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The ecological transformation of Aotearoa/New Zealand



The impact of trout on galaxiid fishes in New Zealand

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Abstract: Compared with the effect of invaders on the native terrestrial fauna of New Zealand, interactions between native fishes and introduced trout (sports fish in the genera *Salmo*, *Oncorhynchus* and *Salvelinus*) are less well known and there have been fewer efforts to remedy their effects. Trout have caused widespread reductions in the distribution and abundance of native galaxiid fishes, a family dominated by threatened species. The effects have been most severe on non-diadromous species (those lacking a marine migratory stage), which are commonly eliminated from streams by trout. Galaxiid populations in lakes, and those with migratory 'whitebait' stages, have also been affected, but the extent of the impacts are less understood. The mechanisms controlling negative interactions between trout and native fish, and how the environment modifies those interactions, will be important for future management. Experiments and field comparisons indicate size-specific predation by trout is the main driver of negative interactions. Large trout (>150 mm long) do the greatest damage and small galaxiids (those with adult sizes <150 mm long) are the most at risk. The fry stage of non-diadromous galaxiids is particularly vulnerable. Despite galaxiid fry production in some trout-invaded reaches, often no fry survive making them population 'sinks' that must be sustained by adult dispersal. Trout are also associated with changes in galaxiid behaviour and alterations to stream benthic communities. However, effects on galaxiid growth and fecundity have been little studied. Recent work also indicates that habitat conditions, especially floods, low flows and natural acidity, can mediate trout–galaxiid interactions. We argue that managers should be more proactive in their response to the plight of galaxiids, and we identify avenues of research that will benefit native fish conservation activities in the future.

Keywords: exotic species management; disturbance; invasion; predation; Salmonid

Introduction

There has been widespread concern for the plight of the native terrestrial fauna of New Zealand in the face of repeated waves of species invasion, particularly by mammals. Indeed, scientific criticisms of mammalian introductions have been publicly voiced for over a century (e.g. Buller 1888), and organised attempts at locally eliminating terrestrial invaders in the name of conservation date to at least the 1950s (Thomas & Taylor 2002). In contrast, non-native fish invasions, particularly by members of the family Salmonidae, have only recently been recognised as contributing to the decline of New Zealand's native fishes. Trout (brown trout *Salmo trutta*; rainbow trout

Oncorhynchus mykiss; and brook charr *Salvelinus fontinalis*) were first imported in the 1800s to create recreational fisheries for European colonists (McDowall 1990a). The introductions were extremely successful and New Zealand is now home to world-class trout fisheries. However, actions aimed at reducing the impacts of trout on native fishes have not yet gained broad support from New Zealanders (Chadderton 2003).

The lack of action may partly reflect an inherent bias towards the conservation of terrestrial ecosystems (e.g. Allan & Flecker 1993), but that is not the whole story. New Zealand has a long history of freshwater ecology research with some renowned contributions (e.g. Allen 1951). Nevertheless, there was, and still is in some quarters, a perception that

trout have had a negligible effect on native fishes in New Zealand. This is evident, for example, in Druett's (1983: 128) summary of the introduction of trout to New Zealand: "The acclimatization of freshwater fish is remarkable among all the importations of animals into New Zealand in that it was an enterprise marked with cooperation and dedication, with no bitterness over the effect on other game or on native wildlife. Everyone saw a benefit and everyone worked towards the common goal of freshwater streams and lakes stocked with piscine beauties."

There were certainly some early remonstrations that trout were having a deleterious effect (e.g. Tillyard 1920), but these were rejected by the trout biologists. K. Radway Allen, for example, wrote: "Workers on various native aquatic animals have realized that the species they were interested in were subject to predation by trout and have suggested that this might threaten their survival. Generally, however, little evidence has been adduced as to the actual extent of the threat and one cannot avoid the feeling that sentiment has played an undue part in the formation of some of the opinions expressed" (Allen 1961: 67). In 1968, McDowall catalogued evidence of trout impacts on native fishes up to that time, in response to proposals to introduce another sports fish, the largemouth bass, *Micropterus salmoides*. Although bass were never introduced, much damage had already been done by trout, and trout liberations continued. It was not until the early 1990s that Townsend and Cowl (1991) convincingly implicated brown trout in the widespread disappearance of native fishes from within the family Galaxiidae.

The Townsend and Cowl (1991) study was revolutionary because, by examining fish distribution patterns in replicate sub-catchments of different land uses in the Taieri River catchment, Otago, it disentangled the influence of trout from the effects of habitat quality associated with land-use change. There had been a longstanding argument (both in Australia and New Zealand) that declines in native fish were due to deteriorating habitat conditions rather than the impacts of salmonid invasions (Weatherley & Lake 1967; Jowett et al. 1998). Certainly, large reductions in the distribution and abundance of native fish, particularly diadromous species (i.e. those migrating to the sea for some part of their lifecycle, see McDowall 1996) have occurred as a result of the land-use changes European settlers imposed on the New Zealand landscape (Hanchet 1990; Rowe et al. 1999; Eikaas & McIntosh 2006). However, in the Taieri study non-diadromous galaxiids were usually only found above barriers to trout invasion, irrespective of catchment conditions (Townsend & Cowl 1991).

Today there is more recognition that trout have had a deleterious influence on native fish (Deans et al. 2004), but progress with managing the threats trout pose to native fish biodiversity has been slow. Trout are found in virtually every accessible waterway on New Zealand's South and North islands, and certainly in every lake or stream thought capable of supporting a significant sports fishery. For example, in the tributaries of the upper Waimakariri River, Canterbury, that have been surveyed by University of Canterbury researchers over the last ten years, > 95% of the fish-occupied river length contains trout. Moreover, trout can be found even in relatively inaccessible streams and lakes of remote areas like Dusky Sound, Fiordland (N. R. Dunn pers. obs.). These observations, in conjunction with the imperilled status of many native fish species (Hitchmough et al. 2007), suggest more effort is needed to minimize existing and future threats imposed by trout on New Zealand's unique freshwater fish fauna.

In light of this situation, our goals here are three-fold. First, we summarise the state of knowledge on the influence of trout on native galaxiid fishes. Specifically, we highlight linkages between trout presence and galaxiid decline; outline the evidence for predation by trout as a potent, but context-dependent mechanism of galaxiid decline; review the sub-lethal and indirect effects of trout on galaxiids; and characterise the potential for environmental control on the outcome of trout encroachment into galaxiid habitats. Second, based on our review, we identify pressing knowledge gaps that, if filled, will enhance galaxiid conservation efforts. Lastly, we aim to stimulate more proactive management of trout to mitigate their impacts on native fish. Although we incorporate knowledge from prior syntheses of trout invasion influences in New Zealand, we refer the interested reader to Cowl et al. (1992), McDowall (2006), and Townsend (2003) for expanded historical, taxon-specific, and ecosystem-level reviews.

The role of trout in galaxiid declines

Members of the families Retropinnidae, Galaxiidae and Lepidogalaxiidae, collectively known as galaxioid fishes (Superfamily Galaxioidea *sensu* McDowall 2006), are "quintessential southern cool-temperate freshwater fishes" (2006: 235). Although they probably share a common salmoniform ancestor with Salmonidae, the galaxioid fishes have special features that make them the aquatic equivalents of New Zealand's unique and ancient avifauna (McDowall 2010), and they are the group of fishes most affected by trout invasions (McDowall 2006).

It is probably not a coincidence that their long evolutionary history in isolation from other salmoniform fish makes galaxioid fishes particularly vulnerable to trout (McDowall 1968; McDowall 1990b), just as isolation from mammals has endangered much of the New Zealand avifauna (Daugherty et al. 1993).

Members of Galaxiidae ('galaxiids' hereafter), the focus of our review, make up the majority of New Zealand's contemporary native freshwater fish fauna. Most species are endemic and at least 65% of New Zealand galaxiid taxa are regarded as threatened in New Zealand or by the World Conservation Union (Hitchmough et al. 2007; Table 1). Moreover, many galaxiid taxa have only recently been 'discovered'. A highly variable river galaxias inhabiting eastern South Island rivers, for instance, has been split into multiple distinct taxa (Waters & Wallis 2001; McDowall 2006) and other cryptic taxa have been described (Gleeson et al. 1999; Ling et al. 2001; McDowall & Waters 2002; McDowall & Waters 2003; McDowall 2004). Further taxa are recognised but await formal description, so the proportion threatened could be closer to 75% (Department of Conservation 2004). Consequently, the Galaxiidae rank amongst the "most endangered fish families in the world" (Helfman 2007).

Before reviewing evidence implicating trout as a key driver of galaxiid decline, it is important to understand the inferential barriers that have hampered efforts at establishing definitive cause-effect linkages. In contrast to the situations reviewed by Bellingham et al. (2010) and Innes et al. (2010) for terrestrial systems, detailed descriptions of galaxiid taxonomy and distribution were not compiled until after trout were dispersed throughout New Zealand (McDowall 2003). Historical accounts demonstrating galaxiid decline upon trout invasion, therefore, do not exist. As vexing as it may seem to

Table 1. List of salmonids (all introduced) and currently-described galaxiids (all native) found in New Zealand, with relevant conservation and life-history details, adapted from McDowall (2006) and Hitchmough et al. (2007).

Family	Common Name	Scientific Name	Diadromous/ Non-migratory	Conservation Status
Salmonidae (trout only)	brown trout	<i>Salmo trutta</i>	D	
	rainbow trout	<i>Oncorhynchus mykiss</i>	N	
	brook trout	<i>Salvelinus fontinalis</i>	N	
Galaxiidae	giant kokopu	<i>Galaxias argenteus</i>	D	gradual decline
	koaro	<i>G. brevipinnis</i>	D	
	banded kokopu	<i>G. fasciatus</i>	D	
	inanga	<i>G. maculatus</i>	D	
	shortjaw kokopu	<i>G. postvectis</i>	D	sparse
	roundhead galaxias	<i>G. anomalus</i>	N	gradual decline
	lowland longjaw galaxias	<i>G. cobitinis</i>	N	nationally critical
	flathead galaxias	<i>G. depressiceps</i>	N	gradual decline
	dwarf galaxias	<i>G. divergens</i>	N	gradual decline
	Eldon's galaxias	<i>G. eldoni</i>	N	nationally vulnerable
	dwarf inanga	<i>G. gracilis</i>	N	serious decline
	Gollum galaxias	<i>G. gollumoides</i>	N	gradual decline
	bignose galaxias	<i>G. macronasus</i>	N	gradual decline
	alpine galaxias	<i>G. paucispondylus</i>	N	
	upland longjaw galaxias	<i>G. prognathus</i>	N	gradual decline
	dusky galaxias	<i>G. pullus</i>	N	gradual decline
	Canterbury galaxias	<i>G. vulgaris</i>	N	
	brown mudfish	<i>Neochanna apoda</i>	N	gradual decline
	Canterbury mudfish	<i>N. burrowsius</i>	N	nationally endangered
	black mudfish	<i>N. diversus</i>	N	
	burgundy mudfish	<i>N. heleioides</i>	N	nationally endangered
	Chatham mudfish	<i>N. rekohua</i>	N	range restricted

those used to terrestrial conservation in New Zealand, there is also a paucity of contemporary data on population response to trout removal (but see Lintermans (2000) for an Australian example). Thus, the general conclusion of negative trout effects is built largely upon correlative studies that examine patterns in species distributions, supported by small-scale mechanistic studies. This applies to both non-diadromous (i.e. freshwater resident) and diadromous (i.e. sea-migratory) galaxiids, which we review in turn below.

Non-diadromous galaxiids

New Zealand non-diadromous galaxiids can be subdivided into four groups of fish; the riverine roundhead (*G. anomalus*, *G. eldoni*, *G. gollumoides*, *G. pullus*) and flathead (*G. depressiceps*, *G. vulgaris*) morphotypes which are similar in the current context; the pencil galaxiids (*G. cobitinis*, *G. divergens*, *G. macronasus*, *G. paucispondylus*, *G. prognathus*); the dune lake galaxias of Northland (*G. gracilis*); and the mudfishes in the genus *Neochanna*. All of these fish are small, with maximum adult total lengths less than 160 mm (most <125 mm). Available evidence suggests they are all vulnerable to the impacts associated with trout invasion.

The roundhead and flathead galaxiids generally occur where trout are absent, as described in the pioneering Taieri study (Townsend 1996). However, there are some important taxon- or catchment-specific variations on this general theme. *Galaxias anomalus* (Otago roundhead galaxias) occurs with trout more frequently than do other taxa in the Taieri River (Townsend 1996), but in the Manuherikia River system (Clutha River catchment) these species have disjunct distributions due to local hydrologic variation (Leprieur et al. 2006). In the Waipori River system in Otago, *G. eldoni* (Eldon's galaxias)

is not found with any other fish species (native or exotic) and *G. pullus* (dusky galaxias) occurs with trout (brook charr) at few sites (Allibone 1999). In streams of the upper Waimakariri River, Canterbury, McIntosh (2000a) found Canterbury galaxias (*G. vulgaris*) with both brown and rainbow trout more frequently than had been observed in the earlier Otago studies of the congeneric taxa (Allibone 1999; Townsend & Crowl 1991; Fig. 1). However, all records of co-occurrence in the Waimakariri study were at sites containing small trout (<150 mm) only. This pattern of size-dependent *G. vulgaris*–trout co-occurrence has been noted for other Canterbury streams (Cadwallader 1975; Glova et al. 1992).

Information on the pencil galaxiids is limited, but available data suggest trout have had an impact on them as well (Hopkins 1971; McIntosh 2000a; Harding et al. 2002; McDowall 2006). On the lower North Island, for example, Death and Death (2005) found that *G. divergens* abundance was two to six times higher above than below a barrier to brown trout invasion in the Wainuiomata River. Similarly, *G. paucispondylus* co-occurs with trout in the Waimakariri River when the trout are either small (<150 mm long) or present at very low levels (i.e. at highly disturbed sites; McIntosh 2000a, Howard 2007).

Less well studied are the effects of trout on the non-diadromous, lacustrine galaxiid assemblage of Northland. Coastal dune lakes contain several lineages of a very small (<80 mm long) and rare lake-dwelling galaxias, *G. gracilis*. While these lakes have been subject to multiple fish introductions (Rowe & Chisnall 1997), a full account by McDowall (2006) indicates *G. gracilis* populations have been impacted by trout introductions, as well as other non-native fishes (e.g. *Gambusia affinis*) and catchment land-use changes.

Lastly, though many mudfish (*Neochanna* spp.) occur in

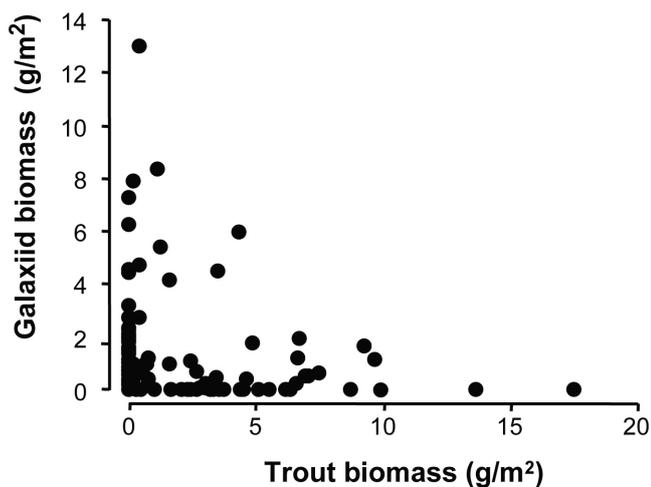


Figure 1. Fish densities (from electrofishing) in streams of the upper Waimakariri River system 1997–2007 indicating much higher rates of co-occurrence between galaxiids (*Galaxias vulgaris*, *G. paucispondylus*, and *G. brevipinnis* combined) and trout (brown [*Salmo trutta*] and rainbow trout [*Oncorhynchus mykiss*] combined) than typically observed in Otago streams (e.g. Townsend and Crowl 1991).

trout-free habitats (e.g. wetlands), instances of co-occurrence with trout can generate intense predator–prey interactions (O’Brien & Dunn 2007). This may in part explain the high level of complementarity in their distributions; there are no records of mudfish–trout co-occurrence for North Island-restricted species (*N. diversus*, *N. heleioides*), and for *N. apoda* and *N. burrowsius* co-occurrence has been observed at <2% of the sites in the New Zealand Freshwater Fish Database (NZFFD; O’Brien & Dunn 2007). Canterbury mudfish (*N. burrowsius*) has the highest recorded co-occurrence with trout (1.6%) of any mudfish species, as it inhabits small spring-fed streams that can provide suitable trout habitat. In one such stream, Eldon (1979) observed substantial predation by brown trout on *N. burrowsius* (e.g. 19 mudfish were found in seven trout stomachs).

Diadromous galaxiids

Correlative information on the influence of trout on the five New Zealand diadromous galaxiid species is poor, even relative to that of the non-diadromous species. First, the smallest species and most prolific contributor to the ‘whitebait’ (i.e. the upstream-migrant juvenile stage of diadromous galaxiids) catch, inanga (*G. maculatus*), is subject to heavy predation by sea-run brown trout (McDowall 2006). Inanga is nevertheless still widely distributed and appears to overlap with trout in many parts of its range. However, there are also clear examples of mutually exclusive inanga–trout distribution patterns (McDowall 2006), and a nationwide analysis revealed significant negative correlations between inanga and both rainbow and brown trout at the site level (Minns 1990).

The larger koaro, banded kokopu, shortjaw kokopu, and giant kokopu (*G. brevipinnis*, *G. fasciatus*, *G. postvectis* and *G. argenteus*, respectively), due to their ability to grow to a larger size than inanga, may have a greater chance for coexistence with trout (McDowall 2006). The three kokopu species are closely associated with instream and/or riparian cover, so their populations have been heavily affected by

forest clearance and other stream-habitat alterations. However, like inanga, kokopu and koaro whitebait are probably subject to high rates of predation by trout during their upstream migrations. There are examples of both adult fish co-occurring with trout, and non-overlapping distributions with trout. For example, McDowall et al. (1996) found no clear evidence that *G. postvectis* and trout had negative interactions, whereas Goodman (2002) demonstrated *G. postvectis* were half as likely to occur in reaches where trout were common than where they were rare. Similarly, Olsson et al. (2006) documented no distributional overlap for these two species. Further, in a survey of West Coast South Island rivers, Main et al. (1985) showed that trout and *G. fasciatus* seldom co-occur at the stream-reach scale. Equally variable in their relationship with trout, *G. argenteus* and trout overlapped in distribution in one survey (Bonnett & Sykes 2002), but rarely co-occurred in another (David et al. 2002).

There are examples of disjunct, complementary distributional patterns for trout and koaro in streams as well (Main et al. 1985; Bell 2001). However, the most compelling evidence that suggests trout have negatively affected koaro comes from lakes. Koaro often form landlocked populations in lakes, where they were very likely abundant and a major food source for Maori prior to trout introduction. Circumstantial accounts indicate that trout likely played a major role in the decline of lake-dwelling koaro populations, especially in the central North Island (McDowall 2006). Unfortunately, a general lack of sizeable trout-free koaro lakes renders it difficult to conduct a large-scale, multi-lake study analogous to those implicating trout in non-diadromous galaxiid decline. Thus, current understanding on the historical and contemporary impacts of non-native trout on lake-dwelling galaxiids is very limited.

In summary, the bulk of distributional data implicates trout in the decline of multiple diadromous and non-diadromous galaxiid populations. In addition, the above review highlights the considerable variability in the strength of trout effects for particular galaxiid species and/or specific locales. We discuss the implications of this variability for galaxiid conservation below.

Trout predation on galaxiids

A dominating feature of interactions between galaxiids and trout is that they are highly size-structured. All non-diadromous galaxiids, which reach maximum sizes of 90–150 mm (McDowall 2000), as well as juveniles and small diadromous individuals, are vulnerable to trout predation. This means the strength of interactions between trout and galaxiids can be determined largely by their disparity in size, the availability of alternative prey resources and/or predator-free refugia, and the underlying productivity of populations.

Size-dependent effects of predatory trout

The occurrence of galaxiids in trout diets is variable and not as high as one might initially expect if there were strong predatory interactions between these taxa (Allibone & McIntosh 1999). Besides the obvious problems of digestion and sample timing, galaxiids may only occur in trout diets in situations where the galaxiid populations are relatively robust. For example, smelt are very common in trout diets in North Island lakes where smelt production exceeds trout predation (Stephens 1984). Conversely, when predation is not sustainable, galaxiids

are likely to be eliminated and hence will no longer appear in trout diets. Lastly, galaxiids co-occur most frequently with small (<150 mm) trout which prey predominantly on invertebrates (Glova & Sagar 1991; Glova et al. 1992; Glova & Sagar 1993).

Experiments are therefore a more useful indicator of interaction strength. Predation trials in stream mesocosms indicate that when brown trout grow longer than 150 mm Fork Length (FL), they are capable of preying on all size classes of *Galaxias vulgaris*, even fish larger than 100 mm in length, whereas small trout (120–130 mm FL) consume only juvenile galaxiids (<60 mm FL; McIntosh 2000a). These results corroborate fish distribution patterns in the Waimakariri River headwaters, where *G. vulgaris* is consistently present in locations where small (<150 mm FL) but not large (>150 mm FL) trout are found (McIntosh 2000a). In another mesocosm experiment, Bonnett and McIntosh (2004) showed that brown trout <116 mm FL had little effect on inanga, whereas Glova (2003) showed larger (255–390 mm FL) brown trout could reduce inanga abundance (Glova 2003).

The consequences of size-specific predation are also evident, albeit in a correlative sense, in the relative abundance of different galaxiid size classes found in the wild. In a survey of the Shag River headwaters, non-diadromous galaxiids co-occurring with small trout (<100 mm) long had size distributions similar to those observed in troutless streams (Fig. 2), whereas small galaxiids were rare in streams containing medium brown trout (100–120 mm; (McIntosh et al. 1994). Thus, even relatively small trout may prey heavily on small galaxiids.

Collectively, these observations imply predation is one of the main drivers of interactions between trout and galaxiids in New Zealand, especially for non-diadromous species. Further, it is clear that trout size moderates the level of predatory impact on galaxiid populations. The corollary to this observation is that galaxiid size, be it life-stage or taxon specific, influences their susceptibility to predation.

Vulnerability of juvenile stages to trout predation

Non-diadromous galaxiids are particularly vulnerable to trout predation because they complete their entire development

in freshwater, including a stream-resident fry stage. The fry of non-diadromous galaxiids studied so far settle in slow-flowing backwater habitats (Jellyman & McIntosh 2008), and although there are species-level differences in fry behaviour, this habitat-use pattern renders them readily accessible to trout as prey. Trout spawned in the same year as galaxiids generally hatch earlier and have a size advantage from the outset. Accordingly, even trout fry (15–20 mm long) are capable of consuming galaxiid fry (Glova 1990; Crowl et al. 1992). The fry of non-diadromous galaxiid species behave in slightly different ways; for example *G. paucispondylus* fry are consistently more benthic when disturbed than *G. vulgaris* fry, which are generally pelagic (Dunn 2003). It remains to be seen whether these behavioural differences affect survivorship in trout-invaded waters.

Available experimental data support the assertion that galaxiid fry are particularly vulnerable to trout predation. In a recent comparison of fry survival patterns between fenced and unfenced backwaters located above and below a trout barrier, Jellyman (2004) demonstrated a clear demographic effect of trout presence on *G. vulgaris*. Fry declines were substantial in unfenced backwaters in the trout-invaded reach, but similar in fenced and unfenced backwaters above the barrier. This pattern matched the disparity in galaxiid fry survivorship documented in a survey of trout and troutless streams in the upper Waimakariri catchment. In that study, there was also a strong negative correlation between reach-scale trout biomass and juvenile-to-adulthood galaxiid survival (P. G. Jellyman & A. R. McIntosh, unpubl. ms.). Together, these results imply local recruitment is minimal in trout-invaded reaches. As a consequence, apparent trout–galaxiid ‘co-existence’ may be driven by landscape- (i.e. immigration) rather than local-scale (i.e. birth) population processes in some instances.

Formation of source–sink metapopulations

If predation risk is patchily distributed within invaded river networks, and these ‘riverscapes’ still contain isolated galaxiid populations (e.g. above barriers), a trout-induced, source–sink metapopulation scenario may develop. The potential for source–sink development is especially pronounced for diadromous galaxiids, as they can be locally productive, and

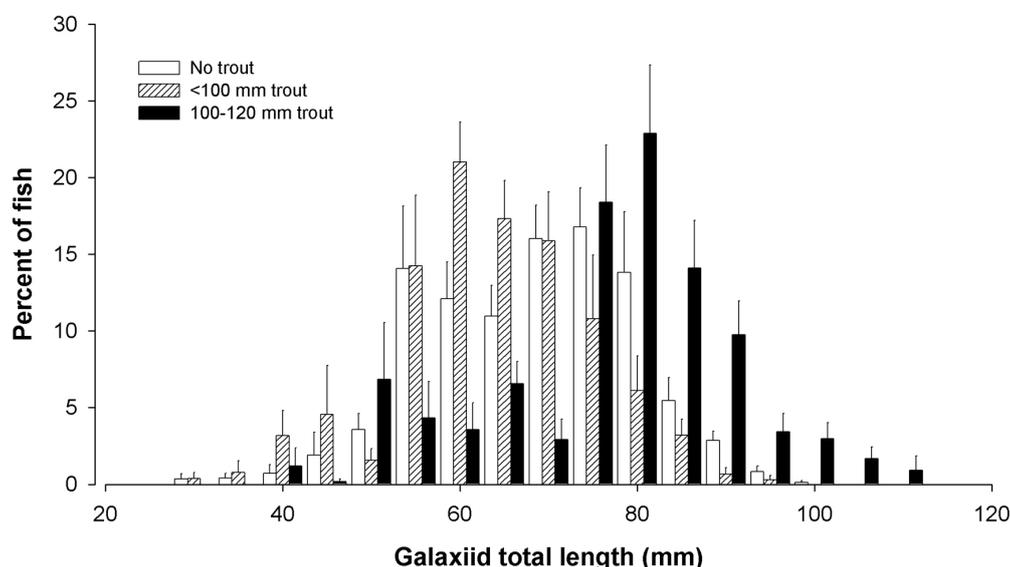


Figure 2. Size distribution of non-diadromous galaxiid populations from 19 locations in the Shag River with either no brown trout ($n = 7$), small (<100 mm Fork Length, FL) brown trout only ($n = 5$) or larger (100–120 mm FL) brown trout ($n = 7$). Bars indicate the mean percentage of a population (+ SE) in a size class (from McIntosh et al. 1994).

spawn larvae that disperse widely and home poorly (McDowall 1990a, 2006). Diadromous galaxiids may, as a result of these traits, begin their life in highly suitable habitats and end their life (perhaps prematurely) in marginally suitable streams. In extreme cases, adult and larval dynamics may be decoupled to such an extent that local population persistence is driven solely by an immigration subsidy (e.g. *Galaxias maculatus* in large West Coast, South Island rivers; MA Hickford & DR Schiel, unpubl. ms.). Nonetheless, if invaded and trout-free habitats are appropriately juxtaposed, diadromy may confer a level of resilience to local populations that might not otherwise exist (McDowall 1996).

Though non-diadromous galaxiids lack obligate migrant life stages, they too may form source–sink metapopulations in catchments containing non-native trout. As above, trout-invaded reaches may be reproductive sink habitats for non-diadromous galaxiids, as only the larger adults can survive and local recruitment seldom occurs under these circumstances (Jellyman 2004). Thus, local persistence must depend on the influx of adults from source habitats (such as those above barriers to trout). This possibility is being actively studied in Canterbury High Country streams, and initial results indicate *G. vulgaris* survives in many trout-invaded reaches due to immigration from troutless source populations rather than through local recruitment (Woodford & McIntosh in press).

Sub-lethal and/or indirect effects of trout on galaxiids

Although predatory impacts of trout are probably a main contributor to galaxiid declines, trout probably also affect galaxiids via other pathways. Possibilities include negative direct effects of trout on galaxiid behaviour, and indirect effects on galaxiid fitness via direct trout influences on the abundance or behaviour of their main food, stream invertebrates. Further, in rare instances, the presence of trout might even benefit galaxiids through complex, indirect interactions. Each of these possibilities has received relatively little attention (McDowall 2003).

First, the results from a pioneering study on trout production and their food supplies (Allen 1951), known as the “Allen paradox”, showed benthic production was insufficient to sustain observed trout production in Horokivi Stream, New Zealand. The implications of Allen’s study are that trout appear capable of exploiting the entire prey base within a stream. In a reappraisal of the Allen paradox, Huryn (1996) demonstrated other prey sources (including smaller trout and terrestrial prey) must be considered for trout production and food availability to be energetically balanced. Given these findings, one might expect trout to strongly affect stream invertebrates.

It is intriguing, therefore, that severe reductions in stream invertebrate abundance have, on the whole, not been detected in natural streams (McIntosh 2000b). However, trout have caused declines in some vulnerable taxa (e.g. *Nesameletus* mayflies and *Zelandopsycha* caddisflies; McIntosh 2002; McIntosh et al. 2005) and altered the composition of invertebrate communities in some streams (Nyström et al. 2003). Flecker and Townsend (1994), for instance, observed substantial reductions in total invertebrate biomass in stream channels containing trout compared with those containing galaxiids or no fish; however, the effects of trout on invertebrate biomass are variable (McIntosh & Townsend 1996). In a comparison of trout and troutless streams (some with galaxiids), Nyström

et al. (2003) noted compositional differences (fewer large taxa in trout-invaded streams) but similar biomasses for different stream types. Lastly, the only New Zealand study of trout effects on the abundance of benthic prey in lakes reported no effect on overall prey biomass and modest negative effects on the abundance of only two large-bodied taxa (Wissing et al. 2006).

The variable response of invertebrate prey to predation is typical of that generally observed for trout streams around the world (Meissner & Muotka 2006). The impacts of trout on benthic communities have proven contingent on many factors, including the availability of alternative terrestrial prey (Nakano et al. 1999), the size of experimental units used (Englund 1997), and the movement of prey (Cooper et al. 1990). Another set of channel experiments, for example, showed the influence of trout on benthic prey was more pronounced in channels subjected to a flood-disturbance treatment than in undisturbed controls (Nyström & McIntosh 2003). Thus, the response of galaxiids to trout-induced shifts in invertebrate abundance and community composition may be quite variable.

Trout-induced alterations to the behaviour and composition of stream benthic prey have been predicted to adversely affect galaxiids (McDowall 2003). Although impacts on invertebrate abundance may be minimal, trout have altered many other aspects of stream ecosystem structure and function (Simon & Townsend 2003; Townsend & Simon 2006). Benthic invertebrates have become more nocturnal (McIntosh & Townsend 1995), invertebrate drift and positioning have been altered (McIntosh & Townsend 1994), and nutrient dynamics have changed (Simon et al. 2004) due to trout invasion. Trout-induced alterations to invertebrate grazing have also been linked to increased algal abundance, comprising a behaviourally-mediated trophic cascade (McIntosh & Townsend 1996). How these changes influence galaxiids and other native fishes has yet to be determined (McDowall 2003).

In terms of direct behavioural effects, early studies of some galaxiid species demonstrated substantial overlap in the habitats and prey used by galaxiids and trout, and suggested competition was avoided through temporal resource partitioning (e.g. Cadwallader 1975; Glova & Sagar 1991; Glova et al. 1992; Glova & Sagar 1993). However, most studies lacked trout-free controls, and important variables associated with galaxiid fitness (e.g. growth) or abundance were not assessed. Subsequent experiments have indicated that even small trout are capable of displacing non-diadromous galaxiids from preferred foraging locations or preventing foraging altogether (McIntosh et al. 1992; Edge et al. 1993). Further, Baker and co-workers (2003) showed *Galaxias depressiceps* was less numerous and confined to shallower depths in streams where brown trout were present than where they were absent. Interestingly, while galaxiids may be influenced by direct agonistic encounters, the one species tested so far (*G. vulgaris*) appears to have little ability or propensity to respond to the chemical cues released by trout (Howard 2007).

To evaluate how non-predatory trout impacts affect galaxiids, examinations of galaxiid growth and abundance under natural conditions at appropriate time scales (i.e. months to years) with replicated comparison to trout-free controls are needed. In the only replicated study of this sort, Howard (2007) fenced off stream reaches and manipulated the presence and size ranges of trout and subsequently quantified differences in *G. vulgaris* growth in reaches containing small (60–100 mm), large (150–224 mm), or no trout. Two striking results emerged from this study. First, a strong relationship was found between the total fish biomass (i.e. trout and galaxiid

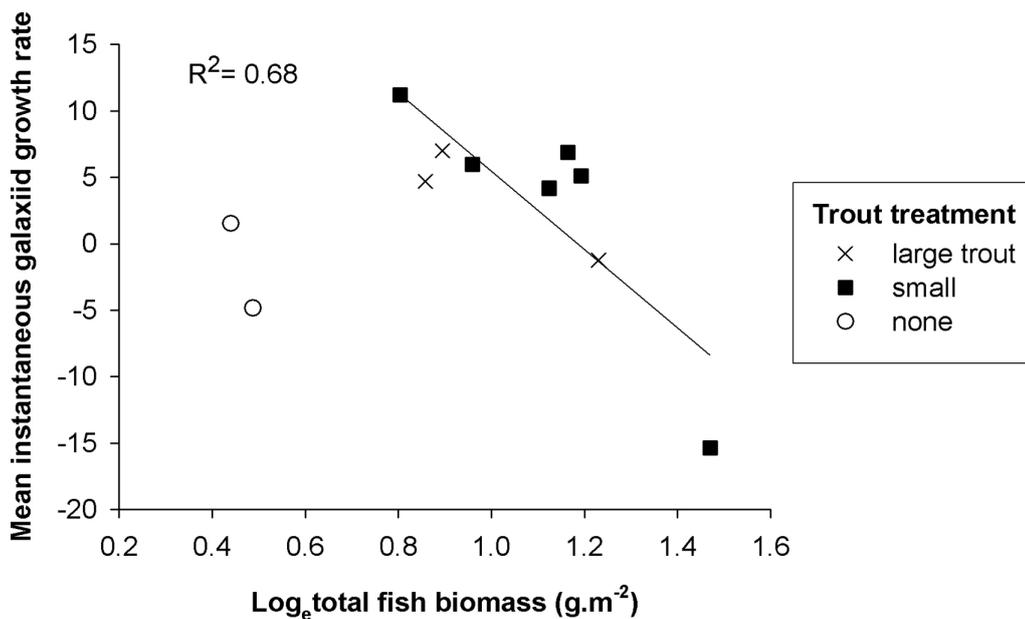


Figure 3. Growth rate of tagged Canterbury galaxias (*Galaxias vulgaris*) in fenced sections of a trout stream with either no trout, small (<150 mm fork length, FL) brown trout (*Salmo trutta*), or large (>150 mm FL) brown trout in relation to the total biomass of fish (trout + galaxiid) in the fenced reach. The regression line is standardized for a block effect and excludes data points for troutless reaches. Instantaneous specific growth rate was calculated as $G_w = [(ln W_{final} - ln W_{initial})/t] \cdot 100$, where W_{final} and $W_{initial}$ are the mass of individual fish at the end and start of the experiment, respectively, and t is the time elapsed, in days (from Howard 2007).

combined) and galaxiid growth rates, for experimental reaches containing trout (Fig. 3). This indicated that, regardless of identity, total fish biomass influenced galaxiid growth in a density-dependent manner. Such a pattern would be expected if fish populations were prey-limited, and is in accordance with the expectation that trout exploit the majority of prey production (Huryn 1996).

The second result of the stream fencing experiment was that, after accounting for fish biomass in a reach, trout had no discernable negative effect on galaxiid growth rates. Rather surprisingly, galaxiids had lower growth rates in trout-free control reaches than in the presence of either small or large trout. Thus, counter to expectations, the results from this initial study suggest trout may positively affect galaxiid growth rates in some situations. Such an effect could be possible if the consequences of trout direct effects on galaxiid behaviour are minor, and the presence of trout in some way enhances galaxiid foraging success (i.e. through facilitation). For instance, by altering the movement and positioning of stream invertebrates (McIntosh & Townsend 1996), trout may increase their vulnerability to benthic galaxiids.

The possibility for yet more complex, non-predatory trout–galaxiid interactions is becoming increasingly apparent. In a recent study of Otago streams, Kelly et al. (2009) found the incidence and severity of parasite infections decreased across a gradient of increasing trout abundance. The authors speculated this ‘infection dilution’ pattern was due to either trout predation on moribund (unsampled) individuals, or trout-induced reductions in galaxiid–intermediate host (i.e. invertebrate) encounter rates. Though counter to Howard (2007) in terms of galaxiid–prey encounter rates, the latter mechanism was similarly attributed to the behavioural response of invertebrates to trout presence. While these studies provide an initial glimpse into the potential for positive trout–galaxiid interactions, more research will be needed to understand how these indirect, life stage-specific interactions fit into the total galaxiid life cycle and, more importantly, galaxiid demographic processes. Further, as highlighted by McDowall (2003), the combination of studies reviewed above highlights the need

for novel perspectives (i.e. beyond viewing predation as the primary mechanism) in fully characterising the relationships between trout and galaxiids.

Environmental controls on co-occurrence

Despite the potential highlighted above for strong deterministic interactions, environmental stochasticity may greatly affect the likelihood of trout–galaxiid coexistence in some streams. Thus, the notion of a predator–prey ‘balance’ or equilibrium may have little relevance to the New Zealand trout–galaxiid situation. Nonetheless, the balance concept has been used to argue that all damage associated with trout invasions has occurred and that management should be limited to preventing further salmonid spread. For example, the 1993 Mavora Lakes Park Conservation Management Plan stated, “The introduced fish [brown and rainbow trout] have impacted on some native fish populations and possibly on native aquatic invertebrates. It is likely, however, that relative stability has been reached and the introduced fish currently in the lakes and rivers now pose no threat to extant native fish populations” (Department of Conservation 1993: 12). This equilibrium perspective is misguided and should not be used to direct management, as we explain below.

First, as suggested previously, trout effects on galaxiids appear highly variable. Many galaxiid populations are still in contact with trout, and this co-occurrence is likely reliant upon processes that mediate the strength of their interactions. In particular, there is accumulating evidence that natural disturbance, mostly associated with extreme high or low flows, can moderate or even nullify the effect of trout on non-diadromous galaxiids. The only streams in which galaxiids and trout co-occurred in the original Taieri River survey, for instance, were braided rivers, which are characteristically unstable environments (Townsend & Crowl 1991). Similarly, stream disturbance limits trout but not galaxiid distributions in the upper Waimakariri River, and thus creates predator-free refugia for galaxiids in an otherwise trout-dominated landscape

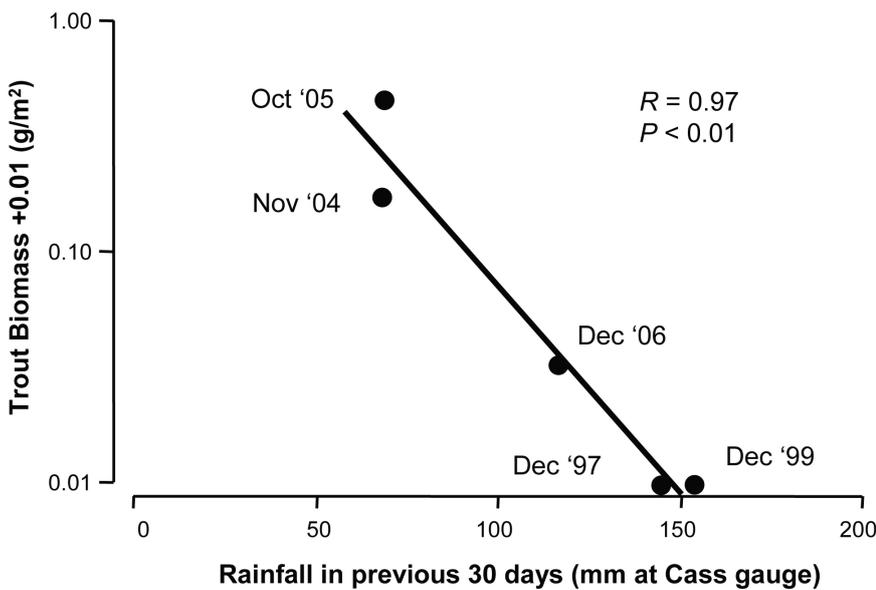


Figure 4. Brown trout (*Salmo trutta*) abundance in the Cass River (Waimakariri catchment) as a function of total rainfall recorded at the University of Canterbury's Cass field station for the preceding 30 days (A. R. McIntosh, unpubl. data). Note that the y -axis is displayed on a \log_{10} scale

(McIntosh 2000a). Additionally, in a recent evaluation of one of the McIntosh (2000a) sites (the Cass River), we found that extreme precipitation and flooding can account for the inter-annual volatility of local trout abundance (Fig. 4). This further supports the assertion that flood-related disturbance may mediate the impact of trout on galaxiids by affecting trout abundance. While this mechanism may underlie the co-occurrence disparity that exists between systems like the upper Waimakariri (Fig. 1) and the Taieri River (Townsend & Crowl 1991), other hydrological conditions may also minimise trout effects.

In Central Otago, a recent study has shown disturbances associated with low flows can also mediate interactions between trout and galaxiids. In the Manuherikia River system (Clutha River catchment), brown trout have effectively eliminated *Galaxias anomalus* from steep, high-flow, upper-catchment reaches (Leprieur et al. 2006). However, stressful low-flow conditions associated with water abstraction have minimised trout impacts on *G. anomalus* in lower-catchment reaches. Similarly, in the upper Waimakariri River system, natural low-flow conditions appear to negatively affect trout more than galaxiids (Dunn 2003). These examples run parallel to work in Australia, where drought-related low flows can strongly affect trout–galaxiid interactions in invaded systems (Closs & Lake 1996).

Multiple studies therefore suggest trout–galaxiid interactions can be highly variable and dependent on flow regime. Mechanistically, extreme flows may minimise interactions by reducing trout abundance (e.g. Fig. 4) and/or growth potential (i.e. by limiting sizes attained). Relative to trout, galaxiids are less impacted by flooding for reasons that are not known. Galaxiids persist in intermittent habitats by using surface water refugia (Davey & Kelly 2007) and/or by burrowing into the streambeds (Hartman 1990; Dunn 2003; Dunn & O'Brien 2006) during extreme low-flow events. As discussed below, future research should be directed at identifying the mechanistic basis for hydrologic mediation of trout impacts.

In addition to stream flow, other environmental circumstances may minimise non-native trout impacts. Naturally acidic waters associated with the leaching of humic acids from forest soils, for instance, appear to exclude brown

trout but not native fish from many forested streams. In a survey of lowland West Coast, South Island streams, naturally acidic sites contained three to four species of diadromous and non-diadromous galaxiids and no trout, whereas neutral pH streams contained trout and few native fish (Olsson et al. 2006). Thus, having a greater tolerance to low pH than trout may confer an additional advantage upon some *Galaxias* spp. Lastly, as implied in the discussion on 'Formation of source–sink metapopulations' above, large-scale factors may prevent trout from eliminating galaxiids from some locations in trout-invaded river networks (Woodford & McIntosh in press). Specifically, the local persistence of galaxiids may be aided by dispersal from productive trout-free refuge populations. This means that the geographic location of source populations and the availability of dispersal pathways within stream landscapes or riverscapes, in addition to environmental conditions, may at times affect the local and regional trout–galaxiid balance. These examples also illustrate that the local co-existence (or lack thereof) of trout and galaxiids is very likely to be a dynamic phenomenon, and that losses of native fish populations may be ongoing, especially if hydrological conditions are stabilised by new engineering works.

Research needs

Inasmuch as this review outlines what is known about the impacts of trout on galaxiids in New Zealand, it highlights that significant gaps in knowledge remain. Given the imperilled status of the Galaxiidae, studies aimed at further quantifying the context-dependent nature of trout impacts will be particularly useful. We advocate research that seeks to characterise how individual traits (e.g. body size), local and landscape-scale population processes (e.g. juvenile production and recruitment), and/or environmental conditions (e.g. hydrology) alter trout impacts. However, we also believe that future conservation efforts will benefit most from trout–galaxiid research that proceeds according to a holistic total life-cycle and landscape-scale vision.

Additionally, as galaxiid conservation and recovery activities progress (Department of Conservation 2004), new information about the risks and benefits of particular strategies

will be needed. For example, it may be tempting to pursue flow or barrier management strategies to give galaxiids an advantage over trout in some systems, based solely upon what is already known. In the absence of information, however, such an approach may do more harm than good for many reasons. For instance, while it is becoming increasingly clear that flow extremes can minimise trout effects in some systems, these same flow patterns can reduce galaxiid abundance (Closs & Lake 1996; McIntosh 2000a; Dunn 2003). Similarly, while barrier management can minimise invasion risk, it can increase the likelihood that random demographic and genetic processes will negatively affect small, fragmented populations (e.g. Peterson et al. 2008).

Finally, more research into pest-fish removal techniques relevant to the New Zealand situation should be undertaken so that trout eradication, when deemed necessary, can proceed according to best scientific practises. To paraphrase Chadderton (2003), today's aquatic scientists and fish conservationists need to follow in the footsteps of New Zealand's terrestrial conservation pioneers; they developed mammal eradication tools in anticipation that New Zealanders would eventually support use of these to preserve native biodiversity.

Galaxiid conservation in a changing Aotearoa – redressing the balance

The “Feathers to fur” symposium was organised to further document the ecological changes that have taken place in Aotearoa/New Zealand. There is no doubt that trout have transformed the riverine ecosystems of New Zealand. ‘Mucous to scales’ would be an appropriate analogy, since galaxiids lack scales and trout (which do have scales) have replaced galaxiids as the dominant fish in New Zealand freshwater ecosystems. As McDowall wrote in *Gamekeepers for the Nation*, a history of the New Zealand Acclimatisation Societies (1994: 466), “Trout populations in lakes and rivers have had a devastating effect on diverse native fishes”. Moreover, during most of the past hundred years, the management of trout has generally taken priority over native fishes. Examples include the prioritization of trout fisheries over indigenous whitebait fisheries, and the continued spread and re-stocking of trout in habitats where their populations are not self-supporting (McDowall 2006). Tellingly, trout and salmon are the only species specifically named in New Zealand's Resource Management Act and therefore have special protection under New Zealand law. Remarkably, at the same time Wildlife Service personnel were working desperately on the conservation of takahe in the Murchison Mountains of Fiordland, they introduced trout to Lake Orbell (McDowall 2006). This double standard is echoed by the paltry efforts at restoration or rehabilitation of native fish populations in New Zealand; there have been far too few!

It is time for energy and funding to be put into restoration and rehabilitation of New Zealand's indigenous native fisheries. This need not result in significant harm to New Zealand's famous trout fisheries, as they are now established and clearly have a high cultural, recreational and economic value. We also recognise the value that indigenous biodiversity derives from the efforts made by the angling community to protect aquatic habitats from degradation (Deans et al. 2004). However, there are many situations where greater priority should be placed on the conservation needs of threatened native fishes than on non-native sport fisheries – particularly in habitats that

are marginal, at best, for trout occupation. Despite examples of successful restoration of galaxiid populations in Australia by removing trout (Lintermans 2000), few such efforts have been undertaken in New Zealand (Chadderton 2003). Given the cultural value of whitebait fisheries and the inherent value of New Zealand's endemic biodiversity, it is surprising that localised trout eradication is not more openly discussed and used as a conservation tool.

Nevertheless, the profile of native fish is on the rise. Increasingly, their plight is being considered in resource consent applications and they are becoming a focus of mainland island restoration plans. As an example, trout removal was recently incorporated into the Karori Wildlife Sanctuary's restoration plan, though as of late 2009 no on-the-ground management has yet occurred. Further, various Department of Conservation, community and iwi-based projects are also being planned. These efforts are being helped by a new generation of freshwater scientists armed with better knowledge of native fish. Thus, we hope that a future symposium will be able to report on the rehabilitation of native fish populations in Aotearoa, the enjoyment that its people have derived from them, and the pride that is taken from our effective kaitiakitanga (guardianship).

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