This letter provides the above information.

Sections 30(1)(fa) and 30(4)

3 As the Panel is aware, it is a function of a regional council, if appropriate, to establish rules in a regional plan to allocate any of the following (section 30(1)(fa)):

3.1 The taking or use of water (other than open coastal water);

3.2 The taking or use of heat or energy from water (other than open coastal water);

3.3 The taking or use of heat or energy from the material surrounding geothermal water; and

3.4 The capacity of air or water to assimilate a discharge of a contaminant.

4 Section 30(4)(f) provides that a rule to allocate a "natural resource" established by a regional council in a plan under section 30(1)(fa) or 1(fb), may do so in any way, subject to a number of listed criteria. This includes the requirement to ensure that the allocation of water does not affect the activities authorised by section 14(3)(b) to (e) (domestic needs, stock drinking water etc).

5 Water is included in section 2 RMA as a "natural and physical resource". Therefore, when establishing rules pursuant to subsection 30(1)(fa), such as, for example, "the taking or use of water", the proposed rule must not offend the criteria listed in section 30(4). Therefore, section 30(4) should be seen as a further gloss on sections 30(1)(fa) and (fb). Rules made under these subsections are subject to subsection 30(4).

6 The use of the word "natural resources" in section 30(4) encompasses more than water. This is likely because sections 30(1)(fa) and (fb) (which are subject to 30(4)) refer to other natural resources, such as air.

7 Both sections 30(1)(fa) and (fb) and section 30(4)(f) RMA were introduced by the Resource Management Amendment Act 2005. It would appear from reviewing parliamentary commentary that these provisions were introduced primarily so as to remove any legal doubt that the allocation of natural resources, including water, is a function of regional councils under the RMA.

8 Accordingly, in Fonterra's submission, when making rules which allocate the taking or use of water (under section 30(1)(fa)(i)), the allocation must not affect the activities authorised by section 14(3)(b) to (e) (nor offend against the other criteria listed in section 30(4)).

Catchments identified in the Primary Sector Water Partnership

9 During the 2008-2009 year, the PSWP met with representatives of all Regional Councils at least once to determine which catchments each Regional Council saw as priority catchments for action by the PSWP. This is documented in the PSWP Annual Report (**attached** as Appendix A). The Annual Report has only just been released and was unavailable at the time Fonterra's evidence in chief was provided. The catchments that were put forward by Regional Councils were:

9.1 Waipu (Northland);

9.2 Hoteo (Auckland);

9.3 Upper Karapiro (Waikato);

9.4 Lower Kaituna (Bay of Plenty);

9.5 Huatokitoki, Porangahau, Ngaruroro, Taharua (Hawkes Bay);

9.6 Upper Manawatu (Manawatu- Wanganui - Horizons);

9.7 Orari, Selwyn Hills (Canterbury);

9.8 South Otago, Upper Taieri (Otago); and

9.9 Waihopai, Balfour, Waimea (Southland);

10 The PSWP selected catchment programmes for uptake on the basis of whether their involvement would add "real value". The final catchment programmes selected were:

10.1 Hoteo (Auckland);

10.2 Upper Karapiro (Waikato);

10.3 Ngaruroro (Hawkes Bay);

10.4 Upper Manawatu (Manawatu/ Wanganui - Horizons);

10.5 Canterbury Plains (Environment Canterbury decided that the greatest value of PSWP involvement would be in providing a conduit for a collaborative discussions on water and nutrient management issues within the Region); and

10.6 Balfour (Southland).

Comments on Revised Schedule D

11 Fonterra's witness, Dr Mike Scarsbrook, has prepared a supplementary statement of evidence about the One Plan's revised Schedule D: Water Quality Standards. His evidence is attached as **Appendix B**.

Impacts of trout on ecosystems

12 **Appendix C** to this letter contains two articles which discuss the impact of trout on New Zealand ecosystems. These are:

12.1 An article by R M McDowall of the National Institute of Water and Atmospheric Research tilted "Impacts of Introduced Salmonids on Native Galaxiids in New Zealand Upland Streams: A New Look at an Old Problem"; and

12.2 An article by Alexander Flecker and Colin Townsend , Department of Zoology, University of Otago, Dunedin, titled "Community-Wide consequences of trout introduction in New Zealand streams."

Data about nitrogen-loss in other regions

13 As indicated by Fonterra's witnesses during the hearing, the gathering of accurate data on regional N-loss from farms is very difficult. Gathering the information for the Manawatu-Wanganui Region was a very resource intensive process. To provide equivalent information for even one or two other regions would require a major resource investment by the farming and fertiliser industries.

14 Given N-loss levels are an outcome of soil type, rainfall, land area in dairying, and cow numbers per hectare, the N-loss levels between regions will differ as markedly as these four factors differ.

15 There is no comprehensive information publically available about N-loss in other regions. While many Overseer files exist for other regions, data confidentiality prevents its release.

16 The increased focus on the issue of diffuse nutrient loss will require imporoved access to such information, and the Dairy and Fertiliser industries are currently working together to address this. It is envisaged that these issues will be addressed within the next 3 months, and data from Horizons and other regions is expected to be used to better understand appropriate benchmarks and targets.

Footnote in Terry Parminter's evidence

17 Footnote 22 of Terry Parminter's evidence in chief says "see paragraph 32 of the Section 42A Report of Dr Monaghan." The specific sentence within paragraph 32 of Dr Monaghan's Report which Dr Parminter was referring to was the following:

> *"While it is unclear whether this scheme can be defined as a regulatory or non-regulatory approach (it can be argued it is a mix of both)."*

18 I trust this information answers the Panel's questions. However, please contact me should you require any further information from Fonterra.

Yours faithfully

Nicky McIndoe
SENIOR SOLICITOR

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APPENDIX A - PRIMARY SECTOR WATER PARTNERSHIP ANNUAL REPORT 2008/ 2009

APPENDIX B – SECOND SUPPLEMENTARY STATEMENT OF EVIDENCE OF DR SCARSBROOK

Before Hearing Commissioners at Palmerston North

under: the Resource Management Act 1991

in the matter of: Submissions on chapters 6, 13 and 15 of the Proposed One Plan

between: **Fonterra Co-operative Group Limited**
Submitter

and: **Manawatu-Wanganui Regional Council**
Respondent

Second statement of supplementary evidence of Dr Michael Robert Scarsbrook for Fonterra Co-operative Group Limited, in response to questions from the Hearing Panel

Dated: 3 March 2010

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SECOND STATEMENT OF SUPPLEMENTARY EVIDENCE OF DR MICHAEL ROBERT SCARSBROOK FOR FONTERRA CO-OPERATIVE GROUP LIMITED IN RESPONSE TO QUESTIONS FROM THE PANEL

INTRODUCTION

1 My full name is Michael Robert Scarsbrook and I have the qualifications and experience described in my Evidence in Chief (*EIC*). I repeat the confirmation given in that statement that I have read and agree to comply with the Code of Conduct for Expert Witnesses.

2 In this second statement of supplementary evidence I respond to a question from the Water Hearing Panel regarding Schedule D: Water Quality Standards, of the Proposed One Plan (*POP*), dated 23 November 2009 (*the Revised Version of Schedule D*). The Panel has asked for my comments on the Revised Version of Schedule D.

COMMENTS ON THE REVISED VERSION OF SCHEDULE D

D1: Standards that apply to all natural streams and rivers (page D-3).

3 I consider that the standard applied to ΔQMCI of "*No statistically significant reduction*" is problematic because sample size is a key determinant of statistical significance in traditional null hypothesis-based statistics. As sample size increases, the detectable difference between two sample means decreases (i.e. the larger the sample, the more likely that a statistically significant result will be produced). I recommend that a standard based on ecological significance (rather than statistical significance) be used. For example, "Maintain existing QMCI values within given range of values relevant to that stream (i.e., >120, 100-120, 80-100 etc.)."

Schedule D: Standards Key (D-18).

4 I have comments on the following terms used:

4.1 "Periphyton (rivers)" - The appropriate statistic for algal biomass (Chl *a*; mg/m^2) needs to be defined. Is it annual average or maximum?

4.2 "DRP" -"*The annual average concentration...shall not exceed...unless natural levels already exceed this standard*". and "SIN". - "*The annual average concentration...shall not exceed...unless natural levels already exceed this standard*". The biggest issue I see here is the definition of "natural levels" – where do these values comes from?

4.3 Accordingly, I recommend the following alternative wording "*The annual average concentration...shall not exceed* *measured or modelled annual average concentrations under appropriate reference conditions. If appropriate reference conditions are not available the annual average concentration…shall not exceed 0.444 g/m*^{3} *SIN OR 0.015 g/m*^{3} *DRP ".* Table D.2a would need to be populated with appropriate reference conditions.

4.4 It is my view that significant uncertainty exists between the levels of DRP and SIN in Table D.2a and periphyton biomass, which is the dependent variable of interest for the purposes of managing a range of values. For this reason I would prefer to see nutrient targets (not "standards") linked to reference conditions estimated through direct measurement or modelling (e.g. CLUES), wherever practicable.

Dr Michael Scarsbrook
3 March 2010

APPENDIX C – ARTICLES ABOUT THE EFFECTS OF TROUT ON STREAM ECOSYSTEMS

Ecological Applications, 4(4), 1994, pp. 798–807

COMMUNITY-WIDE CONSEQUENCES OF TROUT INTRODUCTION IN NEW ZEALAND STREAMS[1]

ALEXANDER S. FLECKER[2] AND COLIN R. TOWNSEND
Department of Zoology, University of Otago, Dunedin, New Zealand

Abstract. Trout provide one of the prime illustrations of the willful introduction of living organisms for recreational purposes. In New Zealand, brown trout were first liberated in the 1860s; today trout are so ubiquitous in the country that they have become enshrined in New Zealand culture. There is abundant evidence that in many streams, trout have largely replaced the indigenous galaxiid fishes. It remains unclear, however, whether their effects in stream communities have propagated through multiple trophic levels.

Here we performed a pair of field experiments to compare the relative impacts of introduced and native fishes on the structure of a New Zealand stream community. We found large differences in the insect assemblages colonizing experimental channels, depending on the fish species present. In general, insect densities and biomass were lowest in channels containing trout compared to either galaxias or no fish treatments. Effects of trout on insect diversity were, however, relatively minor. The influence of fishes on insect abundance cascaded to the bottom trophic level, as algal standing crop was greatest in the presence of trout.

These results suggest that the consequences of trout may extend beyond the replacement of native fish species. Although our approach allows us to ask whether the potential exists for community-wide impacts of invasive fishes, it remains unclear whether multiple trophic-level effects will be readily detectable in many ecological settings. The high degree of spatial and temporal heterogeneity common to running water systems, and the confounding effects of land-use transformations, may impede our ability to discern community-level changes following this and other species introductions.

Key words: biological invasions; community structure; field experiment; Galaxiidae; introduced species; New Zealand; predation; stream; trout.

INTRODUCTION

> *Twenty-five years ago not one of these rivers had the least interest for the angler . . . the rod of the fisherman never cast a shadow on their waters; every one of these mighty rivers, every one of the thousand creeks and streams that flow into them . . . were tenantless and profitless to the sportsman (Spackman 1892, as cited in McDowall 1990a).*
>
> *. . . brown trout have since been stocked in almost every conceivable lake, river, or stream, such that the present naturalized population encompasses every suitable ecological niche within the confines of New Zealand (MacCrimmon and Marshall 1968).*

One of the important challenges linking ecology and conservation is understanding how introduced species influence natural communities (e.g., Elton 1958, Diamond and Case 1986, Mooney and Drake 1986, Drake et al. 1989, Coblentz 1990, Soulé 1990, Pimm 1991). Biological invasions have been of interest to ecologists for decades (e.g., Elton 1958); however, the attention paid to introduced species is today of unprecedented proportions. A clear message from the growing literature is that our knowledge of invasion processes is limited, and serious shortcomings exist in our ability to establish reliable invasion "forecasting rules" (e.g., Mooney and Drake 1986, Drake et al. 1989, Simberloff 1990, Ramakrishnan 1991, Townsend 1991). Regrettably, the staging ground for advances in invasion ecology will occur within the continuing homogenization of the world's biotic realms.

Ecological studies of species introductions largely emphasize how invaders directly affect particular resident species (Simberloff 1990). Much of this work is strongly biased towards conspicuous species or species producing dramatic ecological disruptions (Simberloff 1981, 1985, 1990, Bertness 1984, Herbold and Moyle 1986). In contrast, relatively little is known about subtle effects of invaders on community organization, some of which may be indirect and cascade through multiple trophic levels. There is increasing evidence that indirect interactions are common in natural communities (e.g., Kerfoot and Sih 1987, Pimm 1991, Strauss 1991, Flecker 1992*a*), although effects are often not readily apparent and can be difficult to measure. Thus, the consequences of introduced species could be considerably underestimated by failing to adequately appreciate the importance of subtle impacts of biological invasions (see Pimm 1991, Townsend 1991, Allan and Flecker 1993).

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[1] Manuscript received 18 November 1992; revised 6 October 1993; accepted 9 December 1993.

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In this study, we experimentally examined multiple trophic-level effects of introduced brown trout (*Salmo trutta* L.) in New Zealand tussock grassland streams. Brown trout were first introduced by European settlers into Australasia during the 1860s and have been subsequently transferred to all continents of the world except Antarctica (MacCrimmon and Marshall 1968). In New Zealand, some 60 × 10^6 fish were liberated by 1920; today, brown trout are among the most widely distributed of the country's freshwater fishes (McDowall 1990*a*). There is growing evidence that trout have been a major source of population decline of native fishes and have completely replaced resident species in some locations (e.g., McDowall 1984, 1990*a*, *b*, Minns 1990, Townsend and Crowl 1991, Crowl et al. 1992). For example, Minns (1990) found from his extensive analysis of >4200 stream sites throughout New Zealand, that native fishes generally did not co-occur with exotic species. An issue that remains virtually unexplored, however, is the significance of such broadscale species substitutions to community organization.

The question of focus in this paper is: Does the replacement of native fishes by brown trout have potential community-level consequences in New Zealand tussock streams? Although species substitutions within the guild of insectivorous fishes have been documented, it is unclear whether the impacts are restricted to a single food web component, or whether they are propagated through multiple trophic levels. Understanding the community implications of species replacements is important in shaping our view of stream conservation. Clearly, species are not fully independent entities, and biotic and abiotic connections are essential for the maintenance of the integrity of running water systems.

Study site

The study was conducted in the Shag River, a stony-bottom stream located in Otago Province on the South Island of New Zealand. The Shag River originates in the Kakanui Mountains at an elevation of ≈1200 m and flows southeasterly for 84 km before reaching the Pacific Ocean. The study site is a third-order reach located at 600 m (170°24′ E, 45°11′ S) and varies in width from 2 to 4 m. The stream is open and unshaded, passing through grassland dominated by tussocks (mainly *Festuca* sp. and *Chionochloa rigida*) and shrubs (e.g., *Discaria toumatou*, *Olearia* sp., *Coprosma* sp., and *Aciphylla* spp.). The surrounding area has been grazed by sheep and cattle for >120 yr (Thompson 1949). The climate is typical of the central Otago region in that flows are relatively stable during the summer months when, in general, little rainfall occurs.

Fish fauna and food web complexity

New Zealand streams have a species-poor fish fauna. Characteristically, only two native fish species inhabit the upper reaches of the Shag River, the common river galaxias (Galaxiidae: *Galaxias* cf. *vulgaris*) and long-finned eel (Anguillidae: *Anguilla dieffenbachii*). Galaxiids are southern hemisphere salmoniform fishes, and, in New Zealand, some species are referred to as native or Maori trout. Both galaxiids and eels are predators of invertebrates, although eels become piscivorous once they attain a large body size (McDowall 1990*a*). In addition, the Shag River contains introduced brown trout (Salmonidae: *Salmo trutta*), which were first released into the lower reaches in 1869 by the Otago Acclimatisation Society (Otago Acclimatisation Society 1964). It is unclear when trout first invaded higher elevation sites, because several groups of small waterfalls may have acted as barriers to dispersal. The first known introduction into the study reach was recorded in the 1930s and came from a different genetic stock than the original population (D. Scott, *personal communication*). Like galaxiids, the diet of brown trout is composed mainly of invertebrates; however, larger trout also prey on small galaxiids when present (Crowl et al. 1992). Diet overlap between trout and common river galaxias has led some authors to speculate that interspecific competition might occur between these species (e.g., Cadwallader 1975, Crowl et al. 1992). The occurrence of both trout and galaxiids in the Shag River contrasts with many streams in the region in which the two taxa do not coexist (Townsend and Crowl 1991, Crowl et al. 1992).

Trophic structure in the Shag River during the summer months is relatively simple. Less than 10 taxa of fish and invertebrates comprise the vast bulk of individuals and biomass in the community. Many species can be classified into feeding guilds or functional groups, although some undergo ontogenetic shifts in diet. Virtually all benthic invertebrates found in the Shag River can be considered either browsers (i.e., feed on algae and detritus), filter feeders, or predators (Cowie 1980, Ryder 1983). Thus, there are few food web components, especially if trophically analogous taxa are grouped together as "trophic species" (see Martinez 1991).

METHODS

Experimental design

Our major objective was to explore whether the replacement of native *Galaxias* fishes by introduced brown trout has potential community-wide consequences in New Zealand tussock streams. We conducted two field experiments that compared the effects of the different fish species on lower trophic levels. We aimed to examine: (a) whether stream fishes were strong determinants of patterns of invertebrate abundance, (b) how the fish species might differentially affect insect assemblages, and (c) whether impacts of fishes on insects might cascade to the bottom trophic level (i.e., the algal–detritus resource base).

The first experiment was conducted in January 1992, during the early weeks of the austral summer. Three treatments were established using in situ flow-through stream channels: (1) no fish, (2) galaxiid enclosure, and (3) juvenile brown trout enclosure. Experimental channels were constructed from 5 m lengths of PVC plastic sewer pipe (38 cm inner diameter) cut longitudinally. Each stream channel contained a set of removable screens (7 mm mesh) at each end, permitting free immigration and emigration of invertebrates, but preventing the passage of fishes. The bottom of each channel was covered with a layer of gravel overlaid by cobbles. Substrata were collected from the stream and scrubbed in order to remove attached invertebrates and periphyton. The three experimental treatments were replicated in four randomized complete blocks for a total of 12 channels. Blocks were located in a 0.8-km section of stream, and each block was separated by at least 100 m.

Eight *Galaxias* or juvenile trout were added to each of the experimental enclosures. We attempted to evenly size the two fish species used in the experiment. Galaxias were slightly longer than the juvenile trout (galaxias fork length $\bar{X} \pm 1$ SE = 90.7 ± 1.8 mm; trout fork length 85.3 ± 1.3 mm; $P < 0.02$). Conversely, trout biomass (7.4 ± 0.4 g) was slightly greater than galaxias biomass (6.2 ± 0.4 g), although these differences were not significant ($0.05 < P < 0.10$). Fish biomass represented values from the higher end of the natural range observed in Otago streams (A. D. Huryn and T. A. Crowl, *unpublished data*). Galaxiids were collected in the study reach, whereas juvenile trout were captured in a reach farther downstream containing high trout densities. Fish were collected using a backpack electrofisher and kept in field holding pens for ≈24 h before being added to enclosure channels.

We allowed an initial 10-d period for colonization by algae and invertebrates before stocking fish in any of the channels. We then added fish to the appropriate treatments, placed nylon net covers (3.5 mm mesh) over all channels, and ran the experiment for another 10–11-d period. End screens were brushed gently once each day in order to prevent the mesh from clogging. The experiment was taken down in blocks over a 2-d period for logistical reasons.

At the end of the experiment, a set of fine-mesh nets (200 μm) was placed at both ends of all channels within a block to prevent the escape of invertebrates. Before collecting invertebrates, we measured the size of distinct grazing bands that had developed on the channel walls. Insects were washed from the substrates into the end nets and preserved in 95% ethanol mixed with rose bengal as a colorant. In addition, a 24.6 cm² circle of periphyton was removed with a brush from the top surface of five randomly chosen cobbles from each channel. Algal samples were filtered in the field onto glass fiber filters (Whatman GF/C), wrapped in foil, and immediately preserved on ice.

Invertebrate and algal samples were processed in the laboratory. Invertebrate samples were washed through a 1-mm sieve, which retained the vast majority of insects. Smaller invertebrates (<10 mm body length) were subsampled (≈15% of individuals), whereas larger individuals (≥10 mm body length) were sorted from the entire channel collection. Invertebrates were identified (generally to genus or species) using available keys (e.g., Winterbourn and Gregson 1989). Filtered algal samples were analyzed for chlorophyll *a* and ash-free dry mass (AFDM), as measures of algal standing crop. Chlorophyll was extracted in 90% ethanol and corrected for phaeophytin following methods described by Nusch (1980). After pigment extraction, ash-free dry mass was determined from each algal sample. Samples were dried in an oven at 60°C for 24 h, weighed, ashed in a muffle furnace at 550° for 2 h, and reweighed.

The second experiment was conducted in late summer (March 1992). This experiment differed from the previous one in several ways; however, the main fish treatments were similar. Three fish treatments were established in each of four blocks, corresponding to those described above. Unlike the earlier experiment, channels were divided into two equally sized sections (2.5 m each) using coarse mesh (3.5 mm) partitions placed at the midpoint. In each upstream channel section, an ambient nutrient treatment was maintained, whereas nutrients were added to the downstream sections. Here, we report results from the ambient nutrient sections only, because these provide the comparisons pertinent to the main objectives in this paper. Details about procedures of this experiment are the same as those described above unless noted otherwise.

Statistical analyses

The experiments were analyzed as randomized complete block designs, with blocks representing different locations in the stream (Anderson and McLean 1974). Data were log transformed for taxa in which the variances were not homogeneous. Differences between treatments in the number of invertebrates and algal standing crop (i.e., AFDM and chlorophyll *a*) were analyzed using ANOVA (randomized complete block model). In addition, two a priori orthogonal contrasts (Kirk 1982) were performed that tested for: (1) fish predation effect (fish exclusion vs. galaxias plus trout treatments) and (2) predator species effect (galaxias vs. trout). Because contrasts were both orthogonal and planned, we used a contrast (rather than experimentwise) alpha value of 0.05 as the critical value for considering treatments significantly different (Kirk 1982).

There were few common taxa. We established as a criterion for analyzing a taxon separately that a mean density of >50 individuals/m² be found in at least one treatment. We also analyzed large invertebrate predators (i.e., ≥10 mm body length) even when they failed to meet the above criterion. All statistical analyses were performed using Statistix Version 1.1 (1986).

TABLE 1. Summary of insect densities (number/m², mean ± 1 SE) for different fish treatments from Shag River Experiment 1. No Fish = Fish exclusion channels; Galaxias = Galaxias enclosure channels; Trout = Trout enclosure channels.

	No fish	Galaxias	Trout
Deleatidium	2952.2 ± 255.6	2528.7 ± 392.1	1635.7 ± 265.2
Olinga	947.8 ± 88.2	789.0 ± 68.5	621.9 ± 108.8
Helicopsyche	70.8 ± 17.6	117.2 ± 30.9	30.7 ± 10.8
Total grazers	4003.2 ± 242.5	3462.8 ± 403.3	2317.4 ± 360.6
Coloburiscus	115.6 ± 31.0	158.2 ± 47.0	110.2 ± 25.5
Austrosimulium	167.4 ± 42.5	87.4 ± 20.8	74.2 ± 34.8
Stenoperla	8.2 ± 1.6	8.3 ± 2.3	4.2 ± 1.4
Archichaulodes	2.6 ± 0.6	4.2 ± 1.6	1.2 ± 0.4
Hydrobiosid larvae	11.6 ± 1.1	9.6 ± 2.3	6.2 ± 0.7
Total predators	24.2 ± 2.8	24.8 ± 4.8	12.8 ± 2.2
Total invertebrates	4502.0 ± 190.2	3952.6 ± 456.8	2685.3 ± 404.0
Invertebrate biomass (g/m²)	2.90 ± 0.07	2.90 ± 0.26	1.71 ± 0.28
Species richness	25.5 ± 1.0	24.2 ± 1.0	23.2 ± 0.6
Chlorophyll *a* (μg/cm²)	0.36 ± 0.06	1.18 ± 0.32	1.89 ± 0.82
AFDM (mg/cm²)	4.0 ± 0.6	9.9 ± 2.3	16.2 ± 5.9

RESULTS

Effects on invertebrate abundance and biomass

Density and biomass of colonizing invertebrates were strongly influenced by the experimental treatments (Tables 1–4). In both experiments, densities of total insects were consistently lowest in channels with trout. In early summer (Experiment 1), a significant fish effect was observed (no fish vs. fish contrast, $P < 0.014$, Fig. 1a). Relative to the exclusion treatment, we found fewer total insects when either fish species was present. Nevertheless, there was a substantially greater reduction in insect numbers in trout ($\bar{X} \pm 1$ SE = 2685.3 ± 404.0 individuals/m²) compared to galaxias channels (3952.6 ± 456.8 individuals/m²) ($P < 0.018$, Fig. 1a).

By late summer (Experiment 2), we no longer detected a significant effect of fish per se (i.e., fish vs. no fish contrast, $P < 0.155$), but continued to observe strong overall differences among treatments (Tables 3 and 4). This was because there were highly significant reductions in total insect densities in trout ($\bar{X} \pm 1$ SE = 552.1 ± 99.7 individuals) compared to galaxias (987.4 ± 141.4 individuals/m²) treatments ($P < 0.010$, Fig. 2a).

In neither experiment were significant differences in biomass observed when fish and no fish treatments

TABLE 2. Summary of probabilities for ANOVAs testing for overall treatment effects and orthogonal contrasts for Shag River Experiment 1. ANOVAs were performed on log-transformed data for taxa indicated with an asterisk.

		Contrast	
	Overall	No fish vs. fish	Galaxias vs. trout
Deleatidium	.002	.003	.004
Olinga	.191	.121	.322
Helicopsyche	.099	.925	.039
Total grazers	.007	.009	.015
Coloburiscus	.364	.551	.207
Austrosimulium	.094	.038	.736
Stenoperla	.111	.279	.066
Hydrobiosid larvae*	.033	.028	.082
*Archichaulodes**	.017	.266	.008
Total large predators	.017	.105	.010
Total invertebrates	.010	.014	.018
Invertebrate biomass*	.011	.059	.007
Species richness	.083	.047	.263
Chlorophyll *a**	.034	.014	.460
AFDM*	.023	.010	.266

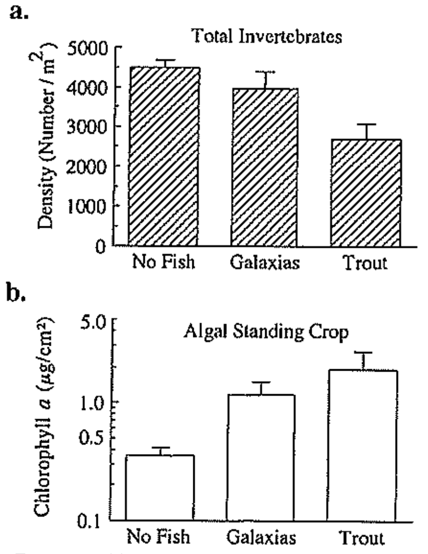

FIG. 1. Total invertebrate density (a) and algal standing crop (b) from the three fish treatments in Experiment 1 (January 1992) (means and 1 SE). Probability values for ANOVAs are given in Table 2.

TABLE 3. Summary of insect densities (number/m², mean ± 1 SE) for different fish treatments from Shag River Experiment 2. No Fish = Fish exclusion channels; Galaxias = Galaxias enclosure channels; Trout = Trout enclosure channels.

	No fish	Galaxias	Trout
Deleatidium	232.0 ± 35.0	202.7 ± 44.8	120.5 ± 25.8
Olinga	617.3 ± 134.3	714.9 ± 117.5	381.3 ± 83.3
Total grazers	873.7 ± 167.3	987.3 ± 104.9	518.2 ± 98.5
Stenoperla	14.5 ± 3.8	13.8 ± 3.7	10.5 ± 5.4
Total predators	16.3 ± 3.4	14.5 ± 3.9	11.3 ± 5.2
Total invertebrates	933.9 ± 162.2	987.4 ± 141.4	552.1 ± 99.7
Invertebrate biomass (g/m²)	2.04 ± 0.68	2.32 ± 0.74	1.21 ± 0.38
Species richness	16.5 ± 1.3	14.0 ± 2.0	13.5 ± 1.9
Chlorophyll *a* (µg/cm²)	0.90 ± 0.14	0.75 ± 0.19	2.00 ± 0.51
AFDM (mg/cm²)	9.7 ± 1.6	7.8 ± 2.8	18.2 ± 3.3

were compared. Insect biomass was remarkably similar between fish exclusion and galaxias channels (Tables 1–4, Fig. 3). In contrast, marked reductions in insect biomass were apparent in trout channels, with biomass generally ≈50–60% of that observed for the other two treatments (Experiment 1: $P < 0.007$, Tables 1 and 2; Experiment 2: $P < 0.026$, Tables 3 and 4).

Few invertebrate species were common, and only five taxa displayed densities >50 individuals/m² over both experiments (the mayflies *Deleatidium* spp. and *Coloburiscus humeralis*, the caddisflies *Olinga feredayi* and *Helicopsyche* sp., and black fly larvae *Austrosimulium* sp.) (Tables 1 and 3). Almost all taxa were less abundant in late summer, after many larval insects had emerged. Effects of the experimental treatments varied according to taxon and date (Tables 1–4). Perhaps the most striking feature was that densities of all taxa were lowest in trout channels compared to the other treatments, although, in some cases, differences were not statistically significant. In contrast, few generalizations could be made to collectively describe the responses of individual taxa to galaxias. In Experiment 1, for example, the most abundant taxon, *Deleatidium* spp., comprised >70% of browsing insects, and exhibited patterns similar to total invertebrates (i.e., densities in no fish channels > galaxias > trout, Table 1). On the other hand, the common caddis *Helicopsyche* displayed the greatest densities in the galaxias channels ($\bar{X} \pm 1$ SE = 117.2 ± 30.9 individuals/m²) relative to both the fish exclusion (70.8 ± 17.6 individuals/m²) and trout enclosure (30.7 ± 10.8 individuals/m²) treatments. Black fly larvae (*Austrosimulium*) displayed yet another pattern, with comparable reductions of black flies in both fish treatments irrespective of the predator species (Tables 1 and 2). Finally, trout markedly reduced the number of invertebrate predators in relation to the galaxias treatment ($P < 0.017$, Tables 1 and 2); however, there were no significant effects of fish per se, because invertebrate predator densities were similar between galaxias enclosures ($\bar{X} \pm 1$ SE = 24.8 ± 4.8) and fish exclusions (24.2 ± 2.8 individuals/m²).

TABLE 4. Summary of probabilities for ANOVAs testing for overall treatment effects and orthogonal contrasts for Shag River Experiment 2. ANOVAs were performed on log-transformed data for taxa indicated with an asterisk.

		Contrast	
	Overall	No fish vs. fish	Galaxias vs. trout
Deleatidium	.038	.052	.050
Olinga	.032	.433	.013
Total grazers	.020	.294	.008
Stenoperla	.715	.607	.544
Total large predators	.622	.466	.540
Total invertebrates	.019	.155	.010
Invertebrate biomass*	.059	.433	.026
Species richness	.011	.004	.506
Chlorophyll *a**	.051	.420	.022
AFDM*	.066	.636	.026

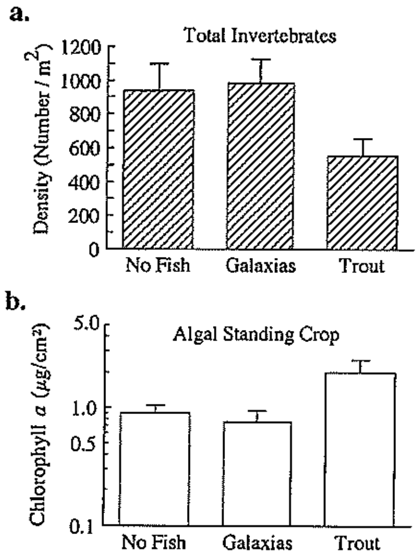

FIG. 2. Total invertebrate density (a) and algal standing crop (b) from the three fish treatments in Experiment 2 (March 1992) (means and 1 SE). Probability values for ANOVAs are given in Table 4.

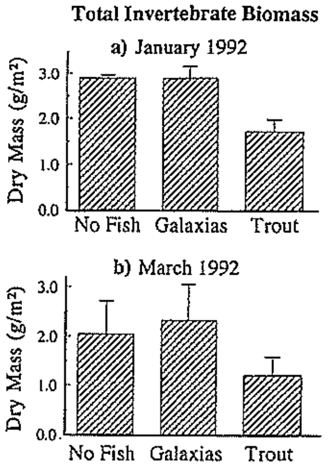

FIG. 3. Total invertebrate biomass from each of the three treatments in the January experiment (a) and March experiment (b) (means and 1 SE). Probability values for ANOVAs are given in Tables 2 and 4.

Only two taxa (*Deleatidium* and *Olinga*) were common in the late summer experiment, and these displayed qualitatively similar patterns (Tables 3 and 4). Strong overall treatment effects were observed for both taxa, yet there were no significant differences when contrasting the fish and no fish treatments. Instead, both taxa displayed significant density reductions in trout channels relative to the galaxias treatment. In contrast to the earlier experiment, no significant differences were observed for large invertebrate predators, although densities were again lowest in trout enclosure channels.

Invertebrate diversity

Approximately 20–25 insect taxa colonized each of the channels during the early summer experiment. Slight differences in species richness were observed among treatments, although the effect was not significant in the overall analysis ($P < 0.083$, Tables 1 and 2). Nevertheless, the small reduction in species richness in channels with fish was significant when contrasted to the fish exclusions (i.e., no fish vs. fish contrast, $P < 0.047$), with a typical decrease of 1–2 insect species.

Similar trends were observed in the late summer experiment, although fewer species of insects were collected (12–17 species per channel) (Tables 3 and 4). In this case, the overall analysis was significant ($P < 0.011$), and a significant fish effect was observed on species richness ($P < 0.004$), but no differences were found in relation to fish species.

Effects on algal standing crop

In both experiments, algal standing crops and total invertebrate density exhibited inverse patterns (Figs. 1 and 2; Tables 1–4). In early summer, algal standing crop from trout channels was >4–5× that of fish exclusions, whereas values in galaxias enclosures were intermediate between trout and no fish treatments (Table 1, Fig. 1b). In this experiment, a significant fish effect on algal standing crop was observed (chlorophyll *a*: $P < 0.034$; AFDM: $P < 0.023$); however, fish species did not differ significantly in their effect on algal standing crop (Table 2). In the late summer experiment, strong treatments differences were once again observed; algal standing crop was greater in trout channels than in galaxias channels (chlorophyll *a*: $P < 0.022$; AFDM: $P < 0.026$) (Fig. 2b, Tables 3 and 4).

Finally, grazing insects left distinct grazing scars (i.e., areas cleared of algae) that differed strongly among treatments (Fig. 4). Insects thoroughly grazed stones and channels when fish were excluded, resulting in wide grazing bands along the channel walls. This contrasted sharply with significantly narrower grazing bands in channels with fish (no fish vs. fish contrast, $P < 0.001$). Moreover, grazing band width was highly dependent on fish species; the width of scars measured in the trout enclosures was about half that in galaxias channels (galaxias vs. trout contrast, $P < 0.008$). These observations suggest that foraging activity of grazing insects may be differentially constrained by the two fish species. This could result if grazers are foraging different distances from refugia in relation to varying predation hazard.

DISCUSSION

Trout provide one of the best illustrations of the willful introduction of fishes in running water communities (MacCrimmon and Marshall 1968, Mac-

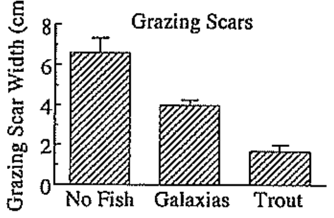

FIG. 4. Width of algal grazing band from the three experimental treatments in the January experiment (means and 1 SE). Probability values are given in *Results: Effects on algal standing crop.*

Crimmon 1971). Historically, questions about their ecological impacts were not thoroughly explored due to social, political, and scientific factors. Recently, a number of reviews have evaluated stream fish introductions (e.g., Courtenay and Stauffer 1984, Moyle 1986, Moyle et al. 1986, Williams et al. 1989, Crowl et al. 1992). The general focus has been on the repercussions of fish invasions for indigenous fish assemblages via a suite of ecological and genetic mechanisms. Such invasions are believed to be one of the major sources of population decline for native stream fishes (e.g., Williams et al. 1989, Moyle and Williams 1990, Allan and Flecker 1993). However, in stream communities there has been remarkably little effort to extend this line of inquiry to other trophic levels. Contrasting with this is the rich literature on multiple trophic-level effects of introduced species in lakes and ponds (e.g., Zaret and Paine 1973, Carpenter 1988, McQueen 1990, Spencer et al. 1991, Carpenter and Kitchell 1992, DeMelo et al. 1992), some of which has formed the basis of the current controversy about whether the introduction of piscivorous species is an effective management tool for controlling algal productivity in lakes (see Carpenter et al. 1985, Gulati et al. 1990).

Here we found differences in the interactions between common river galaxias and brown trout involving lower trophic levels. In our experiments, brown trout caused a consistent reduction in insect abundance, relative to both galaxias and the absence of fish. These effects were manifested in the bottom trophic level where the greatest algal standing crops were measured when trout were present. In contrast, the impacts of native galaxias were considerably more complex and variable. These included density reductions (*Deleatidium* and *Austrosimilium*), increases (*Helicopsyche*), or no effects at all (e.g., large invertebrate predators), depending on the insect species and the seasonal timing of the experiment. Likewise, algal responses reflected the abundance of insect grazers (Figs. 1 and 2). Thus, the consequences of species substitutions in the guild of insectivorous fishes can propagate to the bottom trophic level in this tussock stream community.

We suggest that at least two mechanisms are important in explaining the "top-down" effects of fish that we observed. First, insect density was significantly influenced by fish treatment (Tables 1 and 2). Grazing insects, in particular, displayed strong reductions in response to fish. Further, grazers comprised the major component of the insect assemblage in terms of numbers of individuals. In addition to top-down effects on grazer density, fish appeared to modify insect foraging behavior. This was manifested as differences among treatments in the width of insect grazing scars. Large grazing scars were found in the complete absence of fish (Fig. 4). Moreover, grazing scars were significantly wider in galaxiid compared to trout channels. These patterns suggest that fish constrain activity of grazing invertebrates, whereby the distances that insects venture from refugia differ according to fish species. This interpretation would be consistent with findings that fish modify stream invertebrate behaviors and limit the amount of time foragers spend on exposed surfaces outside of refugia (e.g., Kohler and McPeek 1989, Culp et al. 1991, Huang and Sih 1991, McIntosh and Townsend 1994).

Evidence for community-wide effects of invaders

Whether impacts of invasive species are generally propagated throughout entire communities is a subject of current debate. Certainly, some classes of invaders are likely to wreak havoc in natural systems, especially taxa that constitute new habitat, modify existing habitat, or represent ecological novelties in "naive" communities (Vitousek 1986, Simberloff 1990, Pimm 1991). Based on a literature review, Simberloff (1981, 1990) concluded that there is little evidence that introductions generally result in community-level effects (also see Ebenhard 1988, Lodge 1993). Simberloff argued that in the vast majority of cases, natural communities are resistant to invasions, which add rather than subtract species to communities, and fail to precipitate a chain of secondary extinctions. Furthermore, he contended that innocuous introductions are hardly noticed and rarely reported by the casual observer and reasoned that the bias in this largely anecdotal literature may be towards overestimating the prevalence of community-level impacts.

Several authors have questioned Simberloff's bold assertion (e.g., Herbold and Moyle 1986, Pimm 1991). Herbold and Moyle (1986) maintained that complex effects of introduced species are rarely detected, because they are seldom examined. They suggested that, to the contrary, this has resulted in underestimations of the impacts of introduced species. Moreover, Simberloff's review (1981) considered "effects" as extinctions only, thus overlooking changes in densities which may be the more common community-level consequence of invasions. In his assessment of the invasion literature, Pimm (1991) arrived at the conclusion that species introductions do indeed affect community composition in most cases. He generated a series of predictions about community resistance to invasion based on food web theory, relying on a selected subset of studies to support his arguments. Likewise, Vitousek (1986) examined the evidence that biological invasions can strongly modify ecosystem function. After reviewing a variety of pertinent studies, he concluded unequivocally that ecosystem properties can be altered by invasions in otherwise intact ecosystems. Linked with changes in ecosystem function were effects of invaders on community structure.

This debate serves to underscore that surprisingly few data exist that address the consequences of species introductions at the community level (Simberloff 1990). In particular, relatively little is understood about invasions in which a species substitution occurs within an already existent guild in a community. The direct and indirect effects of species replacements involving ecological analogs may be comparatively subtle and therefore considerably more difficult to document.

How unique are New Zealand streams?

Can we expect to find multiple trophic-level effects of trout elsewhere? A number of authors have suggested that invasions on island ecosystems are often particularly successful. At least two explanations have been proposed: (1) food webs are frequently characterized as relatively simple on islands, and (2) island assemblages are often "naive," having little prior history with many ecological novelties when long isolated from mainlands (Pimm 1991). Classic examples of catastrophic introductions on islands include whole-scale declines of avifaunas from the Australian brown tree snake in Guam (Savidge 1987) and from invasions by mammalian predators in Hawaii (Ebenhard 1988).

Certainly New Zealand streams are species poor. If, indeed, low-diversity food webs are where community-wide consequences of predators are most likely to be manifested (Strong 1992, but see Pimm 1991), then the strong impacts of trout observed in our New Zealand stream may not be surprising. However, it is difficult to generalize about the relative complexity of food webs on islands as opposed to continental land masses. While the number of species on continents may be greater, we know little about the complexity of trophic interactions in different types of streams. Likewise, results from experimental studies in streams on the influence of fish predation are too equivocal to establish whether multi-trophic level effects are generally limited to running waters with few community constituents. Nevertheless, Power (1990*a*) recently described a spectacular four-tiered trophic cascade from a riverine food web in California, suggesting that strong community-level effects of predators can propagate in systems considerably more complex than the stream studied here.

Furthermore, it is hard to judge the degree to which trout represent ecological novelties in New Zealand stream communities. Both trout and galaxiids are insectivorous fishes, belonging to the order Salmoniformes. However, galaxiids are generally small, less aggressive, and considerably more nocturnal than trout. This contrasts with running water communities in North America where the introduction of trout has resulted in species and subspecies substitutions with other native salmonids, often via hybridization (e.g., Williams et al. 1989, Echelle 1991, Goodman 1991). Thus, in North American trout streams, it may not be easy to find species replacements resulting in striking community-level changes. Yet in some regions, trout have been introduced where drift-feeding fishes do not naturally occur, such as mid-elevation streams of the northern Andes (Flecker 1992*b*). In streams where a previously nonexistent guild has become established, community-level effects of invasions are likely to be more readily detectable.

Challenges in detecting community-level effects

Even if community-level effects of biological invasions are commonplace, numerous obstacles may impede our ability to discern their impacts. Notorious problems of spatial and temporal heterogeneity in streams have plagued investigators searching for mechanisms explaining patterns of distribution and abundance. Experimental studies in running waters have often required levels of replication that are ruled out for logistical reasons (see Allan 1984).

Challenges in detecting community-wide effects of introduced species are further complicated by the confounding influences of land use changes. In New Zealand, the onslaught of biological invasions associated with European settlement was accompanied by the widespread conversion of wildlands to pasture (Crosby 1986). Indeed, extensive landscape changes may have been important in setting the stage for successful introductions (see Elton 1958, Orians 1986). Moreover, substantial modifications in nutrient dynamics are likely to have ensued with the introduction of ruminant grazers and heavy fertilizer inputs. Such broadscale changes, whose local effects are not well understood, can only exacerbate problems in documenting impacts of species replacements.

Finally, we may never be able to understand fully the community-level changes that have followed poorly documented extinctions. One can only speculate on the contribution of trout to the extinction of the New Zealand grayling (Prototroctidae: *Prototroctes oxyrhynchus*). This endemic fish species was once so ubiquitous that early European settlers described their taking by the cartload (McDowall 1990*a*). Population declines were noted soon after the introduction of trout; by the turn of the century the species had largely disappeared, and it became extinct in the 1920s (McDowall 1990*a*, *c*). Unlike any living fish species in New Zealand today, the grayling was a highly specialized herbivore which scraped algae from stone surfaces. Evidence from other regions of the world indicates that such algivorous fishes can play a prominent functional role (e.g., Power et al. 1985, Power 1990*b*, Flecker 1992*a*). Interactions between trout, galaxiids and other trophic levels would almost certainly have been modified by the presence of an abundant and comparatively large vertebrate grazer. The demise of the grayling adds a further problematic dimension in attempts to reconstruct how trout introduction has affected the dynamics of New Zealand stream communities.

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Impacts of Introduced Salmonids on Native Galaxiids in New Zealand Upland Streams: A New Look at an Old Problem

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Abstract.—Since brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss* were introduced into New Zealand in the late 1800s, there has been a decline in the abundance of native fish that is often attributed to predation by them. The evidence is largely circumstantial, however, and habitat deterioration may also have played a role. Nor is predation the only means by which introduced trout might be having a negative impact on native fish. Studies of trout population stream ecology show that trout may consume the entire annual benthic insect production of streams, leading to a trophic cascade that is evident in the proliferation of periphyton in the relative absence of invertebrate grazing. Changes in the behavior of both benthic invertebrates and native fish are also believed to have resulted from trout predation. The observed level of benthos predation suggests that an additional impact of trout on native fish may function through a feedback loop: native fish may be less able to obtain food owing to changes in their own behavior, insect behavior, and insect abundance, all of which are induced by trout predation.

New Zealand is known globally for its trout fishing. Trout are abundant owing to extensive areas of hard-rock spawning gravel in small to medium-sized cool, clear-flowing streams in the upland headwaters of New Zealand's many rivers (Hobbs 1948). The size of the trout raises questions as to where the food/energy comes from for them to achieve such size (Hayes 1996a; Hayes et al. 2000). New Zealand's trout are all acclimatized from Europe and North America, having been introduced by settlers during the late 19th century (McDowall 1990a). Most widespread are brown trout *Salmo trutta*, but rainbow trout *Oncorhynchus mykiss* also occur widely and brook trout (also known as brook char) *Salvelinus fontinalis* are present intermittently (McDowall 1990a). There is a strong perception that the trout species introduced into New Zealand have had harmful impacts on the indigenous freshwater fish fauna, especially the galaxiids, which predominate among the country's rather sparse indigenous freshwater fishes (20 of about 36 species; McDowall 1990a, 2000). These alleged impacts have mostly been attributed to predation on the native species by trout (McDowall 1968; Townsend and Crowl 1991; Allibone and McIntosh 1999). However, growing knowledge of the way stream ecosystems function, both in New Zealand (Flecker and Townsend 1994; Huryn 1996, 1998; McIntosh and Townsend 1996; Biggs et al. 2000) and elsewhere (Mittelbach 1986; Gilliam et al. 1989; Power 1992; Cowan and Pekarsky 1994), suggests that other ecosystem processes may also be important in mediating the effects of the introduced trout on the native fauna and ecosystems. It is the purpose of the present paper to explore these processes and their role in the relationships between introduced trout and native galaxiid fishes in New Zealand streams.

Synopsis of the Evidence

Impacts of Trout on Galaxiids: Historical Perspectives

Trout have been highly successful in New Zealand streams. Their "fit" with existing habitats was very good (Moyle and Light 1996), and their success seems to have been almost inevitable (Townsend 1996); certainly, with hindsight it is no surprise. The abundance of cool, swift-flowing streams has undoubtedly been a major contributor to trout success. There was little concern about the effects of trout during the early years, as colonial New Zealand was euphoric about the superb trout fishing that was available (Spackman 1892). Concern for the conservation of native fish began to emerge in the 1960s (McDowall 1968), especially as knowledge of native species grew. These concerns were based mostly on the perception that indigenous fish now had reduced distributions and lowered abundance and that the distributions of native and exotic fish were becoming increasingly complementary (McDowall 1968). Quantitative

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evidence and causal explanations were often lacking, however.

This paucity of information is no surprise. As was usually the case when species were introduced into new habitats (especially in the 19th century), no studies were undertaken before or afterward to assess the potential or actual impacts. Moreover, until about the 1950s, New Zealand's indigenous freshwater fish fauna was so poorly known that there was little basis for comparison. Expressions of concern for native fish were provoked mostly by circumstantial evidence. In addition, proving these sorts of impacts is difficult around the world. Even in North America, where there has been vast research on salmonid fishes, it is still difficult to predict the effects of translocating one salmonid into the habitat of another or even to quantify the effects when such translocations have been undertaken (Fausch 1988; Moyle and Light 1996).

The impacts have sometimes been clearer in New Zealand lakes, such as those of the central North Island, where trout rapidly decimated prolific lacustrine stocks of *Galaxias brevipinnis*—to the extent that trout stocks were in major decline owing to the lack of a forage fish species. They were only "rescued" by the introduction of another indigenous forage fish *Retropinna retropinna*, which, for unknown reasons, has withstood trout predation on a sustained basis (McDowall 1990a, 1990b).

Concern about the apparent, though largely unquantified, decline and loss of stocks of various stream galaxiids has persisted. Habitat deterioration may have played a role in some parts of New Zealand, but this is an unlikely explanation for the decline of native fish in the many areas where stream habitats remain pristine; as a result, the decline in galaxiids has often been attributed to the impacts of trout. The situation became serious enough for the New Zealand Fish and Game Council, which manages New Zealand's trout fisheries, to commission a review of the status of native fish and the threat to them from introduced trout (Allibone and McIntosh 1999).

New Zealand is not unique in its concern about the impacts of trout, especially brown trout, on indigenous galaxiids. There are similar concerns in Australia (Tilzey 1976; Jackson 1981; Lintermans 2000), southern Africa (Ashton et al. 1986), and even the Falkland Islands (McDowall et al. 2001). Ault and White (1994) examined the habitat preferences of brown trout and *G. truttaceus* in Tasmania, claiming that there is "strong evidence that [trout] adversely affect populations of *G. truttaceus*" and that the "similarity of their habitat preferences (in allopatry) strongly suggest[s] . . . interspecific *competition*"; they then pointed to *G. truttaceus*'s having evolved little or no defense against large piscine *predators*" (present author's emphasis), but unsurprisingly conceded that "the causal mechanism [of the harmful impacts of trout] remains to be established." Similar impacts on galaxiids seem likely in Patagonian South America, where trout are widespread (Campos 1970; Navas 1987; Macchi et al. 1999), though such impacts are undocumented.

The Reproduction of Galaxiids and Trout

Upland New Zealand galaxiids spawn in spring (Cadwallader 1976; Allibone and McDowall 1997; Allibone and Townsend 1997; Moore et al. 1999). Larvae hatch at a length of about 10 mm and form small, loose shoals around slack margins of runs and pools. They continue shoaling over the summer until they are around 30–35 mm long (McDowall 1990a), when they become cryptic among the cobble substrate of streams (at least by day).

Brown trout spawn in autumn and early winter, and their young emerge from the gravel at around 30 mm in length during spring (Hobbs 1948). They, too, form loose shoals around slack margins of runs and pools and so will be cohabiting these waters with the much smaller young of galaxiids. When juvenile trout and shoaling galaxiids cooccur in the streams during spring and summer, the trout will always have a big size advantage over the galaxiids. Trout life history thus appears perfectly adapted for emerging trout juveniles to prey on the new cohort of galaxiid larvae and to compete with them for food and space. (There is perhaps a distinct irony that juvenile galaxiids may remain shoaling in open waters to avoid predation by the larger adult galaxiids living within the substrate cobbles of stream riffles and in doing so become vulnerable to trout predation.)

Introduced Trout and Stream Ecology in New Zealand

Allen (1951) endeavored to develop a food-growth budget for the trout population of a New Zealand stream and found that the stream produced inadequate food to support its trout population. Huryn (1996) readdressed this question—not for Allen's Horokiwi Stream, since its trout population was nearly defunct owing to habitat degradation (Jellyman et al. 2000)—but for small streams in southern New Zealand. Like Allen, Huryn found that there was not enough benthic invertebrate production in the stream to support the observed growth of the trout, though this growth became possible when the food supply was augmented by the input of terrestrial and hyporheic invertebrates as well as trout cannibalism. Huryn (1996, 1998) compared ecosystem production from two neighboring tributaries of the Taieri River. In a "galaxiid" stream, less than 20% of benthic production was needed to maintain the fish stock, so that the rich benthic insect community remaining could graze periphyton production and prevent it from proliferating. In a similar "trout" stream, however, the trout preyed heavily on the benthos and so few insects remained to graze the periphyton that there was substantial periphyton proliferation. Biggs et al. (2000) similarly found that the periphyton biomass in several galaxiid streams was lower than that in comparable trout streams and attributed this to the higher biomass of herbivorous benthic insects in the galaxiid streams. Part of the difference in the intensity of prey consumption between galaxiid and trout streams may lie in the fact that trout feed during the long summer days in southern New Zealand, whereas the galaxiids feed during the reciprocally brief summer nights.

McIntosh (McIntosh and Townsend 1996, 1998; McIntosh 2000a, 2000b) compared the behavior of invertebrates in the presence of a native galaxiid predator with their behavior in the presence of brown trout (a novel, introduced predator) in both experimental channels and natural streams. He found that with galaxiids present prey animals spent more time on the exposed surfaces of substrate cobble but that with trout present they were more cryptic, spending more time beneath the cobble. This change of behavior in the presence of trout was interpreted as an evolved adaptive response by prey to heavier predation by trout. It may have implications for the benthic invertebrate drift and consequential impacts on fish feeding.

Thus, where trout population densities are high there are cascading effects on the stream ecosystem (Flecker and Townsend 1994; see also Power 1992; McIntosh and Townsend 1996); a combination of heavy predation by trout on the stream benthos, reduced numbers of insects, and less time being spent on exposed surfaces by invertebrates reduces the consumption of periphyton, which proliferates.

Recent Studies on Trout–Galaxiid Relationships

Townsend and Crowl (1991) examined in detail the relationships between galaxiids (which form a species complex in southern New Zealand; Allibone et al. 1996; Waters and Wallis 2001) and brown trout in one river system, the Taieri. A census of the fish populations across this system showed that trout and indigenous galaxiids had strongly complementary distributions. Of 198 sites examined, only trout were present at 71 sites; only galaxiids were found at 64 sites (typically in headwater streams above falls impassable to trout); both species were present at only 9 sites; and there no fish at 64 sites. The best predictor of the presence of galaxiids was the absence of trout (Townsend 1996). It was concluded that falls were preventing invasions by trout into "fringe" upstream habitats in these small waterways where galaxiids persist but from which trout were excluded. Allibone (1999) described strongly complementary distributions of trout and galaxiids in tributaries of Lake Mahinerangi (a hydroelectricity reservoir) on the Waipori River, a Taieri River tributary less intensively studied by Townsend and Crowl (1991). Although compelling, most of these observations were largely circumstantial: cause and effect were not explicitly identified.

The only study I am aware of that further pursued the question of trout impacts on galaxiids was in Australia, where Lintermans (2000) examined mutually exclusive distributions of rainbow trout and *G. olidus* in a small subalpine stream. Galaxiids were present in headwater streams inaccessible to trout, and trout were in a more downstream reach both above and below an impassable fall. It looked as though the downstream range of *G. olidus* was being limited by the presence of trout. Trout were removed above the barrier, and over a 4-year monitoring period the galaxiids spread downstream into the former trout habitat. Although trout persisted below the barrier, galaxiids were never observed there. It appears that prior to trout removal galaxiids moving downstream did not survive where trout were present and trout were preventing the occupation of this reach of stream by galaxiids. Again, the evidence for trout impacts was circumstantial, and the experiment has not been replicated (though the recovery of the galaxiid population after trout exclusion is compelling evidence for trout impacts on galaxiids).

Mechanisms of Trout Impacts

It has been usual to attribute native fish declines in the face of the trout invasion in New Zealand to predation by trout, or sometimes to competitive displacement (McDowall 1968, 1990a, 1990b;

Townsend and Crowl 1991; Townsend 1996; Allibone and McIntosh 1999). Early discussions of the impacts of trout on galaxiids (McDowall 1968) hypothesized disadvantages of an impoverished, indigenous, remote-island freshwater fish fauna when confronted with larger predatory species from a speciose, continental fauna, a notion that dates back to Darwin (1859; see also Darlington 1957; Elton 1958). Townsend and Crowl (1991) elaborated on this view, arguing that "predation is the most likely mechanism, . . . the strong predation effect [being] probably a result of New Zealand's comparative paucity of native piscivorous fishes, resulting in a native fish fauna having no evolved defenses." There are, no doubt, elements of truth in this view, but it may also be somewhat simplistic. Why, for instance, has the small endemic New Zealand freshwater snail *Potamopyrgus antipodarum* been so strikingly successful in Australia, Europe, and North America (Zaranko et al. 1997; Schreiber et al. 1998; Strayer 1999; Carlsson 2000)? It is easy to attribute causes to such effects but far harder to test such ideas rigorously.

The results of Townsend and Crowl (1991), with galaxiids upstream of falls and trout downstream, do engender the spectre of predatory trout waiting to engulf any galaxiids unwise enough to move downstream. This spectre is reinforced by laboratory observations by Crowl et al. (1992) and Glova (1990), which showed juvenile galaxiids to be vulnerable to trout predation in captivity. Similarly, there is little doubt that the trout populations of the central North Island lakes were initially "driven" by the rich food resource of lacustrine juveniles of *G. brevipinnis* until the prey populations succumbed to predation by the trout (McDowall 1990a, 1990b). Glova and Sagar (1993) concluded that "the more important mechanism in galaxiid–salmonid interactions appears to be predation," though they presented no data. But they also regarded predation as "most probably minimal, as the salmonids . . . comprised, almost exclusively, underyearling fish (too small to be a significant predator on galaxiids)." The possibility that small trout prey upon the much smaller, newly hatched larval and juvenile galaxiids during their co-occurrence in stream habitats in spring was not addressed.

The Role of Competitive Displacement

Indigenous fish may be no better adapted than stream insects to cope with the presence of trout. McIntosh et al. (1992), for instance, found that in artificial stream channels galaxiids spent less time in favored food-gathering sites when trout were present, the galaxiids presumably being unable (or unwilling) to compete with trout for these sites. Glova (1990) also argued for competitive displacement of galaxiids by trout based on agonistic interactions observed in a stream simulator. Despite these observations, Glova et al. (1992) surmised that temporal differences in feeding activity between galaxiids and trout "contribute substantially to lessening the interactions between them" and that overall there was "no apparent evidence of regulatory effect on the abundance and condition of galaxiid populations sympatric with salmonids. . . . The fish appeared to be in good condition" (though they presented no data on condition).

Other Likely Mechanisms of Trout Impacts

Though the tendency in the past has been to look at direct impacts between trout and galaxiids (like predation and competitive exclusion), the situation may not be that simple. It is becoming increasingly recognized that introduced organisms can have widespread effects on the connected aspects of biological communities. As Flecker (1992) pointed out, there has been a shift in focus from "the influence of predators on patterns of prey abundance to the consequences of predation on fish behaviors," with "fish predation [being] an important evolutionary force in shaping drift behavior of lotic mayflies" (see also Cowan and Pekarsky 1994). However, even more subtle interactions seem likely, and particularly feedback effects. These may involve altered animal behaviors that reduce the availability of resources shared with other species or feedback effects that influence interspecific interactions (Power et al. 1985; Gilliam et al. 1989; Wootton 1994). Flecker (1992) showed that "mayflies from . . . streams containing drift feeding fishes displayed a clear nighttime bias in drift" and, moreover, that the mayflies underwent "rapid evolutionary change in behavior when exposed to an exotic predator." That is, mayfly activity was increasingly restricted to the night hours "as predation risk became more intense." This apparently prevalent behavioral adaptation (Mittelbach 1986) may have varied indirect consequences that involve prey behavior and both inter- and intraspecific competition. When stream invertebrates are reduced in abundance and adopt more cryptic behavior, periphyton grazing may be curtailed, which would further depress benthic insect production as well as making the benthos less accessible to fish predators.

Tillyard (1920) long ago suggested that aquatic insect populations in New Zealand had declined as a result of trout predation. Allen (1951), and more recently, Huryn (1996, 1998) have shown that the trout populations present in some New Zealand streams can consume all available benthic invertebrate production. The work of McIntosh (McIntosh and Townsend 1996, 1998; McIntosh 2000a, 2000b) is consistent with Flecker's (1992) findings that novel behavioral traits evolved rapidly to reduce the predatory impacts of introduced trout; invertebrates in a New Zealand stream became more cryptic, spending more time beneath substrate cobble during the daytime when subjected to trout predation.

Impacts other than predation and competition are indicated if we bring together the results of the following New Zealand studies: (1) Huryn (1996, 1998) on the high levels of consumption of benthic prey by trout; (2) Flecker and Townsend (1994), McIntosh and Townsend (1996), and Biggs et al. (2000) on the trophic cascade resulting from heavy trout predation on the benthos, which leads to the proliferation of periphyton owing to low grazing pressure; (3) McIntosh and Townsend (1996, 1998) and McIntosh (2000a) on the behavior of benthic stream invertebrates in response to the introduction of trout and their predatory pressure on benthic prey; and (4) McIntosh (2000b) showing the modified behavior of galaxiids in response to the presence of trout.

Lima and Dill (1990) explored the general question of alterations in behavior by animals exposed to predation risk, pointing to the potential tradeoff between obtaining food or becoming food and concluding that animals are capable of evaluating the costs and benefits involved and modifying their behaviors accordingly (see also Milinski 1986). Possibly this principle applies to galaxiids, which may be more cryptic and spend less time feeding when exposed to trout predation (McIntosh 2000b). Is it then possible that an impact of trout on galaxiids in New Zealand streams is to so reduce the stream insect fauna (food) accessible to them and to so alter their foraging behavior that the galaxiids are seriously food limited? This will, in part, depend on what galaxiids eat and how they obtain their food.

The Diet of New Zealand's Upland Stream Galaxiids

All of the research undertaken on the diets of several indigenous galaxiids inhabiting gravelly headwater streams and rivers shows that they eat stream invertebrates almost exclusively (*G. vulgaris*: Cadwallader 1975; Glova and Sagar 1989a, 1989b, 1993; *G. divergens*: Hopkins 1965; *G. depressiceps*, *G. anomalus*, and *G. eldoni*, Allibone and Townsend 1998; *G. pullus*: Allibone and McDowall 1997; *G. paucispondylus*: Bonnett et al. 1989; Glova and Sagar 1993; *G. prognathus*: Bonnett et al. 1989; Glova and Sagar 1991). Less is known about the feeding behavior of these fish species, though they are thought to be (at least substantially) drift feeders (Cadwallader 1975; Glova and Sagar 1989a; Hayes 1996b; Allibone and McDowall 1997; Allibone and Townsend 1998). The galaxiids seem to adopt a feeding strategy not unlike that of trout (Glova 1990; Glova et al. 1992; Glova and Sagar 1993; Hayes et al. 2000). Thus, there would likely be overlap between galaxiids and trout, both in their feeding positions in streams and in the prey they consume, though there may be diel differences in the timing of feeding (Glova et al. 1992). In general, like brown trout, galaxiids seem to be opportunistic stream invertebrate predators, though they show a bias towards soft-bodied prey (Allibone and Townsend 1998). The overlap in foods taken by galaxiids and brown trout is broad (Glova and Sagar 1991, 1993; Glova et al. 1992).

Nocturnal Feeding Behavior of Galaxiids

Galaxiids are often described as nocturnal in behavior (Glova and Sagar 1989a, 1989b, 1991, 1993; McDowall 1990a; Glova et al. 1992; Biggs et al. 2000). This may provide temporal separation in feeding activity between the nocturnal galaxiids and crepuscular and diurnal trout (Glova and Sagar 1993). But, as discussed above, the short summer nights may restrict the duration of feeding by a nocturnal predator. The long nights of winter seem unlikely to compensate for the short summer nights, given the cold temperatures and likely low levels of activity of galaxiids in submontane streams during winter. The description of galaxiids as nocturnal may, however, be too broad a generalization. Allibone and Townsend (1998) and Allibone and McDowall (1997) reported that galaxiids in the upper Taieri River may also feed by day, and J. W. Hayes (Cawthron Institute, personal communication) has observed them drift feeding by day (Kakanui River). The growth of galaxiids appears to be very slow in the cold submontane streams of southern New Zealand, with some large adult fish showing little or no growth from one year to the next (Allibone and Townsend 1997).

Food availability may be particularly important to galaxiids seeking to sequester energy in preparation for spring spawning (Cadwallader 1976; Allibone and McDowall 1997; Allibone and Townsend 1997). Limited food availability and low temperatures may force galaxiids to seek food whenever it is available, and they may be less nocturnal in these upland streams than they are in less rigorous (warmer) environments. If galaxiids need to forage by day to meet their energy needs, the effects of trout in restricting diurnal foraging will be accentuated.

Conclusions

Predation by trout may be an important mechanism in the decline of galaxiids, as indicated by the complementary distributions of galaxiids and trout described by Townsend and Crowl (1991). Given their size and the timing of their availability, juvenile galaxiids may be providing a fine source of food for young trout during spring. Nor is there any reason to exclude competitive displacement as another mechanism for detrimental effects of trout on galaxiids. However, the work of Townsend and his various collaborators also suggests that the interactions between these taxa may be more complex: If (1) naturally occurring galaxiids in streams consume only a small proportion of the benthos of these streams, as argued by Huryn (1996, 1998), so that enough invertebrates remain to suppress the growth of substrate periphyton by their grazing (Flecker and Townsend 1994; Biggs et al. 2000); (2) by contrast, trout are consuming virtually the entire annual invertebrate production in at least some streams, as Allen (1951) and Huryn (1996, 1998) have argued, to the extent that insect populations are so reduced that there is a consequential proliferation of stream periphyton (Flecker and Townsend 1994; Biggs et al. 2000); (3) the intensity of trout predation on stream insects has induced a significant behavioral shift by leading to more cryptic behavior of prey and reduced benthic production (McIntosh 2000a), thus reducing prey accessibility; and (4) trout predation or agonistic behavior has also led to the exclusion of galaxiids from the best foraging sites and to increasingly nocturnal or cryptic behavior by the galaxiids, then one of the significant causes of the decline in stream galaxiids—and the complementary distributions of galaxiids and trout—seems likely to be that the galaxiids are seriously food limited owing to a combination of all of the above effects (despite the contention of Glova et al. 1992 that galaxiids suffered no loss of condition when coexisting with trout). Glova and Sagar's (1993) observation that galaxiids had lower stomach fullness when cohabiting with brown trout than those in a stream containing no trout is consistent with the view developed here that the presence of trout is constraining galaxiid food consumption. Though Glova and Sagar (1993) concluded that "competition for food and space in the streams [they had] studied was not serious," this conclusion can scarcely be derived from their data. If trout are feeding at the limits of stream benthos production (Allen 1951; Huryn 1996, 1998) and trout are more intensive exploiters of this food source than galaxiids (McIntosh 2000b), food may be a seriously limiting resource for galaxiids.

Allibone and Townsend (1998) have suggested that some upland stream galaxiids focus their predation on soft-bodied invertebrates, whereas trout forage on a wider range of invertebrates (Glova and Sagar 1993). If galaxiids eat a narrower range of invertebrates than is present in streams and consumed by trout, this might further constrain their food choices. Whatever the causes, reduced food supplies have implications for the survival, growth, and ultimately reproductive output of galaxiids.

Given the known ability of trout to prey on galaxiids, predation remains a potentially serious impact. And the fact that galaxiids may already be struggling to get enough food in the severely competitive food environment imposed on them by the invasion of trout may only intensify their need to hunt prey and thereby raise their risk of predation by trout. Food limitation thus seems highly likely to be a partial explanation for the disappearance of native species. The idea of a food shortage and competition between fish species is, of course, not novel, but the perspective added by the research on New Zealand streams and their benthic invertebrates, galaxiid fishes, and trout populations is certainly illuminating. While the effects of habitat degradation cannot be ignored, the impacts of trout on the native galaxiids seem to have been severe.

Future Research Options

How can these ideas be clarified? Only with difficulty, judging by the lack of success in examining these sorts of questions among the extraordinarily well-studied salmonids (Fausch 1988). Competitive interactions of this sort are not easy to document rigorously (Schoener 1982), especially when competition is so intense that one of the competitors is eliminated and there are several mechanisms that may be synergistic in their impacts. Moyle and Light (1996) enunciated a series of principles that may govern both the success and impacts of exotic species introductions. Of particular relevance to the New Zealand scenario is their contention that "[i]n systems that have been minimally altered by human activity fishes most likely to be successful invaders are top predators and omnivores/detritivores." Salmonids in New Zealand streams certainly fit the specification of top predators in minimally altered ecosystems. However, another of their principles, namely, that "[m]ost successful invaders are integrated without major negative effects (e.g., extirpations) on the community being invaded" has not proved correct for Salmonidae in New Zealand. Moyle and Light's (1996) caveat that "a relatively small number of species seem[s] to be responsible for most of the extirpations, reflecting a large number of introductions of predatory fishes, usually for sports fishing" is certainly apposite. Ross (1991) has generalized that "depauperate fish faunas [are] especially susceptible to successful establishment of nonnative fishes" (see also Leidy and Moyle 1998). By most criteria, New Zealand's freshwater fish fauna is depauperate (McDowall 1990a), and the country's relatively simply structured indigenous stream ecosystems, which have few trophic levels and low fish species diversity, seem likely to be bringing two generalized, opportunistic, drift-feeding invertebrate predators like brown trout and galaxiids into head-to-head competition for resources.

Further comparisons of benthic insect abundance between galaxiid and trout streams may clarify the effects of heavy trout predation on the benthos. It might be possible to observe and compare the behaviors of the two fish species when they occupy streams alone with what happens when they coexist. The prospect of introducing one species into the range of the other poses conservation and ethical questions that must be addressed with care. The results of interactions between the two species in artificial stream channels could be heuristic (McIntosh 2000a). Possible scenarios could be established whereby overlaps in the ranges of trout and galaxiids are generated by reversible manipulations of barriers to upstream migration by trout and trout removal (as was done by Lintermans 2000). This has been proposed by Allibone and McDowall (1997) for assisting the conservation of *G. pullus*, which appears to have been displaced by introduced brook trout. Any opportunities to observe the impacts of fish population manipulations should be exploited. Archival distribution records of New Zealand freshwater fish species show that some localities that once had populations of galaxiids no longer do. So the process of trout replacing galaxiids may still be going on. That being so, a search for sites where the behavioral and dietary interactions of trout and galaxiids can be examined ought to be a priority, as such sites would provide a scenario in which to study these interactions and clarify the processes of replacement. Understanding these processes can then form a basis for informed conservation protocols.

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