

Learning the ropes: mussel spat ropes improve fish and shrimp passage through culverts

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Summary

1. Culvert pipes are regularly used around the world for conveying stream flows underground, through embankments or under road crossings. Installation of these features can have significant negative effects on the passage of freshwater biota and potentially exclude many species from large areas of river networks.

2. We investigated the installation of mussel spat ropes as a potentially rapid and cost-effective tool for improving passage of freshwater biota through culvert pipes where internal barrel conditions impede passage. We assessed passage success for two fish species, juvenile rainbow trout *Oncorhynchus mykiss* (Walbaum 1972) and adult inanga *Galaxias maculatus* (Jenyns 1842), and one migratory shrimp, *Paratya curvirostris* (Heller 1862), through culverts of differing length (3 and 6 m), slope (1.5 and 3°) and flow (0.24 and 0.75 L s⁻¹). We hypothesized that ropes would enhance the passage success of these three species, but success rates would differ between species and trial combinations.

3. Ropes resulted in a reduced water velocity within culvert barrels and significantly improved passage success for all three species. Shrimp benefited most by the presence of ropes, being unable to negotiate any of the pipe combinations in their absence, but exhibiting varying rates of success across all combinations with their presence. Both *G. maculatus* and *O. mykiss* were able to negotiate some of the non-rope pipe combinations, but as the level of difficulty increased, successful passage was only achieved with the ropes present.

4. *Synthesis and applications.* We conclude that this relatively inexpensive and easy-to-install tool has the potential to substantially improve passage for a range of aquatic biota through various culvert scenarios. We consider that ropes would be particularly useful in situations where internal culvert access is difficult and where various culvert parameters (slope, flow, length) result in internal barrel hydraulics that would normally limit or exclude passage of aquatic biota.

Key-words: diadromy, fish passage, *Galaxias maculatus*, inanga, *Oncorhynchus mykiss*, *Paratya curvirostris*, rainbow trout, remediation, retrofit, velocity barrier

Introduction

Global biodiversity is currently declining at rates unprecedented in human history (Butchart *et al.* 2010), and freshwater systems in particular appear to be under greater threat than their terrestrial and marine counterparts

(Dudgeon *et al.* 2006; Strayer & Dudgeon 2010). There are many human causes that have led to these declines including various forms of land-use change and habitat degradation (Harding *et al.* 1998; Allan 2004), introduction of invasive species (Olden *et al.* 2004; McDowall 2006) and declines in water quality resulting from the excess nutrients (e.g. Hautier, Niklaus & Hector 2009) and contaminants (e.g. Driscoll *et al.* 2007).

Another major cause of biodiversity decline, and arguably one which may be easier to address on shorter time-scales, is human-mediated disruption of riverscape connectivity. In particular, the installation of physical

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barriers has, in many cases, negatively impacted on the movement of freshwater organisms in both upstream and downstream directions (March *et al.* 2003; Nilsson *et al.* 2005; Liermann *et al.* 2012). In recognition of this world-wide problem, a substantial amount of research has been undertaken on the issue, particularly over the last two decades (Fullerton *et al.* 2010). Despite attempts to improve river connectivity, and a greater general awareness of its importance, human-mediated disruption of river networks seemingly continues at a much greater rate than its remediation (Nilsson *et al.* 2005; Strayer & Dudgeon 2010), while efforts to improve or reinstate fish passage globally have rarely resulted in passage success commensurate with the situation prior to barrier installation (Schilt 2007; Williams 2008).

In rural and urban environments throughout the world, one of the most commonly installed features for conveying water either through embankments or under roads is the culvert pipe, which can have significant deleterious impacts on fish populations (Gibson, Haedrich & Wernerheim 2005; Franklin & Bartels 2010). Although culvert dimensions and material composition may vary and thus affect different species in different ways (Bouska & Paukert 2010), in most cases, their internal structure is purposely smooth (excluding corrugated versions) for improved hydraulic efficiency. As a result of concentrating and conveying flows through a pipe, two common issues typically arise for freshwater biota seeking egress: the first is the potential for culvert 'perching' that occurs as a result of erosion of the bed downstream of the pipe, which effectively suspends the pipe in mid-air (Doehring, Young & McIntosh 2011; David & Hamer 2012), and the second is the potential for a hydraulic barrier to be created resulting from the conveyance of homogenous, high velocity, laminar flows (Macdonald & Davies 2007; Franklin & Bartels 2010; Tonkin, Wright & David 2012). Either or both of these issues may constrain passage for any given culvert, although the degree to which passage is impaired also depends on a range of other factors including culvert installation depth, length, gradient, shape and internal barrel velocity (Ead, Rajaratnam & Katopodis 2002; Bouska & Paukert 2010). Additionally, passage success may vary for a given combination of factors depending on the locomotive abilities of different aquatic species and life stages and in some cases may even favour the spread of invasive over indigenous species (Rahel 2007; Foster & Keller 2011).

To address some of these recognized variables, a range of retrofit options to enable passage through culvert pipes have been developed. These typically include baffle-type structures arranged and designed in different ways (Ead, Rajaratnam & Katopodis 2002; Macdonald & Davies 2007; Feurich, Boubee & Olsen 2012), which are primarily designed to create flow heterogeneity and resting points for aquatic biota on their journey upstream or downstream. Such features can be expensive, however, particularly for

long pipes, and sufficient culvert capacity needs to exist to minimize the potential for upstream flooding.

A recent simplistic and cost-effective approach for addressing passage through culverts has been the installation of mussel spat ropes through pipes (David, Hamer & Collier 2009; David & Hamer 2012). Although ropes in these investigations were primarily used to improve passage success for 'climbing' fish species past 'perched' culverts, it was concluded that substantial potential exists to investigate their effectiveness for improving passage of other species through long, non-perched culverts via the disruption of laminar pipe flows (David & Hamer 2012). Accordingly, a recent small-scale laboratory trial highlighted their applicability for assisting passage of a small benthic fish species through otherwise impassable velocity barriers (Tonkin, Wright & David 2012).

Extending this work, in the present study, we assessed passage performance for two 'swimming' fish species and one migratory shrimp through culverts with and without ropes set at various, realistic combinations of length, gradient and flow. Combinations were designed to provide a grade of passage difficulty to clearly establish the utility of ropes for improving (or otherwise) passage success. In this investigation, we hypothesized that for a given combination of length, flow and slope that (i) ropes would enable passage success where culverts would otherwise be impassable or significantly improve passage success where some passage can be made in their absence, and (ii) success rates of the three species would differ at varying set-up combinations due to species-specific locomotive capabilities and behaviour.

Materials and methods

FISH AND CRUSTACEAN COLLECTION

We sourced *Galaxias maculatus* (Jenyns 1842; inanga; fork length [FL]: 41–129 mm) and *Paratya curvirostris* (Heller 1862; orbit-carapace length: 1.56–9.15 mm) from tributaries of the Raglan Harbour, North Island, New Zealand, between 15 June and 5 July, 2012. Both species were collected using Gee minnow traps (3-mm mesh) or a wide-mouth whitebait net (3-mm mesh, 1060 × 390 mm). Captured fish and shrimp were removed immediately and emptied into separate 20-L buckets fitted with battery operated aerators for transport to the Bay of Plenty aquaculture centre in Tauranga, east coast, North Island. Juvenile *Oncorhynchus mykiss* (Walbaum 1972; FL: 34–109 mm) were sourced from the Department of Conservation (Turangi hatchery wild stock, central North Island, New Zealand) and were transferred to the same locality in a fish transport trailer. Transport of all organisms from capture to destination occurred within 3 h.

Once at the facility, all fish and crustaceans were kept for at least 24 h before being used in trials. Fish were kept in aerated 900-L holding tanks prior to trials, and *P. curvirostris*, in aerated 50-L fish bins. *Galaxias maculatus* were fed once at the end of each day, and *O. mykiss*, three times per day, but never within two hours before a trial run. *P. curvirostris* were only kept for short periods (approximately 2–3 days) and in water with high

levels of organic matter for nourishment. All subjects were kept in water that was within 3 °C of temperatures experienced during trials.

EXPERIMENTAL SET-UP

To assess the effectiveness of mussel spat rope at assisting the two fish species through culverts at various physical settings, we conducted the trial in a four-way full factorial set-up with the following factors: mussel rope (presence/absence), flow (high/low), pipe length (short/long) and slope (low/high). The shrimp *P. curvirostris* was only examined at the two high flow settings (high flow × high/low slope) due to difficulties in capturing sufficient subjects to run all trial combinations without their reuse. A three-way factorial design was thus employed with an assumption that the high flow settings were more challenging to this species for passage than low flow settings.

Trials were run in the laboratory using four individual lengths of 350-mm-diameter PVC culvert pipe (FARMTUFF™; iPlex Pipelines, New Zealand). These were set up in two pairs of 3 and

6 m length, which were each on a closed recirculating system driven by an individual 240-v Onga Pump (Model 413; Pentair Water New Zealand Ltd., Auckland, New Zealand). Each pipe passed between a top and bottom 50-L chamber (625 × 440 × 265 mm) and had a flexible canvas join approximately 500 mm from each end of the pipe to allow for changes in slope (Fig. 1). Each pair had its own 600-L sump from which water was drawn and delivered to each of the individual top chambers associated with each pipe. Once the water had passed through the pipe and into the bottom chambers, it drained directly through a 50-mm drainage outlet into the same sump from which it originated.

The two slopes employed were 1.5° and 3° as these are considered to be within the range of average slopes typically represented by culverts installed in the field (Kelly & Collier 2006). The two flows applied were 0.24 (±0.003) and 0.75 (±0.02) L s⁻¹. We ensured that flow did not differ between the same flow treatments in either the low (one-way ANOVA: $F_{3,24} = 1.41$, $P = 0.27$) or high (one-way ANOVA: $F_{3,24} = 0.47$, $P = 0.7$) flow treatments. We also assessed the velocity at each of the flow and slope settings and with or without rope by measuring the time taken for dye to pass

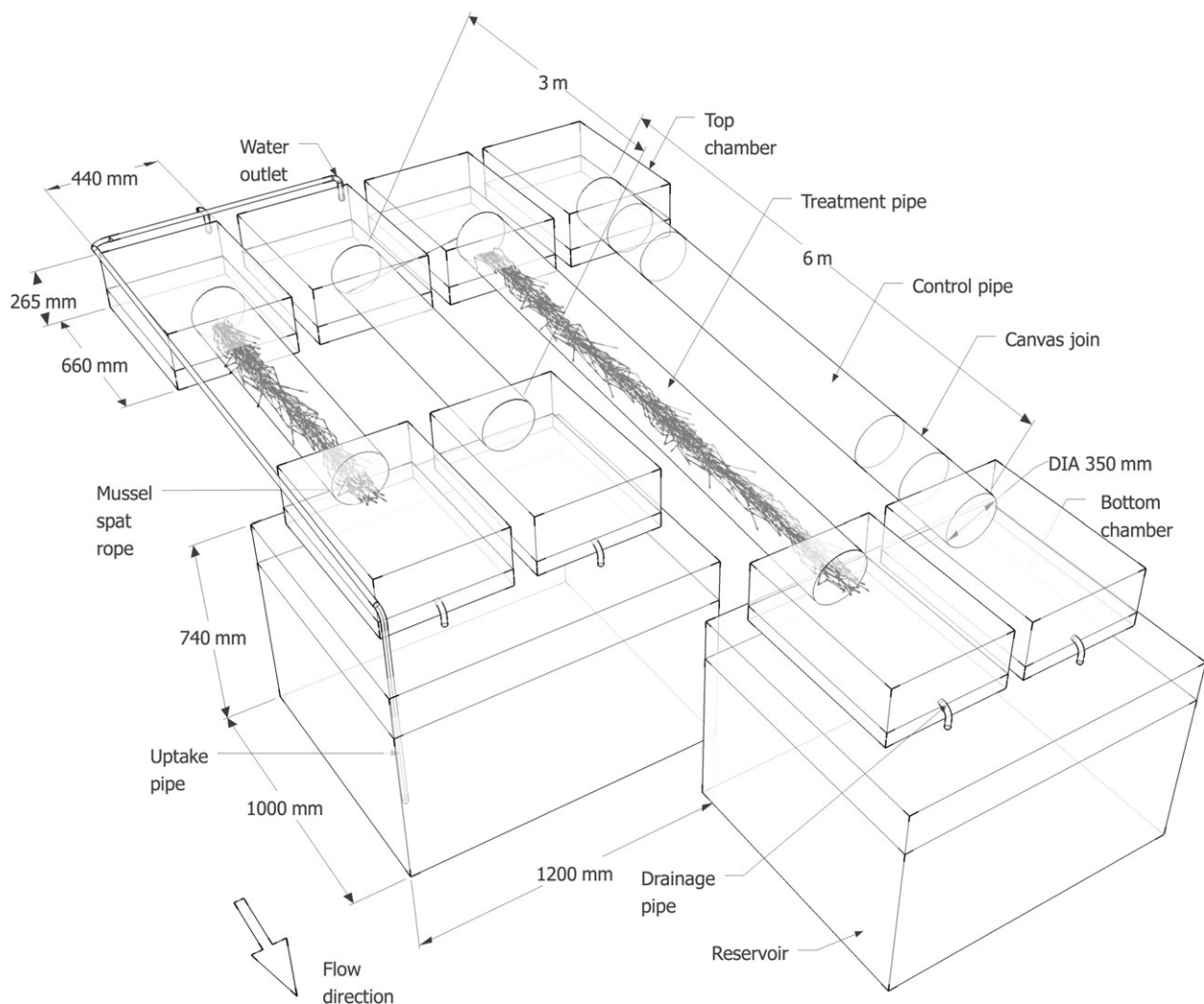


Fig. 1. Schematic diagram of experimental set-up assessing the effects of mussel spat rope on passage success of juvenile rainbow trout *Oncorhynchus mykiss*, inanga *Galaxias maculatus* and the shrimp *Paratya curvirostris* through culverts of differing pipe length (3 and 6 m), slope (1.5 and 3°) and flow (0.24 and 0.75 L s⁻¹). Note: diagram not drawn to scale.

the length of the pipe and then converted this value to m s^{-1} . Finally, the two pipe lengths were 3 and 6 m. The longer setting likely represents a typical two-way country road, while the shorter is representative of a one-way culverted creek crossing typically traversed by quad bikes on farming properties or culverted walking trails.

We ran all trials with four pipes operating simultaneously: two 3-m pipes and two 6-m pipes, each with one treatment (i.e. rope) and one control (no rope) pipe. We randomly allocated the two pipes with rope at the beginning of every trial using a coin toss. We fitted each of these treatment pipes with one doubled length of UV-stabilized polypropylene mussel spat rope ('Super Xmas Tree' brand; Donaghys Industries, Christchurch, New Zealand) to provide two parallel strands that spanned the full length of the culvert. We kept depth constant at 90–100 mm in each of the bottom chambers and ran four replicates at each of the experimental settings for fish and three replicates for *P. curvirostris*. A maximum of four trials were carried out each day between 6.30 am and 11 pm.

Temperatures were maintained and controlled by a combination of the manual addition of Aqua One 300-w Heat Bars (Aqua One, Nelson, New Zealand) to increase the heat to desired levels if necessary within each bottom sump and Aqua One 4-hp Arctic Chillers (Aqua One) that were plumbed into the circular pipe system. Trials were run at $16\text{ }^{\circ}\text{C}$ ($\pm 1\text{ }^{\circ}\text{C}$) for both *G. maculatus* and *P. curvirostris* and at $13\text{ }^{\circ}\text{C}$ ($\pm 1\text{ }^{\circ}\text{C}$) for *O. mykiss*. These temperatures were used to reflect favourable conditions for each of these species: juvenile *O. mykiss* – 11–19 $^{\circ}\text{C}$ (McCauley & Pond 1971; Nielsen, Lisle & Ozaki 1994; Roper, Scarnecchia & La Marr 1994) and *G. maculatus* – 18.1 $^{\circ}\text{C}$ (Richardson, Boubee & West 1994). Little information exists regarding the temperature preferences of *P. curvirostris*, although Quinn *et al.* (1994) assessed their lethal limits, which ranged between 25 and 28 $^{\circ}\text{C}$ depending on the length of exposure. Therefore, we ran the *P. curvirostris* trials at 16 $^{\circ}\text{C}$ as they often inhabit the same streams as *G. maculatus*.

EXPERIMENTAL METHODOLOGY

To avoid any potential issues with 'learning', no fish or crustacean was used more than once throughout the experiment. We used 15 *O. mykiss* ($n = 960$) in each trial and 20 *G. maculatus* ($n = 1280$) and *P. curvirostris* ($n = 480$). We limited *O. mykiss* density to 15 per replicate to minimize stress as they were slightly larger than *G. maculatus*. Animals were placed in the bottom chamber at the beginning of each trial, and (excluding the initial 20 min to assess speed of first ascent, discussed further below) subjects were left for 2 h before checking their position post-trial. Only the front half of the bottom chamber was available to the fish as they were placed within a mesh bag to minimize hiding space and encourage passage attempts.

We placed a one-way mesh 'funnel' device at the top end of each pipe to retain successful subjects in the upper chamber and minimize their potential return downstream. We counted individuals as successfully reaching the top if they were present in the top chamber at the conclusion of the trial. Those found in the pipes or on the rope at the end of trials were counted as having not successfully ascended. To examine any differences in approximate speed of ascent between different treatments, we observed the top four chambers from behind a screen during the initial 20 min of each trial. The time of the first subject to successfully negotiate any of the four set-ups was recorded during this 20-min period.

STATISTICAL ANALYSES

Prior to analyses, individuals reaching the top were converted into proportions and analysed accordingly. We checked for normality and homogeneity by visually inspecting residual plots against fitted values. All statistical analyses were performed using R 2.15.0 (R Development Core Team 2012). To assess the effectiveness of mussel ropes at reducing velocity at each of the two remaining settings (flow and slope), we performed a three-way factorial analysis of variance (ANOVA). To test our primary hypothesis that rope presence improves passage of the two fish species through culverts at various combinations of flow, slope and pipe length (i.e. four different main treatments), we used four-way factorial ANOVA. As we only used the highest flow setting for *P. curvirostris*, we used three-way factorial ANOVA to test for differences in success rates between treatments (rope, slope, pipe length). As we were interested in results specific to settings used in this laboratory trial, all factors were treated as fixed.

Results

VELOCITY

Velocity through the culvert pipes was significantly reduced by the addition of mussel spat rope (Fig. 2, Table 1). Moreover, velocity was greater at both high flows and high slope settings, and there was a significant interaction between rope presence and flow (Fig. 2, Table 1). Velocity ranged from 0.24 to 0.63 m s^{-1} with rope present and from 0.78 to 1.28 m s^{-1} in their absence.

FISH AND SHRIMP RESPONSE

While fish were able to ascend some of the pipe settings without mussel spat rope in place, success was often low, and in agreement with our principal hypothesis, rope provision significantly improved passage of fish and shrimp

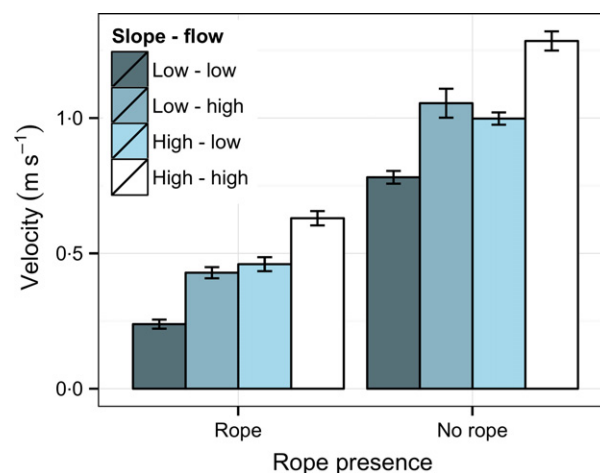


Fig. 2. Mean (± 1 SE) velocity through pipes assessing the effects of mussel spat rope addition, slope (1.5 and 3 $^{\circ}$) and flow (0.24 and 0.75 L s^{-1}); $n = 4$ replicates for each experimental setting tested. Three-way ANOVA results are given in Table 1.

in these trials (Figs 3 and 4, Table 2). At the most extreme settings (6-m pipes, high gradient and flow), no passage was made by any species without rope present (Figs 3 and 4, Table 2). Moreover, in accordance with our second hypothesis, clear differences were evident in the success rate of the different species depending on the settings in which trials were run (slope, flow, pipe length; Figs 3 and 4, Table 2).

Oncorhynchus mykiss

Mussel ropes significantly improved *O. mykiss* passage (Fig. 3a, Table 2). Mean success was highly variable ranging from 0 to 60% depending on trial settings. On average (and irrespective of flow or slope), passage success was greater when ropes were present than when they were

Table 1. Results of three-way factorial ANOVA comparing velocity measurements through pipes between three treatment variables: Mussel spat rope (presence/absence), slope (1.5 and 3°) and flow (0.24 and 0.75 L s⁻¹), n = 4 replicates for each experimental setting tested

Treatment	F _{1,56}	P
Rope	767.56	<0.0001
Slope	104.06	<0.0001
Flow	116.51	<0.0001
Rope × Slope	0.08	0.78
Rope × Flow	5.54	0.02
Slope × Flow	0.01	0.93
Rope × Slope × Flow	0.15	0.7

absent, and the magnitude of the effect was greater for 6-m (mean 5% success no rope, 40% rope) than for 3-m pipes (mean success 34% no rope, 50% rope).

In the 6-m pipes, *O. mykiss* were able to complete passage more often at high flow settings, both with rope present (at both slopes) and without rope (at low gradient only; Fig. 3a, Table 2). No fish were able to ascend 6-m pipes when slope was set to 3° (the higher slope setting)

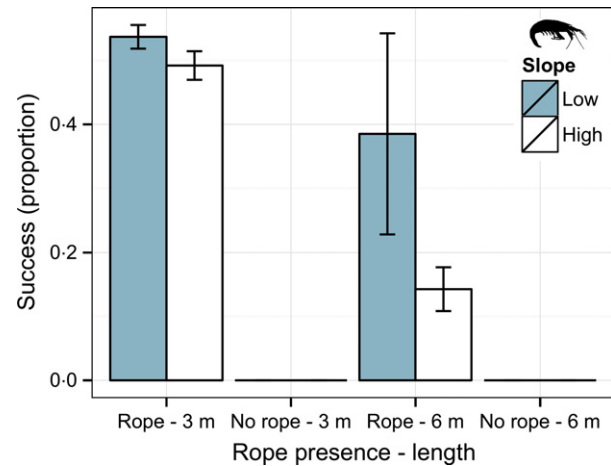


Fig. 4. Mean (±1 SE) proportion of the shrimp *Paratya curvirostris* successfully ascending pipes during two-hour trial periods assessing the effects of mussel spat rope addition, pipe length (3 and 6 m) and slope (1.5 and 3°). Coloured bars indicate either low or high slope. Note: trials were run at high flow settings only (0.75 L s⁻¹); n = 3 replicates for each experimental setting tested. Three-way ANOVA results are given in Table 2.

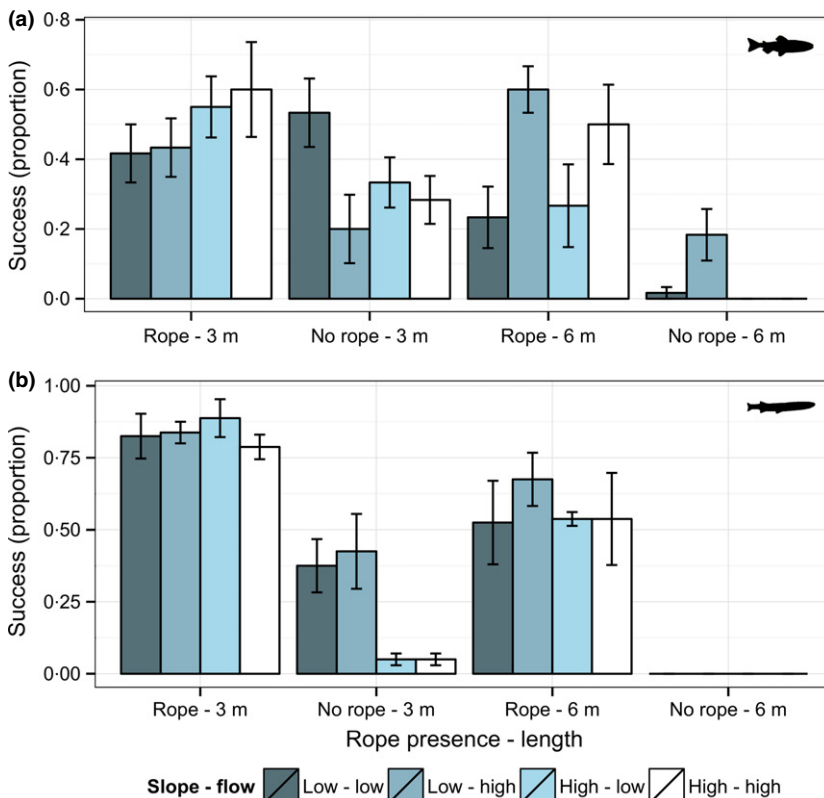


Fig. 3. Mean (±1 SE) proportion of (a) juvenile rainbow trout *Oncorhynchus mykiss* and (b) inanga *Galaxias maculatus* successfully ascending pipes during 2-h trial periods assessing the effects of mussel spat rope addition, pipe length (3 and 6 m), slope (1.5 and 3°) and flow (0.24 and 0.75 L s⁻¹); n = 4 replicates for each experimental setting tested. Four-way ANOVA results are given in Table 2.

without ropes present. Rope provision and pipe length both exhibited significant main effects, but several higher-order interactions were present involving rope, flow and length (Fig. 3a, Table 2). In 3-m pipes without rope present, more *O. mykiss* were able to pass through pipes in the low slope and low flow trials than the remaining three settings without rope.

When considering the rate of passage success within the first 20 min of a trial, some *O. mykiss* individuals were able to negotiate the 3-m pipes rapidly (often within 1 min of trial commencement). These ascents were typically faster in control pipes where fish were required to negotiate the laminar flows in a single rapid sustained burst (see Table S2, Supporting information). Generally, however, ascent times were variable, and successful passage typically took longer for the 6-m pipe combinations (excluding one instance where a single individual negotiated a ropeless 6-m control pipe within 1 min; see Table S2, Supporting information).

Galaxias maculatus

Ropes also significantly improved *G. maculatus* passage with some variation in results depending on pipe length and gradient (Fig. 3b, Table 2). The mean number of fish ascending pipes varied from 0 to 89% depending on the specific parameters. Passage success increased from 23% without ropes to 83% with ropes present in the 3-m pipes and from 0 to 57% in the 6-m pipes. No fish were able to ascend 6-m pipes at any flow or slope setting without the provision of ropes. Moreover, in 3-m pipes, while some fish were able to pass through, success was significantly lower in high slope, compared with low-slope trials, as

indicated by the three-way interaction between rope, slope and length (Table 2). With rope provision, passage success did not vary with the slope or flow settings used, but success was lower in the longer pipes (Table 2).

The ascent times for *G. maculatus* within the 20-min observation period were again highly variable and often within one min of trial commencement at the 3-m low slope settings (see Table S2, Supporting information). However, no ascents were made in the first 20 min in any of the ropeless, high-slope 3-m pipes or any of the 6-m ropeless pipe combinations, irrespective of slope or flow (see Table S2, Supporting information).

Paratya curvirostris

In line with our primary hypothesis, *P. curvirostris* shrimp were unable to ascend any pipes at either length or slope without the provision of rope. In contrast, success ranged from 14 to 54% in the roped pipes (Fig. 4, Table 2). Passage success was lower in the 6-m pipes and at higher slopes with a significant rope \times slope interaction (Fig. 4, Table 2). Only two ascents were made in the first 20 min (12 and 19 min) across all trials for *P. curvirostris*, in both the 3-m roped pipes (see Table S2, Supporting information).

Discussion

In contrast to a multitude of other human pressures impacting freshwater environments, development of tools for reinstating (physical) riverine connectivity for freshwater biota can result in rapid and measurable ecological gains (Hart & Poff 2002; Hart *et al.* 2002; Franklin &

Table 2. Results of four-way factorial ANOVA for juvenile rainbow trout *Oncorhynchus mykiss* and inanga *Galaxias maculatus* and three-way factorial ANOVA for the shrimp *Paratya curvirostris* assessing the proportion successfully ascending culvert pipes during 2-h trial periods at different settings of mussel spat rope (presence/absence), pipe length (3 and 6 m), slope (1.5 and 3°) and flow (0.24 and 0.75 L s⁻¹); $n = 4$ replicates for each experimental setting tested for *Oncorhynchus mykiss* and *Galaxias maculatus* and $n = 3$ for *Paratya curvirostris*

Treatment	<i>Oncorhynchus mykiss</i>		<i>Galaxias maculatus</i>		<i>Paratya curvirostris</i>	
	$F_{1,48}$	P	$F_{1,48}$	P	$F_{1,16}$	P
Rope	36.75	<0.0001	232.36	<0.0001	90.44	<0.0001
Slope	0.06	0.806	6.91	0.011	3.08	0.098
Flow	1.77	0.19	0.13	0.718	–	–
Length	21.01	<0.0001	40.3	<0.0001	9.38	0.007
Rope \times Slope	2.65	0.11	3.61	0.063	3.08	0.098
Rope \times Flow	6.82	0.012	0.002	0.968	–	–
Rope \times Length	4.92	0.031	0.28	0.602	9.38	0.007
Slope \times Flow	0.002	0.961	1.02	0.317	–	–
Slope \times Length	1.77	0.19	3.31	0.075	1.45	0.245
Flow \times Length	10.26	0.002	0.37	0.547	–	–
Rope \times Slope \times Flow	0.41	0.525	0.47	0.495	–	–
Rope \times Slope \times Length	0.7	0.406	7.34	0.009	1.45	0.245
Rope \times Flow \times Length	0.002	0.961	0.87	0.357	–	–
Slope \times Flow \times Length	3.33	0.074	0.002	0.968	–	–
Slope \times Flow \times Length \times Rope	0.7	0.406	0.08	0.778	–	–

For *Paratya curvirostris*, trials were run at high flow settings only (0.75 L s⁻¹).

Bartels 2010). The current laboratory study demonstrated that the presence of mussel ropes in culvert pipes enabled successful passage of the two fish and one shrimp species tested when various realistic combinations of slope, length and flow would have otherwise limited or excluded passage in their absence. Passage success under these conditions was most likely facilitated by reduced barrel water velocities as suggested in other studies (e.g. Larinier 2002; Macdonald & Davies 2007) and a general increase in flow complexity relative to unroped conditions. Observations of fish and shrimp behaviour and video footage revealed that the test subjects often struggled to negotiate unroped culverts, but were able to exploit roped set-ups in various ways to improve passage success (see <http://dx.doi.org/10.6084/m9.figshare.695084>).

Paratya curvirostris

Historically, passage within freshwater systems has typically focused on improving access for larger popular ichthyofauna with little consideration given to other freshwater taxa (Hamano *et al.* 1995; March *et al.* 2003; but see Fievet 2000). Freshwater shrimp can be important functional components in freshwater environments and, when present in high abundances, may be important ecosystem engineers (Pringle *et al.* 1993; Schaller *et al.* 2010; Moulton *et al.* 2012). For diadromous shrimp in particular, anthropogenic disruption of passage within river networks has the potential to result in significant functional changes in upstream reaches (March *et al.* 2001).

The atyid decapod shrimp *P. curvirostris* is endemic to New Zealand and may be locally abundant in freshwater catchments close to the coast (Carpenter 1978). This poorly studied detritivore exhibits a diadromous life history, and therefore, its distribution is likely to be strongly influenced by river connectivity. In our study, laminar flows in unroped culverts prevented upstream egress of this species, while provision of ropes resulted in relatively high passage success across all tested combinations. To gain an insight into the locomotive behaviour used by *P. curvirostris* as they ascended the roped culverts, we constructed a scaled down version of our experimental set-up using ropes fitted to a section of clear perspex pipe. Video footage indicated that a combination of crawling along rope stands and occasional 'boundary layer swimming' enabled these organisms to overcome the hydraulic barrier and progress steadily upstream (see 'paratya perspex pipe behaviour.m4v'; <http://dx.doi.org/10.6084/m9.figshare.695084>). Similar behaviour exhibited by diadromous shrimp has been noted by other researchers (e.g. Benstead *et al.* 1999; Kikkert, Crowl & Covich 2009), and provision of tactile media such as mesh textile matting has been suggested to improve passage of crawling biota through fish ladders (Hamano *et al.* 1995).

Although passage success was lower for the longest and steepest roped set-up, observations of *P. curvirostris* clinging to the ropes at the conclusion of each 2-h trial (as well

as low ascent rates in the first 20-min observation period) suggested that passage success may have been higher if trials were conducted over a longer period. Under natural conditions, shrimp would have unlimited time to negotiate barriers, so we suggest that ropes could be a cost-effective tool for significantly improving culvert passage for similar migratory crustacea globally.

Oncorhynchus mykiss

In contrast to shrimp, juvenile *O. mykiss* displayed a rather complex response to the various set-up combinations. On average, provision of ropes improved passage success of *O. mykiss* relative to unroped pipes. The effectiveness of ropes for facilitating passage was most notable at the most extreme trial settings where 6-m pipes set at high slope enabled some successful passage (at both high and low flows), while equivalent unroped controls did not.

Surprisingly, a small number of trout were able to successfully negotiate 6-m pipes without rope, but only when set at low slope. Under this setting, limited passage was achieved at both high and low flows, with success marginally greater at the higher flow setting. The higher flow setting also appeared to substantially improve passage success for trout in equivalent 6-m pipes with ropes present. Observations and physical measurements of trout body depth (Tonkin, David & Brooke 2013) suggest that a possible explanation for lower passage efficacy at low flow settings in long pipes may be that trout were unable to generate sufficient lateral propulsion over this distance as a result of lower within-culvert water depth.

The variable success exhibited by *O. mykiss* across the different trial combinations in the current study suggests that slope and flow may interact and vary disproportionately for a given pipe length. Nevertheless, and in accordance with the other species examined, results from this study suggest that ropes can substantially improve passage success for small *O. mykiss* when extreme barrier parameters exclude passage in their absence.

Galaxias maculatus

In contrast to *O. mykiss*, which were able to ascend 6-m low-slope pipes, *G. maculatus* were unable to successfully negotiate any of the 6-m pipe combinations without ropes present. Previous research into the swimming capabilities of *G. maculatus* suggests that this species is unable to attain the same burst or sustained swimming speeds as *O. mykiss* (Mitchell 1989; Mitchell & Boubee 1995), although burst speeds up to 0.87 m s⁻¹ for 5 s or less have been recorded for *G. maculatus* (Feurich, Boubee & Olsen 2012). For a given body length, these two species are morphologically quite different with *O. mykiss* being deeper dorsoventrally (Tonkin, David & Brooke 2013). Interestingly, however, when ropes were present within the pipes, *G. maculatus* on average exhibited greater passage success

than trout across all rope configurations tested. Observations in a simulated perspex pipe indicated that *G. maculatus* are able to use their 'tubular' and sinuous body shape to purposely burrow into and rest within the rope strands before continuing their ascent (see 'inanga perspex pipe behaviour.m4v'; <http://dx.doi.org/10.6084/m9.figshare.695084>), a behaviour not exhibited by *O. mykiss* in this study.

A final unreplicated trial demonstrated that even at a slope of 10° combined with high flow, ropes still facilitated the passage of *G. maculatus* through both 3-m (30% success) and 6-m (16% success) pipes, although more than 1 h elapsed before successful passage was achieved by this species. This result, in association with data recorded for a benthic eleotriid *Gobiomorphus huttoni* (Tonkin, Wright & David 2012), indicates that ropes could enable passage of fish through some potentially extreme culvert scenarios.

Considerations for use of mussel ropes in the field

A critical consideration to retrofitting any culvert, particularly culverts operating under outlet control, is culvert capacity. In our experimental set-up, ropes reduced the cross-sectional area for water conveyance by only about 2–5% in the 350-mm-diameter pipes used. This range incorporates a potential doubling and fluctuation of rope diameter from a compressed state to an expanded state (14–28 mm × 2 ropes, respectively). Although this method was developed primarily for promoting the passage of smaller species through long physically inaccessible culverts, potential exists to up-scale the tool for use in larger culverts. Theoretically, up-scaling should be easier in larger culverts since cross-sectional area reduction will decrease proportional to the pipe diameter squared, while the increased roughness produced by the ropes would decrease proportional to culvert diameter.

While small organisms are able to exploit small 'pockets' of reduced velocity generated by the ropes (as exhibited in this study), we acknowledge that the needs of larger organisms through larger structures may not be met using the simple arrangement tested in this investigation. Nevertheless, we consider this to be an issue of scale. That is, where culvert capacity permits, we believe that substantial potential exists to improve the use of this tool for a broader range and size of culvert types and aquatic species. For instance, a single rope line ('Xmas tree') is designed to support tensile weight loads up to 2 t, although other similar options supporting loads up to 24 t exist (<https://www.donaghys.com>), so multiple rope lines laid in larger diameter culverts (see David & Hamer 2012) could be used as a 'scaffolding' structure onto which baffles or other objects could be added or removed to improve passage performance. Theoretically, components for such a structure could easily be transported and constructed on site and deployed/retracted as a single assembled unit, possibly without the need to dewater or physically enter the culvert. Conceivably, the structural

durability and hydraulic performance (including derivation of roughness coefficients, Manning's *n* for different materials and rope types) under a range of flow scenarios would need to be evaluated prior to long-term deployment.

A further consideration to improving connectivity is the potential for facilitating the spread of invasive species (Rahel 2007). In New Zealand and elsewhere, the consequences of salmonids breaching natural and artificial instream barriers on endemic fish biodiversity have been clearly demonstrated (McDowall 2006, McIntosh *et al.* 2010). Our investigation provided some insights into the physical capability of small *O. mykiss* through culverts which indicated that, irrespective of flow setting, a ropeless 6-m culvert enabled limited passage at a 1.5° slope, but excluded passage at 3°. In addition to physical capabilities, observations we made during our experiments suggested that *O. mykiss* and *G. maculatus* may use species-specific behaviours to negotiate barriers. For instance, at steep slopes, *G. maculatus* often used their tubular shape to burrow into rope strands and rest in the benthic region below the ropes on their journey upstream, whereas this behaviour was not observed for *O. mykiss*. Conceivably, closer examination and exploitation of unique behaviours at extreme settings may enable specific designs or barrier settings to favour native species over exotics. To date, detailed investigation of fish behaviour in relation to hydraulics has received limited attention (Fullerton *et al.* 2010; Silva *et al.* 2011), but is likely to be a fruitful area of future research for controlling species connectivity (Taylor, Fahrig & With 2006).

CONCLUSIONS

In this study, the three aquatic organisms displayed unique behaviours in response to various experimental configurations when attempting to surpass culverts with and without the provision of mussel ropes. As demonstrated in this and previous studies, such observations are clearly important for optimizing passage success for aquatic taxa with differing locomotive capabilities. The parameters and experimental configurations used in this study were chosen to reflect realistic conditions frequently encountered for small diameter, difficult-to-retrofit stream culverts. We consider ropes to be a unique option for improving riverscape connectivity under such conditions that typically preclude the use of other existing methods. Substantial potential also exists to modify and test rope configurations to improve their utility across a broader range of culvert types and sizes and to evaluate passage performance for a greater variety of aquatic species. Irrespective of configuration, this study demonstrates that ropes can be used as a rapid and effective low-cost solution for improving passage of various aquatic biota with differing locomotive abilities through small stream culverts.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Summary statistics of juvenile rainbow trout *Oncorhynchus mykiss*, inanga *Galaxias maculatus*, and *Paratya curvirostris* size differences between the top and bottom chambers post-trial.

Table S2. Raw times (in min) recorded for juvenile rainbow trout *Oncorhynchus mykiss*, inanga *Galaxias maculatus*, and *Paratya curvirostris* successfully ascending pipes within the first 20-min observation period.