Assessment of migration barriers in the eastern Otago region: Perched road culverts, climbing galaxiids and non-migratory galaxiid conservation

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Joshua F. Tabak

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ABSTRACT

New Zealand's diadromous fish populations face vast networks of road culverts that often limit upstream dispersal as a function of efficient hydrological design. Migration barriers, such as perched pipe culverts, fragment and isolate viable stream habitat from recruitment by overcoming migratory adaptations of fish, inevitably eroding populations through genetic loss. This study addressed several concerns of conservation managers in the eastern Otago region through examination of impassable perched pipe culvert impacts on local fish distributions, as well as trialling perched migration barriers in the laboratory and field in order to protect a threatened non-migratory galaxiid population from an invasive species. The latter trial was found to have great promise as a freshwater conservation management tool.

The interaction between poor road culvert design and fish dispersal has been examined across New Zealand's differing landscapes. In eastern Otago, commercial forestry plantations provided homogenous land use type and pipe culvert design to examine perched pipe culvert prevalence and fish distribution in relation to pipe culverts as seen in Chapter Two. By using a unique approach identifying pipe culverts as passable or impassable *a priori*, based on previous fish passage understanding and research, the relationship between fish distribution and culverts could be examined despite inherently dynamic interactions between fish migratory adaptations and culvert characteristics. Surveys found just over fifty percent of pipe culverts were perched to some degree, and upon analysis that a negative relationship existed between species richness and fish abundance above versus below pipe culverts. The findings galvanise current understanding of the limiting effects of pipe culverts on upstream fish migration and identify the scale of perched culvert prevalence in commercial forestry plantations of the eastern Otago region.

Abundance trends, although statistically inconclusive but scientifically supported, affirm that impassable pipe culverts likely have a limiting/barrier effect on the dispersal and migration of kōaro (*Galaxias brevipinnis*). The climbing migratory adaptations which kōaro rely on to navigate in-stream obstacles were examined in Chapter Three. The relationship between climbing success and juvenile kōaro size was trialled in a controlled environment and revealed a significant trend in the size of juvenile kōaro climbers that were successful at navigating a simulated migration barrier. Disrupting the wetted margin, and thus hydrological connectivity, through the use of a perched barrier proved totally effective at halting juvenile kōaro climbing.

Kōaro are considered an invasive threat to populations of the rare non-migratory dusky galaxias (*Galaxias pullus*) in several tributaries of the upper Waipori River in eastern Otago. Attempts by the Department of Conservation to install migration barriers on a research weir to limit kōaro recruitment into a dusky galaxias stronghold population had proven unsuccessful. Chapter Four documents the development and deployment of a perched aluminium migration barrier which continued to be extremely successful over a period of several years at halting juvenile kōaro recruitment as confirmed by electrofishing and kōaro relocation data pre and post installation. This system provides conservation managers with a tool to protect non-migratory galaxiids across New Zealand that are at risk of juvenile kōaro invasion, and for the protection of historic habitat for non-migratory galaxiid translocation.

Investigation into kōaro migratory capabilities also raised new questions about the interactions between form and function of climbing adaptations and how these may have influenced the evolutionary ecology of ancestral climbing galaxiids in response to geological processes. Discussions regarding the complexity of kōaro migration as a dynamic process of timing, growth and distance are also presented.

Understanding the mechanisms by which perched pipe culverts limit upstream fish migration, and on which migratory fish species rely, allows for conservation managers to improve fish passage or control invasive fish species encroachment, both with the purpose of conserving endangered species and in-stream habitats. Overall, critical thinking and understanding of fish migratory adaptations, both in a natural setting and a controlled environment, has proven a robust method in developing a useful conservation tool for endangered species isolation management while working closely alongside front line conservation managers.

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CHAPTER ONE

Introduction

Migration has evolved separately in many animal groups; from birds, to mammals, and fishes (Alerstam et al. 2003). Migration is a distinct dispersal between one habitat and another, sometimes over great distances or obstacles (Harris et al. 2009). Strong innate forces are the drivers of migrants, which are often physically adapted to overcome significant challenges (Gwinner 1996); these traits shaping how migratory animals interact with their environment (Tøttrup et al. 2008). In some instances migratory animals are unable to avoid anthropogenic impacts along their migration paths (Pfister et al. 1992), especially where partial or complete “man-made” migratory barriers are encountered (Forman & Alexander 1998; Henningsson & Alerstam 2005). The impacts of anthropogenic disturbance on the migratory dispersal of a species is in most cases detrimental to the population, associated communities and general ecosystem function (Trombulak & Frissell 2000; Stow et al. 2001; Tallmon et al. 2003; Driscoll 2004). Up to date research and well informed conservation strategies provide a necessary and beneficial measure to relieve these negative human impacts on animal migrations (Harris et al. 2009; Hodgson et al. 2009).

Diadromous fishes epitomise animal movement between two distinctly different habitats (Lucas & Baras 2001); for diadromous fish spend essential parts of their lifetimes at sea before migrating up freshwater rivers to breed (McDowall 2000; McDowall 2001). Uninterrupted hydrological and longitudinal connectivity is the primary factor facilitating such diadromous fish migrations (McDowall 1998; Crook et al. 2009; Hall et al. 2011); hence any in-stream barriers, natural or human-made, can create obstacles for diadromous fish migration (MacDonald & Davies 2007; Branco et al. 2011). It is widely accepted that dams, weirs, and road culverts are the most widespread in-stream barriers of anthropogenic origin effecting diadromous fish migration today (Burford et al. 2009). These barriers have historically been designed for effective hydrological management, often with little or no regard for migrating diadromous fish populations (Solcz 2007). Road culverts, in particular, fragment stream habitats and are of major ecological concern worldwide (Jungwirth et al. 2000; Morita & Yamamoto 2002; Copeland 2004; Gibson et al. 2005; Khan & Colbo 2008), especially when considering their extensive use (Park et al. 2008). Road culverts that fragment fish assemblages (Rolls 2011) will over time lead to local and population scale declines eventuating in a loss of genetic potential, adaptive capabilities or extinction (Allendorf et al. 1987; Wofford et al. 2005; Bourne et al. 2011; Nislow et al. 2011). Crucially, momentum is gaining in the study of road culvert design efficaciousness and migratory fish life history and physiology, to ensure both hydrological and environmental functioning is maintained (Clark et al. 2014).

Road culverts have historically been engineered to meet the requirements of efficient hydrological management, transport practices, low manufacturing costs and low installation costs (Johnson & Brown 2000; Jones et al. 2000; O'Hanley & Tomberlin 2005). Pipe culverts for example generally are smooth surfaced, facilitate high water velocities, are installed on steep gradients and are of long lengths to span beneath road surfaces (Bates et al. 2003; Bouska & Paukert 2010). Of particular significance, as a result of pipe culvert installation, is the 'free-hanging' or perching of pipe culvert outlets; a situation posing the greatest obstacle to many migratory fish species internationally (Kemp & O'Hanley 2010) and in New Zealand (McDowall 1984; Boubée et al. 1999; James & Joy 2008; Leathwick et al. 2008; Doehring et al. 2011).

The prevalence of perched road culverts has been discussed by authors in certain localities across New Zealand such as the Manawatu (James & Joy 2008) and Auckland (Barnes 2004). The implications and impacts of perched culverts and other designs on New Zealand's native migratory freshwater fish fauna (and exotic species) have been examined in depth by Boubée et al. (1999) for the National Institute of Water and Atmosphere (NIWA) and the Department of Conservation. Within the eastern Otago region steps have been taken to record natural barriers by the Department of Conservation (D Jack pers. comms 2011, unreferenced). However, surveys to identify perched pipe culverts within the region and analyses of associated fish communities are yet to be completed, despite the region being home to several threatened galaxiids which are likely impacted (Allibone & Barrier 2004).

Perched road culverts are of great concern to conservation managers around the world with aims of protecting and facilitating fish migrations (Bourne et al. 2011). Authors such as Parker (2000) have published guidelines which can be used for the analysis of culvert characteristics to prioritise perched culvert removal or retrofitting in order to restore upstream fish passage and migration (Kemp & O'Hanley 2010). Conservation managers within New

Zealand have also addressed perched culvert issues; for example, authors such as David et al. (2009), from the Environment Waikato Council, have trialled retrofitting techniques to facilitate climbing galaxiid passage through perched road culverts.

While perched road culverts have generally been considered a negative, the ability of a perched pipe culvert to block the upstream passage of an invasive species can have value. Internationally in-stream barriers are effectively used to limit dispersal of invasive fish species (Stainbrook et al. 2005; Dawson et al. 2006); however the use of perched migration barriers internationally for this purpose is uncommon. Investigation of perched migration barriers within New Zealand may prove to be a significant and positive tool for freshwater conservation managers looking to protect threatened freshwater fish populations from other invasive fish species (Allibone & McDowall 1997).

Kōaro (*Galaxias brevipinnis*) (Fig 1.1) are found throughout New Zealand and, although a native, can be considered invasive when encroaching on threatened fish habitats (Allibone 1999). The invasive nature of kōaro is facilitated by its innate adept climbing ability as a juvenile; able to navigate significant in-stream obstacles and gradients (McDowall 2010). The ability of kōaro to readily form landlocked populations [facultative diadromy; (McDowall 1998)] and the impoundment of natural water courses by humans, has allowed for the proliferation and migration of juvenile kōaro deeper into streams where they historically could not reach (Allibone 1999). Within eastern Otago, and since the damming of the Waipori River and subsequent formation of Lake Mahinerangi, the mass migration of juvenile kōaro into rare dusky galaxias (*Galaxias pullus*) (Fig 1.2) habitat is said to have had negative consequences (Allibone & McDowall 1997). Kōaro are thought to out-compete the less fecund dusky galaxias, whose numbers and distribution have drastically shrunk since the forming of Lake Mahinerangi (Jones & Closs 2016) and is of concern to conservation managers responsible for dusky galaxias protection. The opportunity therefore exists to design and trial perched migration barriers as a useful conservation tool to halt climbing kōaro juvenile invasion and in doing so potentially reverse the impacts of kōaro invasion on the dusky galaxias.

Fig. 1.1 A widespread ‘climbing expert’; the kōaro (*Galaxias brevipinnis*) (photo: Paddy Ryan[1])

Fig. 1.2 The threatened dusky galaxias (*Galaxias pullus*) from the eastern Otago region (photo: Simon Madill[2])

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[1] https://teara.govt.nz/en/photograph/11114/koaro-galaxiasbrevipinnis
[2] https://www.doc.govt.nz/nature/native-animals/freshwater-fish/non-migratory-galaxiids/dusky-galaxias/

General hypothesis

To research migratory fish community interactions with perched road culverts, it is not only necessary to determine fish population distribution in relation to perched road culverts but also perched road culvert prevalence. To design an effective migration barrier as a conservation tool for excluding migratory fish species, it is imperative to understand the physical capabilities and limitations of the focal species (Crook et al. 2010), and by incorporating knowledge gained from previous attempts.

The primary goal of this study is to design a useful conservation management tool to isolate endangered dusky galaxias populations from kōaro encroachment. This goal will be achieved in the following three steps: 1) by analysing the literature and the relationship between fish migration and perched culverts in a natural setting; 2) by testing the climbing ability of kōaro and migration barrier design and theory in a controlled setting; and 3) by adapting and testing migration barrier design in the field.

This study will therefore: A) examine road culverts and freshwater fish populations within catchments of the eastern Otago region, B) examine the climbing morphology and behaviours of the kōaro and c) examine a migration barrier installed by the Department of Conservation. Below are the questions which this study aims to answer:

1. What is the prevalence of perched road culverts in the eastern Otago region? (Chapter Two)
2. Have perched road culverts shaped migratory freshwater fish distributions in the eastern Otago region? (Chapter Two)
3. How does the morphology of a climbing migratory fish, the kōaro, influence its ability to climb successfully? (Chapter Three)
4. Can a man-made perched migration barrier stop juvenile kōaro from migrating upstream in a controlled setting? (Chapter Three)
5. Can a man-made perched migration barrier be used as a conservation management tool in streams to disrupt kōaro migration? (Chapter Four)

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CHAPTER TWO

The status of perched pipe culverts installed in exotic forestry road networks and associated freshwater fish communities within the eastern Otago region.

2.1 Introduction

Hydrological connectivity is a primary factor influencing migratory fish dispersal and ecology (Crook et al. 2009). Connectivity between freshwater environments and the sea, for example, is the key element enabling the life history of diadromous fishes (McDowall 1997); migrations between the sea and freshwater having shaped how diadromous fish evolved with their environment (Lucas & Baras 2001) both behaviourally (Leonard et al. 2012) and morphologically (Schoenfuss & Blob 2003). Man-made barriers along migration pathways that overcome behavioural and morphological adaptations severely restrict fish dispersal during upstream migrations (Burford et al. 2009; Branco et al. 2012).

Road culverts are prime examples of widespread anthropogenic barriers (Park et al. 2008) that limit fish dispersal and alter in-stream fish communities (Rolls 2011) by fragmenting habitats (Gibson et al. 2005; Khan & Colbo 2008). The negative impacts of hydrologically effective road culvert designs on upstream fish passage are often exacerbated as a function of their own design (Jones et al. 2000; Solcz 2007). For example, concentrated high water flows through pipe culverts frequently scour stream beds downstream leading to free hanging of pipe culvert outlets (perching) above nominal water flow levels (Gibson et al. 2005; Kemp & O'Hanley 2010; Doehring et al. 2011). This creates a significant break in longitudinal connectivity within streams which can overcome fish migratory capabilities (Bourne et al. 2011). Perhaps the most cost effective and widely used road culvert style is that of pipe culverts (Gibson et al. 2005).

The dynamics of fish dispersal within streams is highly complex with upstream migration reductions altering the basic "population equation" of a fish species (Nislow et al. 2011). Essentially significant decreases in fish species immigration due to impassable perched pipe culverts can potentially lead to local extirpation of that species (Rolls 2011) and reduce the species richness in that locality (Nislow et al. 2011). A better understanding of fish abundance and species richness in relation to perched pipe culverts can provide insight into the impacts these structures have on fish community structure and migration at a catchment scale (Nislow et al. 2011). An example of a perched pipe culvert running below a road can be seen in a photograph taken within the eastern Otago region, New Zealand (Fig 2.1).

Fig. 2.1 A perched pipe culvert, Tokomairiro River tributary, Dunedin (photo: Josh Tabak)

Globally the negative impacts of perched pipe culverts on fish communities are well documented (Park et al. 2008; Kemp & O'Hanley 2010). Within New Zealand the study of perched pipe culverts has also received significant attention with local councils (Barnes 2004; James & Joy 2008; Stevenson et al. 2008; Stevenson & Baker 2009: David & Hamer 2012) and various research institutes (Boubée et al. 1999; Baker & Boubée 2006; Doehring et al. 2011) examining fish passage issues in detail. This research has been conducted to better understand how culvert prevalence and design have impacted New Zealand's freshwater fish fauna, a large proportion of which are migratory (McDowall 2000).

The extent to which perched pipe culverts have structured fish and galaxiid communities within eastern Otago is not well understood and is an area of interest to the Department of Conservation (D Jack pers. comms 2011, unreferenced). Evaluating the prevalence of perched pipe culverts and fish community distribution will contribute to the understanding of the extent of habitat fragmentation effects on native and exotic fish species within the region, and help guide native fish conservation management strategies.

Exotic forestry plantations are prevalent in the eastern Otago region where thousands of hectares of land are dedicated to pine (*Pinus radiata*) and douglas fir (*Pseudotsuga menziesii*) plantations. Significant tracts of threatened galaxiid habitat are found in these exotic forestry planations (Allibone & McDowall 1997), where the installation of roads and pipe culverts are an integral aspect of forestry operations (Pendly 2015), and may have altered the historic distribution of resident native fish communities (Allibone & McDowall 1997). While assessments of road culverts and in-stream structures within New Zealand have surveyed pastoral (James and Joy 2008) and native forest (Barnes 2004) land use types, little published research has investigated culverts in exotic forestry plantations.

Nislow et al. (2011) designed an at the time novel method to assess migration barriers and their impacts on fish communities by classifying culverts as impassable or passable *a priori* based on the degree to which culverts are perched. This method allowed fish abundance and species richness to be assessed upstream and downstream at a catchment scale and across numerous sites providing sufficient power to detect the effects of perched culverts as barriers (Nislow et al. 2011). Such a method is unique as it accounts for the substantial intrinsic variation of culverts and stream dynamics. This approach has not been trialled in New Zealand and could provide a simple method for examining the barrier effects of culverts on our native fish communities; of which diadromous migrations are a key life history for many (McDowall 2000). This chapter therefore aims to survey a sample of road crossings in exotic forestry plantations of eastern Otago, as well as the resident freshwater fish communities, aiming to quantify not only the extent of perched pipe culverts but any relationships relative to pipe culverts that local freshwater fish abundance and species richness may have. Of particular interest is the impact of perched pipe culverts on the upstream migration of galaxiids.

2.2 Methods and materials

Culvert surveys

This study focused on three localities within the eastern Otago region; Mahinerangi, Akatore and Tokomairiro (Fig 2.2). These areas were chosen as the catchment land use is predominantly exotic forestry plantations. Surveys within these forestry plantations allowed for ease of access to multiple culverts on a network of forestry roads. The forestry plantations are owned and administered by two companies, Wenita and City Forests Ltd. Permission, keys and permits were sought and granted for access to the road crossings.

A four step process was first used to assess 180 road crossings across the three localities to find suitable culverts for use in the study [adapted from Parker (2000)]:

1) The first step was to identify all potential road crossings (on a 1:50,000 topographical map of the three locations) on first, second, third and fourth order streams.
2) The second step was to field visit the road crossings before proceeding with the following two steps.
3) Step three was to evaluate if the crossing was indeed a pipe culvert crossing. Sites identified on the map during the first step may not have existed or were other forms of crossing, e.g. bridges or fords.
4) Step four was to identify the channel or stream at the crossing as viable fish habitat. Culverts placed on crossings which had ill-defined stream channels, were completely vegetated, had no or very little water, or had no obvious habitat upstream were not surveyed.

Of the 180 road crossings visited, a subset of culverts that met the criteria of steps 3 and 4 above were chosen to study further (Figs 2.4, 2.5, 2.6). The chosen subset of 60 pipe culverts had the following information documented:

1. Co-ordinates of the pipe culverts were taken with a hand held Global Positioning System unit (GPS).
2. Numbered each pipe culvert according to topographic map location and co-ordinates.
3. Recorded pipe culvert outfall drop and outfall length where a pipe culvert was above the water surface.

4. Recorded whether the culvert was impassable, passable or did not meet the criteria. Perched culverts with an outfall drop equal to or above 12cm in height and an outlet length equal to or greater than 5cm in length were predicted to be impassable (Nislow et al. 2011) by native freshwater fish for the purposes of this study (Fig 2.3). Culverts submerged were considered and recorded as passable. Culverts that were neither impassable nor passable were recorded as not meeting the criteria for analysis.

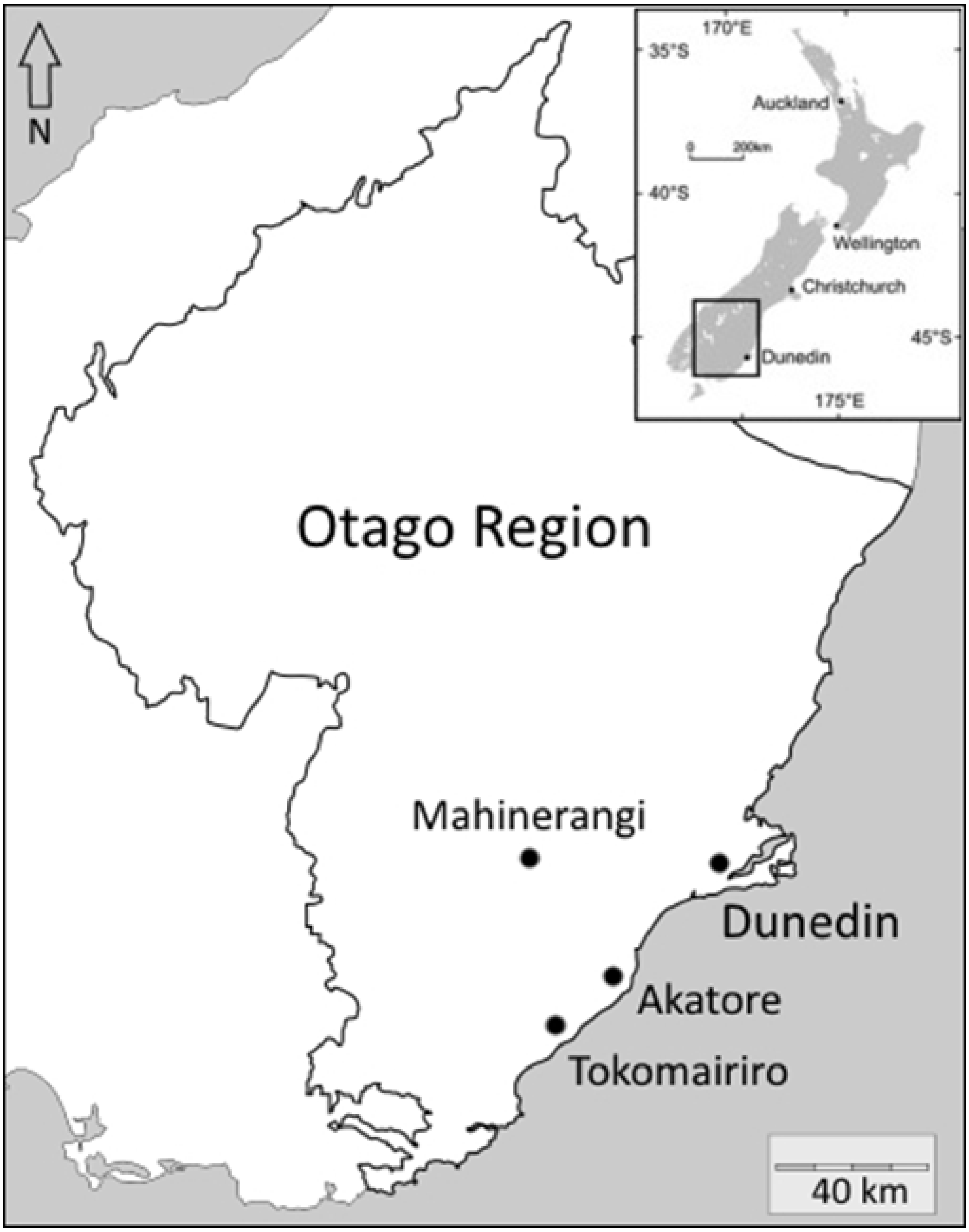

Fig. 2.2 Culvert survey localities in the eastern Otago region.

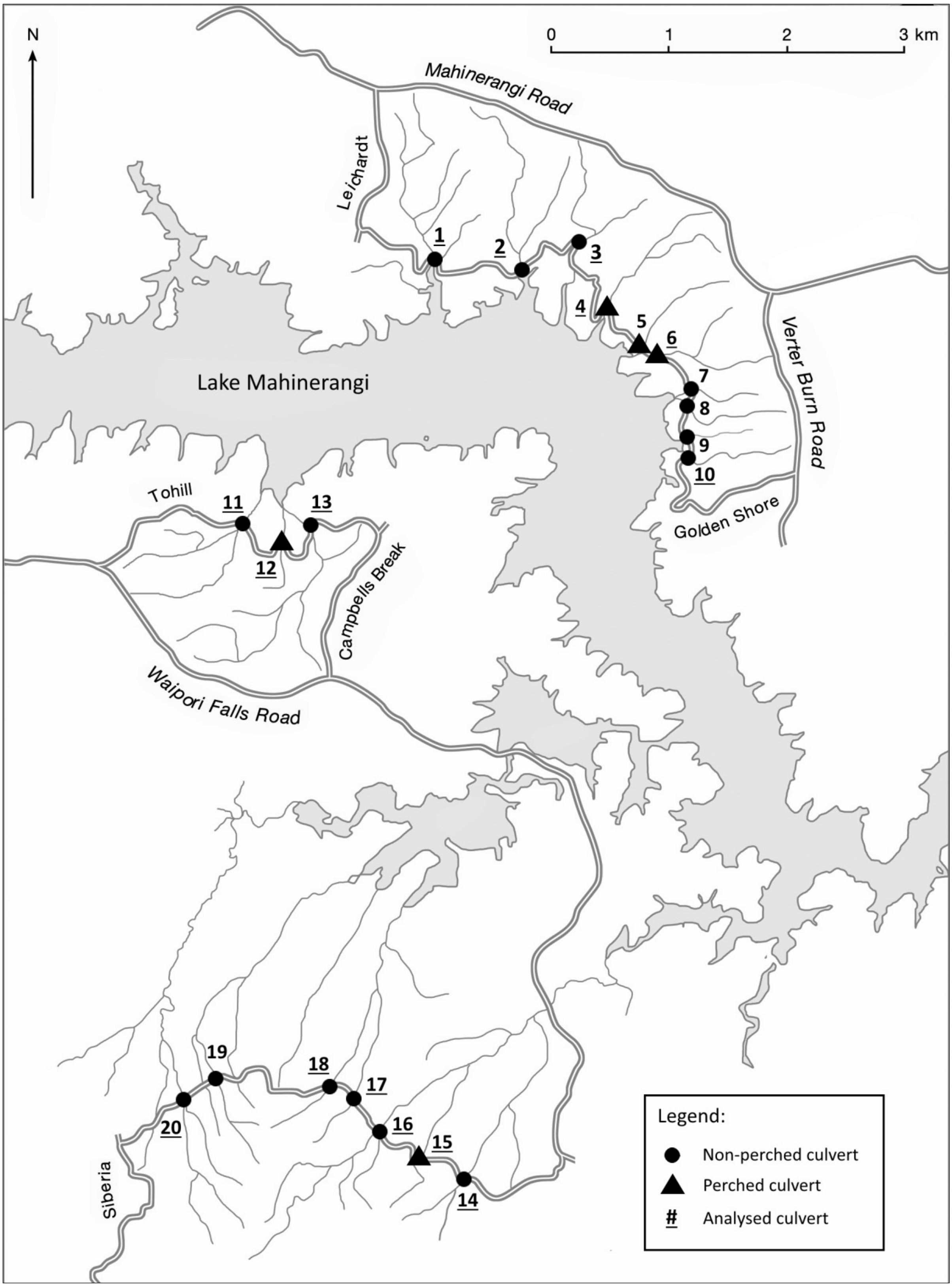

Fig. 2.4 Mahinerangi catchment area with the number of perched and non-perched road culverts surveyed, and the qualifying culverts analysed in models to compare fish abundance and species richness either side of those culverts. Culverts were considered passable or impassable based on predetermined characteristics.

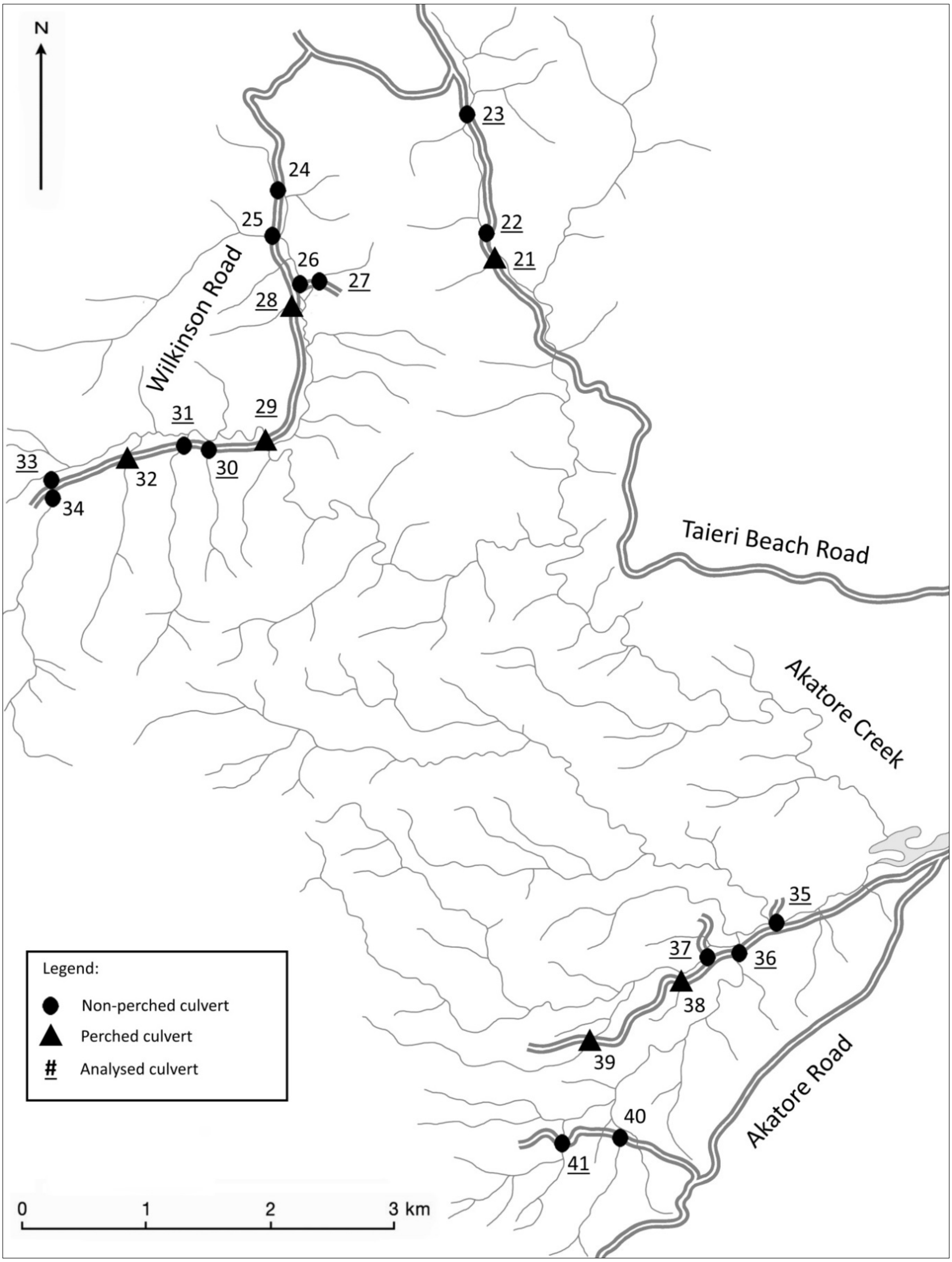

Fig. 2.5 Akatore catchment area with the number of perched and non-perched road culverts surveyed, and the qualifying culverts analysed in models to compare fish abundance and species richness either side of those culverts. Culverts were considered passable or impassable based on predetermined characteristics.

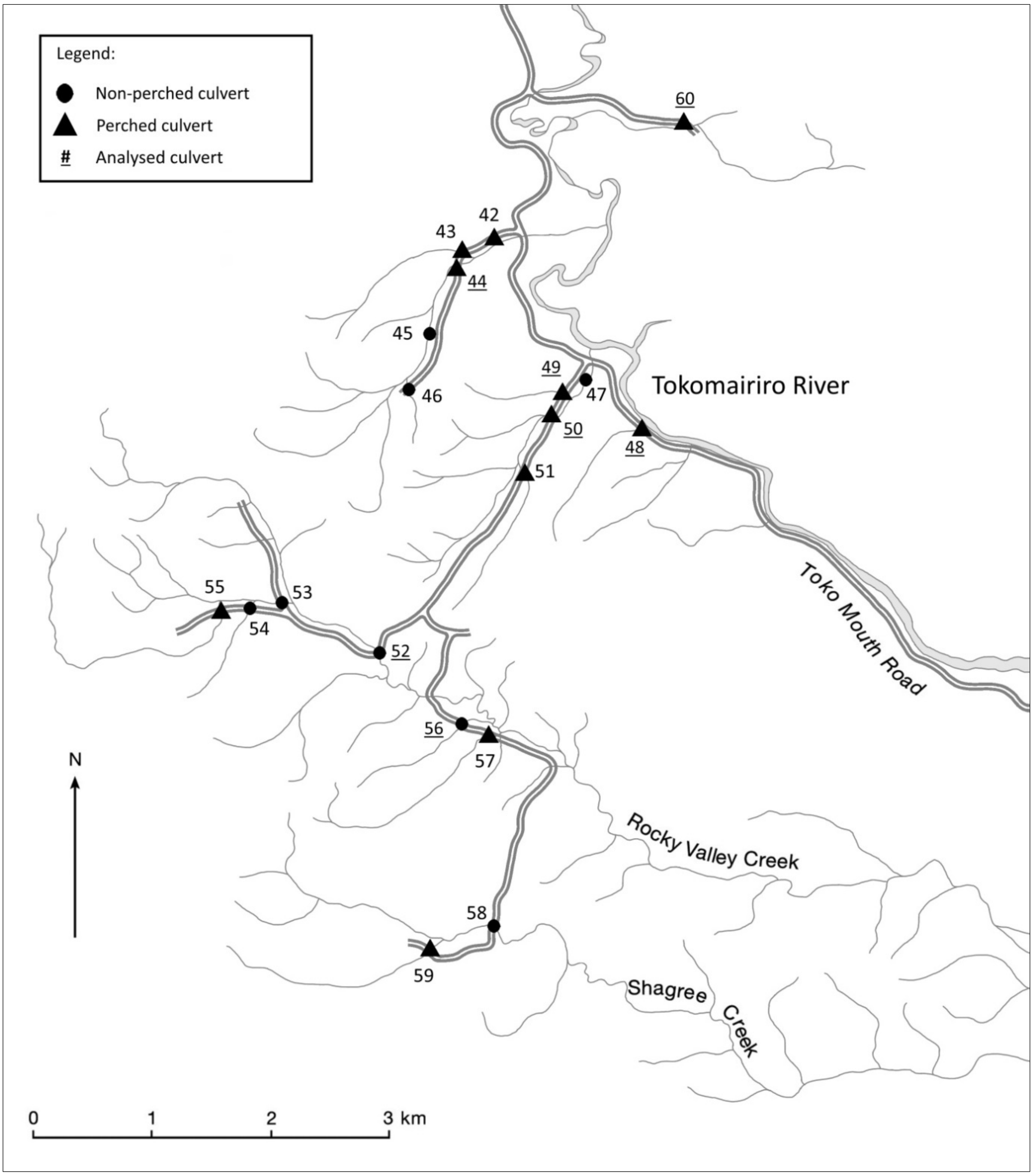

Fig. 2.6 Tributaries of the Tokomairiro river, Rocky Valley creek and Shagree creek with the number of perched and non-perched road culverts surveyed, and the qualifying culverts analysed in models to compare fish abundance and species richness either side of those culverts. Culverts were considered passable or impassable based on predetermined characteristics.

Culvert surveys commenced 1st November 2012 through until 31st March 2013. Assessing culverts using the above criteria at or near base flow conditions ensured that perched culverts were categorised correctly and that only permanent streams were sampled (Park et al. 2008); the assumption being that permanent streams would be more likely to hold stable fish populations (Rosenfeld et al. 2000).

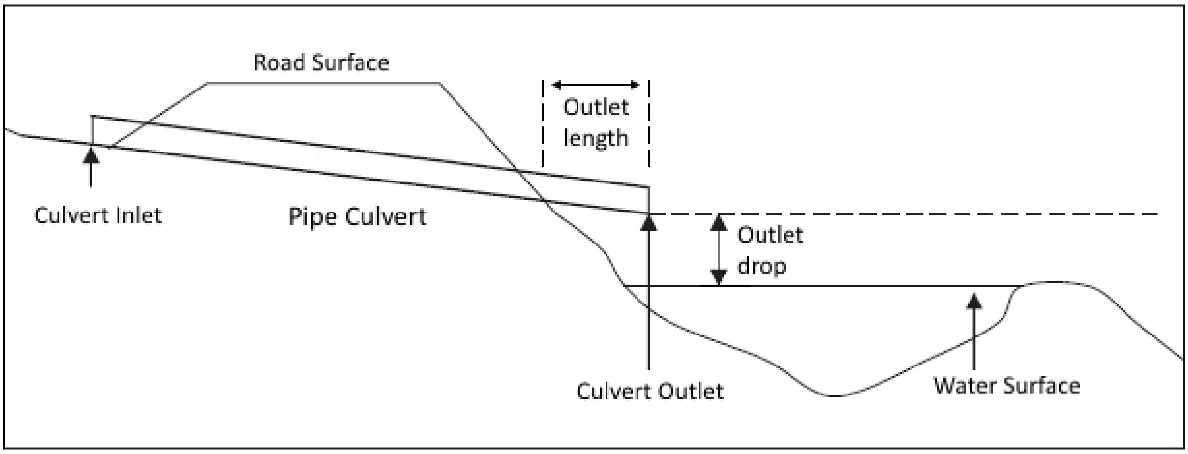

Fig. 2.3 Diagram of a perched pipe culvert with outlet measurements (Adapted from Nislow et al. 2011).

Of the subset of sixty culverts identified, only 36 qualified for the data analysis based on culvert design and fish presence (Table 2.1).

Table 2.1 Means (Standard Deviation) of the qualifying culverts' design characteristics. Average stream order (1st – 4th order) is presented.

	N	Stream Order (1-4)	Culvert Outfall Drop (cm)	Culvert Outfall Length (cm)
Passable	19	2.21	0.26 (1.15)	1.89 (8.26)
Impassable	17	1.82	78.37 (74.08)	38.01 (21.99)

Fish surveys

Spotlight fish surveys were completed after dusk by the author between 02 February and 28 March 2013. The spotlight method described by David et al. (2002) was used to survey the number and species of fish during surveys. This method was chosen as many native fish such as galaxiids are nocturnal (David et al. 2002) and it is a simpler and faster way of sampling many sites compared to electrofishing and fyke netting. This method involves slowly walking upstream searching for fish by scanning the stream with a spotlight from bank to bank c. 2m upstream of the observer using a handheld spotlight and a 12v battery. Fifty meters of stream was surveyed both above and below each culvert, and completed only once for each culvert. This level of effort allows the observer to identify most species present within streams (Nislow et al. 2011).

Spotlighting constraints

Fish abundance can be underestimated when spotlighting due to surface turbulence and water clarity obscuring fish (David et al. 2002). This constraint can be a limiting factor when measuring how fish abundance changes over several sites over time. As this study aims to examine if fish abundance is different at a single point in time, it was reasoned that proportionally any underestimation would be similar both upstream and downstream of a culvert.

It was also acknowledged that some species can be hard to differentiate when spotlighting (David et al. 2002); but that species groups often share dispersal traits (McDowall 1990) and have similar interactions with perched culverts. For instance, both shortfin and longfin eels (*Anguilla spp.*) are hard to identify in-stream but both are excellent climbers as elvers (McDowall 1990). This reasoning was also applied for *Gobiomorphus spp.* that can look similar when small and share a relatively similar intermediate climbing ability (Boubée et al. 1999). It was reasoned interspecific differences in ability within these two family groups, to migrate past culverts, would be minimal and as such could be grouped together.

Data analysis methods

Culverts in streams that did not meet design requirements or did not have fish present were excluded from further analysis (Nislow et al. 2011). Three generalised linear mixed models were used to test fish abundance and species richness of fish communities in relation to the 36 qualifying culverts predicted passable (n=19) or impassable (n=17) (Nislow et al. 2011). The dependent variables for the first two models performed were 1) total number of fish (fish abundance count) and 2) total number of species observed (species richness count). The fixed effects for the above two models were location (upstream or downstream from the culvert), culvert type (predicted passable or impassable), and an interaction between location and culvert type. The third model we performed used a zero-inflated Poisson linear mixed model for which the dependent variable was species-specific fish abundance (a count of the total number of fish for each species) and the fixed effects were location, culvert type, species, and all possible two and three way interactions. The fixed effect “species” was included as an explanatory variable to see if the number of fish present at a location varied by species.

The aim of this study and this analysis was to conclude whether the total number of fish counted differed above and below pipe culverts, whether this effect was dissimilar for predicted impassable and passable pipe culverts, and for different species (Nislow et al. 2011). All models included site as a random effect. Model fitting and selection was performed using the glmmADMB package in program R (Fournier et al. 2012, Skaug et al. 2016; https://www.R-project.org/). Model fitment was selected using Akaike information criteria [AIC] (Burnham & Anderson 2004).

2.3 Results

A total of 244 fish were identified at the 36 qualifying pipe culverts; four species and two genus’ were identified (*Anguilla* spp. and *Gobiomorphus* spp. were unable to be identified to species level and were grouped and treated as one “species”)(Table 2.2). Fish were observed upstream from the pipe culvert at 20 sites, downstream from the pipe culvert at 31 sites, and were observed both upstream and downstream from the pipe culvert at 15 sites. Ten of the 16 sites that had no fish present upstream from the culvert had been predicted to be impassable prior to fish sampling.

Table 2.2 Fish species collected from 36 sites during the summer of 2012-2013 within exotic forestry plantations in the eastern Otago region of New Zealand, organised by occurrence.

Species	Scientific Name	Culverts
Banded kokopu	*Galaxias fasciatus*	17
Kōaro	*Galaxias brevipinnis*	14
Brown trout	*Salmo trutta*	8
Eel	*Anguilla spp.*	8
Bully	*Gobiomorphus spp.*	5
Inanga	*Galaxias maculatus*	5

The first two models revealed that both fish abundance and species richness were lower, on average, upstream than downstream from pipe culverts ($F_{1,70}=6.445$, p = 0.013; $F_{1,70} = 4.876$, p = 0.031). This trend was stronger at sites with impassable pipe culverts (Fig 2.7), but was not statistically significant. That is that the relationship between the total number of fish observed upstream and downstream of the pipe culvert at passable sites is approximately

0.4:1, while the relationship at impassable pipe culverts is weakly negative ($F_{1,68} = 0.261$, $p = 0.61$). Similarly, the relationship between species richness above and below pipe culverts classified as impassable is weakly negative while a positive trend appears for passable pipe culverts ($F_{1,68} = 2.212$, $p = 0.14$).

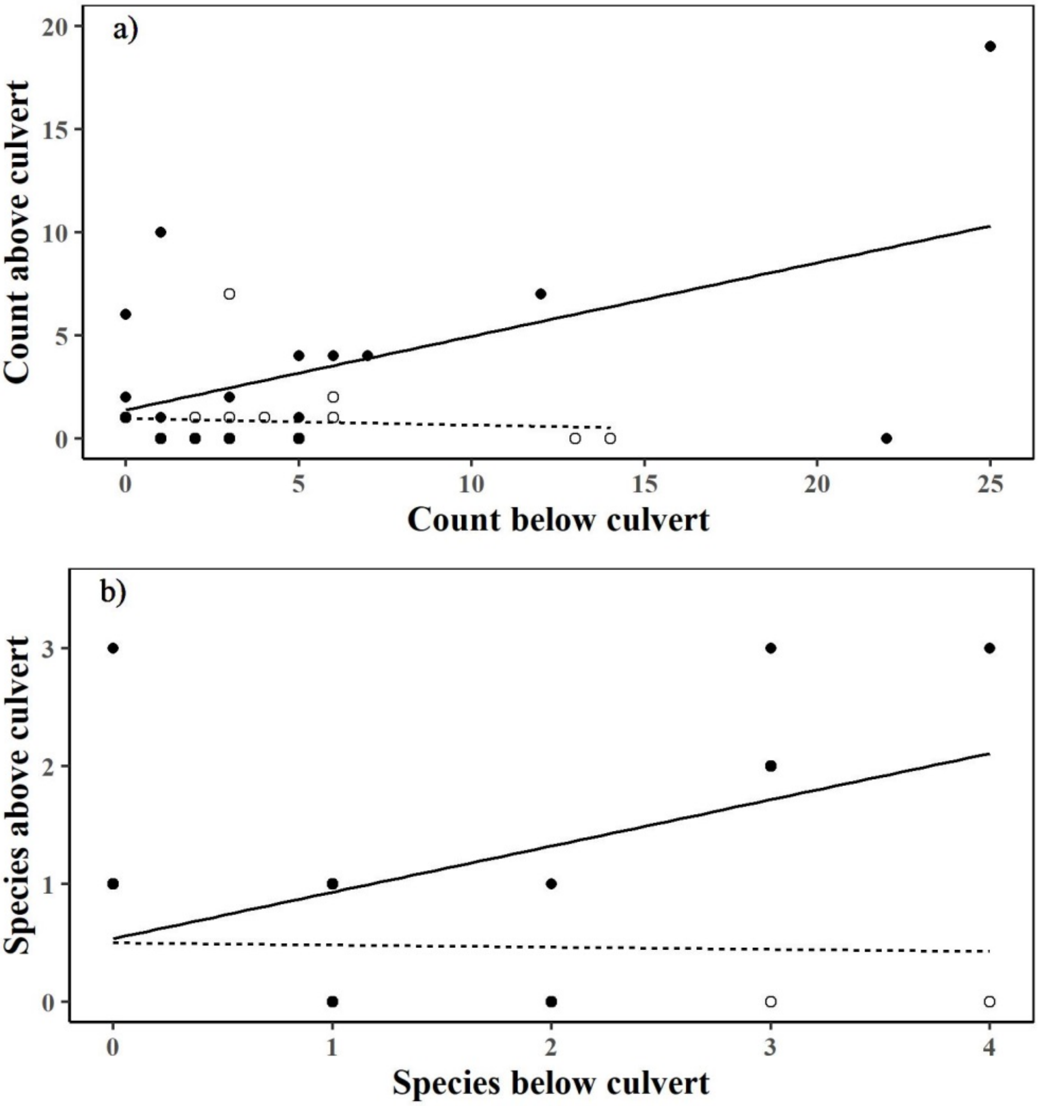

Fig. 2.7 The a) total number of fish counted (fish abundance) and b) the total number of species counted (species richness) upstream from each of 36 (passable and impassable) pipe culverts by the fish abundance or species richness observed below the pipe culvert. Hollow circles represent culverts classified as impassable *a priori*. Solid circles represent culverts classified as passable *a priori*. The solid line represents the relationship for pipe culverts classified as passable, while the dashed line represents the relationship for those pipe culverts classified as impassable. Responses to the categorical variables "passable / impassable" are presented as a continuous variable to show relationships between downstream / upstream reaches within each stream.

The best model for local species-specific abundance included the type of pipe culvert (passable or impassable), the location (up or downstream), and the species, along with two and three way interactions (Table 2.3).

Table 2.3 Model selection results for models of local species-specific fish abundance listed by the fixed effects, in which type represents whether the culvert was predicted impassable and location represents survey position upstream or downstream from culvert, with AIC (Akaike information criteria) and ΔAIC (difference between model AIC and AIC of the top model).

	AIC	ΔAIC
Type*Location*Species	768.70	0.00
Type+Location+Species	770.60	1.90
Type*Species	773.10	4.40
Location*Species	794.00	25.30
Type*Location	798.50	29.80

The model revealed that the interaction between culvert type, location and species was not significant (F 1, 480 = 624, p = 0.6818), and the observed patterns in species-specific abundance were also not statistically significant (Fig 2.8).

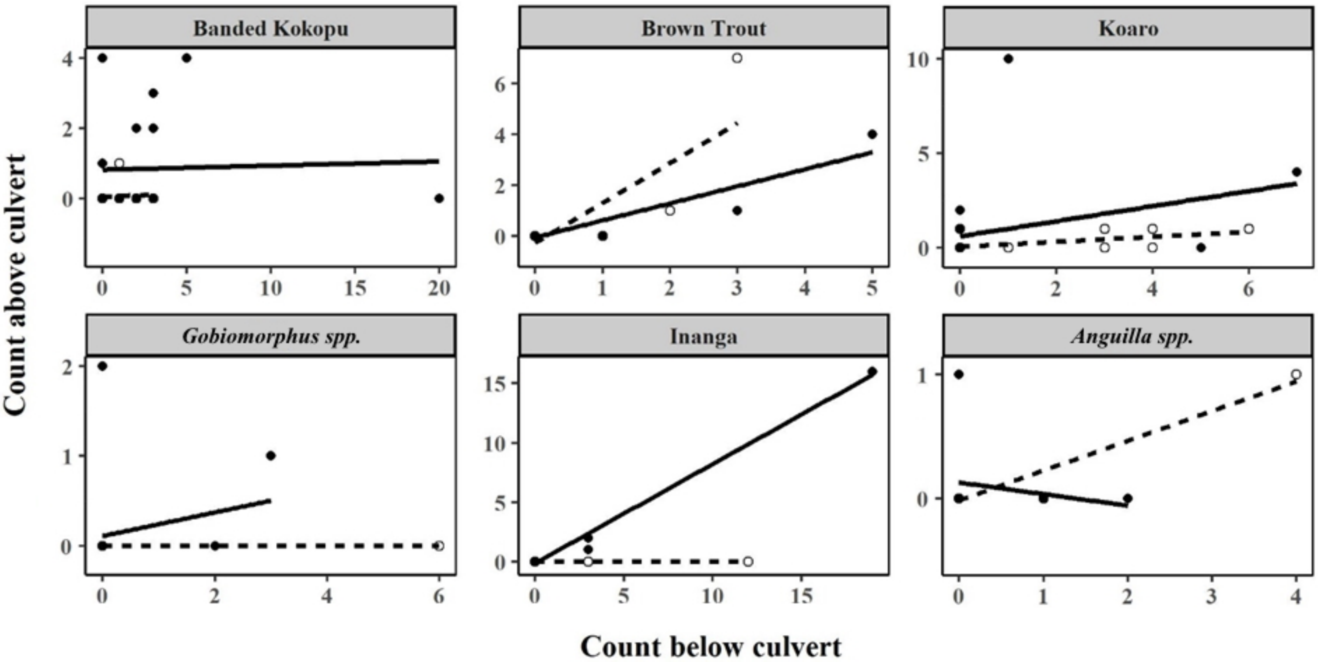

Fig. 2.8 The species-specific fish abundance observed upstream from each of 36 surveyed pipe culverts by the species-specific fish abundance observed below the pipe culvert. Hollow circles represent culverts classified as impassable *a priori*. The solid line represents the relationship for culverts classified as passable, while the dashed line represents the relationship for those classified as impassable. Responses to the categorical variables “passable / impassable” are presented as a continuous variable to show relationships between downstream / upstream reaches within each stream.

2.4 Discussion

It was found that just over half the pipe culverts assessed in exotic forestry plantation streams were perched at the time of surveys with seven fish groups identified. The observed trend was that fish abundance and species richness were reduced upstream of both impassable and passable pipe culverts. Broadly, these findings support the consensus that pipe culvert installation hinders upstream fish migration, river connectivity, and the abundance, species richness and distribution of freshwater fish communities. This result highlights the importance of fish-passage-friendly road crossing installation and the upstream limiting effect on fish migration of pipe culverts.

The trend towards lower fish abundance and species richness upstream of the pipe culverts (relative to downstream) supports international (Bouska & Paukert 2010; Branco et al. 2012) and national evidence (David et al. 2014) that pipe culverts, in general, can be barriers to fish migration, regardless of being perched or not. In New Zealand for example, uniformly fast water velocities through pipe culverts can prevent native fishes passing through those culverts and accessing upstream habitat (Mitchell 1989; Tonkin et al. 2012). Although not statistically significant, the species-specific abundance trends showed that perched (impassable) pipe culverts may have a greater barrier effect compared to non-perched (passable) pipe culverts for some native New Zealand fish species. Similar to overall fish abundance, for example, the relationship between fish abundance above and below the pipe culverts for both kōaro and inanga was positive at passable culverts and weak or negative at impassable pipe culverts. Due to the small sample size it is likely not enough data was available to statistically detect these trends, however, the trends and supporting international (Haro et al. 2004, MacDonald & Davies 2007) and national research (Doehring et al. 2011; David & Hamer 2012) do provide compelling evidence that a more thorough investigation is warranted, that species-specific interactions exist with pipe culverts, and that perched pipe culverts likely have a greater barrier effect for some New Zealand fish species than non-perched pipe culverts.

The large percentage of perched pipe culverts found during this study is not unusual. The work of James and Joy (2008) for instance found that the majority [~90%] of in-stream structures surveyed in pastoral land in the Manawatu River catchment were box or pipe culverts with 66% of all structures being perched to some degree. A similar result was also found by Barnes (2004) with 54 in-stream structures being surveyed in the mostly native forested Hunua and Waharau Regional Parks, of which 47 were culverts and 31 [~65%] were perched. This evidence reinforces that perching of pipe culverts through poor installation is a widespread occurrence, and that considerable stream habitat fragmentation and disruption to fish migration and communities has occurred across New Zealand, not only in exotic forestry plantations but across many land use types (Stevenson & Baker 2009).

Fish surveys of the Mahinerangi catchment did not record the presence of the rare Eldon's galaxias (*Galaxias eldoni*). Populations of this non-migratory galaxiid species are known to inhabit streams that were surveyed (D Jack pers. comms 2011, unreferenced) and it is likely some Eldon's galaxias were mistakenly identified as kōaro which are abundant in Lake Mahinerangi and its tributaries (Allibone & McDowall 1997). However, as with the New Zealand shortfin and longfin eel, these two galaxiids are both excellent climbers with similar morphological features, such as large pectoral and pelvic fins, which aid climbing (McDowall 1990). This suggests any negative trends regarding the barrier effect of pipe culverts on the upstream migration of kōaro would likely be similar for Eldon's galaxias, and perhaps greater for other galaxiids.

Although not statistically conclusive, the results of this study lend support to the theory that perched pipe culverts act as migration barriers to all galaxiids as kōaro and inanga abundance above and below passable pipe culverts shared a positive relationship but shared a weak or negative relationship with impassable pipe culverts. In other words kōaro, as the most capable galaxiid species at navigating in-stream obstacles (McDowall 1990), had the same negative relationship with perched pipe culverts as inanga, which are far less adapted and capable of navigating past obstacles during upstream migration (Doehring et al. 2011). Ultimately, this strengthens the notion that perched pipe culverts likely limit the upstream migration of all the galaxiid species of fishes in New Zealand.

Brown trout were the only species whose abundance had a positive relationship with both impassable and passable pipe culverts. While brown trout may have been present upstream prior to culvert installation (and successfully persist above culverts); they are strong swimmers and will utilise plunge pools to leap and navigate past perched culverts when encountered (Holthe et al. 2005; Baker & Boubée 2006; Solcz 2007). This capability is contrary to the majority of New Zealand's migratory native fish species which are not known to leap to navigate in-stream obstacles (Boubée et al. 1999), instead relying on being able to climb via wetted margins (McDowall 2000). Surpassing the climbing abilities of these fishes, perched pipe culverts effectively break wetted margins and break upstream connectivity (David et al. 2012). Galaxiid and native freshwater fish populations that rely on migration for recruitment are thus at greater risk of habitat fragmentation than brown trout due to their differing migratory adaptations and life histories (Doehring et al. 2011).

In this study, 6 of the 16 sites predicted to be impassable had fish present upstream, and modelling showed no particular relationship between passable or impassable pipe culverts with banded kokopu, *Anguilla spp.* or *Gobiomorphus spp.* and so could not account for their distribution relative to pipe culverts. A possible explanation for this was observed by Barnes (2004) who found that while fish species diversity was similar upstream and downstream of perched culverts during surveys, a distinct difference in some species' age structures were observed. Barnes (2004) concluded that a perched culvert may be limiting galaxiid upstream immigration thus skewing age structure with larger individuals dominating upstream. A likely scenario across New Zealand is that previously installed pipe culverts may have overtime eroded the downstream channel, becoming perched to a point where immigration was no longer possible but individuals remained up and downstream of that perched culvert. Such circumstances would skew age structures and is particularly relevant for long lived species such as longfin and shortfin eels (McDowall 2010). Size was not assessed in this study, but could have clearly indicated whether migration into the stream networks had occurred prior to pipe culvert installation. However, given the longevity of longfin eels, it would take many years before population size structure became markedly skewed due to limited immigration.

Overall the findings of this study align with similar research which documents the negative effect of culverts on New Zealand freshwater fish species (Boubée et al. 1999; Doehring et al. 2011). There were observable differences in fish communities above and below pipe culverts which suggest pipe culverts can be a barrier to upstream movement, and that barriers to upstream movement can influence the structure of fish communities. While this study focused on pipe culverts in exotic forestry plantation road networks, the evidence of perched culvert prevalence throughout New Zealand (Boubée et al. 1999) highlights the opportunity to restore freshwater fish communities across many land use types by removing culverts and migration barriers or modifying them to be fish passage friendly (Barnes 2004; James and Joy 2008). Ultimately, results from this study contribute to the growing body of knowledge on the migratory requirements of native freshwater fish, the importance of maintaining in-stream connectivity, and the necessity for fish-passage-friendly road crossing installation.

The results from this study also have important management applications for forestry plantation road networks and freshwater fish conservation. Firstly, to enhance fish passage, conservation managers must work with exotic forestry managers to ensure fish-passage-friendly road crossings are installed or perched pipe culverts are remediated to ensure fish dispersal throughout stream networks in exotic forestry plantations. Secondly, it is also evident that perched pipe culvert designs could be used as migration barriers to limit invasive fish species migration where necessary [extra design considerations must be made as brown trout can navigate perched pipe culverts in some instances (Baker & Boubée 2006)]. Finally, conservation managers could use perched barriers or remediation of perched pipe culverts to either allow native fish access to historical habitats, or safeguard vulnerable translocated or resident populations of threatened native fish (Burford at al. 2009).

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CHAPTER THREE

The relationship between size, a perched alloy barrier, and the climbing success of kōaro (*Galaxias brevipinnis*) juveniles in laboratory trials.

3.1 Introduction

Worldwide, diadromous fish populations are faced with in-stream barriers as they are migrating upstream (Jungwirth et al. 1998; Lasne et al. 2007; MacDonald & Davies 2007). These migrating fishes often display physical adaptations which allow them to overcome in-stream barriers as they seek to migrate to their adult niche habitats upstream (Schoenfuss & Blob 2003). Fishes make excellent models for studies identifying relationships between body shape and migratory ability in a wide range of circumstances (Wainwright et al. 2002; Walker & Westneat 2002; Lauder et al. 2003; Blake 2004; Carroll et al. 2004; Higham et al. 2005; Blake 2006; Domenici et al. 2008; Blake et al. 2009), and such studies provide understanding of the morphologies required for migratory success in in different environments (Blob et al. 2010). Often the more highly adapted diadromous fish are to navigating obstacles, the more complex or difficult in-stream migration barriers they face (Blob et al. 2010).

The larval stages of several gobiid species, native to Hawaii and other oceanic islands (Berrebi et al. 2005), are diadromous and spend several months in saltwater before migrating upstream into freshwater habitats as juveniles (Maie et al. 2009). The rivers in Hawaii have high elevational origins, fast water flows, powerful discharges and numerous in-stream barriers, such as waterfalls, which must be navigated (Maie et al. 2007). Juveniles of gobiid species in the Hawaiian Islands use powerburst and inching climbing techniques (Maie et al. 2009; Schoenfuss & Blob 2003), in conjunction with oral and fused pectoral fin ventral suckers to climb the wetted margins of these large in-stream obstacles (Blob et al. 2006). The Hawaiian gobies specifically rely on mechanical suction and also the surface tension or capillary action of fluid (Gorb 2008) that generates adhesive-like forces between the fish and any wetted surface (Baker & Boubée 2006). The use of wetted margins to climb also avoids having to resist the forces of drag in the main flow (Schoenfuss & Blob 2003). Several studies have quantified the significance of Hawaiian goby morphological variation, including allometric growth (Maie et al. 2007), to better understand goby climbing technique and its influence on their ecology (Maie et al. 2009; Blob et al. 2008).

New Zealand streams, particularly on the west coast of New Zealand, are similar to those streams inhabited by the climbing goby fauna of Hawaii (Maie et al. 2009). Several galaxiids of New Zealand also share similarities with the Hawaiian gobiid species; they are diadromous and are known for their climbing ability as juveniles (Baker & Hicks 2003; Eikaas & McIntosh 2006). Juvenile kōaro (*Galaxias brevipinnis*) are considered to be the best climbers amongst the galaxiids. Kōaro are widespread around New Zealand with some juveniles migrating great distances and over large obstacles (McDowall 2003a). Kōaro juveniles may also be able to take advantage of surface tension (Baker & Boubée 2006), by utilising their broad ventrally facing pelvic and pectoral fins and under-body surface area to adhere to wet surfaces in order to climb wetted margins (McDowall 2003b). In contrast to the Hawaiian goby species that use mechanical suction, kōaro are said to utilise the series of backward facing callus ridges on their pelvic and pectoral fins to provide extra purchase when climbing (McDowall 2003b). McDowall (2003b) also stated that the large pelvic and pectoral fins of kōaro juveniles may act as depressors due to water flow when submerged.

Despite the adept climbing abilities of some New Zealand galaxiid species, various man-made barriers have altered the distributions of many galaxiid fish as their physiological and behavioural migratory adaptations cannot surpass these obstacles (James & Joy 2008; Doehring et al. 2011). Perched road culverts in particular are a barrier to migrating diadromous fish species (Kemp & Williams 2008; Burford et al. 2009; Perkin et al. 2010; Kilgore et al. 2010) because in most cases, they are impossible to pass, even for the most advanced fish climbers (Boubée et al. 1999). Perched culverts are therefore generally considered undesirable in terms of species conservation with reductions in habitat size and fish dispersal (Warren & Pardew 1998; Cote et al. 2005; Kemp & O'Hanley 2010), especially when the genetic and metapopulation dynamics are considered for affected species (Neraas & Spruell 2001; Wofford et al. 2005; Bourne et al. 2011). However, perched culverts can also act as a barrier to invasive fish which can be beneficial for species of conservation interest upstream of culverts (Allibone & McDowall 1997). The responsible use of perched structures by freshwater managers has been proven to be a valuable conservation tool (Lavis et al. 2003). Although with respect to preventing "climbing fish" migrating upstream through the use of perched structures, little information or previous cases have been identified and studied outside of New Zealand.

Juvenile kōaro have been invading threatened non-migratory galaxiid habitats in Otago since the damming of the Waipori River over one hundred years ago (Allibone & McDowall 1997). Staff from the Department of Conservation in Otago had been exploring the use of perched structures to halt juvenile kōaro migration as when adults they either competitively exclude or predate upon dusky galaxias juveniles (Allibone 1999). Early attempts to limit kōaro migration have proven to be ineffective (Campbell 2011). Eliminating climbing juvenile kōaro migration into non-migratory galaxiid habitats will help protect non-migratory galaxiid populations which are in decline (Allibone & McDowall 1997).

While there are several studies (McDowall 1970; McDowall 1990; McDowall 2010) describing the excellent climbing abilities and climbing morphology of juvenile kōaro; there have been no quantitative trials completed to analyse and compare the variation in juvenile morphological climbing traits and styles. Doehring et al. (2011) wrote that there is an absence of information on the heights and gradients that New Zealand's migratory galaxiids can traverse, and McDowall (2010) believed that understanding the climbing aptitude of galaxiids is important for understanding kōaro ecology. A controlled trial quantifying differences in kōaro juvenile size and the possible significance of these differences effecting climbing ability and success would be a novel approach to better the ecological understanding of kōaro. Research coupled with a controlled trial would also provide valuable insights into the design and success of perched barriers at disrupting juvenile kōaro climbing ability in a laboratory setting, which could then be translated into a useful conservation tool in the field.

Armed with the knowledge of the threatened non-migratory galaxiid plight in Otago, and the need for a successful climbing fish exclusion tool by the Department of Conservation, this study aims to use a controlled laboratory experiment to test a) how factors of size in juvenile kōaro effects their climbing ability, and b) to test the concept that a perched barrier can stop juvenile kōaro from climbing an artificial weir.

3.2 Methods and materials

In February 2013, fresh-run transparent kōaro juveniles were sourced from the mouth of Mount Burke Creek (1301510.491E, 5061156.841N NZTM), which flows into Lake Hawea of the South Island, New Zealand. The juveniles were caught using a Kainga EFM300 electrofishing machine and a stop net. Approximately 600 juvenile kōaro were collected and held in an oxygenated tank containing creek water while being transported back to the laboratory. Transparency of the fish indicated all were fresh recruits into the stream (McDowall et al. 1994). Collection on the same day was assumed to ensure that individuals were within the same relative stage of development (Blob et al. 2010). The juveniles were acclimated for one week after transportation to the laboratory. Kōaro were observed feeding and mortality was approximately 1%, indicating that fish were not overly stressed by transportation (Schoenfuss & Blob 2003). Due to travel distance, time restraints and the seasonality of kōaro migration, only one collection of juveniles took place.

Climbing ability in relation to body size

A simulated concrete weir was erected in the laboratory and 'seasoned' for 6 weeks with living rock to start the nitrogen cycle (bacterial processing of nitrogen excreted by fish) within the tank and frequent water changes were made to ensure any chemical traces from construction and materials were flushed out, and (Fig 3.1). The simulated weir was made of a lower glass tank (500mm x 300mm x 400mm) and a plastic top chamber (300mm x 400mm x 300mm), connected by a right angled, plaster/sand weir. The "vertical" weir face was 250mm wide and 500mm high above the lower tank waterline. The "horizontal" top section of the weir was of a 'flat-bottom V' shape and was 250mm wide by 300mm deep. The 'V' form sides were on 45 degree angles and were 200mm high. The 'V' form shape allowed a controlled and even stream of water to cascade over the weir face. The particular design of the weir was used for a number of reasons. Firstly, the weir design was used to imitate a 'climbable manmade barrier' that would likely be found in the field and which could be retrofitted with a migration barrier. Secondly, the materials were used to mimic the rough nature of rocks as found in a natural setting, and the concrete used in weirs, to provide a suitable surface for kōaro to adhere too. Thirdly, the rough nature of the weir surface also increased the wetted margins of the weir, which kōaro (McDowall 2003b) and other climbing species (Schoenfuss & Blob 2003) use to navigate past fast flowing cascading water. Lastly, the V shape of the weir was used to ensure water recirculating down the weir face be kept in the middle to provide sufficient wetted margins either side for the kōaro to climb. These weir design specifications were to ensure the experiment tested the studies primary objectives.

Fig. 3.1 The concrete weir simulation in the laboratory (photo: Josh Tabak)

An aquarium water pump (240v – Hailea HL-BT700) was used to deliver a constant 7 litres of water per minute (42 gallons per hour) from the lower tank to the top chamber, from where the water was recycled and spilled over and down the weir face into the lower tank. A ‘Gee minnow style’ trap was used to catch kōaro as they navigated over the weir in an ‘upstream’ direction into the top tank, and to stop them returning to the bottom tank (David et al. 2009). A 25mm wide frame was used around the top perimeter of the bottom tank and top tank walls to deter kōaro from escaping over the sides of the tank. The recirculating design was beneficial as Baker and Hicks (2003) found that kōaro displayed a strong upstream drive in their experiments. It was assumed that the flow of water down the weir face would increase the likelihood that kōaro climbed the weir during experiments. Both tanks also had stones and rocks to provide cover for fish.

Based on several test runs, and in order to expose all juveniles to the weir in a controlled, un-cramped manner, ten replicate seven day trials were conducted. A lighting timer was used to keep a diurnal cycle of 12 hours light to dark. Individual fish locations were recorded at the conclusion of each trial. Trials ran for seven days to a) ensure ample time exposure of kōaro to the weir and b) to allow time for kōaro to recover from handling. Fish were used once in trials as experience can affect performances in experiments (Kemp et al. 2009). Thirty fish were used in each trial and were euthanized in ethanol (95%) at the end of each trial. Juvenile kōaro total length and weight were measured from specimens' immediately after they had been euthanised in 95% ethanol so as to avoid any shrinkage which can occur after long periods of ethanol exposure (Maie et al. 2007). Climbing performance was graded as a success or failure depending on kōaro final location at the end of the experiment (Blob et al. 2010). Kōaro locations along the simulation were recorded as either the top tank (TT) or the bottom tank (BT) (David et al. 2009). Between each trial a water change of 90% was made to dilute odours and remove excess nitrogen. The water temperature within the simulation setup was monitored weekly during the trial period.

Fish were held and maintained in a large tank (1500mm x 60mm x 50mm) for the duration of this study. Fish were non-selectively caught from this tank using a scoop net to ensure a random and broad variation in size for each trial. Over the duration of the experiment, being 15 weeks, fish size was expected to increase, which would give a wider range of sizes to trial. Kōaro juvenile size ranged from 32mm to 43mm total length (TL) when collected from Mount Burke creek to between 39 and 52mm TL by the end of the trials. They were fed using a small sized commercial fish feed daily to ensure they had sufficient energy levels to climb. Their tank was cleaned weekly. The freshwater in the tank was mixed with 5% seawater to help prevent microbial infections. On two occasions 'Wunder White Spot Cure' was used to control the spread of white spot infection. The fish used in each trial were caught randomly from this tank using a small scoop net. Ambient temperatures remained constant throughout the experiments.

Perched barrier

The same concrete weir setup and conditions, as pictured and described in the section above were used in this trial. This was because a) kōaro had shown that the weir was navigable and b) this allowed a controlled comparison of climbing success results against the effects a perched alloy barrier may have on the climbing success of kōaro. The perched barrier climbing experiment and non-perched barrier climbing experiment ran in alternate weeks.

The perched alloy barrier in question was constructed using a 1mm thick aluminium plate. The 300mm wide aluminium barrier lip (150mm deep) was centralised and angled 120 degrees downwards from the vertical weir face. The barrier was installed 300mm above the water level in the bottom tank. This was to deter kōaro from leaping onto the barrier lip. The 'V' form weir made for a controlled and even water flow over the barrier lip. A 0.5mm gap between the alloy barrier and the weir allowed a slight stream of water to wet the weir face beneath the barrier lip. This was to simulate a 'splash zone' to ensure the barrier and weir was entirely wetted. Five replicate seven day long trials were to be completed with the barrier installed. Twenty fish were used per trial. Individual fish were used once and euthanized in ethanol (95%) before total length and weight measurement.

Fig. 3.2 Alloy barrier installed on the concrete weir (photo: Josh Tabak)

Data analysis methods

For the non-barrier trials, the effects of weight and total length on the probability of success of juvenile kōaro climbers was analysed separately using logistic regression models (Zar 1999) as they are likely correlated. To compare the simple logistic regression results of successful and unsuccessful kōaro climbers with more complex models, a model with weight and total length was analysed, as well as a model with weight, total length and an interaction term (weight interaction with total length) (Zar 1999). The weight and length variables were centered prior to final model fitting to account for high multicollinearity as indicated by high variance inflation factors (weight VIF = 10.154, total length VIF = 10.154) that were initially generated. Both the more complex models were tested using a chi-squared test for best fit and a probability of success interaction plot of weight and total length was produced. Alpha (α) was set at 0.05 and data were analysed in program R (https://www.R-project.org/).

The non-barrier trials were used as the control for the barrier fitted trials. The effect of the perched barrier on climbing success was tested against non-barrier climbing success using a chi-squared test of association (Baker and Hicks 2003). Baker and Hicks (2003) used a similar chi-square analysis to test odour preference significance in Inanga (*Galaxias maculatus*) and kōaro during laboratory experiments.

The experiments relied upon a primary assumption; that all kōaro juveniles in this experiment attempted to climb and navigate the weir and either failed or succeeded in navigating above the weir. As has been used elsewhere (Holthe et al. 2005), video footage was taken during several trials to confirm if fish attempted, and were unable to navigate past and above the weir.

3.3 Results

In total 366 kōaro juveniles were trialled in the weir simulation experiment. Of the 303 juvenile kōaro placed in the bottom tank of the experiment without the perched barrier fitted; only 82 were successful at navigating the weir over 10 different trial weeks. Within those ten trials, success rates of juvenile kōaro who navigated the weir varied from 17% to 40%, with an overall average of 27%. Both successful and unsuccessful attempts to navigate the weir were captured on video[1].

Logistic regression models (1 and 2) demonstrate that there was a significant difference in the total length (Fig 3.3) and weight (Fig 3.4) of successful versus unsuccessful juvenile kōaro climbers during the non-barrier trials; with larger juvenile kōaro being more likely to successfully navigate the barrier when total length and weight were tested independently of each other (Table 3.1).

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[1] "Juvenile kōaro (*Galaxias brevipinnis*) climbing success" - https://youtu.be/lup5_GXuXz0

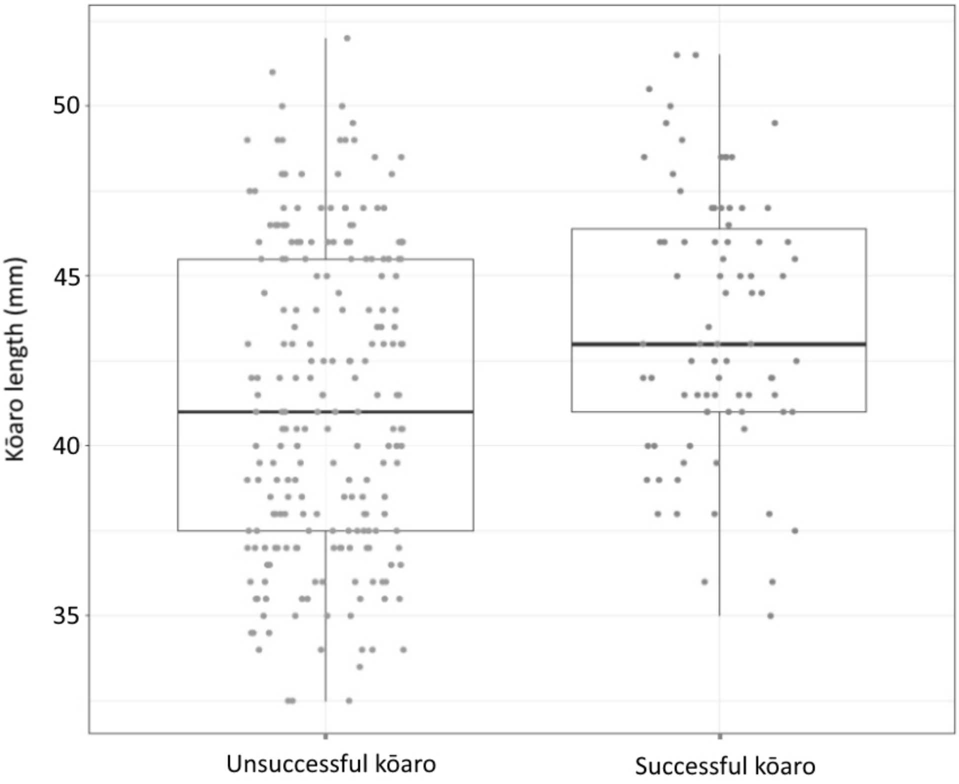

Fig. 3.3 The difference in total length between unsuccessful and successful kōaro juveniles when attempting to navigate a simulated weir under laboratory conditions.

Model 3 (Table 3.1) suggests the effects of weight and total length on climbing success is significant (weight p = .0038, total length p = 0.0001). Model 4 suggests that only total length and the interaction between weight and total length are statistically significant (Table 3.1).

Table 3.1 Logistic regression model results showing the significance that total length, weight, and the weight interaction with total length term had for kōaro juveniles during a weir simulation in laboratory conditions. Positive coefficients indicate a positive correlation between the variable and the likelihood of successfully navigating the weir.

Logistic Regression Model	**Factor**	**Coefficient**	**p-value**
1	Total length	0.11549	<1e-3
2	Weight	2.6098	0.008
3	Weight	-10.0345	0.0038
	Total length	0.3993	0.0001
4	Weight	7.2138	0.0538
	Total length	0.3489	0.0012
	Weight*Total length	-0.6605	0.0285

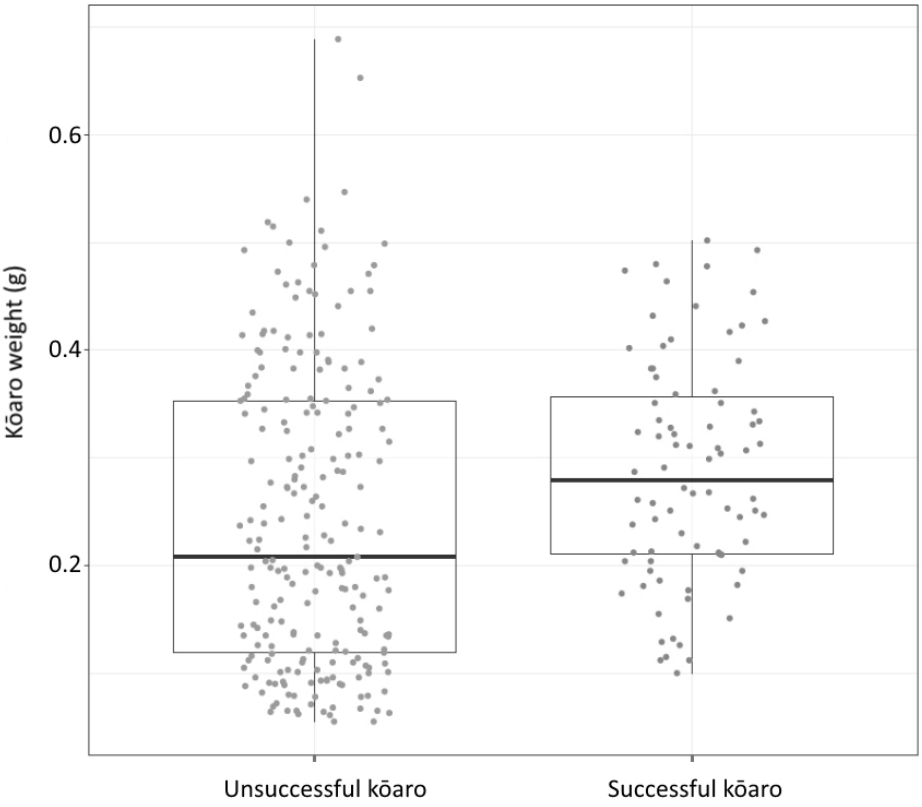

Fig. 3.4 The difference in weight between unsuccessful and successful kōaro juveniles when attempting to navigate a simulated weir under laboratory conditions.

A Chi-squared test showed that the fourth model had a better fit (p = 0.0231, Table 3.2) than the third model. The fourth model was then used to produce a probability of success interaction plot of weight and total length for juvenile kōaro (Fig 3.5).

Table 3.2 Analysis of deviance table.

Model	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
3	300	329.30			
4	299	324.13	1	5.1613	0.0231

The plot shows the predicted impact of weight for different total lengths of juvenile kōaro. It indicates that given a particular total length of a juvenile kōaro, a larger weight reduces the chances of that fish navigating the weir. The predictions of the interaction plot are indicative only because of the high level of multicollinearity between weight and total length.

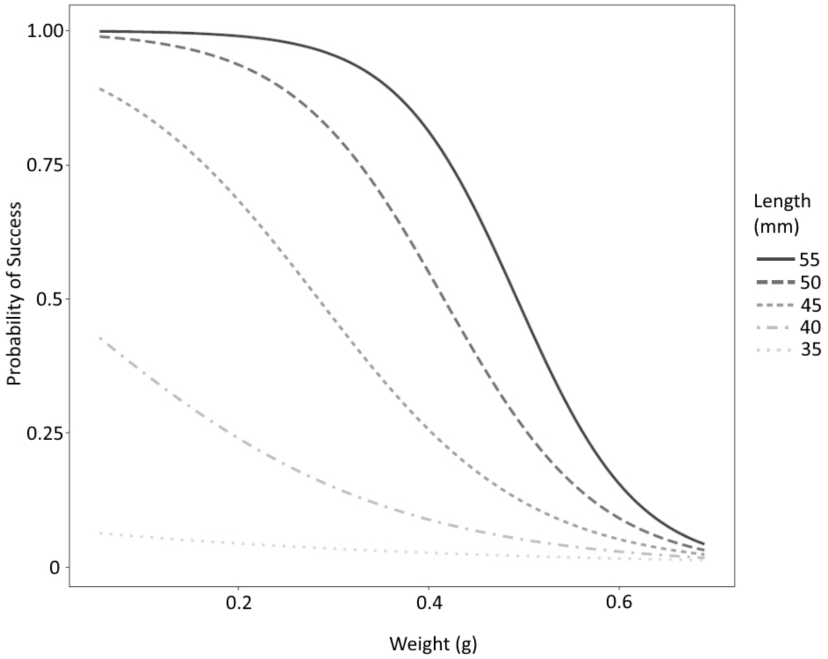

Fig. 3.5 Interaction plot predicting the climbing success of juvenile kōaro with different weights and total lengths.

The relationship between weight, total length and climbing success for juvenile kōaro can also be visualised in a scatterplot of weight versus total length (Fig 3.6). Several long, heavy kōaro failed to navigate the weir whilst long, lighter kōaro are successful.

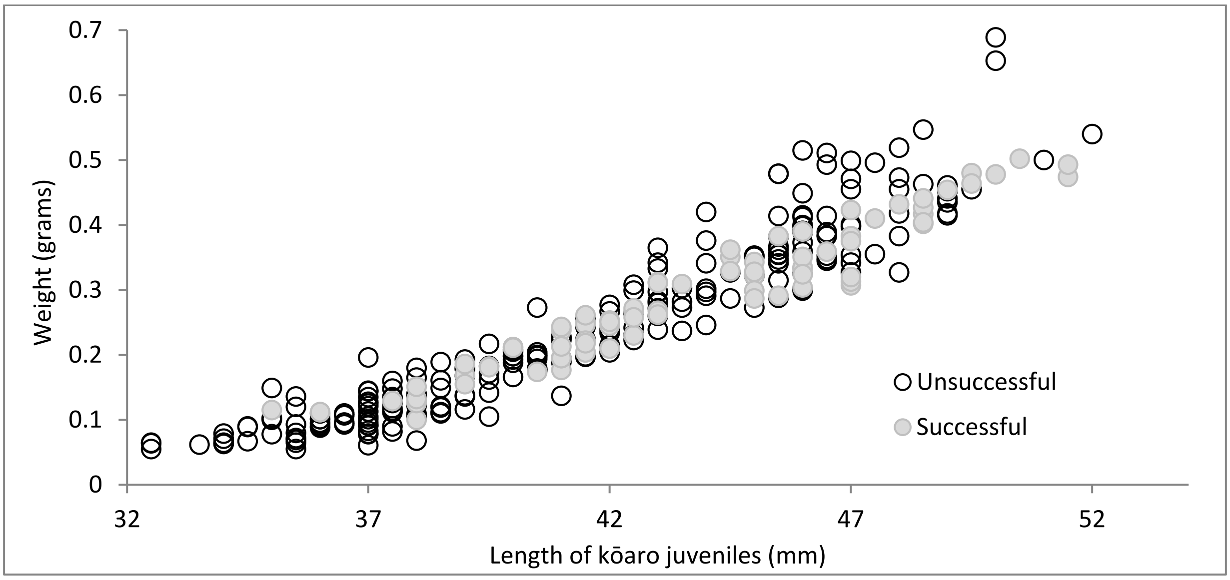

Fig. 3.6 Scatterplot showing the relationship between juvenile kōaro weight, total length and climbing success when navigating an experimental weir.

A total of 63 kōaro juveniles were used in trials with the perched barrier fitted to the experimental weir. In contrast to the non-barrier trials, no juvenile kōaro were successful in reaching the upper tank when the perched barrier was fitted (Table 3.3). It was decided after three trials to discontinue the barrier experiment as it was apparent that no fish were going to be able to navigate past the barrier. A chi-squared test revealed significantly fewer juvenile kōaro were able to navigate the weir when the barrier was fitted (p <1e-3).

Table 3.3 Chi-squared test results showing kōaro climbing success in the absence and presence of a perched barrier.

	Failed	**Success**	**Total**
No Barrier	221	82	303
Barrier	63	0	63
Total	284	82	366

Video observation revealed two climbing styles. Kōaro juveniles were seen to climb in rapid bursts and then rest on the wetted margin of the weir face in between bursts. Kōaro also demonstrated slower climbing motions to move forward while resting on the wetted margin. On several occasions, rapid burst climbers would swerve into the main flow of the water in the centre of the weir face and were forced backward before swerving onto the wetted margin to rest. Slow climbing appeared to occur only on the wetted margins and where the 90 degree angle at the top of the vertical weir face joined the horizontal weir section leading to the top tank.

3.4 Discussion

Climbing ability

The results of this experiment demonstrate that juvenile kōaro climbing ability is influenced by morphology. Longer individuals with lesser body weight were more successful at navigating the weir relative to individuals that were as long, but heavier. The longer and lighter individuals may have been better equipped to navigate the weir because of a larger surface area to volume ratio (relative to the heavier unsuccessful individuals). Successful juvenile kōaro may have had a larger surface area perhaps due to larger pelvic or pectoral fins, increasing their ability to stay attached against the weir face when climbing. Linton et al. (2007) support this notion as they noted climbing eels benefit from a larger surface area to volume ratio increasing adhesive surface tension forces. Lujan and Conway (2015) also suggest that large ventrally flat shaped paired fins can maximise mechanical substrate contact. Larger paired fins could also increase the hydrodynamic down force of kōaro in flowing water (McDowall 2003b)

Compounding the benefits of comparatively larger pelvic and pectoral fins on climbing success is the associated increase in the size of the callused ridges on the fin (McDowall 2003b). These ridges are found only on the pectoral and pelvic fins of the climbing galaxiids, and are much reduced in non-climbing galaxiids, suggesting they play a significant role in climbing (McDowall 2003b). An increase in the size or area of these ridges would increase the overall ventral pelvic and pectoral fin surface area. In light of this it is likely that juvenile kōaro equipped with larger paired fins, have an increased potential for hydrodynamic down force, mechanical traction and capillary adhesion on substrates when climbing wetted margins or in flowing water. Such an advantage would certainly increase migratory and climbing ability and the chances of success when navigating an in-stream obstacle.

The success of juvenile kōaro climbers may have also been due, in part, to behavioural differences and approaches to navigating the weir. Video footage of juvenile kōaro climbing technique showed various combinations of distinct phases in climbing spells alongside periods of resting. Firstly juvenile kōaro juveniles demonstrated the ‘powerburst’ technique, similar to that described by Blob et al. (2006) when studying the specialised climbing behaviour of the Hawaiian gobiid fishes *Awaous guamensis* and *Lentipes concolor*. The powerburst technique involves fish using their pectoral (and pelvic in the case of kōaro) fins to push off surfaces as an initial force to begin a burst of axial undulation. Baker and Boubée (2006) described this climbing technique as a “wriggle” type movement when describing the climbing of banded kokopu and kōaro. The second climbing phase juvenile kōaro demonstrated was a slower version of this technique which could be described as ‘edging’. The kōaro generated leverage by using their pelvic and pectoral fins to create slow deliberate axial undulations. Many combinations of powerburst climbing spells in and beside the main flow were observed along with spells of edging and re-adjusting along the wetted margins. Resting for a long duration during climbing has been strongly correlated with climbing success (Weinstein & Full 1998 - 1999; Edwards & Gleeson 2001) because rest periods allow for fatigue recovery, removal of performance reducing compounds, and restoration of metabolic fuels (Weinstein & Full 2000; Allen & Westerblad 2001).

Video footage observation showed kōaro juveniles struggling to powerburst climb in the main flow of the weir; the main flow pushing kōaro back down the weir face[1]. While a lack of rest time may account for kōaro juveniles being pushed back, other selective environmental forces in the form of drag and gravity can influence climbing success and ultimately morphology and behaviour (Maie et al. 2007). Selection often favours morphological features such as fusiform body shapes or lighter bodies, for example, which help to minimise water drag (Lujan & Conway 2015) and minimise the effects of gravity (Maie et al. 2007). In this study, the longer successful juvenile kōaro climbers may have been more hydrodynamically suited to climbing compared to the shorter heavier juveniles who were unsuccessful at climbing. Locomotor behaviours also interact with these environmental forces. Powerburst climbers for example, where climbing primarily occurs along the edges of water currents, are more likely to be exposed to water drag than climbers who use wetted margins outside the reach of flowing water (Blob et al. 2006) which eliminates water flow force and drag (Schoenfuss & Blob 2003). The larger successful climbers may have been more efficient powerburst climbers along with being better equipped to utilise surface tension to minimise energy use and recovery time.

Fish are met by different environmental challenges simply as a function of their own growth (Maie et al. 2007). With regards to climbing fishes, pectoral fins were shown to grow allometrically in area and length relative to body length and mass in the Hawaiian goby *S. stimpsoni*, which form territories in pools upstream instead of continuously migrating (Maie et al. 2007). It is likely kōaro display some level of allometric growth during their migrations which may influence their climbing aptitude as they age; suggesting that allometric growth and general increases in size are likely to place an age or size limit on kōaro climbing ability. A decrease in climbing aptitude could thus provide a likely explanation for territory formation in climbing galaxiid adults.

While the experiment highlighted the effects of size on climbing success, the result is only indicative of the specific physical demands the experimental weir design placed on the kōaro juveniles in this trial. In a natural setting, physical demands may differ. In streams, the body shape differences of juvenile kōaro such as length, narrowness, flatness, pelvic and pectoral fin shape, size and callus ridges are likely to influence their ability to climb different

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[1] "Juvenile kōaro (*Galaxias brevipinnis*) climbing" - https://youtu.be/PPUU8wxOfnA

obstacles based on the local conditions such as substrate type, water velocity and wetted margin type (Blob et al. 2008; Blob et al. 2010).

Perched barrier

Perched migration barriers have been successfully used by conservation managers across the Great Lakes region of the United States (Lavis et al. 2003). These perched migration barriers, which create a vertical drop of 30cm, overcome the behavioural and physical limits of lamprey climbing ability during migration events (Lavis et al. 2003). Similarly, the results of the trials in this study clearly demonstrate that an appropriately designed perched barrier can block the upstream migration of juvenile kōaro and could therefore be used to a) remediate weirs that represent likely barriers within the natural habitat of kōaro (and other climbing galaxiids), and b) to block the upstream migration of kōaro into streams sustaining populations of threatened non-migratory *Galaxias* species.

The perched aluminium barrier used in these trials exceeded the physical and behavioural limits of juvenile kōaro climbing ability, blocking their upstream migration. Baker and Boubée (2006) found that kōaro climb by ensuring their fins keep constant contact with the substrate. However, the design of the thin perched barrier lip effectively breaks the contact of juvenile kōaro fins and body surface area with the substrate when trying to navigate around the 360 degree angle of the lip. The break in contact is a similar observation to that of Jellyman (1977) who noted that climbing eel elvers in New Zealand could not pass over surfaces that had large breaks in them, or where a substantial break in contact between the substrate and eel body surface occurred. Video observation of the weir experiment showed juvenile kōaro struggled to maintain body and fin contact with the weir (where the vertical face met the top horizontal section of the weir at a 90 degree angle) being pushed backward by the water flow. The perched aluminium barrier experiment therefore highlights the potential for such a perched barrier to prevent juvenile kōaro climbing. Perched barriers may therefore be a potential conservation tool that can be used to halt kōaro juvenile migration into streams beyond their natural range.

Future research

Extreme environments impart severe selective forces that govern the physiological performance limits of individuals (Waterman 1999 - 2001), and this is particularly the case for climbing fish (Lujan & Conway 2015). Navigating waterfalls and difficult in-stream barriers exerts strong selective forces upon migrating Hawaiian goby juveniles, for example, limiting the upstream distance they can travel and habitats they can access in streams (Blob et al. 2006). Constant environmental selective pressures that govern juvenile kōaro migration combined with the findings of the experiment suggest intraspecific variation in individual body types may also influence the abilities of some juvenile kōaro to access certain stream habitats. McDowall (2010) referred extensively in his book to the importance of life history, as the greatest driver of non-diadromous galaxiid speciation in New Zealand; but could intraspecific variation in climbing ability of a galaxiid common ancestor have contributed at some level to this process? This is a very complex and difficult question to answer, but as McDowall (2010) suggested, a greater understanding of galaxiid climbing ability and limits will elucidate more details regarding kōaro ecology.

The climbing success experiment relied upon basic and unsophisticated representations of juvenile kōaro morphology by testing total length, weight, and the interaction of total length and weight. Other approaches to testing climbing ability, such as digitally photographing lateral and ventral views of kōaro juveniles while climbing, may help to determine more specific morphological traits that influence juvenile kōaro climbing success -such as pectoral and pelvic fin size, and specific surface area ratios (Blob et al. 2010). Schoenfuss and Blob (2003) and Kemp et al. (2009) described methods to film and photograph fish climbing and locomotor kinematics using clear plexiglass. Recent photographic work by Ingram and Bennington (2018) has shown modest body shape differences between lake and stream populations of kōaro using morphometric measurement analysis of body shape. Perhaps a similar method could be used to assess galaxiid climbing morphology and behaviour with respect to size and age in more detail. Baker (2003) has already undertaken novel trials in this field by studying two New Zealand diadromous fish species and finding that the age and size of the common bully (*Gobiomorphus cotidianus*) and inanga (*Galaxias maculatus*) influenced their success when attempting to navigate through different weir designs. Testing the maximum size of juvenile kōaro climbing success may also be insightful given that potential allometric growth changes in kōaro may be similar to the processes seen in Hawaiian gobiid species' which limits their adult territories and shapes their ecology (Maie et al. 2007).

Conclusions

Climbing ability in juvenile kōaro appears to be influenced by intraspecific variation in juvenile kōaro body size and behaviour. Morphological differences that exploit surface tension with differing degrees of success perhaps influence juvenile kōaro climbing ability.

Differences in pelvic and pectoral fin size (surface area) and callus ridge rays for example may improve capillary adhesion to surfaces and impart greater hydrodynamic downforce when climbing. Differences in individual climbing style, resting behaviour to minimise energy loss, and body shape drag efficiency may also affect individual climbing ability. Increasing juvenile kōaro age and allometric growth during migration is also likely to impact on climbing ability, performance and final dispersal of adult populations.

The success of the perched aluminium barrier at halting kōaro from climbing introduces a possible new isolation concept to be explored by conservation managers for controlling invasive climbing fish in New Zealand. A successful perched aluminium barrier in the field would allow conservation mangers to protect rare non-migratory galaxiids within New Zealand from migratory invaders.

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CHAPTER FOUR

Assessment of a perched migration barrier as a conservation tool: separating dusky galaxias (*Galaxias pullus*) from the invasive kōaro (*Galaxias brevipinnis*) in a Waipori River tributary.

4.1 Introduction

New Zealand's flora and fauna have evolved alongside a turbulent geological history (Wallis & Trewick 2009). Native freshwater fishes, bound by water, have been subjected in part to several geological processes as uplift and erosion shapes where and how water flows across the land (Craw 2013; Waters & Wallis 2000). New Zealand's native galaxiid fishes in particular display differing life histories (McDowall 1990). The life history and ecology of isolated non-migratory galaxias are at the mercy of changes in water flow, exposed to periods of riverine "inter and dis" connectivity (Waters et al. 2006).

The extent of isolated non-migratory galaxias forms are still being revealed today. For example, the once overarching description of the common river galaxias (*Galaxias vulgaris*) in the South Island of New Zealand (Allibone & McDowall 1997) has now, through genetic analysis and morphological comparison, been divided into the *Galaxias vulgaris* species complex which describes several distinct non-migratory galaxias species (Allibone et al. 1996; Waters et al. 2010). Two galaxias of the *vulgaris* complex (Allibone & Townsend 1997), Eldon's galaxias (*Galaxias eldoni*) and Dusky galaxias (*Galaxias pullus*) described in 1996 (McDowall & Wallis 1996), are confined only to eastern Otago (McDowall 2010). Dusky galaxias and Eldon's galaxias are present in the Waipori River catchment, with smaller populations scattered throughout the upper tributaries of the Tuapeka, Waitahuna and Taieri Rivers (McDowall 2000-2010). Jones and Closs (2016a, 2016b) more recently have described the early life history traits, dispersal mechanisms, metapopulation structure and threats to these upland galaxiid species.

Humans have also played a hand in governing how, where and when water flows across the land. Engineering feats to redirect rivers and the building of dams for hydropower has seen many natural river catchments altered. Lake Mahinerangi, as a prime example, was formed following movements by the Dunedin City Council beginning in 1907 to dam the Waipori River to generate electricity (Beeche 1950). McDowall and Allibone (1994) suggested that the impoundment of the Waipori River had led to ecological change in the upper catchment. McDowall and Allibone (1994) reasoned that new stream invaders such as brown trout (*Salmo trutta*) and particularly kōaro *(Galaxias brevipinnis)*, a native fish which were never very abundant in the upper Waipori River catchment, had been encroaching upon non-migratory galaxias habitat in headwater streams.

Kōaro are usually amphidromous, breeding and laying eggs in freshwater habitats, with larval fish migrating out to sea for several months before migrating back to freshwater as juveniles (McDowall et al. 1994). However, amphidromy in kōaro is facultative, and large freshwater bodies can serve as nursery habitats for young (McDowall 1998). The formation of Lake Mahinerangi gave kōaro a recruitment site 40 kilometres inland (McDowall 1998). From here juvenile kōaro could begin to migrate upstream, further than ever before, into the headwaters of the Waipori River catchment (McDowall 1998; Ravenscroft 2006). Allibone and McDowall (1997) highlighted the threat of kōaro invasion on dusky galaxias populations. Kōaro are suggested to predate upon and/or competitively exclude non-migratory galaxias, and are one of the likely reasons for dusky galaxias decline in the upper Waipori River catchment (Allibone 1999). Kōaro also have much higher fecundity and recruitment rates than dusky galaxias, at least in streams close to downstream impoundments (Jones & Closs 2016b).

McDowall and Allibone (1994) first proposed dusky galaxias populations could be protected through the use of perched barriers. Allibone and McDowall (1997) later detailed the extent of at-risk dusky galaxias populations in the upper Waipori River catchment that would benefit from conservation management. The Forest Research Institute had previously installed hydrological research weirs (Fahey & Watson 1991) where two dusky galaxias populations had been identified in two adjacent tributaries of the upper Waipori River catchment. These structures provided the platform for conservation efforts that started in 1998 to try and stop kōaro recruitment into both tributaries by retrofitting short lengths of railway iron to act as migration barriers (Ravenscroft 2006). The Department of Conservation (DOC) hypothesised these measures would help reduce the invasion pressure of kōaro on these vulnerable dusky galaxias populations.

Allibone and Barrier (2004) wrote the "New Zealand non-migratory galaxiid fishes recovery plan 2003-2013" for the DOC years after these early dusky galaxias conservation efforts had been made. As a statement of intentions and strategic guidance for freshwater conservancy teams, the new recovery plan laid out broad goals, specific actions and objectives to conserve at-risk non-migratory galaxiid populations. The dusky galaxias, labelled as conservation dependant in 2002 (Hitchmough 2002), featured prominently in the recovery plan. The plan stated that: 1) as key dusky galaxias sites, the tributaries were to be protected from kōaro invasion by assessing, maintaining or improving in-stream barriers, and 2) through the continuation of the DOC kōaro removal project which began in 2002 (Campbell 2011).

Conservation managers have successfully used isolation management in streams internationally to control invasive fish migrations (Novinger & Rahel 2003). Isolation management involves migration barrier installations followed by invasive species removal and then native species re-colonisation (Rahel 2004). Fausch et al. (2009) highlights barriers to invasive fish species are often critical to the survival of headwater fish species, which usually lack competitors and predators. For instance, at-risk native cutthroat trout (*Oncorhynchus clarki*) populations in headwater streams of Wyoming were being isolated from competition with other invasive trout species, using migration barrier installations (Kruse et al. 2001). Rahel (2004) suggested repurposing natural and manmade structures within catchments as migration barriers, on a case-by-case basis, to get the best isolation management conservation outcomes possible for afflicted native species.

Access issues meant a comprehensive electrofishing programme was conducted in only one of the dusky galaxias tributaries (Campbell 2011). Electrofishing surveys showed that the railway iron barrier did not halt juvenile kōaro recruitment. This prompted the DOC to trial a stainless steel migration barrier design in 2008. However, continued surveys after its installation showed this design also did not halt juvenile kōaro recruitment. Discussions with the DOC Dunedin suggested another new migration barrier design was needed to isolate the dusky galaxias population.

Perched culverts are known to be effective barriers to diadromous galaxiid migration (Boubée et al. 1999) and perched migration barriers have been used successfully in the United States to halt diadromous migrations of invasive climbing lamprey (Lavis et al 2013). In light of the need for improved conservation outcomes for the endangered dusky galaxias, this chapter aims to trial a new perched migration barrier design as an isolation management tool. The objective of the trial is to examine if the new perched migration barrier design can halt juvenile kōaro recruitment past a research weir in order to isolate the dusky galaxias population living above. This chapter will also evaluate the existing migration barriers used by the DOC, and explain the design and installation of the new perched migration barrier.

4.2 Methods and materials

Study location

In 1981, the Forest Research Institute built two hydrological research weirs in the upper Waipori River catchment to study water discharge differences between a native tussock tributary and an adjacent tributary that was to be planted in pines (Fahey & Watson 1991). The tributaries have nearly identically sized catchments and are typical of dusky galaxias habitat. The tributaries consist of first and second order streams around 1m in width, with alluvium and quartzo-feldpathic schist substrates (Campbell 2011). This chapter focuses on the native tussock tributary where the DOC chose to conduct electrofishing surveys and migration barrier trials. The DOC continues to monitor the kōaro and dusky galaxias populations in the tributary (Fig 4.1).

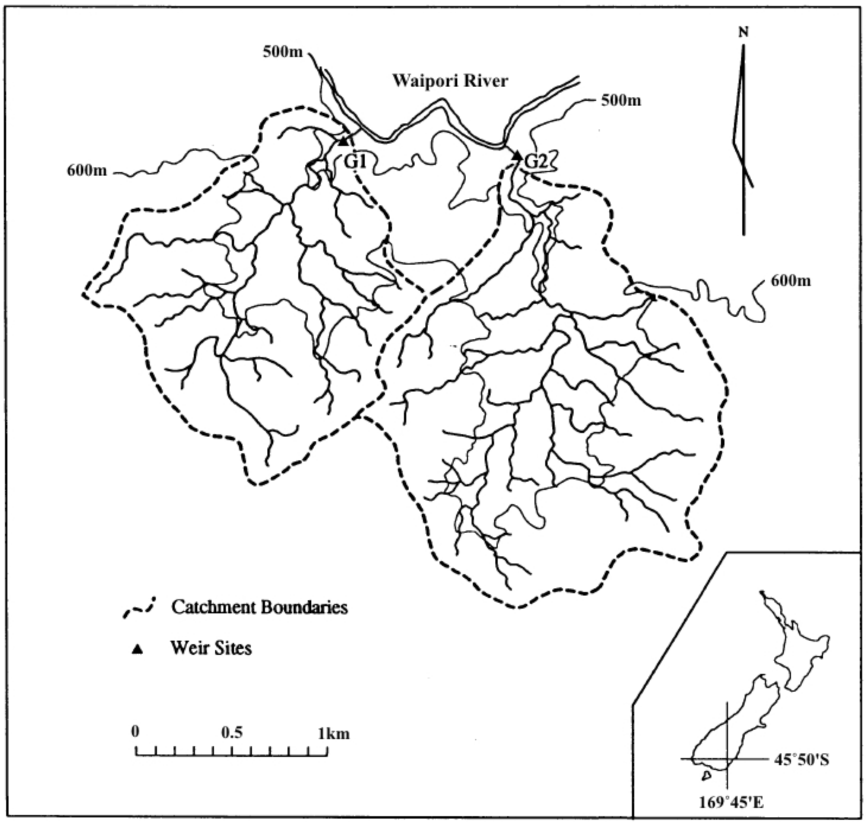

Fig. 4.1 A map that pictures the location of two research weirs (~480m above sea level) installed by the Forest Research Institute on two tributaries that drain into the Waipori River. The dusky galaxias population in tributary G1 is monitored by the DOC and is where migration barrier trials have occurred. The contour lines depict the elevations of typical dusky galaxias habitat. (Map adapted from Fahey and Watson 1991)

Perched migration barrier design

The new perched migration barrier (Fig 4.2) was custom made in three sections using 3mm thick aluminium sheets. The cost to have this migration barrier custom manufactured by Otago Sheetmetal and Engineering Ltd was $251.85 (including G.S.T). Each section of the migration barrier was formed into a perched lip and backing plate by longitudinally bending the 225mm wide aluminium sheets to form a 120 degree internal angle. The perched lip being 175mm wide and the backing plate 50mm high. The lip of each section was braced against the backing plate using triangular supports welded into place. The backing plate was drilled with ten evenly spaced 10mm holes for use when fixing to the concrete weir. The middle section was 3m in length with four evenly spaced braces; the two end braces being drilled with two holes each to act as flanges for joining the end sections. The left and right end sections had drilled braces acting as flanges to join flush with the middle section. The left and right sections equipped with end caps that were 175mm high and 175mm wide. Beyond the end cap the lip extends by 100mm. Overall length of the barrier when assembled was 5.5 metres.

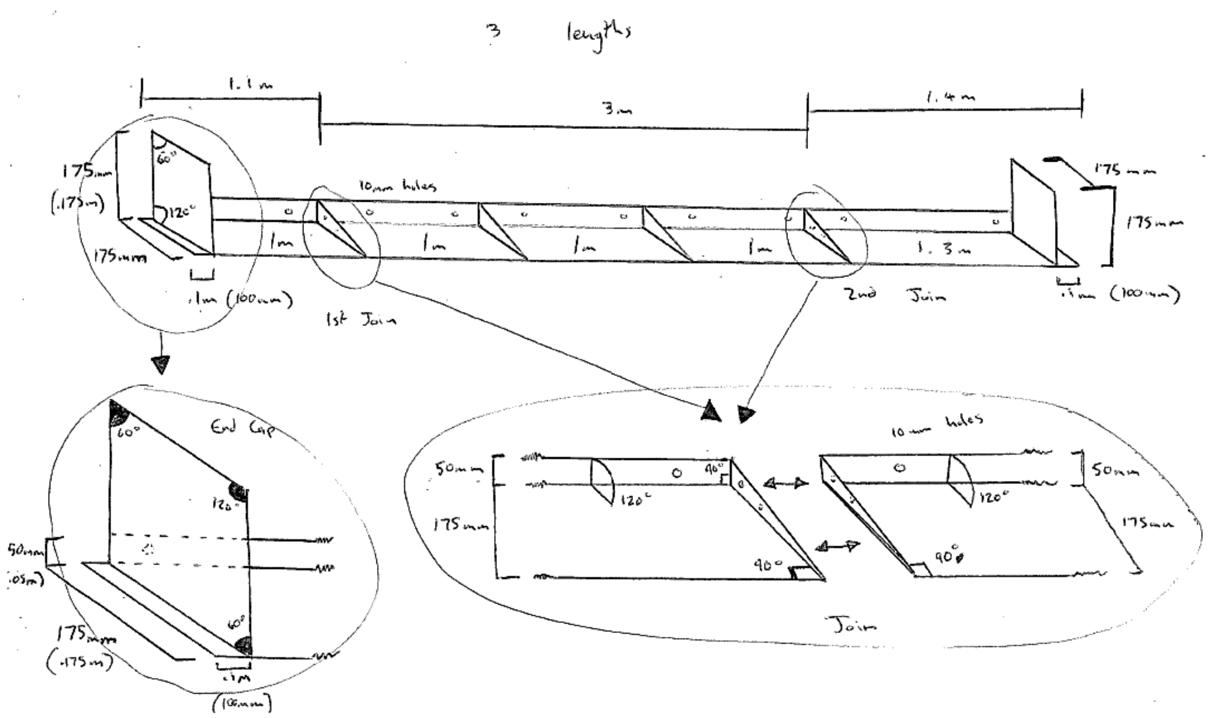

Fig. 4.2 Schematic drawing of the aluminium migration barrier and its dimensions.

Perched migration barrier installation

The new migration barrier was installed on the 22nd February 2013 (Fig 4.3). The three sections were transported to site and bolted together with aluminium bolts. A black bitumen based sealer called "Sika Blackseal – 1" was used between the joining flanges. The new barrier was placed as high as possible on the weir face without the water landing on the lip (approx. 600mm above the splash pad). The barrier was kept level along its length and was fixed to the weir using 10mm x 100mm galvanised "Ramset Dynabolts". The concrete weir face was drilled using a 10mm "Irwin" masonry bit. The barrier backing plate was sealed against the concrete weir using "Sika Blackseal – 1", except where the concrete was wet. A special two part epoxy designed for underwater application, called "Manus Bond Flex Weld 15" (purchased from Trademax in Dunedin), was used to seal behind and over the barrier backing plate where the concrete was wet. The barrier was monitored for two hours after installation then inspected one week later.

Fig. 4.3 A new perched migration barrier design to stop climbing juvenile kōaro (photo: Josh Tabak)

Electrofishing surveys and kōaro relocation

This chapter compares DOC permanent monitoring site (PMS) data (2005-2012) and relocation data (2002-2012) pre and post the new migration barrier installation in 2013. Four electrofishing surveys were completed post barrier installation in 2013 (2014-2017) during the month of February. The sampling method employed by the DOC included the use of a "Kainga EFM3000" backpack electrofishing machine, by an experienced operator, to sweep 3m lengths of stream bed upstream of a 2mm mesh screen net held submerged to collect fish (Campbell 2011). Sections of stream over 1.5m wide had both margins fished. The set PMS covered three 50m reaches that were all fished 2 to 4 times during annual sampling trips.

Sampling sites were considered to be properly fished when a pass of the reach returned at least 90% less fish than the first pass. Fish were collected during each pass and kept in buckets before being measured for length and weight. Dusky galaxias were returned to the PMS reach where they had been collected while kōaro were relocated to below the research weir. Further kōaro capture and relocation work was completed alongside PMS sampling over the first kilometre of the stream above the research weir. Kōaro equal to or less than 70mm in length were classed as juveniles (O'Connor & Koehn 1998) and a dusky galaxias juvenile is defined as being equal to or less than 55mm in length (Cadwallader 1975) for the purposes of this study.

Sub-adult dusky galaxias can be difficult to differentiate from kōaro to the untrained eye. The most reliable method of distinction is to undertake principal tail fin ray counts (McDowall 2000), but this is difficult in the field (Allibone & McDowall 1997). During the electrofishing surveys identification of dusky galaxias relied on experienced DOC staff familiar with the body shape, colouration and patterning unique to dusky galaxias (Allibone & McDowall 1997, McDowall 2000).

Electrofishing survey effort varied noticeably since surveys began, from as low as 68 minutes effort in 2010 to 525 minutes effort in 2011. The timing of electrofishing surveys also varied each year; with surveys taking place between the months September and May.

Data analysis methods

In order to make more informed conclusions about recruitment and population sizes, this study examined kōaro and dusky galaxias abundance counts, fish lengths, and electrofishing effort of fish surveys, pre and post the new migration barrier installation in 2013. To visually compare any changes in captured kōaro and dusky galaxias length, pre and post barrier installation, frequency histograms were first produced (Allibone & McDowall 1997). Linear models were then used for kōaro and dusky galaxias separately to examine captured fish lengths with year as a co-variate and the barrier installation in 2013 as the intervention (Quinn & Keough 2002). Generalised linear models (GLM) were then used to examine captured kōaro and dusky galaxias abundance counts separately, pre and post barrier installation, by comparing yearly captured fish counts while accounting for electrofishing effort (Hilbe 2011). Model selection and fitting was performed using program R (R Core Team 2019; https://www.R-project.org/). Negative Binomial GLM's were selected based on Akaike information criteria [AIC] (Burnham & Anderson 2004).

4.3 Results

By February 2017, no juvenile kōaro had been caught upstream of the new migration barrier post installation (Fig 4.4). This follows 15 years of successful juvenile kōaro navigation past the weir during which time the railway iron and stainless steel barriers previously installed by the DOC were fitted. Prior to the new migration barrier installation, 585 kōaro were measured and 340 dusky galaxias were measured. Since the new migration barrier was installed, 33 kōaro and 105 dusky galaxias have been caught upstream [by February 2017] (Fig 4.4).

Kōaro average size upstream of the barrier increased to 172mm in 2017 which is the largest average size since sampling began in 2002 (Fig 4.4). There has been a significant increase in the length of kōaro captured upstream since the new perched migration barrier was installed in 2013 ($P < 1e\text{-}3$). The smallest captured kōaro upstream, post new barrier installation, was 87mm, caught in 2016. Prior to the new barrier installation, the smallest kōaro captured upstream was 41mm in late January 2008; three other kōaro juveniles less than 50mm were also caught upstream during late January surveys pre 2013 (Fig 4.4).

Juvenile dusky galaxias have been caught upstream pre and post the new migration barrier installation (Fig 4.4), and there has been no significant change in dusky galaxias length post installation ($P = 0.133$). The average size of upstream captured dusky galaxias fluctuated yearly between 61 - 90mm (range of 29mm) pre the new migration barrier installation, and has reduced to 59 - and 69mm (range of 10mm) post installation. This difference was not statistically significant.

The GLM analyses show that there has been a significant reduction in the number of kōaro caught upstream per year post the new migration barrier installation ($P = 0.00132$), while no significant change in the number of dusky galaxias captured upstream per year was observed post installation ($P = 0.703$).

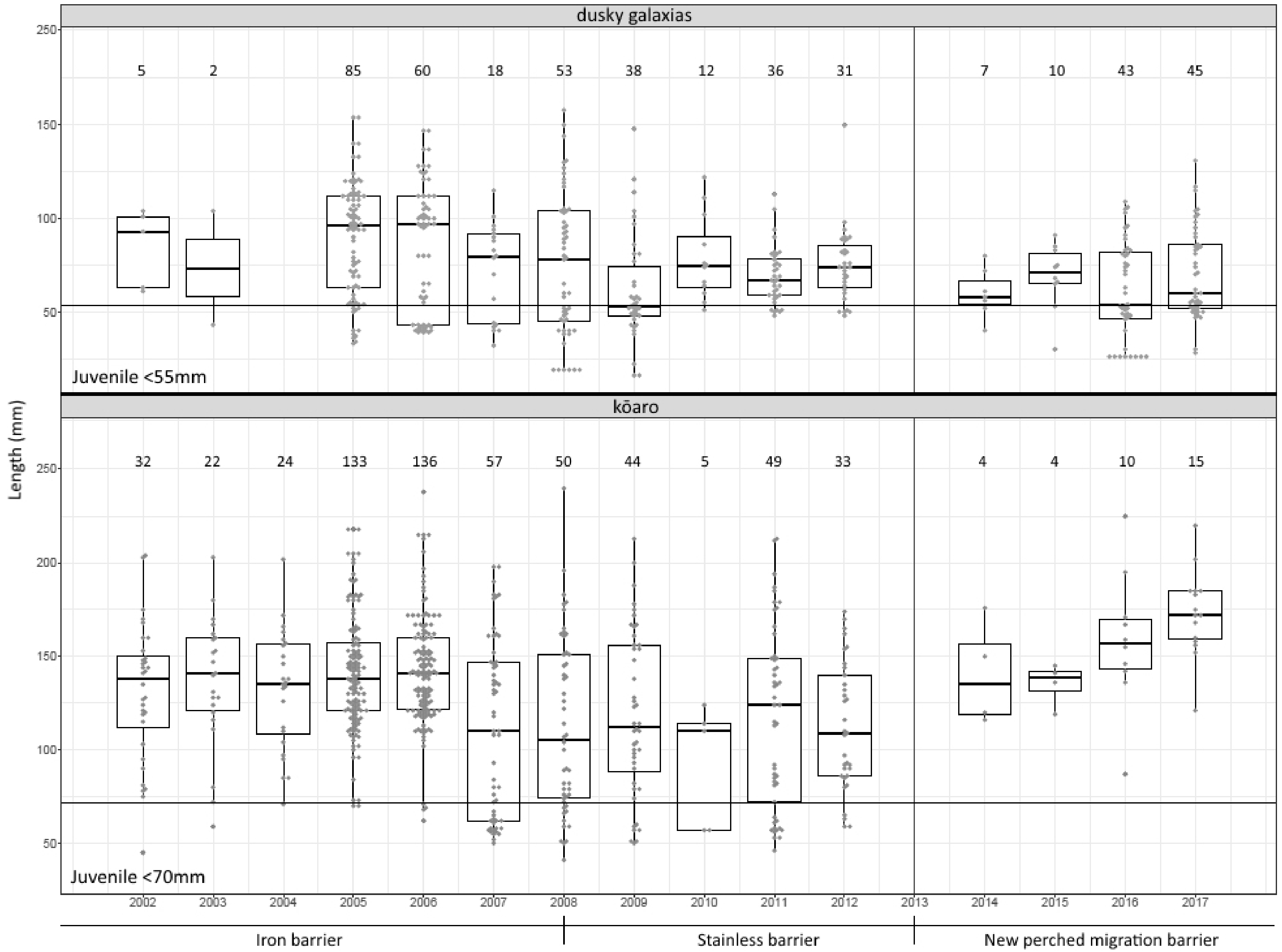

Fig. 4.4 Lengths (mm) and counts of dusky galaxias and kōaro captured upstream of a research weir, in a tributary of the Waipori River, fitted with two DOC migration barriers and the new perched migration barrier installed in 2013 (Data adapted from DOC: Dunedin office). The horizontal line through each plot represents the maximum juvenile length. Zero dusky galaxias were caught in 2004. Fish counts included for each species and year.

4.4 Discussion

As at 1st February 2017, no juvenile kōaro less than 70mm have been found upstream of the new migration barrier which suggests kōaro immigration past the weir has been halted. The new perched migration barrier design and its method of installation appear to be effective and its success strengthens speculation about the migratory kōaro and resident dusky galaxias populations above the barrier.

The capture rate of kōaro following installation of the new migration barrier has fallen to its lowest level since the DOC electrofishing and relocation programme began, with the average size of individuals increasing to its largest length (Fig 4.4). Similar results have been seen by Thompson and Rahel (1998) who used electrofishing to remove invasive brook char which significantly reduced their numbers over several years. The kōaro being caught above the barrier are probably larger residents that have evaded capture since electrofishing surveys began. It is expected that the average size of kōaro being caught upstream of the barrier will continue to increase each year as the population ages without recruitment.

The smallest kōaro caught in electrofishing surveys post the new barrier installation was 87mm; caught on the 2nd of May 2016. The age of this individual was unknown; however, sizes of immigrating juvenile kōaro prior to the new migration barrier trial and the growth rates of non-migratory galaxias suggest its presence upstream of the weir before barrier installation. Juvenile kōaro migration was observed in the focal tributary during the months of January and February with individuals less than 50mm long and as small as 41mm being recorded upstream (Department of Conservation unpublished data). Making assertions about landlocked kōaro growth rates is difficult as this information is unknown, but higher altitude streams often have reduced water temperatures (McDowall 2010) typically correlating with a decrease in stream productivity and growth rate (O'Connor & Koehn 1998; Jones & Closs 2016a). Low temperatures were apparent during electrofishing surveys, with January water temperatures averaging 10.95 degrees from 2008 – 2012 (Department of Conservation unpublished data). Dusky galaxias growth data from long term DOC fish recapture tagging, has shown juvenile dusky galaxias growth rates vary considerably in a proximate high altitude tributary (Ravenscroft et al. 2015), from as low as 3mm per year to 23mm per year (averaging 12.8mm). Considering the juvenile growth data of dusky galaxias, as a close genetic relative of kōaro (Waters et al. 2010), and noting the local stream temperatures and productivity, the 87mm long kōaro with 3 years of growth at 12.8mm per year, could have measured ~50mm in January or February 2013. This suggests it is most likely that this kōaro migrated above the weir just before the new migration barrier installation on the 22nd February 2013.

Laboratory experiments suggest it is extremely unlikely for kōaro to navigate past a perched barrier lip (Chapter Three). While inferring that the 87mm kōaro passed upstream before the new migration barrier installation, other means for its presence upstream of the weir should not be discounted. For instance, during its larval phase this individual may not have emigrated downstream of the weir. Larval kōaro are noted to remain close to the benthos when emigrating downstream (McDowall & Suren 1995) and Jones and Closs (2016b) also report that lowered water velocity in-stream provides refuges for larval non-migratory galaxiids. Because the hydrological weir dams the Waipori tributary, although undocumented, it may be possible that the larval kōaro reared within the pool immediately upstream of the weir structure.

Other possibilities are that the 87mm kōaro navigated through the weir itself or around the weir via overland flow. For example, a migration barrier trial by Thompson & Rahel (1998) found invasive trout were able to navigate upstream through artificial rock weir migration barriers, and Dunn and O'Brien (2006) have referenced several *Galaxias* species accessing interstitial spaces, suggesting juvenile kōaro may be able to navigate through interstitial spaces or cracks in migration barriers. The formation of interstitial spaces may have occurred where a rubber gasket seals a large steel plate over a water bypass at the foot of the concrete research weir. Banded kokopu have also been observed using wetted tree roots to navigate in-stream obstacles (David et al. 2009), and it may be possible that juvenile kōaro could use other vegetation forms to navigate past in-stream obstacles. Bowden et al. (2001) examined the same tributary as this study and noted rain readily flowed overland through moss blankets. Stream or overland flow through moss or vegetation during large rain events could provide connectivity for kōaro migration either side of the perched migration barrier. If further electrofishing surveys in the coming years confirm that juvenile kōaro are being found above the weir, these scenarios should be explored. It is also recommended migration barrier design take these into account.

The results indicate that dusky galaxias have maintained recruitment and their population size since the electrofishing programme began, with no significant increases in numbers or significant changes in size since the new migration barrier installation. Although the results cannot confirm an increase in survival rates of dusky recruits, an observed decrease in dusky galaxias average size suggests it is likely survival rates have increased to some extent post installation. It seems reasonable to accept that this is either a result of decreased predation by kōaro and/or a decrease in competitive exclusion (Allibone 1999). Certainly now that kōaro numbers are significantly reducing in the tributary upstream of the new migration barrier, the dusky galaxias population will likely expand and individuals will start occupying stream positions previously filled by kōaro.

Lessons from Chapter Two

A particular 'chain of events' enable migratory fish to negotiate natural migration barriers; artificial migration barriers must sever these links to be effective. The more links broken, the more robust the barrier. Artificial migration barriers designed to stop invasive fish migrations must be able to a) overcome the physical capabilities of the fish (Kilgore et al. 2010), b) overcome the fishes intrinsic drive and strategies to negotiate barriers (Kilgore et al. 2010) and c) successfully operate under all environmental conditions. As water is the physical medium that links stream networks, hydrological connectivity is generally the primary critical link that needs to be broken (Pringle 2003; Branco et al. 2011).

The climbing behaviour and morphology of kōaro allows them to utilise wetted margins (McDowall 2003) to navigate in-stream obstacles and realise hydrological connectivity. The large surface area to volume ratio of juvenile kōaro, with large pectoral and pelvic fins, exploits the surface tension forces of water on rough surfaces and allows them to propel themselves up obstacles with an anguilliform-like motion (Baker & Hicks 2003). Any wetted margin forming on the weir face must be severed in order to eliminate the surface tension and capillary adhesion of fish to the weir face being climbed. The use of a perched aluminium lip in laboratory trials was shown to stop juvenile kōaro from climbing over an experimental weir (Chapter Three).

Perched migration barrier design must be able to cope with environmental stresses and events. Streams not only provide downstream transport for fauna but also transport sediments, nutrients, and organic debris (Julius et al. 2005). Artificial barriers must not hinder these transport processes, nor should these processes affect the functioning of the barrier. This is necessary to ensure maintenance-free function of barriers and minimise the expense of maintaining them. Maintaining uninterrupted water flow, transport of vegetation, sediments and invertebrates is also necessary to ensure proper ecosystem functioning (Julius et al.

2005). Flooding is an issue which must be considered carefully (Rahel 2004) when designing a migration barrier. It is often during these times when mass transport of sediment and vegetation occur which can damage or bridge perched migration barriers. If a flood is large enough, it is possible the migration barrier could be drowned out, opening up stream margins which will once again allow upstream passage for fish such as kōaro. It may only take one event to reconnect the chain for invasive fish to overcome the migration barrier.

Within New Zealand's context, when designing a perched migration barrier to protect non-migratory galaxiids, it is necessary to consider how trout migration into these populations can be mitigated. The work by Jones and Closs (2016b) demonstrates the importance of excluding trout from non-migratory galaxiid habitats as trout quickly decimate headwater galaxias populations. One design feature is the inclusion of splash pads, which mitigate trout migration past barriers (Novinger & Rahel 2003). Concrete splash pads prevent the formation of plunge pools, which can provide enough resting and jumping space enabling trout to circumvent migration barriers (Thompson & Rahel 1998). However, splash pads generally create large splash zones, and therefore wetted margins for kōaro to climb, and must be factored into kōaro migration barrier design.

The Department of Conservation

The DOC office Dunedin has led efforts to conserve dusky galaxias populations through the use of migration barriers. Early prototypes had proven unsuccessful but paved the way for this field of research. The DOC Dunedin freshwater team who installed and monitored the stainless barrier ascertained that it did not completely sever hydrological connectivity. Examination of the stainless barrier and the weir showed that a wetted margin was still seen either side of the barrier, with water tracking along the top of the barrier and spilling down either side. The freshwater team also highlighted the significant costs with using stainless steel as a barrier and tools required to install a barrier in an isolated area.

A field inspection revealed another design oversight with the stainless barrier lip being supported from underneath with side support panels. This negated the perched lip effect, as water would track along the top and down the side support panels and weir face. Juvenile kōaro could climb the side supports and the weir face, and follow the wetted margin around the top of the barrier.

Fig. 4.5 The stainless steel migration barrier installed by the DOC in 2008 (photo: Josh Tabak)

The rigid stainless steel barrier also did not sit flush to the concrete weir because the weir itself was not square. A tough thick rubber gasket was installed to seal any gaps between the barrier and concrete weir, and a silicone based sealant was used around the perimeter. The silicone sealant appeared to have been used to glue, seal and block remaining gaps between the gasket and the concrete weir. However, in the five years since application, the silicone sealant had swelled, perished and disintegrated to leave small openings between the gasket and concrete weir. This could have provided passage for juvenile kōaro to bypass the barrier. The adhesion of the silicone sealant and/or running water may have also contributed to the erosion of concrete observed behind the barrier as exposed aggregate was visible.

The thick rubber gasket also provided a flat level resting spot for juvenile kōaro which would have helped their metabolic recovery (Weinstein & Full 2000; Allen & Westerblad 2001) during the climb. This resting spot would also have "caught" juvenile kōaro that dislodged during climbing attempts to navigate the weir v notch which would have increased the likelihood of climbing success (Weinstein & Full 1998 - 1999; Edwards & Gleeson 2001).

Perched migration barrier

The new perched migration barrier final design was the culmination of previous barrier trials, the literature and problem solving. The lip depth and internal angle, between the backing plate and the perched lip, was chosen for three reasons. Firstly a downward angle helps shed water, limiting how far water can track either side of the barrier. Secondly the smaller the depth of the lip, the less leverage that is placed upon that lip by water, sediment or debris. This would lessen the chance of weakening the attachment of the barrier to the weir. Thirdly, a greater internal lip angle would increase the depth of the lip needed to ensure the perched end still remained some distance from the weir face. The new barrier was designed to be as wide a perched lip as possible on the weir face. The braces were placed on the top of the lip to ensure a flat underside was presented to climbing juvenile kōaro beneath; this was to ensure no structures were present that may help juvenile kōaro rest or navigate around the lip. Large end caps were predicted to stop water tracking outwards and would be useful at disrupting the wetted margin during high flows when splash zone size increases.

Ramset Dynabolts were used to attach the barrier backing plate to the weir face. As the barrier was retrofitted to the weir face, battery powered drills and Dynabolts were considered the best option to solidly secure the barrier. Dynabolts are a tried and tested means of fastening materials to concrete surfaces. The bitumen sealer was used only on dry concrete to seal the top and joints of the barrier. As the weir faces north, and bitumen stays flexible, it would move with the barrier as it expands and contracts with the sun and heat. Bitumen sealer also has extremely good adhesive properties and does not perish in the sun. A two part epoxy sealant specifically designed for application underwater was used where the concrete was wet. It adhered to the weir and barrier well and was applied generously. The epoxy was suggested to stop water eroding the concrete from behind the barrier attachment, potentially opening up new passages for juvenile kōaro.

Aluminium was chosen as the construction material for the new perched migration barrier for several reasons. Firstly it is lightweight, allowing for ease of transport and installation in the field. Secondly it is strong and highly corrosion resistant, so will last in the field for decades without needing to be replaced. Thirdly it is cheaper to buy than stainless steel, which minimises cost for multiple barriers and if the barrier is damaged and needs replacement or repair. The use of 3mm aluminium sheet was decided as it is very rigid while still maintaining a thin edge.

Like many rare non-migratory fish populations, the dusky galaxias population is in a very remote location; conservation efforts carried out in the stream requires a great dedication of time and resources. Any artificial migration barrier installed in the field must function year round without the need for routine maintenance. Overall maintenance of the new barrier was considered and as a feature requires minimal attention. It is still recommended that prior to the main kōaro migration in spring, a check of the barrier is made to ensure it is functioning correctly ensuring no mass kōaro migration into the tributary.

Conservation outcomes

Novinger and Rahel (2003) suggest that while isolation management holds short term benefits by stopping invasive threats to a species, the need to sustain or enhance gene flow between isolated populations is critical to long term conservation. Using the dusky galaxias as an example, the current fragmented populations are at risk from inbreeding depression and potential genetic bottlenecks which may lead to population collapses (Jones & Closs 2016b) if not reconnected. However, because dusky galaxias are slow growing, long lived and have limited self-dispersal ability as a function of their life history, this makes genetic dispersal and self-recolonisation of habitat unlikely (Jones & Closs 2016b), and may call for conservation interventions. Allibone and McDowall (1997) suggested translocation of dusky galaxias to increase overall population security, and this approach may prove an efficient way to improve genetic exchange.

While translocation of dusky galaxias individuals for the species' genetic maintenance would be beneficial, it does not go without risks. Allibone and McDowall (1997) acknowledged that translocation, particularly to re-establish very small populations or historical habitat, would require significant numbers of dusky galaxias to be translocated. This would need to reoccur over successive years and as such may place current populations at risk of depletion or collapse (Allibone & McDowall 1997). However, reinforcing current dusky galaxias populations *in situ*, by increasing downstream habitat through perched migration barrier installation and kōaro and trout removal, would increase the likelihood that these populations could withstand removal for establishing new populations. The dusky galaxiid tributary in this study, for example, is now on its way to become a true stronghold and source population for future translocation efforts.

Fig. 4.6 Modified waterfall in Burnt Creek, Otago, NZ (photo: Daniel Jack)

Burnt Creek is another upper Waipori River tributary with the same potential to offer a dusky galaxias donor stronghold population (Allibone & McDowall 1997). It has one of the largest known populations of dusky galaxias, confirmed by DOC electrofishing surveys (Ravenscroft et al. 2015). An 11 metre waterfall in the creek midsection stops trout and kōaro invasion into the headwaters; however, the lower section has several significant waterfalls which do not impede trout or kōaro recruitment. Electrofishing surveys reveal few dusky galaxias remain in the bottom section compared with the mid and upper sections (Ravenscroft et al. 2015). Placement of a perched migration barrier on one of the modified waterfalls in the lower section of Burnt Creek, could allow dusky galaxias colonisation downstream (Fig 4.9). This is supported by the work of Lintermans (2000) who found mountain galaxias (*Galaxias olidus*) was able to recolonise downstream habitats after the removal of trout above an enhanced trout barrier which was also shown to stop trout re-invading. Jones and Closs (2016b) note that larval dusky galaxias are capable of surviving dispersal downstream over large waterfalls.

Threatened stronghold and source populations of non-migratory galaxias could be safeguarded against kōaro invasion using the redesigned perched migration barrier. The lowland longjaw galaxias (*Galaxias cobitinis*) and bignose galaxias (*Galaxias macronasus*) of Fraser Spring near Twizel are examples of non-migratory galaxias populations that may benefit from kōaro exclusion (S Bowie 2017 pers. comms; unreferenced). Fitted to manmade or natural in-stream structures which take advantage of height, the new perched migration barrier could be a passive conservation tool that stops kōaro immigration and allows kōaro populations to naturally decline upstream. The new barrier used in conjunction with electrofishing relocation or other fish removal techniques could provide a faster means to protect at-risk galaxias populations. Perched migration barriers may also be used to rehabilitate historical habitats for the reintroduction of non-migratory galaxiids (Allibone & McDowall 1997).

Conclusions

The kōaro is a diadromous native galaxiid species (McDowall 1998) capable of forming self-sustaining landlocked populations in large freshwater bodies. Kōaro can be considered invasive when river impoundments provide larval habitat and allow juvenile dispersal outside of their otherwise normal range (Allibone 1999). Non-migratory galaxiid populations, such as those of the dusky galaxias, are affected by kōaro invasion through predation and/or competitive exclusion (Allibone 1999) and have suffered range contractions as a result. Isolation from the continuing kōaro invasion will secure a promising future for dusky galaxias populations.

Early migration barrier trials by the DOC identified key aspects of kōaro exclusion and improvements to migration barrier design which have paved the way for further research. Careful consideration must be given to perched migration barrier design and installation in order to overcome the migratory adaptations and behaviours of kōaro in all environmental conditions. After more than a decade of kōaro relocation effort and four years trialling the new perched migration barrier, results from electrofishing surveys indicate a reduction in kōaro numbers caught above the barrier and an increase in the size of captured kōaro post installation. It seems the perched migration barrier can limit kōaro recruitment completely, and if the incursion of any juvenile kōaro should occur in future, other strategies to restore the barrier should be investigated. The mitigation of kōaro recruitment and on-going kōaro relocation work will keep reducing the predation and/or competitive exclusion (Allibone 1999) burden on this dusky galaxias population.

Perched migration barriers to limit kōaro invasion can now be considered a valuable conservation tool for freshwater fish managers. The perched migration barrier design in this study could be adapted for installation in other streams, on man-made or even natural rock features. The use of a perched migration barrier has many benefits for protecting non-migratory galaxias populations and other threatened and at risk native fish species throughout New Zealand and more broadly wherever koaro occur (e.g. Australia (O'Connor & Koehn 1998)). Used at key sites, perched migration barrier installation, even without invasive migratory fish removal upstream, would begin the passive process of reclaiming stream habitat for fish species at risk of extirpation.

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CHAPTER FIVE

General Discussion

Perched road culverts are found extensively throughout New Zealand and negatively affect New Zealand's native freshwater fish fauna (Boubée et al. 1999). Perched culverts disrupt in-stream connectivity which prevents fish migration, thus fragmenting fish populations and restructuring native fish communities (Stevenson & Baker 2009). In the eastern Otago region, little targeted information on the prevalence of perched culverts and associated impacts on freshwater fish populations had been available to conservation managers (Allibone et al. 2010) up until now.

Survey results from this study revealed perched pipe culvert prevalence within exotic forestry plantations of the eastern Otago region was about fifty percent in 2013. This finding is consistent nationally (Barnes 2004; James & Joy 2008) and suggests many fish communities have likely been impacted and restructured by perched culvert migration barriers (Boubée et al. 1999). Modelling results revealed fish abundance and species richness certainly were lower above pipe culverts than below, and although statistically inconclusive, but with the support of international evidence and research from within New Zealand, that perched pipe culverts are greater migration barriers for some New Zealand fish species.

One constraint of the fish survey methodology was it failed to allow for age structure identification within fish communities observed. However, Barnes (2004) found that large galaxiids dominated above a perched culvert as recruitment had been compromised. The perching of the culvert and the halting of recruitment poses a significant problem for the continuation of that galaxiid population upstream, with the potential for emigration and deaths to outweigh immigration (see Nislow et al. 2011). This would eventually lead to the loss of those mature breeding fish over time from viable habitat (Wofford et al. 2005). Galaxiids can live for long periods of time. For example, aging studies suggest Banded kokopu can live up to 15 years (West et al. 2005). As such, the effects of poor road culvert installation or the perching of a pipe culvert may not be fully realised for some time until an aging breeding population collapses. Careful attention must furthermore be paid to the presence of juvenile fish species to confirm viable recruitment through. New road culverts must also be designed and installed so as not to become perched in the future.

Contributing to the impact of pipe culvert perching on fish migration in exotic forestry plantations in New Zealand had been a lack of nationally consistent guidelines regulating pipe culvert installation with respect to providing for fish passage (Pendly 2015). Pendly (2015) established that significant inconsistencies existed between permitted activity rules and best management practices implemented by regional councils which suggested that streams and fish populations were subjected to differing environmental impacts in exotic forestry plantations across New Zealand. While the Otago region had published guidelines for fish-friendly culvert installation (Pendly 2015), given the age of some forestry plantation road networks, it is perhaps not surprising that over fifty percent of pipe culverts were perched. However, moving forward, new national environmental standards[1] were introduced to guide exotic forestry plantation managers when maintaining pipe culverts or installing road crossings. It is expected therefore that the percentage of perched pipe culverts in these catchments will, in time, drop as they are replaced or remediated with fish-passage-friendly designs. Ensuring fish passage in existing and new exotic forestry plantations through appropriate culvert installation will undoubtedly benefit local fish communities by increasing and ensuring access to historic habitat in those catchments.

The national environmental standards for plantation forestry regulations (see footnote) are a positive step toward ensuring fish passage in exotic forestry plantations. However, given reporting requirements and the detrimental effects of perched pipe culverts on fish passage, discretion ultimately falls on forestry managers to install and remediate pipe culverts and road stream crossings correctly. Regional councils must in that case ensure monitoring and the maintenance of fish passage to truly benefit the protection of fish communities in exotic forestry plantations. This will also serve to provide assurance to conservation managers that fish species can maintain healthy populations and communities in exotic forestry plantations.

The presence of perched culverts within exotic forestry plantations has been identified as one of the contributing factors which are threatening galaxiid populations in New Zealand (Allibone 2000; Hanchet 1990; Joy 2009; Rowe et al. 1999, Rowe et al. 2000). For example, the endangered dusky galaxias (*Galaxias pullus*) had 65% of its habitat and distribution

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[1] Which define road crossings “that provide for fish passage by maintaining river bed material in any structure that would be in place of the river bed” as permitted activities. Section 40(2) – Resource Management (National Environmental Standards for Plantation Forestry) Regulations 2017.

overlapping with exotic forestry plantation boundaries and perched culverts were identified as a significant dispersal problem (Allibone & McDowall 1997). However, while logging operations and road crossing installations in exotic forestry plantations are identified as a threat to dusky galaxias, it was proposed that exotic forestry plantations could also provide areas of refuge for the species (Allibone & McDowall 1997). Strategic perched pipe culvert installation used for invasive kōaro and salmonid restriction was suggested as a means to facilitate dusky galaxias population recovery and cement their survival in critical stream habitats (Allibone & McDowall 1997). This study, building on previous experience and knowledge (Ravenscroft et al. 2015), has since confirmed the use of a perched migration barrier as being extremely effective in excluding kōaro from dusky galaxias populations. Therefore the combination of exotic forestry perched culvert remediation, the use of perched migration barriers, and the removal of salmonids and kōaro could see strategic sites become recolonised by dusky galaxiids both naturally or through translocation (Allibone & McDowall 1997).

McDowall & Allibone (1994) first expressed the idea that a perched culvert could provide a means of kōaro exclusion. Having demonstrated their effectiveness within the short-medium term, expanding the use of perched barriers as a conservation tool could also help protect key non-migratory galaxiid core refuges and historical stream habitat. Strategic placement of perched migration barriers would help to expand source populations and reverse the downward trajectory of threatened non-migratory galaxiids toward extinction (Allibone et al. 2010). Similar strategies could also be implemented where other New Zealand fish populations are identified as under threat from kōaro and salmonid encroachment (Bowie et al. 2018).

Climbing Success and Migration Barriers

Before the construction of Lake Mahinerangi it was considered likely that sparse populations of kōaro lived in the upper Waipori River, although this cannot be confirmed (McDowall & Allibone 1994). However, evidence to support their existence in the upper Waipori River does exist in that kōaro are significant diadromous migrants that are capable of migrating tens of kilometres inland, as seen in large river systems such as the Buller and Grey Rivers (Hicks 2012). Tributaries of the Taieri River, another large river system, which happen to be home to non-migratory galaxiids (McDowall 2010), also hold small numbers of kōaro which are recorded rarely and intermittently, it is said, at the very upper limits of their distribution in these headwater reaches (McDowall & Allibone 1994). While providing evidence that diadromous kōaro likely would have accessed the upper Waipori River, these examples further highlight that a complex relationship exists between migratory distances, river system characteristics, migration barriers and kōaro migratory adaptations, as seen by the limits of dispersal in diadromous and landlocked kōaro populations. The dynamics of this relationship even more complex when considering allometric growth and the time and place migration barriers are encountered as juveniles or in the right circumstances where river system characteristics allow upstream migration of adults.

The findings of this study certainly suggest a relationship exists between climbing ability and juvenile kōaro body shape, with some individuals better equipped to climb wetted margins and navigate in-stream obstacles than others. The climbing ability of juvenile kōaro is also likely to change as a factor of allometric growth over time, with a decrease in surface area to volume ratio and the ability to climb steep gradients as weight overcomes the forces of surface tension that aids juvenile kōaro adherence to wet surfaces. A similar relationship between individual migratory success and body shape is observed in the gobiid species of Hawaii (Blob et al. 2006). Intraspecific variation and allometric growth has been found to regulate the dispersal of individuals during upstream migration (Blob et al. 2008; Maie et al. 2007). This intraspecific variation between gobiid individuals and the likelihood of climbing success is also influenced by intraspecific behaviour, adding another layer of dynamism that defines the climbing performance of individuals and their dispersal (Blob et al. 2006). When applied to juvenile kōaro, allometric growth and intraspecific variations in body shape and behaviours are therefore likely to limit the migratory distances and distribution of individuals within stream networks and would likely account for kōaro distribution patterns [prior to the introduction of trout (Townsend & Crowl 1991)].

When examining kōaro migration in light of intraspecific variation in migratory ability, inferences can be made as to the interactions individuals may have with migration barriers and how this may impact kōaro distribution. For example, juvenile kōaro with more efficient body shapes for climbing are better able to navigate larger in-stream obstacles than less efficient climbers, allowing them to penetrate further upstream in time into headwater reaches before allometric growth limited their climbing efficiency (Blob et al. 2006). This may be reflected with measurable differences in juvenile kōaro body shape over elevational distributions, and where larger in-stream obstacles can be navigated past or higher elevations attained when in closer proximity, in terms of distance and time, to larval rearing sites when kōaro body size is most climbing proficient. However such a relationship has not yet been identified and could be explored. Evidence of an elevational/migratory distance relationship would also help to confirm that only sparse numbers of kōaro likely occupied the upper Waipori catchment prior to the formation of Lake Mahinerangi (McDowall & Allibone 1994).

Sparse numbers of kōaro in the upper Waipori catchment would suggest that low rates of habitat overlap existed between kōaro and those non-migratory galaxiids, as seen in the upper Taieri catchment (McDowall & Allibone 1994). This lends weight to the accepted theory that kōaro numbers have increased in the upper Waipori catchment placing dusky galaxias, for example, under greater competitive or predatory pressure since the building of the Lake Mahinerangi Dam. The fact populations of dusky galaxias have survived in the wake of increased kōaro numbers for the last 100 years is surely an indication that dusky galaxias were able to or had coexisted alongside some level of kōaro presence prior to kōaro insurgence. This perhaps indicates a level of in-stream niche difference between kōaro and dusky galaxias and that kōaro are not completely dominant over their non-migratory dusky galaxias cousins (McDowall 2010).

Genetic work by Waters et al. (2010) has recently revealed that a single loss of diadromy in a common ancestor of the kōaro, has led to the possible vicariant speciation of the non-migratory *Galaxias vulgaris* complex (including the dusky galaxias) since. However, this is an area McDowall (2010) stated needs further clarification, as how the biogeography of non-migratory galaxiids in the region came to be is highly complex. While the cause for this loss of diadromy and speciation within the *Galaxias vulgaris* complex is yet unknown, it seems highly likely that geological processes have played a major role (McDowall 2010). As interactions between diadromous galaxiid migration and episodic geological events are explicitly linked as a function of their life history (Waters & Wallis 2000), it seems likely that newly created migration barriers arising from these events would have been faced by migrating individuals (Ingram & Bennington 2018). Blob et al. (2006) suggests intraspecific variation in climbing ability might play an important role in determining not only dispersal along stream continuums, but which individuals will breed together along that stream continuum. Could intraspecific differences in juvenile morphology and climbing ability, in response to a geological event, such as a sudden uplift or a landslide, have played a role in the evolutionary history of the kōaro and the *Galaxias vulgaris* complex?

Jones and Closs (2016) have shown that larvae of the different species within the *Galaxias vulgaris* complex generally maintain interspecific variation in morphology during development and have varying levels of swimming ability, with the higher headwater species being larger post-hatch. Although little information is available for post-larvae of these species, given the findings for juvenile kōaro, testing the morphological and behavioural adaptations of juvenile non-migratory galaxiids of the *Galaxias vulgaris* complex may also highlight differences in interspecific and intraspecific climbing abilities and behaviour. The work of Ingram and Bennington (2018) has shown a weak but parallel divergence for kōaro in adjacent but differing habitats in the South Island, New Zealand. So it appears possible that intraspecific differences in climbing ability and/or behaviour could differ in their response to geological processes and may have played a role alongside vicariant speciation in the *Galaxias vulgaris* complex (McDowall 2010).

Supposition aside, one certainty is that migration barriers do impart selective pressures on New Zealand's diadromous freshwater fish populations which can ultimately shape fish abundance and distribution through stream networks. Over the past century, since the installation of vast road networks with poorly installed pipe culverts, the abundance and distribution of New Zealand's native fish communities have suffered significantly with vast losses in historic habitat. However, given the research, new understanding, new legislation and new developments regarding fish-passage-friendly road crossings and culvert installations, the future for re-establishing historic fish habitats and populations looks promising. Considering that restoration and maintenance of fish passage is increasingly expected, and given the important work of others, and the findings of this study, that attention can shift away from proving the negative effects of poor culvert installation into facilitating fish-passage-friendly culvert and road crossing installation or remediation. To contribute to this growing body of research, efforts in the future to further understand New Zealand native fish migratory ability and adaptations will help guide the development of novel fish passage structures. Efforts should also prioritise the remediation or implementation of fish passage barriers to secure vulnerable and endangered fish species' populations in the short term, prior to examining fish species and populations of lower conservation concern.

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