Risk assessment and mitigations of the potential impacts of trout predation on

New Zealand's indigenous fish species

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Abstract

Trout were introduced into New Zealand freshwater ecosystems ~150 years ago as a prized sports fish, despite unknown potential impacts of this introduction. New Zealand's native fish are experiencing widespread decline, with trout implicated as one potential key stressor. The concurrent introduction of trout with large-scale land use change have made attributing decline to specific stressors difficult. However, understanding the effect of specific stressors is necessary for management of healthy populations of both the native fauna and valued introduced species. This thesis unpacks the predatory impacts of trout on native fish by (1) using the literature to develop a risk assessment matrix to identify fish species at high risk of detrimental impact from trout predation, and (2) experimentally examine whether trout presence alters the habitat preferences of a small non-migratory galaxiid.

Risk assessments provide an avenue for wildlife managers to prioritise conservation and remediation efforts towards reducing the impacts of trout predation on the most at-risk native fish. The risk assessment matrix created in this thesis has triaged species most at-risk of detrimental population impact from trout predation. Perhaps unsurprisingly, the risk assessment identified non-diadromous galaxiids and mudfish as the most vulnerable groups to trout predation. Nationally, approximately 10% of river reaches occupied by trout also overlap with locations of at least one native fish species at high risk of trout impact. These reaches should be a focus for future investigation and mitigation efforts, such as physical habitat restoration, water quality improvements, restoration of hydrological regimes, and active population control.

Dwarf galaxiids (a non-migratory native fish) were identified as highly vulnerable to trout predation. I investigated potential impacts of trout on the habitat preference of dwarf galaxiids in replicated mesocosms. The experiments examined two contrasting habitats, comparing sand and cobble substrate, and vegetation and no vegetation. Potential changes in refuge seeking behaviours were examined in the physical presence of trout, the presence of trout odour, and the absence of trout. In the gravel substrate experiment, galaxiids were noted in refuge more frequently when exposed to trout odour, no other significant differences were observed. This indicates that dwarf galaxiids are unlikely to alter their refuge seeking behaviour in the presence of trout, which may leave them exposed to trout predation, and further indicates the importance of instream and riparian refuge for dwarf galaxiids.
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Chapter One: Introduction

Freshwater fish globally are threatened by population declines (Arthington et al., 2016). In New Zealand, 92% of species are endemic and suffer population fragmentation and reduction in abundance and distribution (Joy & Death, 2013; Moffat et al., 2020). Many species are locally extinct over much of their pre-European range (Canning, 2018; Joy & Death, 2013) largely attributed to loss of habitat, eutrophication, sedimentation, hydrological changes, and introduced species (Foote et al., 2015; Joy et al., 2019). Halting and reversing these declines will require knowledge and resources to drive policy and management interventions (Moffat et al., 2020).

Brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) were introduced in the late 1800's to New Zealand as highly valued sports fish (McDowall, 1968). However, their introduction has been associated with declines in native fish abundance and distribution, particularly non-diadromous galaxiids (McDowall, 2003; Woodford & Mcintosh, 2010). There is a need to balance the requirement for a highly valued trout fishery with those of an increasingly threatened native fish fauna (Jellyman et al., 2018) to prioritise where impacts of trout on native fish are likely to be the greatest to focus management actions of controlling trout impacts where needed.

The objectives of this thesis are two-fold. Firstly, to identify which native fish populations are at high risk being detrimentally impacted by trout predation and where that may be occurring. Secondly, to examine whether the presence of trout drives a change in the habitat preferences of a non-migratory galaxiid.

Chapter two presents a literature informed multi-criteria risk assessment of vulnerability of New Zealand native fish species to deleterious population impacts caused by trout predation. The extent to which trout overlap with highly vulnerable native fish populations was estimated by using existing species distribution predictions, and a priority subset of river reaches for intervention identified. I also suggest a toolbox of potential options for impact mitigation in these reaches.

Chapter three describes an experiment assessing refuge seeking behaviours by dwarf galaxiids (*Galaxias divergens*) in the presence of large rainbow trout. The hiding behaviour of dwarf galaxiids in the presence of trout and when exposed to the odour from the trout was analysed against a control group of galaxiids free from any trout input. Two contrasting habitat options were compared, with and without vegetation, and fine and coarse substrate.

Chapter four presents conclusions and discussion.

Chapter Two: A risk-assessment of trout impacts on native fish populations

Introduction.

New Zealand's freshwater fish fauna is exposed to a multitude of stressors including climate change, urban and agricultural intensification, exotic fish species introductions, decreasing water quality and quantity, and reductions of freshwater habitat (Joy et al., 2018). New Zealand's native freshwater fish species are largely endemic, and while a few, generally lowland, species are pelagic and shoaling, the majority are cryptic, nocturnal, and benthic, giving the impression of an impoverished native fauna (McDowall, 2006b). Salmonids are considered to have reduced the abundance and distribution of native fish species (McIntosh et al., 2010), based primarily on earlier research finding a negative association between brown trout and Canterbury galaxiids (Townsend & Crowl, 1991). Despite this, salmonids are also highly valued as a sports fishery and have legislated protections and management to ensure their sustainability. Trout were introduced into New Zealand in the 1860s as a sports fish, and prior to this information on native freshwater fauna was scarce. As a result, understanding the impacts of trout on native fish populations is challenging, with contemporary examinations typically confounded with anthropogenic impacts (Howard, 2007; McDowall, 2006a). Recent legislation changes, such as the National Policy Statement for Freshwater Management (Ministry for the Environment, 2020), and the Conservation (Indigenous Freshwater Fish) Amendment Bill (2019) have bolstered the protection and management of native fish, including the development of native freshwater fish management plans. If managers are to be effective in ensuring the overall sustainability of both native and sports fish, then management needs to be informed of both the extent to which trout are highly detrimental to native fish assemblages, and the management options available. With conservation management often facing highly limited resources, it is may also be necessary to prioritise responses.

Risk assessment frameworks can offer a systematic approach for assessing potential ecological risk of novel species on native biodiversity at multiple scales and assist in focussing and prioritising management actions (Probert et al., 2020). Such risk assessments generate objectively derived numeric scores for a given species based on an assessment of specific traits (Rowe & Wilding, 2012). While the most frequently used framework is the Australian Weed Risk Assessment (Pheloung et al., 1999), which has been adapted for use in several countries (Gordon et al., 2008), risk assessments for freshwater fish are becoming more common, and have now been developed for the USA, Australia, and the UK (Rowe & Wilding, 2012). Risk assessments may also provide an effective method of triaging New

Zealand's native freshwater fish populations at risk from trout predation for additional conservation interventions.

Any risk assessment evaluating the potential impacts of trout on native fish will need to recognise that impacts will be species-specific. The impact trout predation has on each species will largely depend on the frequency and extent of interactions with trout (e.g., diel activity overlap), population dynamics (e.g., recruitment potential), and behaviour (Carpenter et al., 2010). The ability of native fish to withstand disturbances (e.g., floods and drought), and the availability of food and refugia will also play an important role in determining the outcome of interactions with trout (Joy & Death, 2013; McIntosh et al., 2010). The multiple interconnected factors affecting trout predation impacts have made quantification of such impacts difficult. Furthermore, this is complicated by dependence on studies with generally small sample sizes, distinct habitat differences between trout vs non-trout streams, and the changes in habitat preferences across life stages of the studied species (Baker et al., 2003).

This chapter reviewed the literature on the life histories, biology, and ecology of native freshwater fish and used this information to develop and systematically populate a risk assessment matrix which assesses the risk of substantial population-level impacts by trout predation in New Zealand rivers. Once each species was assigned a vulnerability score, species distribution predictions were then used to identify locations where trout are predicted to overlap with species with high, moderate, or minor risk scores. Although competition between native species and trout across different life-cycle stages is likely, predation seems to be the trout-induced stressor on native fish (McDowall, 2003; Townsend & Crowl, 1991).

Methods.

Risk assessment matrix derivation. Risk assessments of invasive species have previously predominantly focussed on evaluating the biological traits of the introduced species and those of the receiving community to understand potential risk to native ecosystems. However, trait focussed risk assessments often overlook potential ecosystem modulators, including environmental disturbances and native species resilience (Probert et al., 2020). For this risk assessment framework, native fish were scored and triaged based on their biological and species resilience traits that may increase vulnerability to trout predation and encounter rates.

The overall impact of trout predation on a given native fish population is determined by the population dynamics of native fish species, which are in turn governed by fecundity and frequency of spawning events (Stevens et al., 2016). Rapid growth, early maturation, short life span, high fecundity and widespread dispersal and distribution (r-selected traits)

allow for high population resilience to disturbance events (Rowe & Wilding, 2012). Those migratory and long lived, late maturing fish species (K-selected traits) are exposed to increased ontogenetic jeopardy due to movements between very different habitats or increased time spent in vulnerable life stages (Arthington et al., 2016). In addition to population growth strategies, the initial health of the population will also affect recovery from disturbances, as impacts are often cumulative. In the risk assessment framework, initial population health was indicated by the New Zealand Threat Classification System (NZTCS) conservation status, which quantifies the current risk of extinction for each native freshwater fish species (Department of Conservation, 2020; Dunn et al., 2018).

For all native fish, literature was used to appraise the risk of substantial negative impacts at the local population-level by trout predation. Each species was scored between zero and 31, composed of the weighted sum of nine potential risk factors (See Table 2.1 for risk factors, scoring, weighting and justification). For each risk factor, species were assigned a score from 1-3, with 1 indicating little to no risk, and 3 indicating high risk. Not all risk factors were considered equal: fecundity and egg size, age at reproductive maturity, threat status and adult body size were considered to be of increased importance when considering interactions with trout and were therefore given twice the weighting in overall scoring. All scores were assigned using literature-informed judgement and are presented, with referenced material, in Table 2.2. Once scores were assigned, species were then triaged into groups of high risk (scoring between 26 and 31), moderate risk (scoring between 21-26) and minor or low risk (scoring between 16 -20).

Following risk assessment development, the overlap distributions of trout and native fish were determined using predictions from the New Zealand Freshwater Fish Database (Stoffels, 2022). Locations and extent of river reaches with at least one high-risk native fish potentially interacting with trout were determined. This allows prioritisation of conservation efforts to where the most at-risk species are likely to interact with trout.

Table 2.1. Native fish vulnerability table and weightings

Mediating factors	Assessment	Score	Weighting	Example
Overlapping physical habitat with trout (micro-niche habitat proximity increases interaction likelihood)	No or rare overlap	1	1	Dwarf galaxiids (*Galaxias divergens*, Appendix A1-9.6) score 2 out of a potential 3 with macro-habitat overlaps with trout across a proportion of their wide range. Benthic adults utilise differing microhabitat from trout species, however fry and juveniles are pelagic, increasing risk of predation.
	Intermittent overlap	2		
	Persistent overlap	3		
Diel activity patterns (activities at similar times as trout: e.g., crepuscular activity patterns increase likelihood of interactions)	No or rare overlap	1	1	Dwarf galaxiids receive a 2 out of 3 as they are primarily diurnal. While trout have predominantly crepuscular feeding patterns they will feed during the day, indicating some feeding time overlap is likely.
	Intermittent overlap	2		
	Similar diel patterns to trout	3		
Diet similarities (increase potential for competitive interactions)	No or few similarities	1	1	A diet of terrestrial and benthic invertebrates is likely to increase the chance of interactions between dwarf galaxiids and trout, leading to the given score of 2 of a possible 3.
	Similar (aquatic inverts)	2		
	Very similar (aquatic & terrestrial inverts/piscivorous)	3		
Fecundity & egg size (many small eggs aid population resilience by increased numbers of larvae)	Many	1	2	Dwarf galaxiids score 2 out of a possible 6, spawning moderate quantities of large eggs in two annual spawning peaks.
	Few, small eggs	2		
	Few, large eggs	3		
Age at reproductive maturity (longer maturation time increases likelihood of individuals not surviving to breed)	1 year	1	1	Female dwarf galaxiids mature in the beginning of their second year of life, giving them their score of 2.
	1-3 years	2		
	>3 years	3		
Larval dispersal ability (source/sink repopulation potential, population replenishment and resilience)	Diadromous	1	2	Dwarf galaxiids score the highest possible risk score here of 6, due to their large fry's limited dispersal ability reducing the likelihood of population recruitment from any upstream populations.
	Non-diadromous, widespread dispersal	2		
	Non-diadromous, limited dispersal	3		
Threatened species ranking (Dunn et al, 2018)	Not threatened	1	2	The threatened species rating of Declining gives dwarf galaxiids their vulnerability score of 4.
	Declining	2		
	Naturally uncommon	2		
	Nationally vulnerable	2		
	Data deficient	2		
	Nationally endangered	3		
	Nationally critical	3		
Adult body length (smaller adults more easily predated)	>12 cm	1	2	With a maximum length of 8 cm, dwarf galaxiids are in the highest risk bracket for their small size, with a score of 6.
	8-12 cm	2		
	<8 cm	3		

Results.

The most at-risk species included many of the non-diadromous galaxiids and mudfish species. Species deemed at least risk from trout prediction included torrentfish, eels, bullies, smelt, flounder, and lamprey (Table 2.2).

Nationally, trout are predicted to overlap with at least one native fish species across a total stream length of 25,059.37 km. Of this overlapping distribution, 1,626.01 km of reach contain both trout and high-risk native fish species, 5,317.96 km of waterway contains both trout and medium risk native fish species, and the remaining overlapping distribution of 18,115.4 km only contained species designated as low risk (Figure 2.1). Across all river reaches nationally, approximately 10% of river reaches (1, 626 km) were found to have both trout of any size and at least one high-risk native fish (Figure 2.1). Rounded to the nearest kilometre, an additional 5,318 km were found to have at least one moderate risk rated native fish, and the remaining overlapping distribution of 18,115 km contained freshwater fish species designated as low risk (Figure 2.1). This indicates approximately 0.4% of all national reaches are predicted to contain at least one high-risk species (Table 2.3).
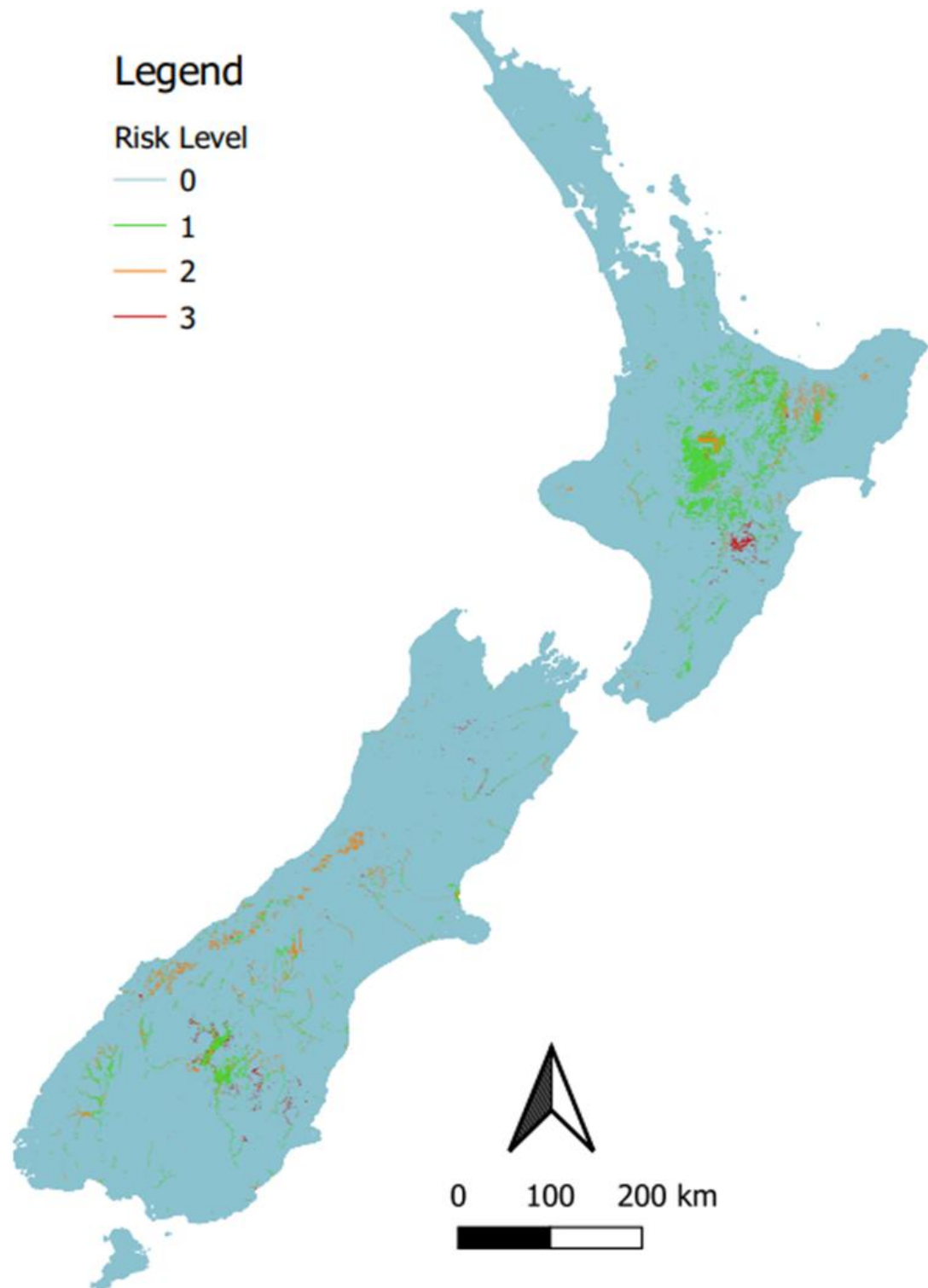
Figure 2.1. Map of New Zealand showing river reaches where native species at high (3), moderate (2), or low (1) risk of negative population impacts due to trout predation overlap with trout presence. A no possible impact score (0) is in place where there are no trout present.

Table 2.2. Risk assessment matrix for New Zealand freshwater fish species: vulnerability scores and references.

Species	Risk factors and weightings								References	Score	Vulnerability rating
	Overlapping mesohabitat / niche with trout	Diet similarities	Diel activity patterns	Fecundity and egg size	Age at maturity	Larval dispersal (recolonisation)	Threat ranking	Adult size			
	1	1	1	2	1	2	2	2			
Dusky galaxiid (*Galaxias pullus*)	2	2	2	3	3	3	3	2	(Allibone et al., 2015; Allibone, 2000; Allibone & McIntosh, 1999; Closs et al., 2013; Dunn et al., 2018; Jellyman et al., 2013). See Appendix A-9.5.	31	High
Lowland longjaw galaxiid (*Galaxias cobinitis*)	2	2	2	3	1	3	3	3	(Allibone et al., 2010; Allibone et al., 2015; Baker et al., 2003; Dunn et al., 2018; Dunn & Brien, 2006; Jellyman et al., 2013; McDowall & Waters, 2002). See Appendix A-9.9.	31	High
Eldon's galaxiid (*Galaxias eldoni*)	2	2	2	3	2	3	3	2	(Allibone et al., 2015; Allibone & McIntosh, 1999; Allibone, 2000; Allibone & Townsend, 1997; Dunn et al., 2018; Jellyman et al., 2013) See Appendix A-9.7.	30	High
Bignose galaxiid (*Galaxias macronasus*)	2	2	2	3	2	3	2	3	(Allibone et al., 2015; Allibone & Gray, 2018; Dunn et al., 2018; Howard, 2014; Jellyman et al., 2013). See Appendix A-9.2.	30	High
Upland longjaw galaxiid (*Galaxias prognathus*)	2	2	2	3	1	3	2	3	(Allibone et al., 2015; Allibone et al., 2010; Allibone & Gray, 2018; Bonnett, 1992; Dunn et al., 2018; Howard, 2014; Jellyman et al., 2013; McDowall, 1990). See Appendix A-9.11.	29	High
Canterbury mudfish (*Neochanna burrowsius*)	2	2	1	3	2	3	3	2	(Cadwallader, 1975b; Eldon, 1979a; Eldon 1979b; Jellyman et al., 2013; Ling & Gleeson, 2001; McDowall, 1990a; McIntosh et al., 2010; O'Brien, 2005a; O'Brien & Dunn, 2007; West et al., 2015) See Appendix A-2.	29	High
Brown mudfish (*Neochanna apoda*)	2	2	1	3	2	3	2	2	(Dunn et al., 2018; Eldon, 1968; Jellyman et al., 2013; McDowall, 1990a; O'Brien & Dunn, 2007; West et al., 2015). See Appendix A-2.	27	High

Species									References	Score	Rating
Black mudfish (*Neochanna diversus)*	2	2	1	3	2	3	2	2	(Closs et al., 2013; Dunn et al., 2018; Jellyman et al., 2013; McDowall, 2010; O'Brien & Dunn, 2007; West et al., 2015). See Appendix A-2.	27	High
Northland mudfish (*Neochanna heleosis)*	2	2	1	3	2	3	2	2	(Dunn et al., 2018; Jellyman et al., 2013; McDowall, 1990a; O'Brien & Dunn, 2007; West et al., 2015). See Appendix A-2.	27	High
Chatham Island mudfish (*Neochanna rekohua)*	2	2	1	3	2	3	2	2	(Dunn et al., 2018; Jellyman et al., 2013; McDowall, 2004; O'Brien & Dunn, 2007). See Appendix A-2.	27	High
Taieri Flathead galaxiid (*Galaxias depressiceps*)	2	2	2	2	2	3	2	2	(Allibone & Townsend, 1997; Baker et al., 2003; Dunn et al., 2018; McDowall & Wallis, 1996; Moore et al., 1999; Smith, 2014; Wager, 2015; Woodford & McIntosh, 2013). See Appendix A-9.10.	26	High
Dwarf galaxiid (*Galaxias divergens*)	2	2	2	1	2	3	2	3	(Allibone, 2002a; Dunn et al., 2018; Hay, 2009a; Hay 2009b; Hayes et al., 2019; Hopkins, 1971; Jowett et al., 1996; McDowall, 1990a; West et al., 2015). See Appendix A-9.6.	26	High
Roundhead galaxiid (*Galaxias anomalus*)	2	2	1	1	2	3	3	2	(Allibone, 2002; Allibone et al., 2015; Allibone & Townsend, 1997; Baker et al., 2003; Dunn et al., 2018; Jellyman et al., 2013; McDowall & Wallis, 1996; Moore et al., 1999). See Appendix A-9.4.	25	Moderate
Gollum galaxiid (*Galaxias gollumoides*)	2	2	2	1	1	3	2	3	(Allibone et al., 2015; Dunn et al., 2018; Jellyman et al., 2013; McDowall & Chaddertoi, 1999). See Appendix A-9.8.	25	Moderate
Tarndale bully (*Gobiomorphus alpinus*)	2	2	2	1	1	3	2	3	(Dunn et al., 2018; Jellyman et al., 2000; Jellyman et al., 2013; Ling et al., 2015; McDowall, 1994; McDowall & Stevens, 2007; Smith et al., 2003) See Appendix A-11.2.	25	Moderate
Canterbury galaxiid (*Galaxias vulgaris*)	2	2	2	1	2	2	2	3	(Allibone et al., 2015; Allibone & Townsend, 1997; Cadwallader, 1973; Dunn et al., 2018; Glova et al., 1992; Glova & Sagar, 1989b; Howard, 2007; Jellyman et al., 2013; Jones, 2014; McDowall & Hewitt, 2004; McDowall & Wallis, 1996; Townsend & Crowl, 1991; Waters et al., 2020; Woodford, 2009; Woodford & Mcintosh, 2010; Woodford & McIntosh, 2013). See Appendix A-9.3.	24	Moderate
Alpine galaxiid (*Galaxias paucispondylus*)	2	2	2	1	2	3	2	2	(Allibone et al., 2015; Bonnett, 1990; Bonnett, 1992; Dunn et al., 2018; Jellyman et al., 2013; McDowall, 1990a; Sagar & Eldon, 1983). See Appendix A-9.1.	24	Moderate
Upland bully (*Gobiomorphus breviceps)*	2	2	2	3	1	2	1	2	(Dunn et al., 2018; Hayes et al., 2019; Jellyman et al., 2013; Jowett & Boustead, 2001; McDowall, 1990a; McDowall & Eldon, 1997; Minns, 1990; West et al., 2015; Woodford & Mcintosh, 2010). See Appendix A-11.3.	23	Moderate
Koaro (*Galaxias brevipinnis*)	3	3	2	1	2	1	2	2	(Allibone & McIntosh, 1999; Bell, 2001; David et al., 2014; Dunn et al., 2018; Glova, 2003; Hayes, 1996; Hayes et al., 1989; Jowett & Richardson, 1995; Kusabs & Swales, 1991; Main & Winterbourn,	22	Moderate

									1987; McDowall, 1990a; Rowe et al., 1992; Sagar & Eldon, 1983, McEwan & Joy, 2014a). See Appendix A-8.4.		
Giant kokopu (*Galaxias argenteus*)	3	3	3	1	3	1	2	1	(Bonnett & Lambert, 2002; Bonnett & Sykes, 2002; David, 2003; David et al., 2002; David et al., 2004; Dunn et al., 2018; Franklin et al., 2015; Hansen et al., 2004; Jellyman & Harding, 2012; Main, 1988; McDowall, 1990a; West et al., 2015; Whitehead et al., 2002; Yungnickel et al., 2020). See Appendix A-8.2.	22	Moderate
Shortjaw kokopu (*Galaxias postvectis*)	3	3	2	1	3	1	2	1	(Allibone et al., 2003; Charteris et al., 2003; Dunn et al., 2018; Goodman, 2002; McDowall, 1990a; McDowall et al., 1996; West et al., 2015, McEwan & Joy, 2014a). See Appendix A-8.5.	21	Moderate
Bluegill bully (*Gobiomorphus hubbsi*)	2	2	2	1	1	1	2	3	(Allibone et al., 2015; Atkinson & Joy, 2009; Dunn et al., 2018; Jarvis, 2015; Jellyman et al., 2013; Jowett & Boustead, 2001; Jowett & Richardson, 2003; McDowall, 1990a; McIntosh & Townsend, 2008; Sagar & Eldon, 1983; Sagar & Glova, 1998; Scrimgeour & Winterbourn, 1987). See Appendix A-10.1.	21	Moderate
Inanga (*Galaxias maculatus*)	3	2	2	1	1	1	2	2	(Allibone et al., 2010; Benzie, 1968; Bonnett & McIntosh, 2004; David et al., 2015; Dunn et al., 2018; Hayes et al., 1989; Hayes et al., 2008; Hickford & Schiel, 2014; Jellyman et al., 2013; Jowett, 2002; Jowett et al., 1996; Jowett & Richardson, 2003; Joy & Death, 2001; Main, 1988; McDowall, 1990a; McLean et al., 2007; Orchard et al., 2018; Robertson et al., 2016; Rowe et al., 1999; Yungnickel et al., 2020). See Appendix A-8.3.	20	Minor
Torrentfish (*Cheimarrichthys fosteri*)	2	2	2	1	2	1	2	2	(Allibone et al., 2015; Dunn et al., 2018; Glova et al., 1987a; Jellyman et al., 2013; McDowall, 1990a; McDowall, 2000; Richardson & Jowett, 1995; Sagar & Eldon, 1983; Scrimgeour & Eldon, 1989; Tana, 2009; Warburton, 2015). See Appendix A-5.	20	Minor
Stokell's smelt (*Stokellia anisodon*)	3	1	3	1	1	1	2	2	(Allen, 1961; David et al., 2015; Dunn et al., 2018; Hicks & McCaughan, 1997; Jellyman et al., 2013; Joy & Atkinson, 2012; McDowall, 1990a). See Appendix A-3.	20	Minor
Banded kokopu (*Galaxias fasciatus*)	3	3	2	1	3	1	1	1	(Baker & Smith, 2007; David et al., 2002; Dunn et al., 2018; Hicks & McCaughan, 1997; Main, 1988; McCullough, 1998; Mitchell & Penlington, 1982; Rowe et al., 2000; West et al., 2015; West et al., 2005). See Appendix A-8.1.	19	Minor
Cran's bully (*Gobiomorphus basalis*)	2	2	2	1	1	2	1	2	(Closs et al., 2013; Dunn et al., 2018; P. Franklin et al., 2015; Hicks & McCaughan, 1997; Jowett & Boustead, 2001; McDowall, 1990a; Riddell, 1982; Stokell, 1940). See Appendix A-11.1.	19	Minor
Common smelt (*Retropinna retropinna*)	3	2	3	1	1	1	1	2	(Allibone & McIntosh, 1999; Dunn et al., 2018; Franklin et al., 2015; Jellyman et al., 2013; Joy & Atkinson, 2012; McDowall,	19	Minor

Species									References	Total	Rating
									1990a; Richardson et al., 2001; Rowe, 1984; Rowe, 1993; Rowe & Taumoepeau, 2004; Ward et al., 2005). See Appendix A-3.		
Longfin eel (*Anguilla dieffenbachii*)	2	3	1	1	3	1	2	1	(Allen, 1961; Beentjes et al., 2006; Broad, 2002; Burnet, 1969a; Burnet, 1969b; Burnet, 1969c; Cadwallader, 1975c; Dunn et al., 2018; Glova et al., 1998; Hicks & McCaughan, 1997; Jellyman, 2012; Jellyman, 1989; Jellyman, 2007; Jellyman, 2012; Jellyman, 1996; Jellyman et al., 2003; McDowall, 1990a; McDowall, 2010; Pike et al., 2015b; Sagar & Eldon, 1983). See Appendix A-4.	19	Minor
Giant bully (*Gobiomorphus gobiodes*)	2	2	2	1	2	1	2	1	(Dunn et al., 2018; Jellyman et al., 2000; Jellyman et al., 2013; Ling et al., 2015; McDowall, 1990a, McDowall, 1997). See Appendix A-10.3.	18	Minor
Redfin bully (*Gobiomorphus huttoni*)	2	2	2	1	2	1	1	2	(Dunn et al., 2018; Jellyman et al., 2013; Jowett & Boustead, 2001; Ling et al., 2015; McDowall, 1990a; McEwan & Joy, 2013; McEwan & Joy, 2014b). See Appendix A-10.4.	18	Minor
Shortfin eel (*Anguilla australis*)	2	3	1	1	3	1	1	1	(Beentjes et al., 2006; Cadwallader, 1975c; Dunn et al., 2018; Hicks & McCaughan, 1997; Jellyman, 1989; Jellyman et al., 2003; Joy & Atkinson, 2012; Kelly & Jellyman, 2007; McDowall, 1990a; McDowall, 2010; Pike et al., 2015a; Sagar & Glova, 1998). See Appendix A-4.	17	Minor
Common bully (*Gobiomorphus cotidianus*)	2	2	2	1	1	1	1	2	(Bleackley, 2008; Closs et al., 2003; David et al., 2002; Dunn et al., 2018; Jellyman et al., 2000; Jellyman et al., 2013; Landman et al., 2005; McDowall, 1990a; West et al., 2015). See Appendix A-10.2.	17	Minor
Black flounder (*Rhombosolea retiarii*)	1	3	2	1	2	1	1	1	(David et al., 2015; Dunn et al., 2018; Jellyman et al., 2013; Jellyman & Harding, 2012; McDowall, 1990a; McDowall, 2016; McEwan & Joy, 2013; Minns, 1990; Waimaori, 2017). See Appendix A-7.	16	Minor
Pouched lamprey (*Geotria australis*)	1	1	1	1	3	1	2	1	(Allibone & McIntosh, 1999; Baker et al., 2016; Closs et al., 2015; Dunn et al., 2018; James, 2008; Jellyman et al., 2002; Jellyman & Glova, 2002; Jowett et al., 1996; Kelso & Glova, 1993; McDowall, 1990a; Mittelbach & Persson, 1998; Paton et al., 2019; Robbins, 2007; Todd, 1992). See Appendix A-6.	16	Minor

Table 2.3. Length of stream sections where trout are present with native fish species (to the nearest km)

Risk	Length of waterway (km)	Prop of all waterways each risk class (%)	Prop of all waterways where trout overlap with risk class (%)
Low	18115	4.4	7.5
Mod	5318	1.3	8.9
High	1626	0.4	10.1

Discussion.

The literature informed risk assessment matrix presented here is a step towards identifying species, such as mudfish and non-diadromous galaxiids, whose populations are more vulnerable to disturbances of any sort due to small or fragmented populations (Dunn et al., 2018), which are therefore deemed more vulnerable to impacts of any kind. Other risk factors include the maximum adult fish size, as smaller species are at greater risk of predation throughout their entire life cycles (Mittelbach & Persson, 1998), and overlapping microhabitats with trout. Crepuscular feeding behaviour and dietary overlaps also may place trout and native fish in closer proximity, increasing chances of interactions (Table 2.2 and Appendix A). Mudfish and many non-diadromous galaxiid species have populations at high risk of deleterious impacts from any predation, including from trout (Table 2.3). Mudfish have highly fragmented populations and are restricted in range due to ongoing habitat loss. While Canterbury mudfish have higher fecundity levels, other mudfish species show low recruitment potential, hence any loss to predation could have a significantly negative impact on mudfish populations (Appendix A-2). Dusky, lowland longjaw, Eldon's, bignose, upland longjaw, Taieri flathead and dwarf galaxiids are all at high risk of negative impacts from trout predation due to low recruitment rates, small adult size, and similarities in diet and habitat requirements (see Appendix A-9). Figure 2.2 shows (in red) that reaches where trout currently overlap with high-risk species is highly localised, rather than widespread nationally. These locations are primarily in the Otago region (non-diadromous galaxiids) and Hawkes Bay (dwarf galaxiids).

Those species at a moderate risk of impact by trout predation either have differing habitat preferences to trout, are classified with a highly vulnerable threat-ranking or limited fecundity (roundhead and Gollum galaxiids, Appendix A-9, or Tarndale bully Appendix A-11) or very similar habitat preferences but co-exist with trout in unstable rivers due to microhabitat differences and higher fecundity (Canterbury and alpine galaxiids). The large

diadromous galaxiid species (giant kokopu, shortjaw kokopu and koaro) are vulnerable to predation during their juvenile migrations as whitebait, and adults have habitat and diet preference overlaps with trout. Bluegill bullies inhabit torrents and are often spatially segregated from trout within the same river reach. While upland bullies often coexist closely with trout, their moderate risk classification owes to their threat ranking, late maturation, and low fecundity traits.

Longfin and shortfin eels (Appendix A-4), pouched lamprey (Appendix A-6), and black flounder (Appendix A-7) are likely to be minimally affected by trout due to their large size and differing feeding and habitat preferences. Other low risk species, including inanga, Stokell's and common smelt (Appendix A-3), and common, redfin and Cran's bullies have resilience boosting traits such as high fecundity and fast maturation as well as wide dispersal and distribution, and spawn multiple times in one year (Appendix A-10). Torrentfish (Appendix A-5), banded kokopu (Appendix A-8) and giant bully (Appendix A-10) were also considered at low risk given their large adult size and the torrent habitat preferences of torrentfish, microhabitat preferences of banded kokopu, and the high fecundity of giant bully.

The risk assessment presented here has likely been limited by the availability of research on New Zealand native fish species. There are some fundamental knowledge gaps around biology, spawning, habitat requirements and behaviours of many species (Department of Conservation, 2020). The literature limitations also extend to the risk assessment factors which were designed to capture the full range of biological, ecological and life history factors that could mitigate or exacerbate interactions between trout and native fish. As research advances and fills knowledge gaps, or perspectives change, habitats change, or the health of native populations change, so should this risk assessment. There should be periodic reviews with management adapted accordingly. Nonetheless, this assessment provides a transparent and systematic method, informed by the available literature, to indicate potential predatory pressure by trout and hopefully prioritise conservation efforts.

The broad decline in abundance and distribution of native and introduced freshwater fish including trout is widespread across New Zealand (Joy, 2014; Joy et al., 2019; Weeks et al., 2016). Evidence presented in this chapter suggests that these losses (with exceptions for localised impacts of trout on high-risk native species) are likely attributable to habitat loss and degradation, loss of spawning habitats, fish passage barriers, and source and sink population dynamics. Notably, that native species continue to cohabit with trout in many of the remaining enviros indicates trout are less likely responsible for recorded populations declines compared to these anthropogenic factors. Sedimentation and water abstraction are

further factors that confound the ability to delineate the actual impacts of trout on indigenous fish populations. Anthropogenic habitat degradation and contraction may be exacerbating trout predation pressures by reducing population resilience and bringing trout in closer, more regular contact with native fish in the available space that remains. Addressing the issues of habitat loss and providing more space for native species may influence this interaction.

The research presented in this thesis indicates that multiple factors, and multifactor interactions will contribute to the persistence of native fish populations within New Zealand, of which interactions with salmonids is but one. A more nuanced perspective of the interactions between biotic and abiotic factors may help explain conflicting patterns of cohabitation between trout and native freshwater fish species across the postulated risk spectrum

The spatial analysis carried out here relies on modelled predictions of presence-absence and does not indicate local population health or predator-prey dynamics. Conservation managers should prioritise further work in the identified locations to assess the health of high-risk native fish populations and the extent to which consumption occurs by trout. For areas where trout predation impacts are evident, a scoping exercise should identify potential mitigation interventions that may help to reduce trout predation pressures and/or increase the resilience of the affected population. These mitigations may include any or all the management strategies outlined in Table 2.4, with a focus on protecting and restoring habitat variables known to foster cohabitation between trout and native species and, if required, removing large trout to reduce predation pressure (e.g., through allowing increased numbers of large trout to be fished from the site). Any removal of trout should also be preceded by an assessment of all potential impacts of their removal to reduce the chance of unanticipated negative outcomes on other species, such as large eels and piscivorous birds that may predate on trout. Efforts that focus on improving the quality and extent of native fish habitat will not only help native fish resilience to trout predation but also any other disturbances they face.

Table 2.4. Actionable management strategies to mediate and mitigate impact of trout predation on native fish species

Mitigation	Actions	Rationale
Flow variability	Advocate for a natural flow regime, reduce water abstraction for any use, and allow a return to a natural cycle of drought and flood.	Streamflow major variable affecting abundance and distribution of freshwater species. Trout only linked to significant negative impacts on native species in stable streams. Natural flow peaks and droughts assists cohabitation with native species and native species spawning and recruitment. (See Appendix B-1).
Stream morphology and size	Advocate for variety and variability of natural stream processes to positively influence biological diversity by providing for species specific habitat and life history needs. Discourage and find alternatives to channelisation and water abstraction where possible.	Habitat heterogeneity allows cohabitation of many species, including trout and native fish species across differing life stages. Edgewater habitats increases recruitment potential to bolster populations. Dynamic river structure vital for fish species. (See Appendix B-2).
Sediment and substrate size	Advocate for reduced sediment and a range of substrate sizes, minimise sediment inputs into waterways, and allow riparian overhanging structures and wood inputs.	Interstitial space provides habitat, access to food, and refuge for many native fish species and is thus necessary for multi-species communities. Sediment infills substrate, reduces waterway depth, and homogenizes habitat, which may preclude cohabitation. (See Appendix B-3).
Nutrients and pollutants	Advocate for minimised inputs of nutrients and pollutants from any source.	Nutrient inputs can infill waterways and interstitial spaces with aquatic flora and cause hypoxic conditions overnight. Metal and chemical pollutants impair fish species greatly decreasing predator avoidance ability. (See Appendix B-4).
Source and sink populations	Tools: Correctly identify source vs sink populations and connectivity between them, maintain source populations and work to bolster recruitment for sink populations. Ensure fish abundance alone isn't the metric for population health, analyse age groups and site fecundity.	Sink populations of species lose more individuals than they create, and therefore must be bolstered by immigration from healthier populations (source populations). Sink populations are highly vulnerable to extirpation from any threat, including trout or other predator. Source populations may sustain other populations in the face of pressures. (See Appendix B-5).
Marine - freshwater connectivity	Advocate for increased marine - freshwater connectivity in both upstream and downstream directions and remove fish passage barriers where possible	The high incidence of diadromy in freshwater fish indicates the importance of access between marine and freshwater environments in replenishing freshwater communities in the face of biological and environmental pressures. (See Appendix B-6).
Riparian vegetation	Advocate for appropriate riparian vegetation extending throughout as much as the catchment as is practicable.	Many fish species require robust riparian vegetation, inputs of food and woody debris as shelter can sustain inter-species cohabitation as well as partially mitigate other environmental impacts. (See Appendix B-7).
Temperature	Advocate for natural temperature fluctuations, reduce or remove anthropogenic sources of thermal pollutants into waterways, ensure water abstraction does not interfere with the riverine ecosystem.	Water temperature outside any species preferred range overrides any biological interactions by changing all species behaviours (including feeding and breeding), and negative impacts of these unfavourable conditions will increase any impact of predation. (See Appendix B-8).
Trout size	While environment plays a larger role in mediating cohabitation between trout and native species, large trout (>150mm FL) in deep, stable rivers may pose a threat to threatened native fish if any such are inhabiting the same waterbody. Therefore, removal of large trout may be occasionally required if these circumstances occur.	Trout can become piscivorous once over 150mm FL. After this size, fish remain a small portion of trout diet (<10%, on average), and this proportion is governed primarily by the abundance of small fish and the availability of refuge for the prey. Non-diadromous species with highly fragmented and impacted habitats need to be protected from introductions of any large piscivorous fish, including trout. (See Appendix B-9).

Chapter Three: Influence of trout on dwarf galaxiid habitat preferences

Introduction.

Humans are altering the composition and ecology of Earth's biota via introduction of novel species, particularly in communities where resident species are highly specialised (Davis, 2003). Managing undesirable interactions between native and introduced species has become a global conservation challenge (Simberloff, 2003). However, not all introduced species are considered invasive or cause substantial ecological damage (Ling, 2004), some introduced species are considered beneficial depending on the desired ecological and/or human values (Simberloff, 2003). Decisions as to whether introduced species are suppressed, eradicated, or even enhanced are, therefore, dependent on local values and management objectives.

New Zealand's freshwater fish biodiversity mirrors the global trend of an increasing decline in distribution, with 62% of native species experiencing significant declines in distribution (Joy et al., 2018). There is increasing interest nationally to halt and reverse these trends (Weeks et al., 2016). The introduction of salmonids (particularly rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta*), is frequently implicated as a major driver of population fragmentation and decline of several species of native fish (Woodford & Mcintosh, 2010).

However, trout are often observed coexisting with several native fish species in some waterways but not others (Townsend & Crowl, 1991; Woodford, 2009). Species coexistence likely hinges on both the native fish species population resilience to predation, the abundance and availability of food, and the accessibility of habitat refuge to reduce predation. The extent to which habitat refuge protects a species from being predated is not only dependent on habitat availability, but the ability of prey species to utilise such refuge. The use of a variety of substrates by New Zealand fish species as refuge from predation by fish and birds, as well as refuge from floods has been well documented (Davey & Kelly, 2007; Jowett & Richardson, 1994). Many native fish species are benthic and inhabit interstitial substrate spaces, including bullies and some non-diadromous galaxiids (McEwan & Joy, 2014b; Woodford, 2009). Riparian vegetation may increase the density of dwarf galaxiid and other freshwater fish populations by providing refugia and food resources. Graynoth (1979) noted changes in between dwarf galaxiid populations within a Nelson catchment, with a large reduction in dwarf galaxiid abundance following clear-felling of vegetation to the stream edge when compared with the populations of dwarf galaxiids inhabiting streams with intact riparian vegetation. Habitat preference and/or use may change in the presence of a predator, as has been observed in previous examinations between trout and native fish (Crowl et al., 1992; Edge et al., 1993; McLean et al., 2007). However, the

observed outcomes may have been influenced by differences in experimental set up, the species tested, and the size of trout used. For example, experiments exposing galaxiids to the odours of predators (trout and eels) have demonstrated that larval and juvenile inanga and Canterbury galaxiid species avoid water with chemical cues from eels, but not trout chemical cues, even when the galaxiids used have prior experience with trout (Howard, 2007; McLean et al., 2007). This may indicate lack of familiarity with trout aroma, and/or a recognition of eels as the apex predator of New Zealand's freshwater ecosystem (Jellyman, 2012). Understanding the influence of predator presence on habitat use requires experimental manipulations examining a range of species and habitats.

Predation from brown and rainbow trout has been implicated in the fragmentation of dwarf galaxiid (*Galaxias divergens*) populations (McDowall, 1990b; West et al., 2015). The risk assessment matrix (see Table 2.2) suggests dwarf galaxiids are highly vulnerable to negative population impacts from trout population due to their small size, similarities in diet and habitat needs and low fecundity (see Appendix A-9), although they do coexist with brown trout (Glova et al., 1992; Hay, 2009). McDowall (1990b) states that evidence suggesting dwarf galaxiids are excluded from trout streams or can only be found in abundance upstream of brown trout is at best circumstantial. A later survey by Jowett & Richardson (2003) found 63% of sites with dwarf galaxiids also had brown trout present. It has been previously hypothesised that New Zealand's native fish are unlikely to possess salmonid-avoidance behaviours (freezing or dashing, avoidance, or increased refuge use) as they evolved in isolation from these introduced species (McLean et al., 2007; Milano et al., 2010; Whitehead et al., 2002), and thus have had only a short evolutionary history with which to recognise the specific chemical cues of trout (Milano et al., 2010). However, Kristensen & Closs (2004) demonstrated that a single exposure to conspecific mortality cues alongside the predator chemical simultaneously is enough for some naïve prey species (i.e., common bullies taken from an isolated perch-free pond who therefore had no exposure to perch chemical cues) to associate novel predator (perch) odour with danger. The bullies then exhibited predator avoidance behaviour when exposed to that odour after a single exposure. Thomas et al. (2016) also noted distinct predator avoidance behaviour in inanga after a chemical alarm cue (ground up inanga and water) was added to experimental water, so it is plausible that the behaviour of other native fish has adapted in response to the presence of salmonids after 150 years of interactions.

One way to examine potential behavioural responses of dwarf galaxiids to trout is through experimental manipulations. This study examined whether dwarf galaxiids alter their habitat preference in response to the presence, absence, and odour, of rainbow trout. Two contrasting habitats were examined: (1) sandy vs cobbly substrates, and (2) the

presence and absence of overhanging vegetation; each pairing offering one choice with greater refuge possibilities (cobbles and riparian refuge). It was hypothesised that dwarf galaxiids would preferentially seek refuge in the cobbly benthos or overhanging vegetation in the presence of trout odour, but not when trout and their odour is absent.

Methods.

Dwarf galaxiids and their collection. Dwarf galaxiids are a benthic non-migratory species endemic to New Zealand, attaining a maximum length of 90 mm (Hopkins, 1971). Dwarf galaxiids inhabit cobble and gravel substrates in the riffles of small streams and the shallow margins of larger rivers, predominantly in foothill catchments (Hay, 2009), and feed diurnally on aquatic and terrestrial invertebrates found on the benthos or in the drift (Glova et al., 1987). The life span of dwarf galaxiids is approximately three years, reaching maturity at one - two years: females produce moderate amounts of large eggs during spring and possibly autumn spawning seasons (Hay, 2009; Jowett & Richardson, 2003; Simberloff, 2003). Adult fish can burrow into gravel in response to reduced water levels (Hay, 2009). Dwarf galaxiids are listed as endangered in the IUCN Red List (West et al., 2015), and are thought to be especially vulnerable to anthropogenic threats and impacts of predation from a variety of avian and fish species, including trout, herons, and terns, due to their small size, wide and overlapping distribution with trout, population fragmentation and range reductions, and slow life history (Hay, 2009; Jowett & Richardson, 1994; Joy & Atkinson, 2012). Dwarf galaxiid populations are extremely fragmented, and the isolation of dwarf galaxiid populations have led to genetic differences between some populations (Allibone, 2002a), indicating at least some of this fragmentation is geomorphological in origin, and predates human interference of any type. The vulnerability of dwarf galaxiids to trout predation and the wide overlap of habitat occupation between this species and both brown and rainbow trout make dwarf galaxiids particularly suitable for testing trout interaction behaviours.

The dwarf galaxiids used in this experiment were sourced from the Manga-o-nuku Stream, Hawkes Bay, North Island New Zealand, using a combination of backpack electric fishing and herding via foot shuffling into stop nets. Approximately 400 fish were collected and transported to the Fish & Game hatchery facility in Napier, North Island, New Zealand, where the experiment was conducted. The galaxiids were acclimatised to the hatchery facility within a large, aerated tank, where they were liberally fed Ridley 4mm Tasman Freshwater palleted fish food (47% protein, 24% fat) which they readily consumed. The galaxiids were then allowed to adjust to changes in temperature, light, and location for seven days prior to the experiment beginning.

Predation experiment. The entire experiment was conducted within the Hawkes Bay Fish and Game hatchery facility which ensured all treatments were of the same size and had the same water flow, light, temperature, and water quality. All rainbow trout used in this experiment were approximately two years old and between 190-290 mm long (FL) and reared on-site in large exterior ponds. Selecting trout larger than 150 mm ensured they were of piscivorous length (Sánchez-Hernández et al., 2019). The trout were fed with their usual trout pellets for the duration of the experiment to reduce any risk of direct predation on the galaxiids as the focus of this experiment was on changes in habitat preference, not predation, as per animal ethic requirements (ethics protocol number 19/75, see Appendix C).

Each experimental replicate was a channel system consisting of three troughs in series, each trough measuring 2 m in length, approximately 50 cm in depth and width, with a constant water flow of ~0.18 m^3 from the uppermost trough to the lowest. Each trough contained material (vegetation or substrate) which either provided or denied the dwarf galaxiids places to hide. The two habitats were clearly delineated within a trough but randomly ordered. Inter-trough connectors were extended to allow for enough water volume in each tank for all fish to move around in a natural fashion, and mesh screens were placed at the lower side of each section to prevent any fish being moved into a lower section of the trough by the water flow.
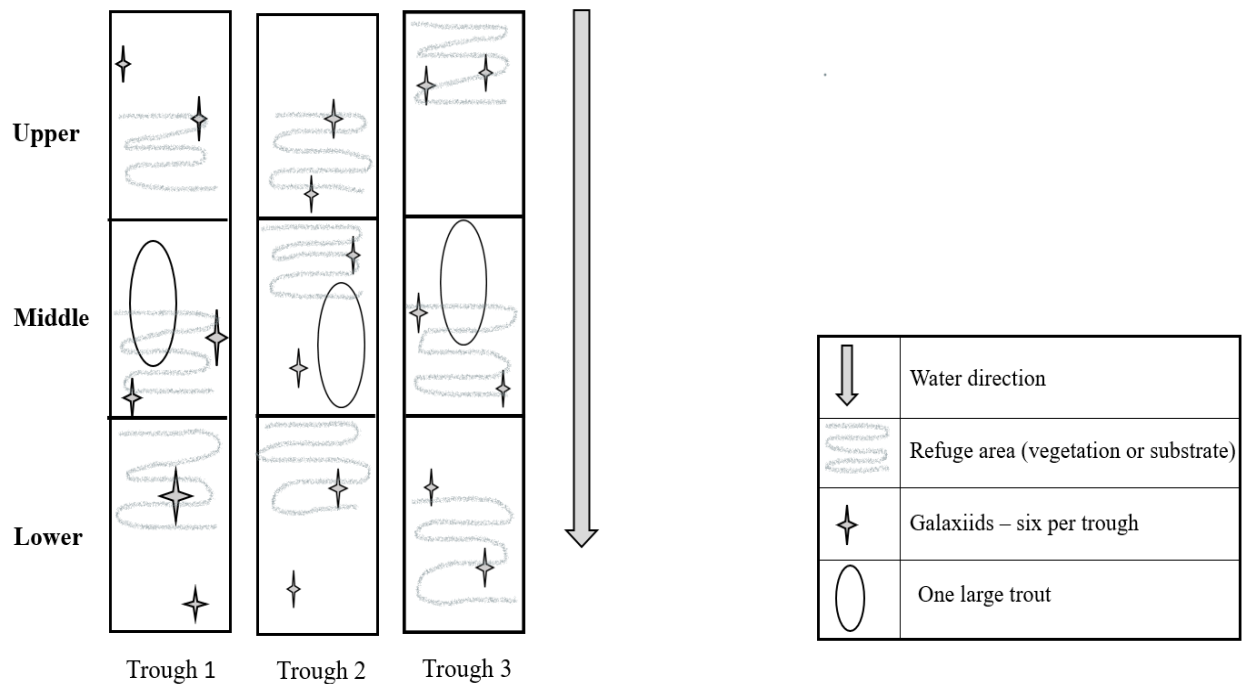
Figure 3.1: Experiment setup diagram showing upper, middle, and lower trough sections and direction of water flow. Dwarf galaxiids are present in upper and lower sections, trout and galaxiids are together in the middle section. Fish icons are not shown to scale.

Six randomly selected dwarf galaxiids were introduced into each section of the trough, this corresponds to a moderate-high stocking density which should give rise to observable habitat preferences. Galaxiids were fed palleted fish food and allowed to adjust to the new troughs which contained the same water supply they had been acclimated in. After the dwarf galaxiids adjustment period was completed, one rainbow trout was introduced into the middle trough section of each replicate. The upper trough sections containing dwarf galaxiids remained absent of trout or trout odour and were the control. The lower trough sections were also absent of trout but exposed to the odour of trout from the middle trough. The number of dwarf galaxiids in each habitat were recorded immediately before trout addition, approximately every hour after trout addition, and then after trout were removed. Observations were made by two observers randomly assigned to each trough in each instance to minimise observer bias. Dwarf galaxiids are known to be preyed on by black fronted terns and other piscivorous birds (Friberg et al., 2011), and it was noted that fish would rapidly mobilise around the tank if startled by observers. Therefore, consistent with Hay (2009), each observer would position themselves beside the trough and then wait for two minutes for fish to resume normal movement and behaviour prior to counting.

The riparian experiment used twelve replicates and ran with trout present for five hours (between 1630-2130 hrs). One half of each of the three sections of each replicate was draped with artificial ivy plants, forming floating riparian refuges (see Appendix D-1). Riparian coverage was randomly allocated to moderate any possible impact of differences in lighting and other variables. The bottoms of each of the troughs were lined with white paper to assist with dwarf galaxiid visibility as some of the fish were small (~3cm) and dark and thus difficult to spot against the concrete.

The substrate preference experiment used ten replicates and ran with trout present for four hours (between 1820 - 2220 hrs). Each section of the ten replicate troughs was randomly assigned half cobbles and larger stones, and the other half was fine gravel with no interstitial spaces (see Appendix D-2). The dwarf galaxiids were easily visible over the light-coloured gravel. Water was run over the replicates until any mobile sediment was flushed out, and once the water was flowing clear for an hour then the fish were added to the troughs as per the riparian experiment.

Following the experiment, trout were returned to their pond of origin at the Hawkes Bay Fish & Game facility, and dwarf galaxiids were utilised by the Hawkes Bay Regional Council for the purposes of designing effective fish passages, in accordance with animal ethics protocol number 19/75 (Appendix C), as conservation and biosecurity regulations do not permit their return to waterways.

Statistical analysis. Multi-factor Analysis of Variance (ANOVA) was used to examine whether the number of Dwarf Galaxiids observed in open habitat (sand or no vegetation) differed between treatments (control, trout, & odour), observation time, and paired-replicates. All analyses was carried out using the statistical software R (version 3.4.3, R Foundation for Statistical Computing., 2017). Posthoc paired t-tests were used to isolate which habitat treatments were different.

Results.

In the substrate choice experiment, channel and time had no significant effect on the number of Dwarf galaxiids observed over fine substrate (Table 3.1, Figure 3.1). The posthoc pairwise t-tests indicated that numbers of galaxiids observed in fine sediment did not differ significantly between trout physical absence and presence (p=0.83), while the odour-only treatments had more galaxiids observed over the fine sediment than both the trout-absent treatment (p=0.002) and the trout-present treatment (p=0.001).

In the vegetation choice experiment, there was no significant difference in the number of galaxiids observed in open water, although this did differ with time and channel (Table 3.1). The posthoc pairwise t-tests did not identify any significant differences between any individual time periods or individual channels (all p>0.05).

Table 3.1. Table and probability values comparing treatments (trout absent, trout present, and trout odour only), time, and channel.

Treatment type	Factor	DF	Sum sq	Mean sq	F value	Pr (>F)
Substrate	Treatments	2	10.03	5.02	6.97	0.001
	Time	1	0.96	0.96	1.34	0.25
	Channel	9	7.27	0.81	1.12	0.35
	Treatment:Time	2	3.45	1.73	2.40	0.09
	Residuals	165	118.83	0.72	-	-
Vegetation	Treatments	2	5.76	2.88	2.42	0.09
	Time	1	40.85	40.85	34.36	<0.001
	Channel	11	35.30	3.21	2.70	0.003
	Treatment:Time	2	0.33	0.17	0.14	0.87
	Residuals	202	240.19	1.19	-	-

Figure 3.2. Number of galaxiids observed over fine gravel in substrate experiment.
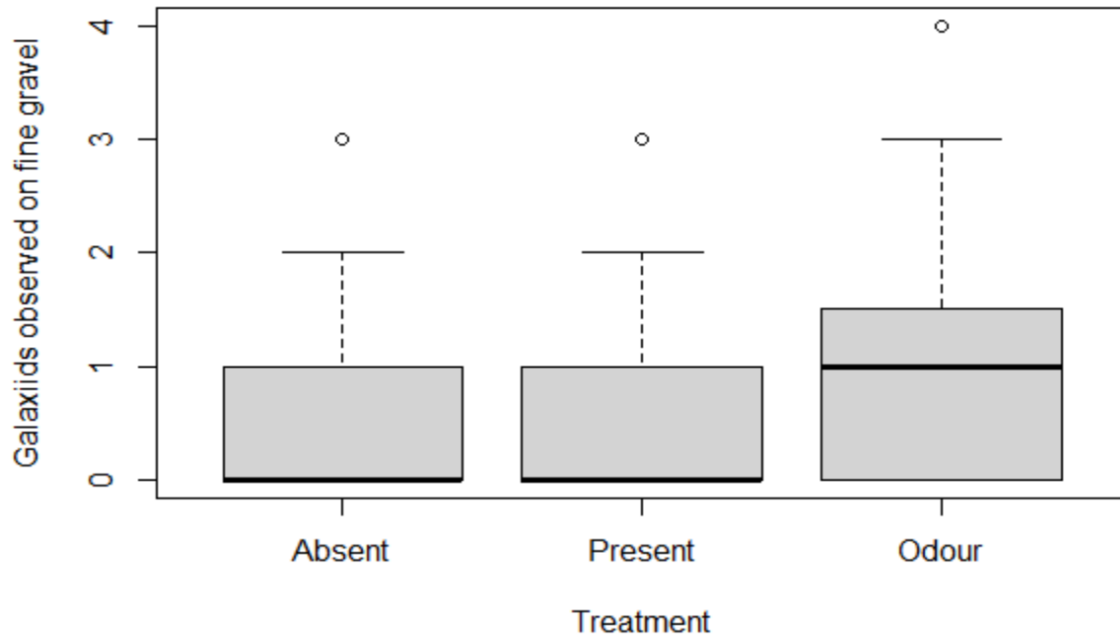
Figure 3.3. Number of galaxiids observed in the open in riparian experiment
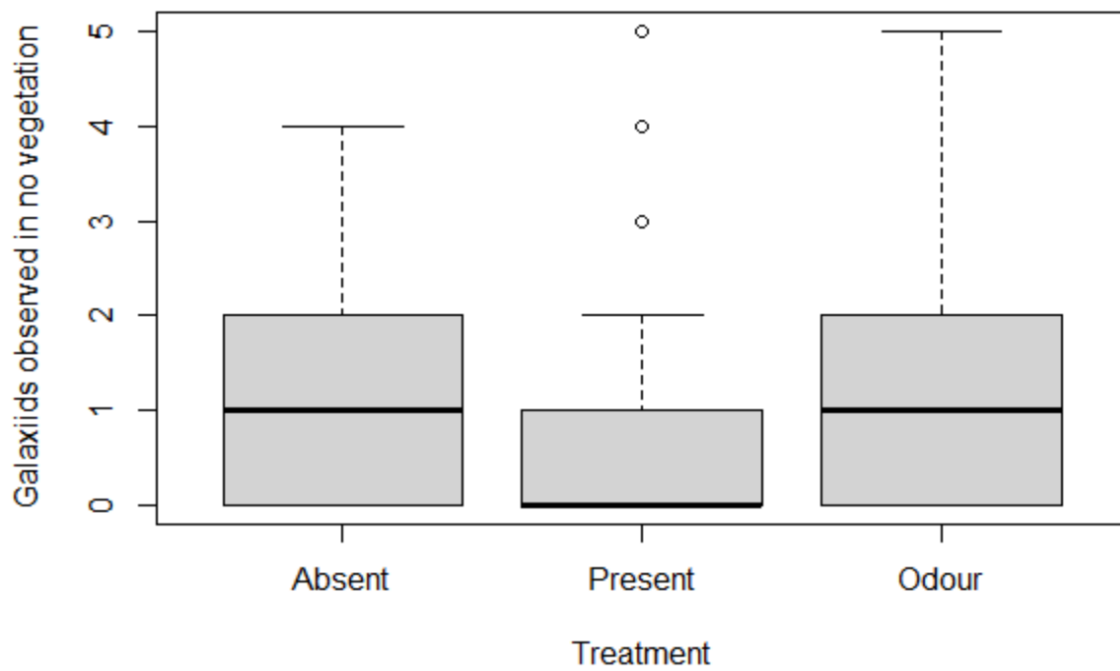
Discussion.

Dwarf galaxiids were observed over fine gravel significantly more in the odour only treatment than in any other treatment, although the difference in number of fish observed was small. Interestingly, there was no significant difference between numbers of galaxiids observed over fine substrate in trout present or trout absent treatments, possibly indicating the observed preference for substrate refuge is unrelated to the presence of a predator. No difference in number of dwarf galaxiids observed in the open was noted between any of the riparian treatments, channels, or time.

A cobble substrate preference by various native fish species has been demonstrated in previous literature. McIntosh et al. (1992) tested the substrate preference of Canterbury galaxiids with and without trout and noted the galaxiids demonstrated an overwhelming preference for large substrate regardless of the presence or absence of trout. Further experimentation showed galaxiids in gravel habitats with no refuge spent more time in slow velocity microhabitats when trout were present, in contrast to the behaviour noted by the author during stream surveys, and potentially indicating that real world variables complicate witnessed biological interactions. Sowersby et al. (2016) created a choice experiment whereby Australian riffle galaxiids could freely enter and exit habitats which contained a rainbow trout over either cobble or sand substrates and found that where the substrate was sand the galaxiids spent significantly more time in the trout free zone, however on cobble substrates the galaxiids cohabited with the trout. Riffle galaxiids also showed a clear preference for cobble substrate in the absence of trout. Howard (2007) found no changes in type or frequency of Canterbury galaxiid refuge seeking behaviour when exposed to trout odour regardless of past trout experience, however they did show a strong preference for refuge use during the day. The previously noted cobble substrate preference of dwarf galaxiids potentially provides refuge from disturbance and predation and may offer foraging benefits due to the high abundance of benthic invertebrates (Hay, 2009; Sowersby et al., 2016).

Research suggests that cohabitation between trout and galaxiids may be facilitated by availability of refuges and with certain size classes of trout. Woodford & McIntosh (2013) tested the potential predatory threat posed by large and small trout on the survival of Canterbury and alpine galaxiids, and whether trout species, size, or presence of vegetative cover impacted the predation rate. Results showed more Canterbury galaxiids disappeared from pens containing large trout (150-220mm FL) than from pens with small trout or no trout, and more alpine galaxiids were recaptured from the small trout (100-120mm FL), treatment compared with both large trout and no trout treatments. It was noted 13% of Canterbury galaxiids and 31% of alpine galaxiids were retrieved from different pens they

had been placed in and may have escaped the experimental area altogether. The noted substrate burrowing capabilities of these galaxiids may have impaired the recapture process and some fish assumed to be consumed may, in fact, have escaped. It was also stated that juvenile trout (30-50 mm TL) were left in the pens, and other, larger trout were unexpectedly found in the pens on recapture: if some pens had more trout in them than others this could change the large fish/small fish ratio in those pens, increase competition for invertebrate food, and provoke a higher rate of predation than would be normally expected. Woodford (2009) investigated predation of large (>150mm FL) brown trout on alpine galaxiids with and without aquatic macrophyte cover. "Significant mortality" (no numbers given) of alpine galaxiids was noted regardless of presence or absence of macrophytes. However, *Deleatidium* larvae were added to each tank prior to the experiment beginning at a minimum density rate, and the galaxiids were added 16 hours prior to the trout being introduced. As there was no substrate for the invertebrates to seek refuge within, trout may not have been preferentially preying on galaxiids, merely without any other accessible food source. A second experiment compared ability of large brown trout (169-187mm FL) and rainbow trout (179-195mm FL) to prey on small alpine or Canterbury galaxiids. No difference was noted in the relative ability of either trout species to consume galaxiids or either species. Eight alpine galaxiids and three Canterbury galaxiids were consumed during this experiment.

During the riparian experiment research conducted for this thesis, one trout was seen to consume a small dwarf galaxiid. No predation or chasing of galaxiids was seen at any other time during the experiments. Within five minutes of the predation occurring a photo was taken with a galaxiid within the same trough prone on the substrate less than five centimetres from the trout (See appendix D-3). This prone position is common to a benthic fish species, and this individual had to leave the riparian refuge to sit in the open with the trout. One observation is insufficient to begin to attempt to extrapolate possible reasons for this behaviour, however it would be interesting to see if this proximity between dwarf galaxiids and trout is an unusual occurrence. Behavioural change related to the immediate presence of predators, or their signals, was tested by Edge et al. (1993) using body positioning and activity level changes of three differing populations of Canterbury galaxiids and their response to the presence of brown trout or trout odour. They found that in the presence of trout Type A galaxiids displayed more prostrate behaviours, Type B showed no difference in behaviour or activity levels, and Type C were more active. Type A and B galaxiids fed at a lower rate in the presence of trout, whereas the feeding rate of Type C was not significantly reduced. The authors theorise that trout may pose less of a risk to the Type C galaxiid which explains the increase in activity and lack of impact on feeding behaviours,

but no explanation is given as to why this should be so. The trout were 115-120mm TL, so likely posed no predation threat.

Edge et al. (1993) also assessed the impact of trout chemicals in water on galaxiids. Only Type A galaxiids (who demonstrated the greatest degree of prone positioning in the presence of trout) were used in the trout odour test, however they demonstrated no behavioural changes when exposed to trout odour, and the dwarf galaxiids in our experiment similarly showed no behavioural changes to trout odour. McLean et al (2007) used a two-chamber choice experiment to determine whether larval and juvenile inanga exhibited avoidance behaviours when exposed to rainbow trout odour and short-finned eel odour. Inanga were placed a tank which contained one non-odour water chamber, and one with either trout or eel odour water. It was noted that both larval and juvenile inanga showed a significant avoidance response to eel odour water, whereas there was no statistically significant avoidance of the trout odour water It should be noted that galaxiids are commonly predated by fish other than trout. Larger bodied native fish such as the kokopu species, koaro and all eel species are also noted to prey on smaller fish, and predation on juvenile giant kokopu by adult conspecifics is considered a significant threat (Whitehead et al., 2002), and thus eels, as the largest and most widespread predator fish species in New Zealand water, may trigger more dramatic predator avoidance behaviour in smaller native fish species.

It is uncertain why dwarf galaxiids in the riparian experiment were affected significantly by the isle they were in. A paired t-test (Appendix C-5: table 3.5) showed significant differences predominantly in isle K: this isle was also used for the substrate experiment which showed no such differences. Perhaps some difference in light or other variable that was not perceived by the experimenters altered the behaviours of the dwarf galaxiids solely on the day of the riparian experiment.

Conclusion.

Literature commonly states that vulnerable non-diadromous native galaxiid species, including dwarf galaxiids, are negatively impacted by trout, and are unlikely to co-exist with them. Fish survey data shows co-occurrence between trout and dwarf galaxiids is relatively common, potentially owing to refuge seeking behaviours of dwarf galaxiids. This experiment showed more galaxiids sought refuge in gravel substrates in the trout odour test only, and no other significant differences in galaxiid behaviour when exposed to trout presence or odour in both riparian and substrate experiments were noted. Although not significant, that there were more galaxiids seen in the open in the riparian experiment control

group than in the trout presence group may have biological importance: further experiments of longer duration may help to determine if this trend is of relevance.

These experiments demonstrate the preference of dwarf galaxiids for cobbled substrates and riparian vegetation, and these preferences provide refuges which could help mitigate the impacts of trout predation. Future waterway management in areas containing trout and dwarf galaxiids should find this data helpful, as it explains this species requirements and preferences for overhanging riparian vegetation and the provision of in-stream structures and deposited sediment management and may help protect these vulnerable galaxiids against threats by aquatic and avian predators.

Chapter Four: Conclusion

Multiple factors will contribute to the persistence of native fish populations within New Zealand of which interactions with salmonids is but one (Hayes et al., 2019). Predicting which species are most vulnerable to biological or environmental disturbance is aided by knowledge gained from a thorough literature search which indicates that higher altitude, cooler water species tend to be less fecund (e.g., have ~40% larger eggs and much lower larval abundance) and take longer to reach maturity, and thus may not be as resilient to disturbance of any sort (large flood, pollutants, predation) as those who have developed faster life histories. Fast life history traits (large numbers of small eggs, earlier maturation, and higher larval abundance) act as a 'resilience buffer' for the population and are traits generally found in species inhabiting lower catchment systems where these disturbances are more common (Jones & Closs, 2018), and is likely the reason why there are no diadromous species assessed as highly vulnerable in the risk assessment matrix. Those species who produce smaller numbers of larger and more physically able offspring offset with a protracted timeframe until sexual maturity is reached have fewer individuals, and any losses prior to breeding could have a disproportionate impact on population size. Once these high-risk species were identified, work can begin on locating and protecting sites which contain these fish and enhancing those environmental factors which allow for coexistence between all our valued freshwater fish species.

The development in this thesis of a risk assessment matrix to prioritise the most at risk species can lead to identifying those reaches where such species are in proximity to trout. Research based on understanding of species traits, environmental, behavioural, and biological requirements can drive focussed management frameworks (Probert et al., 2020). The behavioural experiment conducted here, and previous research, indicates that environmental mitigations should take priority for the needs of native freshwater fish species, in particular a need for food resources, natural waterway forms with high levels of habitat heterogeneity, natural flow regimes, and abundant refuge in the form of riparian vegetation and plentiful interstitial spaces in the substrate. While some highly vulnerable species populations may require a removal of predators such as large trout to ensure their survival, attempted eradications may not achieve enhanced biodiversity outcomes, and a focus on the holistic ecosystem health of an area is strongly recommended for any management program.

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Appendix A: Species specific interactions between native fish and trout

A-1: Grayling

The only native New Zealand fish species known to become extinct is the New Zealand grayling (*Prototroctes oxyrhynchus*), a small, amphidromous, shoaling species which was found in abundance across much of the country. The grayling was the sole herbivorous fish species and was abundant in 1860 but abundance had declined considerable by 1870 (Lee & Perry, 2019). The last recorded grayling sighting was in 1923, and the year of extinction is estimated to be between 1924 and 1979. The introduction of trout has previously been implicated in the cause of extinction (Flecker & Townsend, 1994; McDowall, 2006b). However, grayling also disappeared from isolated streams where trout were not present, and the overall impact of over-harvesting and the overwhelming modification of habitat which occurred with European settlement potentially acted as a significant stressor to the grayling population. It is likely that all factors combined with source-sink dynamics to create the extinction event (Lee & Perry, 2019). As grayling are extinct, biological interactions with trout were not assessed or included in this thesis.

A-2: Mudfish

New Zealand's mudfish species include the black mudfish *(Neochanna diversus*, threat status declining), brown mudfish *(N. apoda*, threat status declining), Canterbury mudfish (*N. burrowsius*, threat status nationally critical), Chatham Island mudfish (*N. rekohua*, threat status naturally uncommon), and the Northland mudfish (*N. heleosis* threat status nationally vulnerable).

Mudfish are scale-less, non-diadromous native freshwater fish, primarily nocturnal and benthic, have a life expectancy of up to 11 years (O'Brien & Dunn, 2007), grow to 175 mm (McDowall, 2004), and are now only found inhabiting slow moving and often temporary waters like ephemeral palustrine wetlands, ephemeral streams and drains (Cadwallader, 1975b; Eldon, 1979b; Ling & Gleeson, 2001; McIntosh et al., 2010; O'Brien, 2005; West et al., 2015). These species usually spawn once a year but may have prolonged or multiple broods if conditions permit (O'Brien & Dunn, 2007). Black and brown mudfish lay few, moderately large eggs, while Canterbury mudfish lay many small eggs. Mudfish can breathe air, burrow into wet soils throughout summer, and survive drying of temporary wetlands and hypoxic water – conditions that most other fish cannot (Eldon, 1979b; O'Brien, 2005).

While the original habitat for Canterbury and brown mudfish was likely to be deep, slow flowing streams between large areas of swamp (McDowall, 1990a), New Zealand now

has less than 10% of pre-human wetlands and associated connecting waterways remaining, with the vast majority converted to agricultural land (Belliss et al., 2015). It is this loss of habitat and the degradation of remaining lowland waterways that has largely driven the decline of mudfish abundance (Eldon, 1968; Foote et al., 2015; West et al., 2015). It has been noted the habitats in which mudfish are now found are difficult to sample efficiently, and this may pose difficulty in accurately estimating abundance and distribution (Cadwallader, 1975b).

Using the risk assessment matrix (Table 2.3), the risk of a negative interaction between trout and mudfish to significantly impact populations is likely high for all species and requires further investigation. Whilst trout have been recorded consuming mudfish, mudfish has only been reported in stomach contents of seven trout in one study (Eldon, 1979a). The relative impact of trout consumption on population abundance has not been assessed. As mudfish occupy temporary wetlands and burrow in mud, the likelihood of predation by trout is minimal as large trout prefer deep, cool, permanent waters (Holmes & Hayes, 2011; Young et al., 2010). Nonetheless, trout presence may contribute to the marginalisation of mudfish to farm drains which are typically unsuitable habitat for trout (Eldon, 1979b; O'Brien, 2005), although mudfish presence in drains may also be driven by habitat preference, given the loss of original habitat options. Mudfish vulnerability to predation is heightened by their often small and fragmented populations (O'Brien & Dunn, 207; Dunn et al., 2018; West et al., 2015) and the limited recruitment potential for all mudfish species excepting the more fecund Canterbury mudfish (McDowall, 1990a; West et al., 2015).

A-3: Smelt

Common smelt (*Retropinna retropinna*, threat status not threatened) grow to a maximum size of 125 mm (Jellyman et al, 2013), and live for a maximum of two years (McDowall, 1990a). They are diadromous and typically constrained to slow velocity, lowland waterways (up to 15 km inland and 140 m above sea level), though they can travel further inland if low gradients and velocities permit (Joy & Atkinson, 2012; McDowall, 1990a). Stokell's smelt (*Stokellia anisodon*, threat status naturally uncommon) are a predominantly marine species which can only be found in coastal freshwater areas of the eastern South Island during spawning; they do not eat in freshwater, and die after breeding (Allen, 1961; David et al., 2015; Franklin et al., 2015; Rowe & Taumoepeau, 2004).

Common smelt were deliberately introduced to North Island lakes as a forage fish for trout (Rowe, 1984; Ward et al., 2005). Using the risk assessment matrix (Table 2.3), it is considered the risk of negative interactions with trout to be deleterious to smelt populations of either species to be minor. Migrating smelt have pelagic shoaling movements through the

centre of waterways, potentially increasing the risk of predation by trout (Allibone & McIntosh, 1999; David et al., 2015; Richardson et al., 2001; Rowe, 1993). However, trout and smelt often co-exist in coastal areas and land-locked lakes where stocking of both species has occurred, likely due to their high fecundity, early maturation, widespread dispersal, and generalist habitat preferences of smelt (Joy & Atkinson, 2012; McDowall, 1990a).

A-4: Eel

Both longfin eel (*Anguilla dieffenbachii*, threat status declining) and shortfin eel (*Anguilla australis*, threat status not threatened) species are catadromous, migrating to sea to breed as fully grown adults, with the larval eels returning to freshwater systems to grow to maturity (McDowall, 1990a; McDowall, 2010; Pike et al., 2015a; Pike at al., 2015b). Eels are widely distributed across New Zealand and are slow growing (males migrate to breed >25 years old and females >40 years), long lived, nocturnal and carnivorous (Beentjes et al., 2006; Glova et al., 1998; Jellyman, 1989; Sagar & Glova, 1998). Longfin eels are New Zealand's largest native freshwater fish: females can obtain sizes of 2 m long and exceed 25 kg (Jellyman, 2007). Large eels are the apex freshwater predator of any given area and support a significant commercial fishery despite their vulnerability status (Jellyman, 2012). Elvers (up to ~300 mm long) inhabit shallow lowland habitats with loose cobble substrate, while larger eels (>500 mm) seek deep, slow flowing water and are strongly associated with undercut banks and debris (Cadwallader, 1975a; Hicks & McCaughan, 1997; Jellyman, 2012; Jellyman, 1989; Jellyman et al., 2003; Sagar & Eldon, 1983). Eels prefer low flow velocities but can tolerate a variety of velocities (Broad, 2002; Richardson & Jowett, 1995).

Using the risk assessment matrix (Table 2.3), it is considered the risk of negative interactions with trout to be deleterious to eel populations of either species to be minor. Differences in diel feeding patterns may reduce the likelihood of interaction, although during summer both trout and eels are most active during twilight (Sagar & Glova, 1998). While juvenile eels can migrate in shoals, their consumption by trout is likely to be low due to their nocturnal and refuge seeking behaviours (McDowall, 1990a). Adult eels typically reside in undercut banks and backwaters during the day and are generally avoided by trout due to eels' status as apex predators (Broad, 2002; Burnet, 1969; Jellyman et al., 2003). Large eels are piscivorous and aggressive hunters that frequently consume trout (Allen, 1961; Cadwallader, 1975c; Jellyman, 1996) and it is therefore unlikely that trout will have a negative impact on populations of eels of either species.

A-5: Torrentfish

Torrentfish (*Cheimarrichthys fosteri,* threat status declining) reach a maximum size of 200 mm with a life expectancy of eight years. They are diadromous with a flattened body and downward facing mouth which enables the consumption of benthic invertebrates in the fast-flowing riffles of shallow braided or gravel bed rivers (Jowett & Richardson, 1995; McDowall, 2000; Tana, 2009). They are primarily nocturnal, likely burrow into substrate during the day (Glova et al., 1987), and are widely distributed around New Zealand with females often migrating further inland than males (McDowall, 1990a; Tana, 2009).

It has been suggested that female torrentfish move downstream to spawn before returning upstream (Glova et al., 1987; Scrimgeour & Eldon, 1989; Warburton, 2015), which may render them vulnerable to predation by large trout as they migrate through their habitats. However, an investigation by McDowall (2000) did not find compelling evidence of long-distance spawning migrations in torrentfish, and Tana (2009) suggests spawning journeys are likely to vary between river systems. While it is possible that trout presence excludes torrentfish from other microhabitat use, the morphological adaptation of torrentfish to rapid flowing water and riffles indicates that these are preferred habitat, regardless of predator presence (Glova et al., 1987).

Using the risk assessment matrix (Table 2.3), it is considered the risk of negative interactions with trout to be deleterious to torrentfish populations to be minor. McDowall (1990a) identified a 2.5 kg trout with eight torrentfish in its stomach, indicating interspecific predation does occur. However, predation by trout is likely to be uncommon as torrentfish occupy riffle and torrent habitats which seldom host large trout (Hayes & Jowett, 1994; McLennan & Macmillan, 1984; Young et al., 2010). Torrentfish vulnerability to predation is likely highest if they move into pools to feed, however, as pools are frequently scoured or infilled and contain fewer invertebrate prey than riffles and runs such movements are unlikely (Glova et al., 1987; Logan & Brooker, 1983; Pridmore & Roper, 1985; Winterbourn, 1978). The widespread distribution, limited interaction potential and low threat ranking of torrentfish indicates this species is likely resilient to negative outcomes of interactions with trout.

A-6: Pouched Lamprey

Pouched lamprey (*Geotria australis,* threat status nationally vulnerable) are a strictly nocturnal anadromous species whose adults reach a maximum of 700 mm long, spawn in freshwater and die after protecting and aerating their eggs (Baker et al., 2016; Closs et al., 2015; Paton et al., 2019). The juveniles (ammocoetes) live in shaded, shallow, slow water

with fine substrate into which they burrow if disturbed (Jellyman & Glova, 2002; Jowett et al., 1996; Todd, 1992) and filter feed on algae and organic detritus (Paton et al., 2019; Todd, 1992) for approximately four years before migrating to sea to parasitise marine animals. They are located in Australia, South America and New Zealand where, although widely distributed, they are threatened due to fish passage barriers and loss of freshwater spawning habitat (James, 2008; Closs et al., 2015; Jellyman & Glova, 2002). Adult lamprey congregate under boulders, are rarely found above the substratum and do not feed in freshwater (Closs et al., 2015; Jellyman et al., 2002; Kelso & Glova, 1993; Todd, 1992).

Using the risk assessment matrix (Table 2.3), it is considered the risk of negative interactions with trout to be deleterious to pouched lamprey populations to be minor. The pool or under boulder habitat usage of adult lamprey may provide refuge from all predators except for large longfin eels (Baker et al., 2016), and the adult lamprey are too large to be eaten by even the largest trout (Allibone & McIntosh, 1999; Mittelbach & Persson, 1998; Robbins, 2007). As trout move upwards into the water column to feed (Hayes & Jowett, 1994), and allowing that there is no overlap of diet, it is unlikely that the benthic ammocoetes would be exposed to predation by trout. The cryptic nature of lamprey makes assessing their abundance, distribution, and fecundity difficult, complicating any actual assessment of any impact of trout on the population.

A-7: Black Flounder

Black flounder (*Rhombosolea retiarii*, threat status not threatened) are a diadromous flatfish species which grow to 350 mm, predominantly inhabit freshwater systems and spawn large numbers of small eggs at sea (David et al., 2015; Jellyman et al., 2013). They consume benthic invertebrates and have been observed consuming whitebait (McDowall, 2016). Flounder are widespread in coastal waterways (Minns, 1990) where they inhabit slow flowing sandy pools, estuaries, and lakes. Adults can be found up to 250km inland along low gradient, large rivers and can occasionally be found in faster flowing, cobbled rivers (David et al., 2015; Jellyman & Harding, 2012; McDowall, 2010). Their life expectancy is unknown.

A study in one coastal lagoon found many flounder bones in the stomachs of trout; however, the report concluded the bones were flounder carcasses discarded by fishers and solely consumed by trout due to scarcity of other food (Rutledge, 1991). Adult black flounder may interact with trout in lowland waterways during the migrations of whitebait as both species prey on juvenile whitebait (McDowall, 2006a), though predation of adult flounder by trout is unlikely due to the large body size and strict benthic positioning of flounder.

Using the risk assessment matrix (Table 2.3), it is considered the risk of negative interactions with trout to be deleterious to black flounder populations to be minor. Studies examining interactions between trout and black flounder have not been sourced, however predation risks from trout are likely to be restricted to the migration of juvenile black flounder from the sea into estuarine and backwater systems during spring (David et al., 2015; McDowall, 1990a). The limited information on flounder abundance (Crisp et al., 2014) and late onset of breeding age (as predation may occur before reproduction) of flounder may increase the vulnerability of the species to negative impacts of any type.

A-8: Diadromous galaxiid

Adults of the diadromous galaxiid (also referred to in literature as galaxias) species spawn in temporarily submerged terrestrial vegetation in freshwater or estuarine habitats: the eggs develop, then hatch when re-inundated by later high flow events and are washed out to sea, the juveniles (often called 'whitebait') return after several months and migrate upstream (David et al., 2004; Franklin et al., 2015). Adults feed on aquatic and terrestrial invertebrates anywhere in the water column or from the benthos, and tend to be nocturnal, though they can be active at any time (Bonnett & Lambert, 2002; Hansen et al., 2004; Main & Winterbourn, 1987; McCullough, 1998; McDowall, 1990a; West et al., 2005). The four large galaxiids (shortjaw kokopu, banded kokopu, giant kokopu and koaro) are slow growing and strongly favour habitat with riparian vegetation (Allibone et al., 2003; Bonnett & Sykes, 2002; McDowall et al., 1996; Rowe et al., 2000; Rowe et al., 1999).

David et al (2004) found that giant kokopu, koaro, inanga and banded kokopu populations can preferentially recruit within freshwater or estuarine systems. Of the five whitebait species only shortjaw kokopu does not appear capable of forming landlocked populations (McDowall, 2010). Populations which preferentially breed in freshwater are at greater risk of negative impacts from anthropogenic activities than those who incorporate a marine life phase.

A-8.1 Banded kokopu

Banded kokopu (*Galaxias fasciatus*, threat ranking not threatened) can grow to 300 mm long and live up to 10 years. Males mature in two years and females in four, spawning large quantities of small eggs, potentially sustaining widespread populations (Mitchell & Penlington, 1982; West, et al., 2015). Banded kokopu often inhabit small, slow flowing pools with fine substrate and undercut banks, often in first and second order streams though they can be found in deeper water in larger rivers (Baker & Smith, 2007; McCullough, 1998;

West et al., 2005). A study by Rowe et al (2000) concluded that juvenile banded kokopu were more sensitive to suspended sediment than other native fish and actively avoided rivers with turbid lower reaches despite presence of suitable upstream habitat. This factor should be considered when assessing banded kokopu distributions.

During 60 hours of observations of trout and banded kokopu interactions in an artificial pond and stream simulator, Main (1988) noted that trout-maintained territories and reacted to the presence of banded kokopu by leaving cover and acting aggressively towards the kokopu, and the banded kokopu swam in a loose shoal and at times reacted with aggression to the trout. West et al (2005) also noted evidence of intraspecific territorial and aggressive behaviours among banded kokopu where the density of the fish was highest. It is possible that banded kokopu could be excluded from some habitat by large trout in reaches where both could co-occur, or alternatively that trout may be excluded by banded kokopu.

A-8.2 Giant kokopu

Giant kokopu (*Galaxias argenteus*, threat ranking declining) are the largest galaxiid species potentially reaching 580 mm long (Whitehead et al., 2002). They are highly fecund with large numbers of small eggs, live up to 30 years and reach maturation in three years (McDowall, 1990a; West et al., 2015; Yungnickel et al., 2020). Small individuals (<80 mm) tend to inhabit shallower backwaters adjacent to fast flowing water, while adult giant kokopu prefer pool habitat in slow flowing, clean lowland waterways with instream cover and abundant riparian vegetation (Bonnett & Lambert, 2002; Bonnett & Sykes, 2002; David, 2003), thus displaying similar shifts in habitat use with increasing size as rainbow trout (Whitehead et al., 2002).

Giant kokopu are regularly found with brown trout in the same waterway but cohabit less frequently at finer spatial scales, potentially due to the kokopu's large size, aggressive territorial behaviour, and predatory nature (Bonnett & Sykes, 2002; David, 2003; Main, 1988). It is noted they are more likely to be absent where trout abundance is high (David et al., 2002; Goodman, 2002; Jellyman, 2012); although a survey by David et al (2002) did observe both species in the same pools in one stream. It is unknown whether the lack of co-occurrence in short reaches is driven by competition/predation between giant kokopu and trout or by fine-scale habitat preferences.

A-8.3 Inanga

Inanga (*Galaxias maculatus*, threat ranking declining) are the most widespread and abundant of the diadromous galaxiids. This species grows to a maximum of 110 mm long and

produces numerous small eggs: most adult inanga die after the first spawning but some reach three years of age (Main, 1988; McDowall, 1990a). They spawn in dense riparian vegetation during high spring tides, eggs hatch in response to re-inundation after two - four weeks (Hickford & Schiel, 2014; McDowall, 1990a; Orchard et al., 2018). Larger females have higher levels of fecundity; it is currently undetermined whether food availability during oceanic life stage or better stream habitat quality are responsible for the increased condition of the fish (Stevens et al., 2016). Juvenile fish return to freshwater ecosystems after several months at sea often following a flood event (Benzie, 1968). Inanga are opportunistic and generalised feeders of aquatic and terrestrial invertebrates (Jowett, 2002; McDowall et al., 1996). Juvenile inanga drift feed along the water column in schools in slower water and pools, and they remain shoaling and pelagic as adults (Jowett, 2002), increasing likelihood of interactions with trout.

Inanga are associated with pasture sites (Jowett & Richardson, 2003; Rowe et al., 1999), slow, deep water, fine substrate within a gentle upstream gradient from the river mouth and are unable to progress past instream barriers (Hayes et al., 1989; Hayes et al., 2008; Joy & Death, 2001). Inanga habitat criteria is dictated by swimming ability and bio-energetic requirements rather than the river and surrounding environment as most individuals spend only a short time (~ seven months) in freshwater (Jowett, 2002; Yungnickel et al., 2020). The short life span of inanga indicates that populations could suffer serious declines should year class recruitment falter or fail (Yungnickel et al., 2020).

An artificial stream experiment analysing habitat use by 50 inanga with and without brown trout present (255-390 mm FL) showed trout predated inanga at a rate of 0-40% (mean 14.5%), and when trout where present inanga utilised run habitats more often than when they were absent (Glova, 2003). In contrast, Bonnett & McIntosh (2004) found that inanga display no behavioural change by inanga in experiments in the presence of small/medium trout. McLean et al., (2007) conducted a choice chamber experiment whereby juvenile inanga were given a choice between water imbued with rainbow trout or shortfin eel odours. Inanga avoided water with eel odour but showed no response to water with trout odour. Results may indicate a lack of recognition of trout as a predator, potentially exposing inanga to predation risk, or a recognition of eels as more significant apex predator than trout.

A-8.4 Koaro

Koaro (*Galaxias brevipinnis*, threat ranking declining) have a life span of 15+ years, reach a maximum length of 270 mm, and the females spawn large numbers of small eggs, likely close to adult habitat (Bell, 2001; McDowall, 1990a). They have excellent climbing ability

which allows their widespread distribution. The species inhabits riffles and pools where they are most often found under large boulders and are negatively buoyant so rest on the substrate then rise into water column to feed in a manner similar to juvenile trout (Bell, 2001; Hayes, 1996; Kusabs & Swales, 1991; Main & Winterbourn, 1987). They often inhabit the riffles and torrents in native forest streams (Hayes et al., 1989; McDowall, 1990a; Richardson & Jowett, 1995) and are rarely found where the riparian cover has been removed (Rowe et al., 1992).

Two surveys have noted pool dwelling populations of koaro in waterways where trout are rare or absent, and it has been suggested that trout may exclude koaro from preferred habitats (Bell, 2001; Hayes, 1996). Kusab & Swales (1991) noted diel feeding differences in Lake Taupo tributaries reduced competitive pressure between rainbow trout and koaro and suggested that trout presence may have led to some exclusion of koaro in rivers with low habitat heterogeneity. In a series of experiments Bell (2001) found that the presence of medium sized trout (up to 140 mm) had no significant effect on the growth rate of small, medium, or large koaro over a one-month period, but that small koaro avoided both medium trout and large koaro suggesting predator avoidance may be of more importance to juvenile koaro than competition factors regardless of species.

A-8.5 Shortjaw kokopu

Shortjaw kokopu (*Galaxias postvectis*, threat ranking nationally vulnerable) has a life span of up to 15 years and can reach 350 mm, matures at three years, and spawns many large eggs (McDowall, 1990a). It is the rarest of the large galaxiids, and inhabits small, clear streams in native forests with logs or boulders as instream cover (Goodman, 2002). They are predominantly nocturnal and feed at all levels in the water column, but feed most frequently from the benthos or the surface and least frequently from the drift. Their preferred diet of cased caddis larvae from the benthos indicates importance of low sedimentation and minimal growths of filamentous algae (Allibone et al., 2003; McDowall et al., 1996).

A survey by Allibone et al., (2003) found that shortjaw kokopu had irregular recruitment patterns and were widely but sparsely distributed, and often found in low abundance. However, the species is cryptic and difficult to sample, and may more abundant than currently recorded. During the study, one reach was cleared of riparian vegetation and the resident kokopu emigrated, despite previously displaying high site fidelity. This response demonstrates the importance of vegetated cover to the species. In an unpublished master's thesis, Goodman (2002) spotlight surveyed fish assemblages in 148 streams across northern parts of New Zealand's South Island and observed trout co-occurrence with shortjaw kokopu

at over the half the sites trout were present. It is, however, unknown which factors, or combinations thereof, explain the lack of co-occurrence at the remaining sites.

Diadromous galaxiids and trout interaction risk

Using the risk assessment matrix (Table 2.3), it is considered the risk of negative interactions with trout to be deleterious to inanga and banded kokopu populations to be minor, and shortjaw kokopu, giant kokopu and koaro populations to be moderate. This increased risk to the latter three species reflects broad dietary, habitat and feeding overlaps between these species and trout, as well as the increased vulnerability to predation encountered by migrating galaxiids (especially juveniles), and the potential for competitive exclusion. These vulnerabilities may be offset by differences in microhabitat and diel feeding preferences; the four large diadromous galaxiids species are likely to grow too big to be consumed by trout and have been observed excluding trout from preferred habitat (Baker & Smith, 2007; David et al., 2002): the increased risk for shortjaw kokopu is linked to its low abundance and giant kokopu is considered more vulnerable due to its late maturation time and almost identical habitat and feeding preferences to trout.

Many of the studies mentioned have indicated potential for competitive interactions between diadromous galaxiids and trout, which have similar diets and feeding habits (Main, 1988; McCullough, 1998) and this may partially explain limited co-occurrence patterns between the species (McDowall, 1968; West et al., 2005). Habitat preferences and environmental variables will impact on spatial distributions of the species also. It is noted that populations of diadromous galaxiid species have suffered major declines in areas where river channelisation, deforestation, wetland drainage and conversion of land to pasture have occurred (Hickford & Schiel, 2014; Whitehead et al., 2002; Yungnickel et al., 2020). Negative interactions between these species and any predator / competitor are likely to be exacerbated under degraded environmental conditions.

A-9: Non-diadromous galaxiid

Non-diadromous galaxiid species complete their entire life cycles within the freshwater system, and often have larger eggs and fry in comparison to diadromous galaxiids (Closs et al., 2013). These galaxiids often have restricted distributions due to habitat fragmentation and reduced larval dispersal ability (Leathwick et al., 2008; Waters et al., 2020) and may be more vulnerable to changes in flow regimes or negative interactions with other fauna. They are generally cryptic and relatively unstudied, with many non-migratory species described only recently based on genetic analysis (Howard, 2014; Waters & Wallis, 2001).

A-9.1 Alpine galaxiid

Alpine galaxiids (*Galaxias paucispondylus*, threat ranking nationally vulnerable) can grow to 112 mm, live ~5 years in shallow, fast flowing streams of the central South Island high country and spawn few, large eggs in winter in their second year (Bonnett, 1990; Bonnett 1992). This species is generally avoidant of overhanging vegetation and positively associated with altitude, temperatures of less than 18^0C, and emergent aquatic vegetation. Juvenile recruitment is highest in permanent upwellings in small, shallow sites with low bed stability and plentiful substrate interstitial spaces (Woodford, 2009; Woodford & Mcintosh, 2011).

Bonnett (1992) noted that sites with alpine galaxiids also had quinnat salmon, rainbow trout, brown trout, Canterbury galaxiid and upland bully present. In a catchment scale survey, Woodford (2009) found that the presence or absence of trout did not change the occurrence of alpine galaxiids or alter juvenile recruitment. Woodford & McIntosh (2013) surveyed the effect of predation pressure from trout on Canterbury and alpine galaxiids across the Waimakariri River catchment and found that alpine galaxiid distribution was less affected by trout than other galaxiids in the study.

A-9.2 Bignose galaxiid

Bignose galaxiid (*Galaxias macronasus*, threat ranking nationally vulnerable) is a cryptic, largely sub-alpine species reaching a maximum length of 100 mm, currently found in 13 sites within the Waitaki River catchment, Canterbury, South Island (Allibone et al., 2015). This species inhabits swiftly flowing, gravelled or cobbled reaches in small springs associated with small wetlands, and females spawn few, small eggs in winter in cobble substrates in streams and headwaters of springs (Allibone et al., 2015). Juveniles are pelagic and shoaling (Allibone & Gray, 2018). Bignose galaxias can be very abundant in low discharge environments lacking other fish species, so may avoid coexisting with any other species (Howard, 2014; McDowall, 2003).

During interaction experiments, Howard (2014) found no significant relationships between bignose galaxiids and trout biomass, however mean bignose biomass was lower when associated with higher mean biomass of other galaxiid species. It is suggested that the main threats to the bignose galaxiids are wetland drainage, habitat degradation and loss including siltation of spawning sites, predation and competition from trout, and river water abstraction as this will reduce habitat availability and potentially remove juveniles with the pumped water (Allibone et al., 2015).

A-9.3 Canterbury galaxiid

Canterbury galaxiids (*Galaxias vulgaris*, threat ranking declining) are widespread in the rivers of Canterbury, Otago, and Southland in New Zealand, are commonly found in moderately velocity waters in gravel and boulder streams, often seek refuge in substrate during the day, and feed nocturnally on small aquatic and terrestrial invertebrates in the drift and benthos (Glova & Sagar, 1989b; McDowall & Wallis, 1996). They mature at two years old and can reach 170 mm long, with a life expectancy of four - six years. (Glova & Sagar, 1989b). Adults become diurnal and highly aggressive during the breeding season (Cadwallader, 1973). Females spawn large numbers of large eggs in riffles (Allibone & Townsend, 1997). Young are often found in large shoals in the slow-moving backwaters and river margins near adult habitat (Allibone et al., 2015; McDowall & Wallis, 1996). Canterbury galaxiid was previously thought to be just one species, however genetic investigation has indicated there are at least 10 taxa under the umbrella name with speciation likely caused by the geographical history of the region (Waters et al., 2020); these species are now commonly known as the *G. vulgaris* species complex (McDowall & Hewitt, 2004). Egg sizes and fecundity vary greatly across the differing species, with the species demonstrating the lowest fecundity and delayed maturation rates associated with stable headwater creeks and the fastest maturing and most fecund species occurring in disturbed lower catchment systems (Jones, 2014).

Allibone et al (2015) postulates the main threats to Canterbury galaxiid population abundance and distribution are ongoing habitat loss and introduced trout. Townsend & Crowl (1991) noted that historically Canterbury galaxiids were widespread through the Taieri River system, Otago, however most galaxiids are now found upstream of waterfalls > 3m high which exclude aquatic apex predators. However, the study did find trout and galaxiids co-occurring in sites within unstable braided streams with high proportions of gravels. Several other surveys have recorded multiple instances of Canterbury galaxiids and trout co-occurrence, so such is evidently possible (Howard, 2007; Woodford, 2009; Woodford & Mcintosh, 2010; Woodford & McIntosh, 2013). High fecundity and widespread larvae dispersal traits may assist Canterbury galaxiids in co-occurring with salmonids in many areas (Allibone et al., 2015; Woodford, 2009). However, the recent findings that many species previously identified as Canterbury galaxiid may, in fact, be wholly separate species with differing biology and life histories demonstrates how biogeographical segregation may further complicate historical research and anecdotal knowledge.

A-9.4 Central Otago roundhead galaxiid

Central Otago roundhead galaxiid species (*Galaxias anomalus,* threat ranking nationally endangered) are found in either swift, shallow gravel/ cobble streams or small, slow, deep creeks with sandy/gravel substrates in Central Otago. The species often utilises instream or bankside cover (Allibone, 2002; McDowall & Wallis, 1996). Roundhead galaxiid has a moderate climbing ability allowing individuals to access sites upstream of waterfalls over 3m (Allibone, 2002). This species inhabits deep low velocity pools or backwaters as juveniles and can be active at any time of day (Baker et al., 2003). The roundhead galaxiid spawns moderate numbers of large eggs in substrate under boulders (Allibone & Townsend, 1997; Moore et al., 1999), lives up to five years and matures in two years (Allibone et al., 2015).

Allibone (2002) states that while this species population is declining, it can survive in easily disturbed, small substrate streams due to high fecundity and its climbing ability which assist in finding upstream sites which may be more suitable due to better spawning habitat or reduced aquatic predators and competitors. A survey of the Manuherikia River, Otago, observed that while brown trout and roundhead galaxiids were largely non-overlapping at the reach scale, they did co-occur in reaches with low valley slope, high risk of intermittent waterway drying, and good representation of riffles and runs close to the mainstem of the Manuherikia River. Bed instability and disturbance may potentially create positive conditions for cohabitation (Leprieur et al., 2006).   -

A-9.5 Dusky galaxiid

Dusky galaxiid (*Galaxias pullus,* threat ranking nationally endangered) are found in small, fragmented reaches in eastern Otago, South Island. This species achieves a maximum length of 150 mm and live up to 15 years, reaching maturity in their fourth year. Dusky galaxiids spawn small numbers of very large eggs in stream margins in spring; the larvae show very limited dispersal from spawning habitat, and the survival of eggs are highly vulnerable to any reduction in water height (Allibone et al., 2015; Allibone, 2000).

A survey of 14 sites containing dusky galaxiids found trout or koaro cohabiting with this species at one site; no longfin eels were found in any dusky galaxiid site (Allibone, 1999). It was postulated that in the absence of predation pressure and population control by eels on koaro and trout those species are now freer to predate non-migratory galaxiids, thereby excluding the smaller galaxiids with slow life histories from previously occupied habitats. No information on other habitat variables was given.

A-9.6 Dwarf galaxiid

Dwarf galaxiids (*Galaxias divergens,* threat ranking declining) are widespread throughout New Zealand, and feed diurnally on benthic and terrestrial invertebrates (Allibone, 2002b). Adults reach a maximum of 80mm in length, have a life expectancy of 3 years, and mature in their second year (Hopkins, 1971). The fry are pelagic and shoaling, becoming cryptic and benthic at two - three months. Adult dwarf galaxiids inhabit edges and riffles in shallow cobbled streams in native forest (Jowett et al., 1996), and utilise interstitial refugia in low flows (Hay, 2009; Hayes et al., 2019).

It has been suggested that the widely dispersed dwarf galaxiid population has been fragmented by salmonids (West et al., 2015), however, the species co-exists with salmonids in many parts of its range (Hayes et al., 2019; West et al., 2015). A survey by Jowett et al., (1996) found no indication that the presence of brown trout influenced the occurrence of dwarf galaxiids even where large trout (up to 280mm) where more abundant. Hayes et al., (2019) also found no evidence of trout (up to 220mm) supressing the abundance of dwarf galaxiids, and this outcome was not influenced by flooding or low-flow disturbances.

A-9.7 Eldon's galaxiid

Eldon's galaxiid (*Galaxias eldoni,* threat ranking nationally endangered) is endemic to eastern Otago, South Island. This species has a highly fragmented population with very restricted distribution, tending to occupy high altitude streams with stony substrates in tussockland or native forest. Adults have a life expectancy of ~15 years, maturing in their second year, and reaching a maximum length of 158mm (Allibone et al., 2015). Females have few, large eggs, and spawn in riffle cobble substrate (Allibone, 2000). The fry are large and have very restricted dispersal ability (Allibone et al., 2015; Allibone & Townsend, 1997), and the species appears to be restricted to very small streams (Allibone, 1999a).

The abundance and distribution of Eldon's galaxiids have substantially declined since 2000, rendering them more vulnerable to any threats and habitat degradation (Allibone et al., 2015).

A-9.8 Gollum galaxiid

Gollum galaxiid (*Galaxias gollumoides*, threat ranking nationally vulnerable) is found in Southland and South Otago, South Island, and on Stewart Island. This species inhabits small lowland low velocity streams and swamps with a silty substrate and emergent vegetation (Allibone et al., 2015). Adults can reach 100mm in length, mature in their first year, and

likely spawn large numbers of small eggs in spring (Allibone et al., 2015). Gollum galaxiids often shoal in open water but have been observed utilising instream debris and undercut banks as cover (McDowall & Chaddertoi, 1999).

Allibone et al., (2015) suggests habitat modification due to water abstraction, stream channelisation and nutrient and sediment loading are the primary threats to this species. Specific research into interactions between trout and this species was not found.

A-9.9 Lowland longjaw galaxiid

Lowland longjaw galaxiid (*Galaxias cobinitis*, threat ranking nationally critical) reach a maximum length of 90 mm, most individuals survive for one year, spawning very few eggs, although in stable flow years the population can increase in abundance rapidly.
This species is found only in two river systems in North Otago within gently flowing shallow water along riffle margins and runs and prefer small-medium cobble substrate with plentiful interstitial spaces (Allibone et al., 2015). Juveniles shoal openly in cold upwellings in stream riffles with very low flow (Baker et al., 2003; McDowall & Waters, 2002). Adult lowland longjaw are cryptic and adept at burrowing, this movement through cobbles is likely an adaptive facet of their biology allowing some protection from drought and predators and thus they may be more abundant than presently known (Dunn & Brien, 2006).

Allibone et al (2010) state that lowland longjaw galaxiid populations are rapidly becoming restricted to areas behind barriers which could exclude large trout. It is considered that pockets of cool, upwelling ground water could be the key to the survival of this species in the Kauru River, as drought can remove surface water from all but these groundwater pools which then may become both refuge and permanent habitat for this species (Dunn & Brien, 2006; McDowall & Waters, 2002). Upwellings may remove fine sediments from within the substrate, which may also help explain the preference of lowland longjaw for groundwater upwellings (Dunn & Brien, 2006). The reliance of lowland longjaw on these pools indicates that water abstraction or change to ground water inputs pose a significant extinction threat (Department of Conservation, 2004; McDowall & Waters, 2002).

A-9.10 Taieri flathead galaxiid

The Taieri flathead galaxiid (*Galaxias depressiceps*, threat ranking nationally vulnerable) inhabits riffles and runs in small-moderate size swiftly flowing boulder/cobble streams with poorly sorted substrates, most often in open tussock countryside (McDowall & Wallis, 1996; Moore et al., 1999). They can live for eight years and grow to 110mm, spawning few, large eggs on the underside of boulders in fast flowing waters in winter (Allibone & Townsend,

1997; Jellyman et al., 2013; Moore et al., 1999)**.** Juveniles prefer deeper, slower water than adults (Baker et al., 2003). Of the other flathead galaxiid species (for example *Galaxias 'species D', G. southern*, and *G. teviot*); little is known about their specific ecologies or any relationship with trout (Woodford & McIntosh, 2013).

Baker et al (2003) found the presence of trout appeared to change the depths at which adult flathead galaxiids were found in Otago streams. Where trout were absent adult flatheads were found in depths up to 0.7m, but where trout were present all adult flatheads were found above 0.3m. No shifts in velocity ranges used by adult or juvenile flatheads were observed regardless of presence or absence of trout, and juveniles displayed no habitat or depth changes. It was noted that juveniles were more common in gravel substrate when trout were present. However, gravel was only present in pools at trout sites, and as juveniles preferentially inhabit pools, this habitat 'change' seems unlikely to be due to trout presence. This is a clear example of the complexities involved in determining impacts of trout against habitat variables and preferences of the native fish species.

A-9.11 Upland longjaw galaxiid

The upland longjaw galaxiid (*Galaxias prognathus*, threat ranking nationally vulnerable), inhabits braided mainstems, tributaries and springs at high elevations in central South Island (Bonnett, 1992; Howard, 2014). This species can live for > three years and reach a maximum length of 87 mm, spawning few, small eggs in autumn and/or spring of their first year. It is undetermined if individuals spawn twice in one year or if there are separate spawning populations (Bonnett, 1992).

Upland longjaw galaxiid populations and distribution are declining due to water abstraction causing the loss of critical spring fed high altitude streams (Allibone et al., 2015; Allibone et al., 2010). Their sparse distribution and presence in volatile riverbeds (with associated reductions in food and habitat resources post flood events) may reduce their interactions with other fish species to those also capable of surviving in small, disturbance prone waterways, but renders the species vulnerable to displacement by floods (Allibone et al., 2015; Allibone et al., 2010; Howard, 2014). A survey by Bonnett (1992) found quinnat salmon, rainbow and brown trout were present in streams with upland longjaw galaxiid, although the scale of interactions or habitat variables were not stated.

Non-diadromous galaxiid and trout interaction risk

Woodford (2009) performed a series of instream experiments assessing the impact of small and large trout on the biomass of alpine and Canterbury galaxiids when confined to fenced

pens. It was noted that the proportion of galaxiid biomass retrieved post experiment was less in large trout treatments than in trout free treatments likely due to emigration and burrowing as well as predation, and that both alpine and Canterbury galaxiids moved through the substrate to different pens, potentially to avoid predation by the trout. At the conclusion of the experiment there was a higher biomass of alpine galaxiids in the small trout treatments than the no trout pens, adding further support to research demonstrating co-occurrence between alpine galaxiids and trout.

Many non-migratory galaxiids have been excluded from historical habitats by water quality and quantity changes leading to fragmented habitats, as well as trout and other introduced species (Baker et al., 2003; Townsend & Crowl, 1991; Waters et al., 2015). However, there are many noted sites where galaxiids and trout co-exist. Areas where cohabitation is more likely to occur include locations with a higher level of disturbance size and frequency, those with interstitial or vegetation refuges, and those at higher altitudes or where the smaller stream size precludes large trout (Woodford & Mcintosh, 2010; Woodford & McIntosh, 2013). Behavioural changes by galaxiids in the presence of trout have also been suggested as a limiter for galaxiid populations (Edge et al., 1993; Jones & Closs, 2018), however experimental studies (predominantly utilising Canterbury galaxiid species) show no or very limited behavioural changes among galaxiids in the presence of trout or trout aroma (Edge et al., 1993; Howard, 2007).

 It is claimed that trout have reduced the distributions of non-diadromous galaxiids to small fragments of their historical habitats (McDowall, 2003; McIntosh et al., 1994). Recent studies of the distributions of Eldon's, flathead, roundhead and dusky galaxiids of the Taieri River have suggested tectonic and glacial processes have altered riverscapes and created vast geomorphological changes and instream barriers which led to speciation of the resident fish population and the published non-overlapping distributions (Waters et al., 2015; Waters et al., 2020).

Using the risk assessment matrix (Table 2.3), it is considered the risk of negative interactions with trout to be deleterious to Central Otago roundhead, Gollum, Canterbury and alpine galaxiids populations to be moderate, and to dwarf, upland longjaw, lowland longjaw, Eldon's, dusky and the Taeiri flathead galaxiid populations to be high. The calculation reflects the capacity for broad diet and habitat overlaps between non-diadromous galaxiid species and trout, as well as the increased vulnerability to predation created by the small size of these galaxiids, and the more limited recruitment potential of those species who have large eggs or fry with limited dispersal. The severe range restriction of many of these species increases the vulnerability of the population to extirpation by any form of disturbance. While literature is not clear on the impact trout have on non-migratory

galaxiids, habitat preservation and restoration and reduction of all threats to these species is of utmost importance.

A-10: Diadromous bully

Diadromous bully species migrate between freshwater and marine environments at different stages in their life cycles (Joy & Death, 2013). Female bullies lay eggs on or under any hard surface with the resulting fry generally pelagic and consuming zooplankton. Adult bully species are benthic, occupy a wide variety of habitats including lakes, rivers, streams, and wetlands and eat aquatic invertebrates from the benthos (Bleackley, 2008; Hicks & McCaughan, 1997; Main, 1988; McDowall, 1990a).

A-10.1 Bluegill bully

Bluegill bullies (*Gobiomorphus hubbsi*, threat ranking declining) generally inhabit fast flowing torrents and riffles with gravel or cobble substrates, often in larger streams, and have a close association with torrentfish due to habitat preference overlaps (Allibone et al., 2015; Jowett & Richardson, 2003; McDowall, 2000; Sagar & Eldon, 1983). They can reach 92mm long, live up to three years (Allibone et al., 2015; Jellyman et al., 2013), and spawn an unknown quantity of very small eggs in spring and summer (Jellyman et al., 2000; McDowall, 1990a). They are obligatorily diadromous, and larvae migrate to sea within a few hours of sunset on the day of hatching (Jarvis, 2015). Older and larger bluegill adults live furthest upstream, indicating continuous upstream migrations of individuals throughout their lives (Atkinson & Joy, 2009). They have a patchy distribution across the North and South and Great Barrier Islands but are often locally abundant (Allibone et al., 2015).

The primary threat to bluegill bully populations is habitat loss caused by water abstraction and sedimentation of river substrate leading to interstitial infill (Allibone et al., 2015; Jowett & Boustead, 2001). Bluegill bullies inhabit heads of rapids and avoid pools, so interactions with large trout are likely minimised spatially (McDowall, 1990a). In a study of 720 bluegill bullies, Scrimgeour & Winterbourn (1987) noted the strongly crepuscular feeding activity of the species will not be related to aquatic predator avoidance, as the only local potential predators (longfin eel and brown trout) occupy different habitats within the river and are also often actively feeding during this period, a statement corroborated by Sagar & Glova (1998), and McIntosh & Townsend (2008).

A-10.2 Common bully

Common bullies (*Gobiomorphus cotidianus*, threat ranking not threatened) reach a maximum length of 140 mm (Jellyman et al., 2013) and have a four to five- year life span, maturing at one year. Large numbers of eggs are laid, possibly multiple times a year, and the territorial male guards the nest. This species is widespread and abundant through its range; however, IUCN Red List records indicated a 25% decline in riverine populations over the 12 years preceding the 2015 report (Jellyman et al., 2000; West et al., 2015). The common bully can form landlocked populations even when access to the marine environment is available and has tolerance to low oxygen levels (Bleackley, 2008; Closs et al., 2003; Landman et al., 2005).

Common bullies are abundant in lakes and rivers and often coexist with trout of all sizes (McDowall, 1990a). David et al (2002) noted that common bullies and brown trout were both abundant in their spotlighting survey of Lee Creek, although no statement was made regarding the extent of any local habitat overlaps.

A-10.3 Giant bully

Giant bullies (*Gobiomorphus gobiodes*, threat ranking naturally uncommon) are slow growing but can reach 250 mm, live for ~10 years, and are found in estuaries and coastal areas of both North and South islands (Ling et al., 2015). This species is highly fecund, possibly spawning multiple times and releasing very large numbers of small eggs during spring and summer (Jellyman et al., 2000; McDowall, 1990a), and juveniles are likely to be misidentified as common bullies (Jellyman et al., 2000; McDowall, 1997).

This species is cryptic and difficult to sample so much of its biology, ecology and population trends are unknown. They are thought to feed on aquatic invertebrates and fish, and while it is seldom recorded, it can be very widespread and at least locally abundant at low elevations and close to the sea (Jellyman et al., 2000; McDowall, 1997). These habitat preferences may bring giant bullies into proximity to large sea-run brown trout, therefore potentially increasing predation risk (McDowall, 1990a).

A-10.4 Redfin bully

Redfin bullies (*Gobiomorphus huttoni*, threat ranking not threatened) can reach 120 mm and live to three-four years, reaching maturity in their second year (Ling et al., 2015; McDowall, 1990a). They inhabit riffles, runs, and pools in fast flowing streams with boulder substrates

(McEwan & Joy, 2014b). Redfin bully spawn large numbers of small eggs twice a year (McDowall & Eldon, 1997).

This species utilises deeper macrohabitats with larger substrate and interstitial spaces during the day and will thus be negatively impacted by interstitial sedimentation (Jowett & Boustead, 2001) which may partially explain the steady rate of population decline. They are nocturnally active, occupying all available habitats at night, including pools which may increase their proximity to larger trout (McEwan & Joy, 2014b). They remain locally abundant where conditions allow (Ling et al., 2015).

Diadromous bully and trout interaction risk

Using the risk assessment matrix (Table 2.3), it is considered the risk of negative interactions with trout to be deleterious to common, giant and redfin bully populations to be minor, and for bluegill bullies to be moderate. The high fecundity, nest guarding, multiple spawning events, early onset of maturity and wide dispersal of fry allows for the common coexistence most diadromous bullies and predators including trout. The patchy distribution of bluegill bullies indicates negative impacts from any source pose a greater risk for that entire species.

A-11: Non-diadromous bully species

Non migratory bully species live their complete life cycle in freshwater, generally spawn larger eggs comparative to diadromous bullies, which leads to smaller clutch sizes but larger larvae with possibly greater swimming ability. Late summer/early autumn spawning seasons may assist potential recruitment to streams that have been disturbed by summer drought conditions (McDowall and Eldon, 1997).

A-11.1 Cran's bully

Cran's bully (*Gobiomorphus basalis*, threat ranking not threatened) is commonly found in rocky streams in native forest through the North Island of New Zealand. They spawn a moderate abundance of large eggs, can live for eight years, reaching maturity at one year, and grow to 107mm (Jellyman et al., 2013). The juveniles mature rapidly, inhabiting slower flowing river margins (Franklin et al., 2015; McDowall, 1990a; Riddell, 1982). Cran's bully tolerates a wide range of conditions and is often found in mid-altitudes and in low-medium gradient creeks and streams with moderate flow in inland areas of the North Island. Populations can locally abundant (Franklin et al., 2015).

The habitat of Cran's bully has been negatively impacted by interstitial sedimentation (Jowett & Boustead, 2001). Stokell (1940) considered the species was likely introduced into the Lake Taupo and Lake Georgina regions as food for trout, however, no research was found detailing impacts of trout on abundance and distribution of this bully within these lakes or in any other waterbody.

A-11.2 Tarndale bully

The Tarndale bully (*Gobiomorphus alpinus*, threat status: naturally uncommon) inhabits coarse cobble substrates along the shores of five small sub-alpine lakes in the Tarndale Hills, South Island (McDowall, 1994; Smith et al., 2003). Tarndale bullies are genetically similar to common bullies but morphologically different, reaching a maximum of 75 mm (Jellyman et al., 2000). This species spawns an unknown number of small eggs, and the fry are minute and pelagic (McDowall & Stevens, 2007).

Brown trout are present in several of the tarn lakes (Smith et al., 2003). No research was found on potential impacts of trout on the abundance or distribution of the Tarndale bully. The predominant threat to this species is habitat degradation by sedimentation and weed growth.

A-11.3 Upland bully

Upland bully (*Gobiomorphus breviceps*, threat ranking not threatened) attain a maximum length of 131mm (Jellyman et al., 2013), can live up to four years and mature after their first year (Hayes et al., 2019). They spawn eight or more times a year over a long period. Females lay moderate numbers of large eggs, and the male guards the nest (Hayes et al., 2019; McDowall & Eldon, 1997). The fry inhabit slow or still river margins and backwaters (Hayes et al., 2019). Adult upland bullies occupy diverse habitats (Hayes et al., 2019), but have been shown in experiments to strongly avoid areas where substrate is heavily infilled by sediment (Jowett & Boustead, 2001).

Surveys have noted a strong positive association between upland bully and trout, where both species coexist in abundance at the site level (Minns, 1990; Woodford & Mcintosh, 2010). Prolonged spawning season, potential for multiple spawning events, and flexible habitat tolerances make the species highly productive and may help explain the population abundance and ease of cohabitation with trout (McDowall & Eldon, 1997).

Non diadromous bully and trout interaction risk

Using the risk assessment matrix (Table 2.3), it is considered the risk of negative interactions with trout to be deleterious to Cran's bully populations to be minor, and for upland and Tarndale bully populations to be moderate. The outcome reflects the mitigating effects of the flexible reproductive strategies and wide habitat tolerances of bully species and noted instances of coexistence in abundance with trout. Species such as upland and Tarndale bullies are geographically isolated and have fewer recruitment opportunities, and so will be more vulnerable to incursions from predators including trout.

Appendix B: Environmental factors mitigating or exacerbating negative interactions between trout and native fish species

B-1. Flow variability

Streamflow is likely the major variable affecting abundance and distribution of riverine species. (Arthington et al., 2006; Boddy et al., 2019; Poff et al., 1997). Trout appear to only have a significant effect on native fish species within stable stream systems which do not experience frequent flooding or severe drying events (Hayes et al., 2019; Jellyman & Mcintosh, 2010; Joy & Atkinson, 2012). Mid to high range flows can move substrate, control riparian vegetation, flush interstitial sediment and periphyton, maintain channel size and form, and provide migration cues and assistance for fish. (Gluckman et al., 2017).

Diadromous galaxiid species use high flow events as triggers for spawning and migration events, and restrictions on floods could cause population declines of those species (Benzie, 1968; Franklin et al., 2015; Mitchell & Penlington, 1982). Floods potentially reduce brown and rainbow trout abundance by 60-100% depending on the size of the trout, the flood event, and the mobility of the substrate of the river it occurs in (Hayes et al., 2019a; Jowett & Richardson, 1989; Warren et al., 2015; Young et al., 2010).

Low flow and drought in riverine environments can be induced by water abstraction for agricultural or urban purposes and has significant negative impacts on all species in the waterways (McEwan & Joy, 2014a., Gluckman et al., 2017; Warren et al., 2015; Xu, 2018). Water abstraction can destroy wetland without direct interferences (Howard, 2014; McDowall, 1984). Low flow events may assist native fish who are more tolerant of warm temperatures than trout, however they may lead to catastrophic loss of native fish as well as trout, and trout potentially recover faster than certain native fish species due to closer source populations (Joy et al., 2018, McIntosh et al, 2010). Native generalist fish populations dominate unregulated rivers while introduced species dominate regulated rivers (Canning et al., 2017; Howard, 2014), therefore disturbance and allowance of natural flow regimes becomes a vital tool for allowing healthy cohabitation and increased biodiversity (Boddy et al., 2019; Glova & Sagar, 1989a; Jowett & Davey, 2007; Poff et al., 1997; Woodford & Mcintosh, 2010).

B-2. Stream morphology and size

The severity of any impact of trout predation on native fish is moderated by the morphology of the waterways they inhabit. Coexistence occurs in complicated and unstable riverine environments due to the increase in habitat heterogeneity providing refuge and optimal

microhabitats for a variety of species throughout differing life stages (Jones & Closs, 2018; Richardson & Taylor, 2002; Woodford, 2009). Complex natural stream processes create a dynamic habitat mosaic which is largely responsible for the high biodiversity of these systems (Allan, 2004). The channelisation of New Zealand rivers for flood protection and to increase land availability for agriculture can thus also increase the vulnerability of native fish to the impacts of predators (David et al., 2019; Gluckman et al., 2017a; Speirs, 2001).

As different fish species have differing refuge requirements, environmental heterogeneity is a vital need for increased biodiversity (Boddy & McIntosh, 2017, Boddy et al, 2019, Davey & Kelly, 2007, McIntosh et al, 2010.). Larger streams may have more habitat diversity with more niches available for different species needs (Allan, 2007). Woodford & McIntosh (2010) found a correlation between stream width / habitat size and trout and galaxiid interaction outcomes, whereby the smaller the stream size the fewer fry survived in the presence of trout. This stream size to fry survival outcome was not correlated when trout were absent. Other studies have specified the importance of suitable spawning and fry rearing habitats close to adult populations for non-diadromous species, in some cases increasing a tenfold increase in fry abundance with suitable backwater habitat availability and suggesting that lack of such habitat may be a critical limiting factor (Jellyman & McIntosh, 2008). Thus, preserving and protecting a variety of habitats critical to each life stages becomes essential, and may also be of particular importance for those species which migrate through different habitats to complete their life histories (Hickford & Schiel, 2011; Moore et al., 1999). Stream channelisation and water abstraction removes edge and backwater habitat, and these can be especially problematic in the first to second order streams in regions where vulnerable non-diadromous high-country fish can be found such as in the Canterbury and Otago regions of the South Island, New Zealand (Allibone et al., 2010).

B-3. Sediment and substrate size

Substrate composition is influenced by catchment geology and morphology as well as stream size, and larger substrate can support great diversity due to the presence of interstitial spaces which create microhabitats and refugia which are utilised by several native freshwater fish species (Joy & Death, 2013). Conversely, fewer interstitial refuges can make the biota of a waterway more vulnerable to disturbance (Allibone, 2002). Refuge from biotic or abiotic disturbances are important for sustained, multi-species fish communities. and it has been noted most native species require large, unstable gravel and cobble substrates for successful cohabitation with other species or for protection from flood and drought (Joy & Atkinson, 2012; Smith, 2014; Woodford & Mcintosh, 2010). It has been postulated that smaller fish

seek refuge to avoid predation and these safe microhabitats may have limited access to food (Mills et al., 2004), however it should be noted that large interstitial spaces are also the preferred habitat for many of New Zealand's benthic invertebrates, and silt and sand dominated sites have the lowest invertebrate diversity and abundance (Jowett & Richardson, 1989; Quinn & Hickey, 1990). This increases the likelihood that interstitial space habitation trends evolved in native fish prior to the introduction of any non-native species, and further emphasises the need to minimise sediment inputs to allow for greater abundance of fish and invertebrates.

Sediment infill reduces the depths of pools and waterways, increases velocity and flow homogeneity, and reduces or removes low velocity areas in the stream which allow the survival of fry and juvenile fish (Richardson & Taylor, 2002; Smith, 2014). Heavy siltation from surface run off or flood events can reduce fish spawning habitat to zero, with lower river reaches particularly vulnerable to sediment build-up (Allibone & Townsend, 1997; Hickford & Schiel, 2011; Warburton, 2015). Reducing sediment loads while increasing the transport ability of the river (by allowing natural flood events or flushing flows) can minimise the inputs of sediment (Jowett & Boustead, 2001). A study of lowland longjaw galaxiids noted that the species burrowing ability is dependent on the presence of large interstitial spaces created with minimal sediment, large substrate, and loosely consolidated substrate (Dunn & Brien, 2006). Boddy & McIntosh (2017) found that the presence of large substrate was so important to alpine galaxiids that they would only inhabit an area with substrate larger than 36mm.

Sediment in suspension can also have deleterious effects on aquatic biota. A study by Rowe et al (2000) concluded that juvenile banded kokopu were more sensitive to suspended sediment than other native fish and actively avoided rivers with turbid lower reaches. This apparent behaviour may lead to declines in populations in rivers with high turbidity in the lower reaches regardless of the presence of suitable upstream habitat, as the juvenile fish will not navigate upstream through the lower portion of the waterway to reach the upstream habitat.

B-4. Nutrients and pollutants

Impacts from agricultural and urban land use are well-known to be deleterious to riparian and waterway habitat and ecology (Joy, 2009). Agriculture can input sediments, nitrogen, dissolved phosphorus and pesticides into streams, industrial discharges have created elevated dissolved metals in sediment in many locations, and multiple pollutants including cadmium, copper, zinc, and lead enter urban waterways (Allan, 2004; Laurie, 2004). Waterborne metals can have a significant disruptive effect on the ability of resident fish species to

forage, migrate, and recognise and appropriately respond to predation risk via direct physiological damage or impairment of biochemical pathways (Greig et al., 2010; Thomas et al., 2016; Yui et al., 2017). Thomas et al (2016) noted that exposure to dissolved copper caused changes in the swimming behaviour of inanga on exposure to a conspecific chemical alarm cue and propose that such changes could impact normal movements in inanga on exposure to copper, particularly in estuarine environments following storm events, and the failure of inanga to reduce movement with alarm cues could expose affected fish to greater risk of predation.

Greig et al (2010) surveyed streams on the West Coast, South Island, comparing fish communities across naturally acidic streams, naturally pH neutral streams, streams draining catchments impacted by coal mining with reduced pH and elevated dissolved metal concentrations. They consider that diadromy likely contributes to the development of generalist traits which may assist in the adaptation of New Zealand's fish fauna to a wide range of physiochemical conditions, but it is likely that high concentrations of bioavailable dissolved metals can have pronounced negative impacts on fish.

Nutrient inputs into waterway, particularly nitrogen and phosphorus, can lead to excessive algal growth which traps sediment, clogs interstitial spaces, and lead to dissolved oxygen depletion during periods of nocturnal respiration by the algae and injury or death of local aquatic species (Ausseil & Clark, 2007; Death et al., 2018). Anthropogenic inputs of both nitrogen and phosphorus need to be closely managed to avoid eutrophication and significantly detrimental impacts on fish species (Elser et al., 2007), and guidelines exist which will assist statutory bodies and river managers set healthy limits of these nutrients (see (Death et al., 2018).

B-5. Source and sink populations

Source and sink population dynamics requires understanding metapopulation theory, where separate potential populations amongst which dispersal may occur are assessed as a single unit (Kean, 1999; Warburton, 2015). Source and sink population dynamics (where extirpation from less productive sites is prevented by recruitment into the local population by individuals from a connected highly productive site) can be created through patchy suitable habitat and food availability, or the presence/absence patterns of predators (Woodford & McIntosh, 2010). Source and sink dynamics may sustain diadromous fish populations facing predation and environmental pressures. Diadromous galaxiids spawn disperse widely, so accumulations of juveniles may form source populations if they are in a favourable area (Allibone et al., 2010; Goodman, 2002; Woodford & Mcintosh, 2011). Larger rivers

disproportionately attract juvenile whitebait due to their larger intrusion of fresh water into the marine environment, however rivers with heavily modified catchments and reduced spawning habitats have reduced inanga egg production compared with smaller waterways with resources: the combination of high concentrations of adult inanga with limited spawning habitat can turn large, modified river systems into sink populations (Jones & Hamilton, 2014).

Source populations may also allow persistent coexistence of non-diadromous native fish and trout if they are able to add juveniles or adults to the sink population. Increasing or creating upstream, trout free source populations could be a viable action to mitigate predatory and competitive actions by trout and help enable a self-sustaining native fish population. (Woodford & Mcintosh, 2010). There is a risk, however, that rapid species decline can occur once source populations can no longer sustain the sink regions, or if connectivity between the two is broken (Joy et al., 2019, McIntosh et al 2010, Boddy et al, 2019).

It has been stated the disappearance of grayling from isolated and pristine rivers without the presence of fishing or introduced species indicates the importance of source population species replenishment, particularly for amphidromous species (Lee & Perry, 2019). It is of vital importance that sites are correctly established as source or sink by measuring local recruitment; species may be present in abundance in degraded rivers which are functional sinks, and failure to correctly identify them as such greatly exacerbates extinction risk for the species (Allibone et al., 2010; Hickford & Schiel, 2011; Lee & Perry, 2019).

B-6. Marine and freshwater connectivity

The prevalence of diadromy in NZ freshwater fish indicates that access between marine and freshwater habitats may be the most important habitat attribute for fish communities (Franklin & Gee, 2019; Gluckman et al., 2017; Jowett & Richardson, 2003; Joy & Death, 2001; Richardson & Taylor, 2002). Several physically distant habitat types may be used by the individual fish of each migratory species at different life stages, and free access between these is required as barriers can fatally delay downstream larval drift; starvation is likely if fry cannot reach marine environment prior to exhausting their endogenous energy resources (yolk) and prevent upstream migrations by small juvenile fish (Franklin & Gee, 2019; McDowall, 2006b).

Barriers at low elevation / low gradient waterways have the potential to have more serious impacts on fish communities than those further from the sea: dams, weirs, culverts

and other barriers impact fish distribution and reduce upstream species richness to those individuals and species able negotiate the barrier (Baker, 2003; Joy & Death, 2001) and may also prevent movement of fish seeking refuge from high-flow events (David, 2003), while fish passage facilities are often ineffective (Arthington et al., 2016)

B-7. Riparian vegetation

There is a clear link between riparian vegetation characteristics and the presence of fish species; with fish species richness and abundance declining at pasture sites and improving in scrub and native forested streams (Joy et al., 2018; Larned et al., 2020). Riparian vegetation reduces algal growth by absorbing nutrient runoff from land, cooling and shading river bed, contributes allochthonous inputs including terrestrial invertebrates into waterways, and increases habitat diversity via bank stabilisation, root structures and woody debris which could potentially decrease competitive and predatory interactions (Canning, 2018; David, 2003; Gluckman et al., 2017; Goodman, 2002; Montori et al., 2006; Niyogi et al., 2007; Sagar & Glova, 1995; Smokorowski & Pratt, 2007; West et al., 2005).

It has been noted that large bodied galaxiids (koaro, shortjaw, banded, and giant kokopu species) are associated with waterways surrounded by native forest and their decline and fragmentation has been linked to deforestation and wetland clearance (Jowett et al., 1998; McDowall et al., 1996; Swales, 1990), therefore protection and restoration of riparian vegetation is likely to be a significant factor in the conservation and management of these species (Bonnett & Lambert, 2002; Goodman, 2002). Diadromous galaxiids require dense riparian vegetation to spawn in, and reduction or damage to these areas by stock grazing or mowing can destroy eggs or greatly reduce their chances of hatching (Hickford & Schiel, 2011).

Streams with added food inputs from riparian vegetation could potentially decrease competitive and predatory interactions and may encourage native fish coexistence with introduced species (David, 2003; Montori et al., 2006), and as headwater impacts seem to have the largest impacts on stream health, riparian trees should extend as far up the headwaters, and cover as much of the catchment as is practical (Niyogi et al., 2007; Orchard, 2017; Rutherford et al., 1997). Allibone et al (2003) found that previously site loyal shortjaw kokopu changed residence following accidental removal of riparian vegetation which infilled some of the smaller pools, decreased stream shading, and increased interstitial sediment. Graynoth (1979) noted greatly decreased abundance of dwarf galaxiids in streams where the riparian forests had been removed compared to those with intact riparian vegetation or a 150m buffer alongside the stream. Important refuge and habitat can also be provided by wood debris and instream structures (Joy & Atkinson, 2012). In an experiment where some

sections of stream five sections were left natural and others were cleared of woody debris and overhanging bank cover, four times as many inanga were later found in the sections with natural cover than the cleared streams (Richardson & Taylor, 2002).

B-8. Temperature

Anthropogenic activities such as heated industrial or geothermal discharge, water abstraction and removal of riparian shading alter the thermal regime of a waterway (Quinn et al., 1994). Water temperature has a profound effect on fish behaviour, growth rate, survival, and abundance, and on other ecosystem processes and communities (Ausseil & Clark, 2007; Richardson et al., 1994). Sub-lethal temperatures can negatively affect fish reproductive and mortality rates; for example, trout cease feeding at temperatures over 19 degrees, and waterways which regularly experience temperatures higher than this may exclude trout (Xu, 2018). Any temperature outside of the preferred temperature range of each species will override any top-down control by fish despite any abundance of predators (Hayes et al., 2019; Kishi et al., 2005; Young et al., 2010). Native fish species have a wide variety of thermal tolerances, but most species have lethal temperatures at ranges higher than that of trout (Richardson et al., 1994). Aquatic invertebrates are also limited in distribution and abundance by thermal preferences (Quinn et al., 1994), therefore increased water temperature can impact the food source for fish as well as affecting fish directly.

The most effective method of reducing water temperature in streams narrower than 10 m is riparian stream shading (Richardson & Jowett, 2005); warmer temperatures in waterways where trout may be larger may assist cohabitation with more thermally tolerant species.

B-9. Trout size

A study of lacustrine brown trout found that the fish first become piscivorous at 2+ years and sized between 130-160mm: most studies agree onset of piscivory in trout occurs when trout are ~150mm FL (Klemetsen et al., 2003; McIntosh, 2000; Mittelbach & Persson, 1998). Prey capture by trout is restricted by the gape and gill raker sizing of trout, and large or abundant prey are preferred because they offer greater energy return for foraging effort, with the size of the prey taken increasing as the trout size does (Bannon & Ringler, 1986; Montori et al., 2006; Shearer & Hayes, 2019). After the onset of piscivory, fish make up <10% of the diet of the brown trout, with invertebrates remaining the main prey sources, particularly in the middle to upper reaches of New Zealand rivers; the amount of fish consumed by trout increases with trout body size and prevalence of small bodied prey, mediated by availability

of refuge for the prey (Crowl et al., 1992; Jellyman et al., 2018; Jones & Closs, 2018; Mittelbach & Persson, 1998; Shearer & Hayes, 2019).

Although opinion is divided on whether trout have had a consistently negative effect on native fish, large trout have been implicated in reducing the abundance and distribution of native fish. Some studies on galaxiid and trout cohabitation have shown that where trout >150mm (FL) are present there are likely to be fewer adult galaxiids and reduced or absent juveniles: however this only applies to certain species of galaxiids: Canterbury galaxias appeared to have less abundant population in the presence of large trout, however alpine galaxias did not: further there have been noted reports of galaxiids co-occurring with trout larger than 150mm, indicating that species behaviour and abiotic influences likely have great influence on fish community creation than the size of trout present (McIntosh et al., 2010; McIntosh, 2000; McIntosh et al., 1994; Townsend, 2003; Woodford & Mcintosh, 2010; Woodford & McIntosh, 2013). Predation pressure by trout is likely to be highest in deep rivers where infrequent flooding allows high densities of large trout and where there are few refuges for native fish (Woodford & McIntosh, 2013).

Appendix C: Photographs of experimental design.

C-1: **Finalised riparian experiment set up**.

Upper trough is closest to the top of the photo. Screens prevent accidental fish transfer between troughs. Riparian cover is shown in this trough pairing closest to the bottom of the photo.

C-2: Finalised substrate experiment set up.

The left-hand trough shows the cobble substrate closest to the bottom of the photo, the right-hand trough shows the sand / fine gravel substrate. The screens prevent fish being carried into a lower trough, and the mesh on the drainpipes prevents fish being carried out of the experiment entirely.

C-3: **Trout and dwarf galaxiid**

Poor quality cell phone photo of a trout (riparian experiment, trough A2). This was the only trout seen to consume a dwarf galaxiid. The predation on the galaxiid occurred approximately one minute before this photo was taken. The small pale stripe in the bottom of the second blue outline is another dwarf galaxiid which came to rest in close proximity to the trout just after the predation incident. Neither of these fish are under riparian cover. This predation incident was the only one witnessed during the course of either experiment, and numbers of dwarf galaxiids recovered post experiment suggested no other galaxiids were consumed.

C-3: **Trout and dwarf galaxiid**