

# Industrial road crossings drive changes in community structure and instream habitat for freshwater fishes in the boreal forest

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## SUMMARY

1. Stream crossing structures are an increasingly prevalent anthropogenic feature on North American riverscapes, particularly in watersheds affected by industrial resource development in sensitive boreal environments. If improperly managed, stream crossings have the potential to alter fish habitat and impede fish movement.

2. This study assessed instream habitat characteristics and fish communities from 33 culverted, bridged and reference streams in an industrialising region of the boreal forest in west-central Alberta. Mixed-effects modelling and multivariate analysis were used to determine impacts of stream crossings at three scales: whole-stream scale, within-stream scale and the interaction of scales.

3. Instream habitat characteristics such as mean depth, water velocity, percent fines, turbidity, water temperature and dissolved oxygen showed significant between-stream as well as within-stream differences among stream crossings. The majority of fish species exhibited significantly lower densities ( $n\ m^{-2}$ ) in upstream habitats as compared to downstream habitats, including a significant reduction in Slimy Sculpin densities in culverted streams. Multivariate tests corroborated these results, showing that fish assemblages differ as a function of stream type.

4. This study suggests industrial stream crossings influence abiotic habitat characteristics in freshwater ecosystems, restrict biotic connectivity and impact fish community structure at the whole-stream and within-stream scales. Alterations to stream ecosystems associated with stream crossings may be driving large-scale changes in stream fish communities in the boreal forest. With expanded development expected in much of North America's boreal region, mitigation measures which limit impacts from stream crossings are needed to ensure proper ecosystem function in freshwater systems.

*Keywords:* bridges, culverts, fragmentation, freshwater, habitat alteration

## Introduction

Freshwater ecosystems are globally imperilled by threats from anthropogenic development (Dudgeon, 2014). As humans continue to alter the landscape (Vitousek *et al.*, 1997), their footprint is rapidly growing and causing alterations to freshwater environments and fish communities (Maitland, 1995; Schindler, 2001). Expansion of this footprint is predominately driven by rising demands for fossil fuels, natural gas, minerals and forest products

(Laurance & Balmford, 2013), resulting in the development and proliferation of linear features (Cott *et al.*, 2015). In North America's boreal forest region – an oligotrophic biome comprising 58.5% of Canada's landmass (Anielski & Wilson, 2009) and containing 25% of the world's remaining intact forests (Lee *et al.*, 2003) – the amount and extent of exploration and development activities has increased dramatically in recent years (Schindler & Lee, 2010; White *et al.*, 2011; Kreutzweiser *et al.*, 2013) and is expected to affect aquatic ecosystems

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in myriad ways (Schindler & Lee, 2010). A direct result of the proliferation of linear features such as industrially-installed resource roads has been the installation of hundreds of thousands of stream crossing structures (Miller, 2012; Januchowski-Hartley *et al.*, 2013). These crossings are particularly prevalent on small streams in forested boreal watersheds experiencing industrial resource development (Prévost, Plamondon & Lévesque, 2002; Scrimgeour *et al.*, 2003; Park *et al.*, 2008) where culverts and single-span bridges are the dominant structures used (Park *et al.*, 2008; MacPherson *et al.*, 2012).

Crossing structures such as culverts and bridges alter stream systems through changes to physical habitat structure, hydrology and water quality (Otterburg & Blank, 2015), potentially leading to species loss and altered communities (Gordon *et al.*, 2013). Habitat quality is affected from sediment mobilisation and deposition which can impact fish both directly (health and behaviour) and indirectly (changes to habitat). For example, a meta-analysis on the effects of sediment on freshwater fish showed that increases in suspended and deposited sediments had negative effects on feeding behaviour, spawning success and species composition and richness (Chapman *et al.*, 2014). Deposited sediments, in turn, can have significant impacts on fish occurrence and distribution as species differ in their substratum preferences and requirements. For example, benthic species such as Slimy Sculpin *Cottus cognatus* and salmonids such as Bull Trout *Salvelinus confluentus* are highly influenced by substratum composition; if excess silt enters a stream, it can form a mat over beds of coarse rocky substratum and severely degrade habitat suitability (Gordon *et al.*, 2013). Alterations to fish habitat are also of concern as they may contribute to fish species homogenisation by facilitating the dominance of tolerant species (e.g. Brook Stickleback *Culaea inconstans*) over sensitive species (e.g. Bull Trout) in degraded streams (Walters, Leigh & Bearden, 2003; Rahel, 2010). For instance, Bull Trout are expected to be extirpated from 24 to 43% of stream reaches that support them in a boreal forest watershed by 2025 due to their negative relation to forest harvest and percent fines (Ripley, Scrimgeour & Boyce, 2005).

Stream crossings such as culverts can act as barriers to instream fish movement and thus disrupt ecological connectivity and reduce the quantity of available suitable habitat. Improperly designed or installed culverts result in physical barriers (e.g. outlet drop, velocity, slope) to fish movement (Belford & Gould, 1989; Norman *et al.*, 2009; MacPherson *et al.*, 2012) and prevent fish from accessing different habitats necessary for life-history

processes or colonisation (Warren & Pardew, 1998; Nislow *et al.*, 2011; MacPherson *et al.*, 2012). As road networks expand, stream crossing densities have grown rapidly in stream networks (Kemp & O'hanley, 2010). For example, in the Great Lakes Basin, Januchowski-Hartley *et al.* (2013) found *c.* 268 000 potential stream crossing barriers, of which they estimated 36% to be impeding fish movement. Similar trends are found in western Canada. In British Columbia, there is an estimated 320 000 stream crossings along *c.* 550 000 km of resource roads (Miller, 2012). In Alberta's boreal forest, it is estimated that several thousand hanging culverts are fragmenting tens of thousands of stream kilometres (Park *et al.*, 2008). Stream habitat fragmentation has additionally been shown to alter fish assemblages (Perkin & Gido, 2012), as well as reduce population resilience to environmental disturbance and reduce genetic mixing (Tortorotot *et al.*, 2014).

In addition to growing anthropogenic stressors, northern boreal environments host a range of significant abiotic stressors that will likely intensify human impacts (Park *et al.*, 2008; Schindler & Lee, 2010). Environmental dynamics in the boreal forest, such as long, annual periods of ice cover combined with other relatively common stochastic events, such as drought and fire, have been suggested to act as a strong regulator of fish population dynamics (Park, 2006; Park *et al.*, 2008). Fish sensitivity to environmental dynamics is exacerbated in northern environments, and the relationship between habitat size and population persistence may be especially strong (Park *et al.*, 2008). Thus, the influence of environmental dynamics in northern environments contributes to the vulnerability of northern fishes to habitat fragmentation and degradation impacts arising from industrial resource development (Reist *et al.*, 2006; Cott *et al.*, 2015). Given the rapid increases in expansion of human activities in the boreal forest over the past four decades (Schindler & Lee, 2010), assessing the impacts of fragmentation from industrial stream crossings is imperative to informing adaptive management, restoration decisions and future land-use planning (Brandt *et al.*, 2013).

Relative to stream systems in Appalachia, the North American Prairies, Eastern Europe and the Pacific Northwest, boreal stream systems have received little attention in regard to the direct influences of stream crossings on fish populations and instream habitat. This is an important research gap as the North American boreal forest is facing increasing pressure from industry (Henry, 2005; Schindler & Lee, 2010), and there are signs that resource development may negatively impact freshwater fish through increased sediment loads (Ripley

*et al.*, 2005; Scrimgeour, Hvenegaard & Tchir, 2008), or problem culverts (Browne, 2007; Park *et al.*, 2008). The aim of this study was to assess the influence of culverts and bridges on instream habitat characteristics and stream fish communities in a boreal forest watershed undergoing expanding resource development. We compared physicochemical habitat characteristics and fish communities among three stream types: (i) streams crossed by culverts, (ii) streams crossed by bridges and (iii) reference streams without culverts or bridges; stream types were further stratified by location within the stream (i.e. upstream or downstream of crossing structures). Fish response was measured in terms of fish density and species richness as suggested by Nislow *et al.* (2011). We assessed four hypotheses within the context of this study. (i) Instream habitat characteristics differ significantly among stream types. This would suggest whole-stream scale impacts on fish habitat, perhaps from altered flow regimes, changes to bed morphology or sinuosity. (ii) Total fish density and species richness would be significantly lower in culverted and bridged streams as compared to reference streams. This would suggest whole-stream scale impacts of crossings on fish populations, likely from stream-wide extirpations induced by habitat fragmentation (Hanski *et al.*, 1995; Favaro *et al.*, 2014). (iii) Habitats upstream of culverts would have significantly lower fish densities and richness than downstream habitats. This would provide evidence of impeded dispersal at the within-stream scale (Bouska & Paukert, 2010; Nislow *et al.*, 2011; Favaro *et al.*, 2014). (iv) Fish assemblages differ among stream types, and in particular, culverted streams will be associated with species more tolerant to increased levels of sediment (e.g. *Chrosomus* spp., Brook Stickleback, or Lake Chub *Couesius plumbeus*).

## Methods

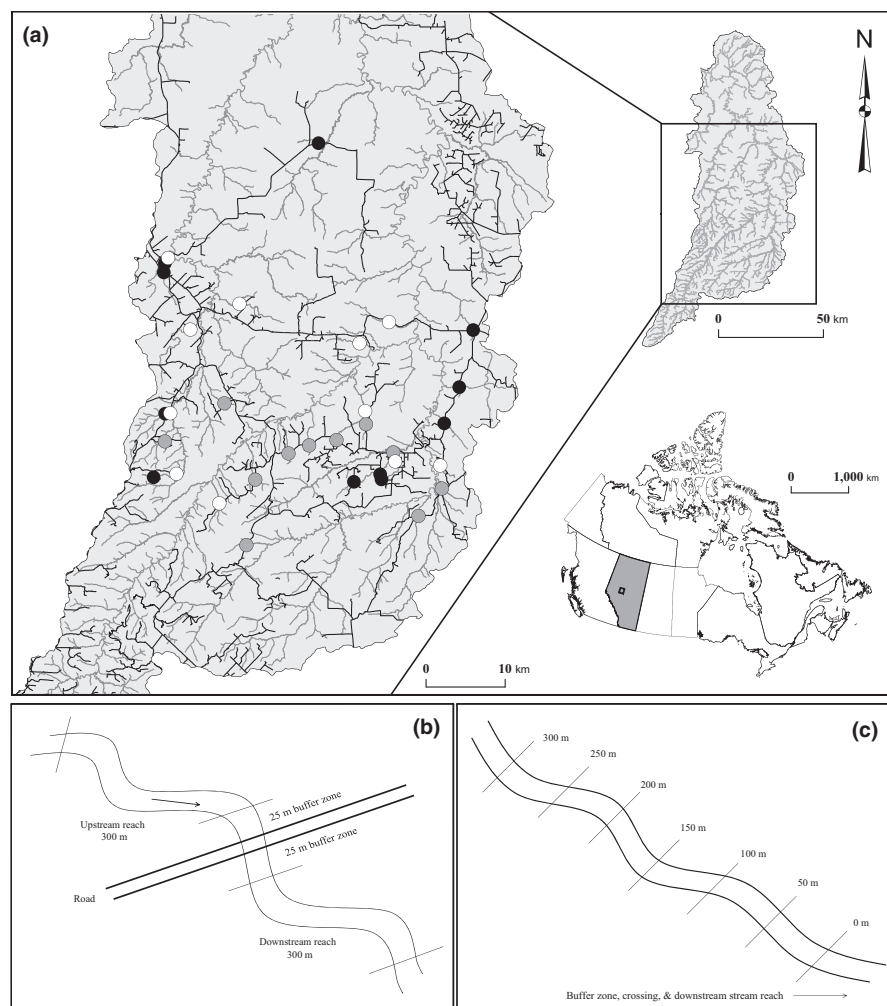
The boreal forest has long, cold winters and short, warm summers (mean annual temperature 0.2 °C–1.1 °C) and contains a principal forest type of closed-canopy mixed-woods (NRC, 2006). This study focussed on tributary streams in the Simonette watershed (5390 km<sup>2</sup>) located in the Upper Peace River Basin of west-central Alberta, Canada (Fig. 1). The watershed is located predominately within the boreal forest Natural Region of Alberta where it flows northward and drains into the Smokey River, eventually feeding the Peace River (NRC, 2006). The streams in the Simonette are characterised by low gradient, meandering reaches (Scrimgeour *et al.*, 2008) which feed the Simonette mainstem. This region has experi-

enced high levels of land-use disturbance from intensive forest harvesting and oil and gas exploration/extraction activities (e.g. roads, forest cutblocks, oil and gas well sites, pipelines; Scrimgeour *et al.*, 2008; White *et al.*, 2011). Industrial activity accounts for 18.7% of land disturbance in the Simonette; of that, forest harvest accounts for 84%, with roads, pipelines and seismic lines making up the remainder (Scrimgeour *et al.*, 2003). These numbers are likely higher today as the aggregate area of industrial activity has increased in recent years (Schindler & Lee, 2010; White *et al.*, 2011) and is expected to further grow over the next century (Kreutzweiser *et al.*, 2013). Indeed, overall mean road density in individual sub-watersheds in the Simonette has increased from  $0.33 \pm 0.02$  km km<sup>-2</sup> (Scrimgeour *et al.*, 2008) to  $0.47 \pm 0.29$  km km<sup>-2</sup> between 2008 and 2015. Watercourses were located south of the confluence of the mainstem Simonette and the Latornell rivers because we were particularly interested in the impacts of stream crossing structures that were installed on resource roads, and land use in the northern portion of the watershed is dominated by private land and agriculture.

Small streams in the boreal forest of Alberta support a relatively depauperate ichthyofauna as a result of its northern location and harsh climate (Nelson & Paetz, 1992). Provincial records indicate that 22 species of fish representing nine families have been recorded in the Simonette River watershed (Alberta Fish & Wildlife Management Information System, accessed April 2015). Among the most common fishes include those from the family Cyprinidae (Northern Redbelly Dace *Chrosomus eos*; Finescale Dace *Chrosomus neogaeus*; Lake Chub; Pearl Dace *Margariscus margarita*; Longnose Dace *Rhinichthys cataractae*; Redside Shiner *Richardsonius balteatus*; Northern Pikeminnow *Ptychocheilus oregonensis*), Cottidae (Slimy Sculpin; Spoonhead Sculpin *Cottus ricei*), Catostomidae (White Sucker *Catostomus commersoni*; Longnose Sucker *Catostomus catostomus*) and salmonids (Arctic Grayling *Thymallus arcticus*; Bull Trout; Mountain Whitefish *Prosopium williamsoni*). Less common species include Brook Stickleback, Trout-perch *Percopsis omiscomaycus*, Burbot *Lota lota*, Walleye *Sander vitreus* and Northern Pike *Esox lucius* (Nelson & Paetz, 1992; Joynt & Sullivan, 2003; Scrimgeour *et al.*, 2003, 2008).

## Study design

We used a balanced spatial comparison with replication among and within streams (McLaughlin *et al.*, 2006; Mueller, Pander & Geist, 2011; Favaro *et al.*, 2014) to investigate patterns in physicochemical habitat charac-



**Fig. 1** Panel diagram depicting study watershed and sampling sites for summer 2013, and sample design for this study in the Simonette Watershed, Alberta, Canada. (a) Study map showing study stream locations. Circles represent stream types; black = culvert, grey = bridge, white = reference. Black lines represent resource roads. (b) Schematic of 300-m stream reaches above and below culverts, bridges and hypothetical crossing structures (references) (note 25-m buffer section between 300-m sample reaches and road crossing). (c) Within each 300-m stream reach, physicochemical habitat characteristics were quantified along seven transects spaced 50 m apart.

teristics and fish communities. We sampled 33 watercourses (see Table S1) of similar size (order 2–4; Strahler, 1957) during summer low flow, 2013. Sample stream reaches were selected using a stream crossing inventory completed in the watershed in 2001 (Johns *et al.*, 2004), field scouting, and local knowledge of crossings and fish occurrence from government employees. Streams crossed by culverts ( $n = 11$ ), streams crossed by bridges ( $n = 11$ ) and reference streams ( $n = 11$ ) were evaluated (hereafter ‘stream type’). Stream types were stratified into upstream and downstream reaches (i.e. above and below crossing structures, and above and below a hypothetical crossing structure on reference streams), yielding a total of 66 sample reaches (Fig. 1). Each sample reach was 300 m in length (AESRD, 2013) and contained seven transects spaced 50 m apart where physicochemical habitat measurements were taken (Fig. 1). Pertinent physical features of crossings were measured (e.g. culvert hang height, outlet water velocity, slope, length). Potential fish passability ratings were determined (i.e. complete barrier to all fish, partial barrier to some fish,

no barrier) for each culvert based on physical measurements of the structure (AESRD, 2014). All culverts were closed-bottom corrugated metal pipes and – with the exception of two – were devoid of substratum within. All bridges were single-span with either concrete or wood abutments. While reference streams did not have a stream crossing within or downstream of sampling, there are four instances in which a reference location is downstream of a culvert, one instance in which a culvert is located below another culvert, and one in which a bridge is located below a culvert. While the bridge located downstream of the culvert does not confound fish passage inference, the culvert located below another culvert may. This factor was impossible to avoid given to the non-random distribution of stream crossings across the riverscape, along with access and logistical constraints.

#### *Physicochemical habitat characteristics*

We used a modified habitat assessment procedure to evaluate common physicochemical habitat parameters



known to influence fish presence (Gorman & Karr, 1978). Streams were sampled consistently with respect to rain events to reduce their influence on water chemistry observations (i.e. sampled at least 24 h after rainfall events). At each transect, we measured wetted width (m), bankfull width (m) and mean water depth (averaged between three point measurements at 25, 50 and 75% of cross-sectional width). Temperature ( $^{\circ}\text{C}$ ), dissolved oxygen ( $\text{DO}$ ;  $\text{mg L}^{-1}$ ), pH, velocity ( $\text{m s}^{-1}$ ), specific conductance ( $\mu\text{S cm}^{-1}$ ) and turbidity (NTU) were also measured. Temperature, DO, pH and specific conductance were measured using a handheld multiprobe meter (YSI, Yellow Springs, OH, USA), and velocity was measured with a handheld acoustic Doppler velocimeter (SonTek/Xylem Inc., San Diego, CA, USA). The velocity at each transect was recorded as the average of three point measurements (at 25, 50 and 75% of cross-sectional width). Substratum composition was visually classified by separating substratum components within  $1\text{-m}^{-2}$  quadrats into four categories based on size [ $<2$  mm (fines), 2–64 mm (gravel), 64–256 mm (cobble) and  $>256$  mm (boulder)], and the proportion of each within each transect was estimated (MacPherson *et al.*, 2012). The proportion of instream habitat types (i.e. pool, riffle and run habitat) was qualitatively estimated for sections between transects (AESRD, 2013). Substratum and habitat type measurements were all taken by a single observer to reduce observer bias. Substratum components were subsequently grouped into a 'Fines' category and a 'Coarse Rocky' category (gravel, cobble and boulder). Physicochemical variables were averaged for each stream reach from the seven transects. We measured physical characteristics of culverts related to fish passage including diameter, length, culvert slope and hang height (Table S2) as outlined in AESRD (2014).

#### Fish data collection

During low flow of summer and early fall 2013, we captured fish using single-pass backpack electrofishing in an upstream direction (Reid, Yunker & Jones, 2009; Smith Root LR-24 Backpack Electrofisher with one dipnetter). Consistent with other studies (McLaughlin *et al.*, 2006; Nislow *et al.*, 2011) and given site field assessments, we established a buffer area (25 m; Fig. 1) that separated the crossing structures from sample reaches to reduce the influence of local habitat alterations from the road and crossing structures (e.g. plunge pools). Direct current voltage and frequency settings were set in accordance with variations in stream conductivity. Mean volt-

age was 296 V (range: 250–330 V) at 30 Hz and 4 or 6 millisecond pulse width. Care was taken to ensure adequate sampling of all habitat types (riffles, runs, pools, undercut banks, etc.). All fish collected were identified to species, enumerated, measured for fork length (mm) and released alive. Voucher specimens of small-bodied species were retained for laboratory confirmation of identification. Electrofishing effort was recorded in seconds per 300-m reach (mean =  $963.9 \pm 58.6$  s per reach).

#### Data analyses

We used a combination of mixed-effects modelling and multivariate analyses to examine differences in patterns of variation observed in the physicochemical habitat characteristics and fish metrics among and within streams. We grouped together salmonids (Arctic Grayling, Bull Trout, Mountain Whitefish), *Chrosomus* spp. (Northern Redbelly Dace, Finescale Dace, Northern Redbelly Dace  $\times$  Finescale Dace) and *Catostomus* spp. (White Sucker, Longnose Sucker) because of small sample sizes (salmonids), broadly similar life histories (salmonids, *Chrosomus* spp., *Catostomus* spp.) and field identification errors (*Chrosomus* spp.), and they gave comparable quantitative results (data not shown). For each stream reach, we computed variable means for each habitat parameter. Total fish density ( $n \text{ m}^{-2}$ ) and species richness were computed for each stream reach. Relative densities ( $n \text{ m}^{-2}$ ) were then calculated for each species for each stream reach.

Given the nested structure of our data (i.e. stream location is nested within stream type), we used the analytical framework developed by Favaro *et al.* (2014). Mixed-effects models were used in three steps. In each model, we examined two main effects (i.e. stream type, location) and their interaction (i.e. stream type  $\times$  location). Stream type was treated as a fixed factor with three levels (culvert, bridge and reference) and stream location with two levels (upstream and downstream). To account for stream-specific random variation in environmental variables, a random intercept term for each stream was included in all models (Zuur *et al.*, 2009). In interpreting model outputs, we follow Favaro *et al.* (2014): a main effect for stream type would indicate whole-stream scale impacts (from stream-wide extirpations); a main effect for stream location would indicate general differences in upstream versus downstream locations (from gradients in fish distributions along the stream corridor); and an interaction effect would suggest impacts of culverts and bridges at the within-stream

scale. All models were built in the open-source software R (R Core Team, 2014) with the *lme* function of the nlme package (Pinheiro *et al.*, 2015) and the *glmmadmb* function of the glmmADMB package (Skaug *et al.*, 2015). Statistical significance was declared at  $\alpha = 0.05$ . Residual plots of all models were visually inspected to ensure variance homoscedasticity.

### Mixed-effects modelling

Linear mixed-effects models (LMEs) were first used to test for differences in the physicochemical habitat characteristics among stream reaches. Multiple habitat variables were log-transformed (depth, velocity, fines, pool habitat, turbidity) to ensure normal residuals. Each variable was modelled as a function of stream type, stream position, the interaction of stream type and location and a random intercept for stream-specific effects. Following this analysis, we used generalised linear mixed models (GLMMs) to test whether significant physical habitat variables affected individual fish responses. If significant, these variables would need to be accounted for in subsequent models testing the effect of stream crossings on fish response metrics. We tested whether mean depth, wetted width, velocity, percent fines or percent coarse substratum (physical variables commonly associated with fish distributions; Favaro *et al.*, 2014) affected fish densities. For GLMMs, we specified a negative binomial error structure for species counts and a Poisson error structure for species richness data (Zuur *et al.*, 2009). In addition, we included an offset for reach area in all models ( $\log \text{ m}^2$ ) except for the species richness model (O'hara & Kotze, 2010) to present count data as densities and account for different areas sampled (Favaro *et al.*, 2014).

The effects of stream crossings on overall fish density, richness and species-specific densities were then examined using GLMMs. Fish responses were modelled as a function of stream type, stream location, the interaction of stream type and location, a random intercept for stream-specific effects and with a reach area offset. Wetted width and mean depth were included as fixed covariates as they were found to influence species-specific density responses (Table S4).

### Multivariate analysis

Multivariate analyses were used to explore differences at the assemblage level and assess the importance of physicochemical habitat characteristics on the observed fish communities among sites (Mueller *et al.*, 2011;

Favaro *et al.*, 2014). Bray–Curtis dissimilarity indices (Clarke & Warwick, 2001) were calculated for all stream pairs based on fish density data and ordinated using non-metric multidimensional scaling (NMDS). NMDS is unconstrained by environmental variables and thus reflects only dissimilarities between species composition data. Environmental gradients were identified by fitting, as regressed vectors, the physicochemical habitat variables to the ordination in a second step. Vectors are interpreted as the direction of environmental change (i.e. of a gradient); the length of which indicates the strength of the correlation between the NMDS configuration and environmental variables. Significance tests for these correlations were carried out using permutation tests with 10 000 randomly permuted correlations. We used two-way permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) on rank dissimilarities from the Bray–Curtis dissimilarity matrix to test for significant differences in species assemblages among stream types, within streams and at the interaction between stream type and location. The PERMANOVA model included a strata term to account for stream-specific differences. Multivariate analyses were carried out in R (R Core Team, 2014). The NMDS analysis was carried out using the *nmds* function in the ecodist package (Goslee & Urban, 2007). Permutation tests were performed with the *envfit* function and PERMANOVA with the *adonis* function in the vegan package (Oksanen *et al.*, 2013) with 9999 permutations.

### Results

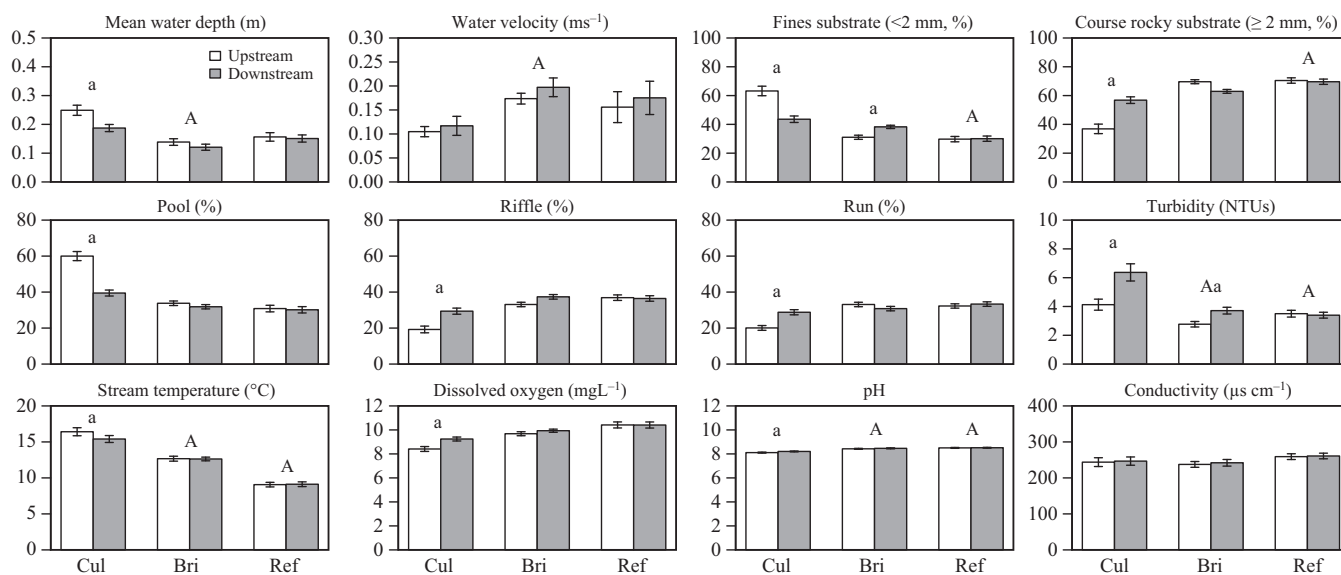
We captured 2987 individuals representing 16 species and 7 families among 66 sample stream reaches (Table S3). Slimy Sculpin was the most abundant and common species (35% of catch) followed by Lake Chub (19%), Northern Redbelly Dace (12%), Finescale Dace (11%) and Brook Stickleback (8%). Following in decreasing order of abundance were Reside Shiner (4%), Longnose Dace (3%), White Sucker (3%), Longnose Sucker (2%), Trout-perch (1%), Pearl Dace (0.8%), Mountain Whitefish (0.7%), Burbot (0.5%), Arctic Grayling (0.4%), Northern Redbelly Dace  $\times$  Finescale Dace (0.1%) and Bull Trout (0.03%). Overall mean density of fish was 7.48 individuals per 100  $\text{m}^2$ , similar to previous estimates from this watershed (7.32 individuals per 100  $\text{m}^2$ ; Scrimgeour *et al.*, 2008). Of the 11 culverts examined, eight were classed as complete barriers to fish movement (all species and life stages), two as partial barriers (passage inadequate for benthic species and fry of all species) and one as fully passable (Table S2).

### Physicochemical habitat characteristics

Consistent with our predictions, we observed strong differences in physicochemical habitat characteristics both among and within streams (Table S4; Fig. 2). Wetted width was similar across stream type and location. Mean water depth was on average 0.5 m lower in bridged versus culverted streams [LME:  $\beta = -0.5$ , standard error (SE) = 0.2, degrees of freedom (d.f.) = 30,  $t = -2.8$ ,  $P = 0.01$ ] and 0.3 m higher upstream versus downstream of culverts (LME:  $\beta = -0.3$ , SE = 0.1, d.f. = 30,  $t = 2.8$ ,  $P = 0.009$ ). Water velocity was on average  $0.7 \text{ m s}^{-1}$  slower in culverted versus bridged streams (LME:  $\beta = 0.7$ , SE = 0.3, d.f. = 30,  $t = 2.2$ ,  $P = 0.038$ ). Culverted streams had an average of 14% more fines than reference streams (LME:  $\beta = -13.5$ , SE = 5.8, d.f. = 30,  $t = -2.3$ ,  $P = 0.026$ ). The percent of fines was also 21% higher upstream compared to downstream in culverted streams (LME:  $\beta = 20.6$ , SE = 4.4, d.f. = 30,  $t = 4.7$ ,  $P < 0.001$ ) and 28% lower upstream compared to downstream in bridged streams (LME:  $\beta = -27.8$ , SE = 6.2, d.f. = 30,  $t = -4.5$ ,  $P < 0.001$ ). Coarse rocky substratum percentages followed a similar trend. The percent of coarse rocky substratum was 4% higher at reference streams compared to culverted streams (LME:  $\beta = 4.3$ , SE = 2.0, d.f. = 30,  $t = 2.2$ ,  $P = 0.037$ ), 7% lower upstream compared to downstream in culverted streams (LME:  $\beta = -7.0$ , SE = 1.5, d.f. = 30,  $t = -4.6$ ,  $P < 0.001$ ) and 9% higher upstream versus downstream in bridged streams (LME:  $\beta = 9.2$ , SE = 2.1,

d.f. = 30,  $t = 4.3$ ,  $P < 0.001$ ). Pool, riffle and run habitat percentages varied within stream types. There was 21% more pool habitat (LME:  $\beta = 20.9$ , SE = 3.4, d.f. = 30,  $t = 6.2$ ,  $P < 0.001$ ), 11% less riffle habitat (LME:  $\beta = 10.5$ , SE = 2.6, d.f. = 30,  $t = -4.0$ ,  $P < 0.000$ ) and 9% less run habitat (LME:  $\beta = 8.8$ , SE = 2.2, d.f. = 30,  $t = -4.0$ ,  $P \leq 0.001$ ) upstream of culverted streams compared to downstream reaches. There was also 20% less pool habitat (LME:  $\beta = -20.2$ , SE = 4.8, d.f. = 30,  $t = -3.4$ ,  $P < 0.001$ ), 8% more riffle habitat (LME:  $\beta = 7.6$ , SE = 3.7, d.f. = 30,  $t = 2.1$ ,  $P = 0.047$ ) and 11% more run habitat (LME:  $\beta = 10.8$ , SE = 3.2, d.f. = 30,  $t = 3.3$ ,  $P = 0.002$ ) upstream versus downstream of bridged streams.

Chemical water characteristics also varied by the interaction of stream type and location (Table S5; Fig. 2). Mean water temperature was  $2.8^\circ\text{C}$  colder in bridged stream (LME:  $\beta = -2.8$ , SE = 1.1, d.f. = 30,  $t = -2.5$ ,  $P = 0.017$ ) and  $6.3^\circ\text{C}$  colder in reference streams (LME:  $\beta = -6.3$ , SE = 1.1, d.f. = 30,  $t = -5.7$ ,  $P < 0.001$ ) as compared with culverted streams. Mean water temperature was on average  $1^\circ\text{C}$  warmer upstream versus downstream of culverted streams (LME:  $\beta = 1.0$ , SE = 0.35, d.f. = 30,  $t = 3.0$ ,  $P = 0.006$ ). Dissolved oxygen was  $0.8 \text{ mg L}^{-1}$  lower upstream versus downstream of culverted streams (LME:  $\beta = -0.8$ , SE = 0.13, d.f. = 30,  $t = -6.3$ ,  $P < 0.001$ ). pH was 0.3 units higher in bridged (LME:  $\beta = 0.3$ , SE = 0.1, d.f. = 30,  $t = 2.4$ ,  $P = 0.022$ ) and reference streams (LME:  $\beta = 0.3$ , SE = 0.1, d.f. = 30,  $t = 2.8$ ,  $P = 0.009$ ) as compared with culverted streams, and 0.1 units lower



**Fig. 2** Physicochemical habitat characteristics (mean  $\pm$  SE) in each stream type and location. Sample sizes for stream types are as follows: culvert,  $N = 11$ ; bridge,  $N = 11$ ; reference,  $N = 11$ . Cul, culverted streams; Bri, bridged streams; Ref, reference streams. Significant differences across stream types are identified by 'A' above bars, while significant differences between upstream and downstream reaches within streams are identified with lower case 'a'.

upstream versus downstream on culverted streams (LME:  $\beta = -0.1$ , SE = 0.03, d.f. = 30,  $t = -3.6$ ,  $P = 0.001$ ). Conductivity did not vary across stream type or location. Finally, turbidity was on average 2.7 NTUs lower in bridged (LME:  $\beta = -2.7$ , SE = 0.99, d.f. = 30,  $t = -2.7$ ,  $P = 0.012$ ) and 3.0 NTUs lower in reference streams (LME:  $\beta = -3.0$ , SE = 0.2, d.f. = 30,  $t = -3.0$ ,  $P = 0.005$ ) versus culverted streams, and 2.1 NTUs lower upstream versus downstream of culverted streams (LME:  $\beta = -2.1$ , SE = 0.48, d.f. = 30,  $t = -4.3$ ,  $P < 0.001$ ).

Both wetted width and mean water depth influence fish response metrics (Table S6). Total density and Brook Stickleback densities were negatively associated with larger wetted widths (GLMM:  $\beta = -0.28$ , SE = 0.14,  $z = -1.99$ ,  $P = 0.046$ ; GLMM:  $\beta = -0.43$ , SE = 0.09,  $z = -4.74$ ,  $P < 0.001$ , respectively), while richness and Slimy Sculpin, Lake Chub and Longnose Dace densities were positively associated with increased wetted width (GLMM:  $\beta = 0.55$ , SE = 0.23,  $z = 2.34$ ,  $P = 0.019$ ; GLMM:  $\beta = 0.43$ , SE = 0.21,  $z = -1.99$ ,  $P = 0.046$ ; GLMM:  $\beta = 0.085$ , SE = 0.38,  $z = -2.24$ ,  $P = 0.025$ ; GLMM:  $\beta = 2.45$ , SE = 0.77,  $z = -3.19$ ,  $P = 0.001$ , respectively). Species richness and Slimy Sculpin and *Chrosomus* spp. densities were negatively associated with increasing mean water depth (GLMM:  $\beta = -11.24$ , SE = 1.86,  $z = -6.06$ ,  $P \leq 0.000$ ; GLMM:  $\beta = -9.66$ , SE = 0.173,  $z = -5.58$ ,  $P < 0.001$ ; GLMM:  $\beta = -0.43$ , SE = 0.09,  $z = -4.47$ ,  $P < 0.000$ ).

### Stream fish communities

Species richness was affected by stream type and the interaction of stream type and location, and total fish density ( $n\ m^{-2}$ ) was affected by the interaction of stream type and location after controlling for variation in wetted stream width and depth (Table 1; Fig. 3). There were on average 0.5 fewer species on bridged versus culverted streams, providing evidence of whole-stream scale effects (GLMM:  $\beta = -0.50$ , SE = 0.24,  $z = 2.04$ ,  $P = 0.041$ ). On culverted streams, total density was on average 4.6% lower (GLMM:  $\beta = -1.73$ , SE = 0.17,  $z = -10.43$ ,  $P < 0.001$ ) and there were on average 1.9 less species upstream versus downstream (GLMM:  $\beta = -1.18$ , SE = 0.27,  $z = -4.43$ ,  $P < 0.001$ ), providing evidence of within-stream scale impacts. In addition to impacts on total density and richness, the effects of stream type were species specific (Table 1, Fig. 4). Slimy Sculpin densities were positively associated with bridged and reference streams. Sculpin densities were on average 6 times higher in reference streams (GLMM:  $\beta = 1.30$ , SE = 0.57,  $z = 2.29$ ,  $P = 0.022$ ) and 6 times higher in bridged streams (GLMM:  $\beta = 1.65$ , SE = 0.57,

$z = 2.88$ ,  $P = 0.004$ ) as compared with culverted streams. *Chrosomus* spp. and *Catostomus* spp. densities were positively associated with culverted streams as compared with bridged streams. On average, *Chrosomus* spp. densities were 1.3 times higher (GLMM:  $\beta = -3.26$ , SE = 1.34,  $z = -2.44$ ,  $P = 0.015$ ) and *Catostomus* spp. densities were 10 times higher in culverted streams (GLMM:  $\beta = -2.91$ , SE = 1.21,  $z = -2.42$ ,  $P = 0.016$ ).

Slimy Sculpin (GLMM:  $\beta = -1.49$ , SE = 0.38,  $z = -3.92$ ,  $P < 0.001$ ), Lake Chub (GLMM:  $\beta = -2.20$ , SE = 0.45,  $z = -4.89$ ,  $P < 0.001$ ), *Chrosomus* spp. (GLMM:  $\beta = -1.55$ , SE = 0.27,  $z = -5.78$ ,  $P < 0.001$ ), Brook Stickleback (GLMM:  $\beta = -3.66$ , SE = 1.43,  $z = -2.55$ ,  $P = 0.011$ ), Redside Shiner (GLMM:  $\beta = -2.35$ , SE = 0.63,  $z = -3.76$ ,  $P < 0.001$ ) and Longnose Dace (GLMM:  $\beta = -1.81$ , SE = 0.61,  $z = -2.98$ ,  $P = 0.003$ ) densities were all affected by the stream type  $\times$  location interaction (Table 1, Fig. 4). This provides evidence of effects at the within-stream scale. For each of these species, densities varied as a function of location, but only on culverted streams; average densities were markedly lower upstream as compared with downstream.

PERMANOVA showed that fish assemblages varied with stream type, but it depended on stream location as the interaction term was significant ( $F_{2,58} = 1.11$ ,  $P = 0.011$ ; Table 2). Ordination differentiated culverted stream reaches from bridged and reference streams, and to a lesser extent bridged streams from references (Fig. 5a). Whereas strong dissimilarities in species composition between upstream and downstream reaches on culverted streams are apparent, they were not for bridged or reference streams (Fig. 5a). The stress of the NMDS ordination of species densities was evaluated at two dimensions. Results suggested a two-dimensional solution suitably represented fish assemblages and revealed broad patterns of dissimilarity in species composition between stream reaches (2-D stress = 0.24; Fig. 5). Correlation of NMDS ordination scores with physicochemical habitat parameters and individual fish species densities indicate the presence of an environmental gradient across study stream reaches with associated differences in where species plot out (Fig. 5b). A primary gradient in physicochemical habitat characteristics is discernable from the left to right. The percentage of fines, pool habitat, temperature, turbidity and water depth are associated with each other, whereas increasing percentages of cobble, gravel and boulder substratum, riffle and run habitat, DO and water velocity align opposite. Brook Stickleback, *Chrosomus* spp., *Catostomus* spp. and Lake Chub are associated with each other and align opposite salmonids, Burbot and Slimy Sculpin.



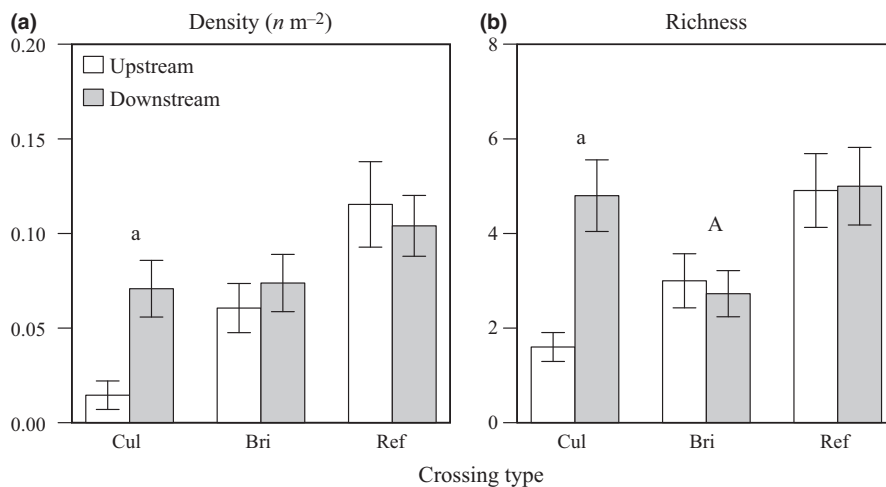
**Table 1** Parameter estimates from generalised linear mixed models investigating fish response metrics across stream type (culvert versus bridge versus reference), stream location (upstream versus downstream) and the interaction of stream type  $\times$  location. Boldface indicates significance at  $\alpha = 0.05$ 

Response	Variable	Coefficient	SE	z value	P
Total density ( $n\ m^2$ )	Intercept	-2.31	0.33	-6.96	0.000
	Bridge	-0.05	0.24	-0.21	0.830
	Reference	0.38	0.24	1.60	0.110
	Upstream	-1.73	0.17	-10.43	<b>&lt;2e<sup>-16</sup></b>
	Wet width	-0.13	0.11	-1.19	0.240
	Depth	-0.62	1.07	-0.58	0.560
	Bridge $\times$ upstream	1.55	0.19	8.05	<b>0.000</b>
	Reference $\times$ upstream	1.67	0.19	8.66	<b>&lt;2e<sup>-16</sup></b>
Richness	Intercept	0.52	0.30	1.75	0.079
	Bridge	-0.50	0.24	-2.04	<b>0.041</b>
	Reference	0.11	0.21	0.52	0.603
	Upstream	-1.18	0.27	-4.43	<b>0.000</b>
	Wet width	0.27	0.08	3.20	0.001
	Depth	2.25	0.93	2.41	0.016
	Bridge $\times$ upstream	1.22	0.36	3.37	<b>0.001</b>
	Reference $\times$ upstream	1.18	0.33	3.60	<b>0.000</b>
Slimy Sculpin ( $n\ m^2$ )	Intercept	-5.43	0.70	-7.76	0.000
	Bridge	1.65	0.57	2.88	<b>0.004</b>
	Reference	1.30	0.57	2.29	<b>0.022</b>
	Upstream	-1.49	0.38	-3.92	0.000
	Wet width	0.29	0.18	1.60	0.109
	Depth	-4.20	1.90	-2.20	0.027
	Bridge $\times$ upstream	1.34	0.37	3.60	<b>0.000</b>
	Reference $\times$ upstream	1.50	0.39	3.87	<b>0.000</b>
Lake Chub ( $n\ m^2$ )	Intercept	-6.97	1.18	-5.92	0.000
	Bridge	-1.46	1.15	-1.26	0.210
	Reference	1.49	1.05	1.43	0.150
	Upstream	-2.20	0.45	-4.89	<b>0.000</b>
	Wet width	0.31	0.31	0.99	0.320
	Depth	2.71	3.03	0.89	0.370
	Bridge $\times$ upstream	2.14	0.45	4.79	<b>0.000</b>
	Reference $\times$ upstream	2.04	0.44	4.62	<b>0.000</b>
<i>Chrosomus</i> spp. ( $n\ m^2$ )	Intercept	-3.68	1.18	-3.11	0.002
	Bridge	-3.26	1.34	-2.44	<b>0.015</b>
	Reference	-0.62	1.19	-0.52	0.602
	Upstream	-1.55	0.27	-5.78	<b>0.000</b>
	Wet width	-0.04	0.32	-0.14	0.890
	Depth	-3.85	1.67	-2.30	0.021
	Bridge $\times$ upstream	1.57	0.37	4.27	<b>0.000</b>
	Reference $\times$ upstream	1.53	0.30	5.05	<b>0.000</b>
Brook Stickleback ( $n\ m^2$ )	Intercept	-7.29	4.51	-1.62	0.106
	Bridge	-4.62	2.87	-1.61	0.107
	Reference	-2.39	2.49	-0.96	0.337
	Upstream	-3.66	1.43	-2.55	<b>0.011</b>
	Wet width	-1.31	1.13	-1.16	0.247
	Depth	10.72	10.71	1.00	0.317
	Bridge $\times$ upstream	5.56	2.29	2.43	<b>0.015</b>
	Reference $\times$ upstream	2.88	1.47	1.96	0.050
Redside Shiner ( $n\ m^2$ )	Intercept	-12.49	1.97	-6.35	0.000
	Bridge	-2.96	1.86	-1.59	0.113
	Reference	-0.24	1.44	-0.16	0.870
	Upstream	-2.35	0.63	-3.76	<b>0.000</b>
	Wet width	1.40	0.66	2.12	0.034
	Depth	5.61	4.84	1.16	0.246
	Bridge $\times$ upstream	1.79	0.64	2.80	<b>0.005</b>
	Reference $\times$ upstream	2.58	0.73	3.52	<b>0.000</b>

Table 1 (Continued)

Response	Variable	Coefficient	SE	z value	P
<i>Catostomus</i> spp. ( $n\ m^{-2}$ )	Intercept	-7.31	1.14	-6.44	0.000
	Bridge	-2.91	1.21	-2.42	<b>0.016</b>
	Reference	0.48	0.83	0.58	0.559
	Upstream	-2.10	0.58	-3.62	<b>0.000</b>
	Wet width	0.13	0.30	0.43	0.664
	Depth	4.19	3.91	1.07	0.284
	Bridge $\times$ upstream	1.11	0.86	1.29	0.196
	Reference $\times$ upstream	2.30	0.60	3.81	<b>0.000</b>
Longnose Dace ( $n\ m^{-2}$ )	Intercept	-15.92	3.98	-4.00	0.000
	Bridge	-5.03	3.17	-1.59	0.113
	Reference	-1.83	2.09	-0.88	0.381
	Upstream	-1.81	0.61	-2.98	<b>0.003</b>
	Wet width	2.75	1.26	2.19	0.028
	Depth	1.14	6.17	0.18	0.853
	Bridge $\times$ upstream	1.02	0.64	1.60	<b>0.109</b>
	Reference $\times$ upstream	2.32	0.90	2.59	<b>0.010</b>
Salmonids ( $n\ m^{-2}$ )	Intercept	-12.69	2.35	-5.41	0.000
	Bridge	0.42	1.57	0.27	0.788
	Reference	1.83	1.43	1.28	0.200
	Upstream	-0.11	1.26	-0.09	0.931
	Wet width	1.08	0.65	1.66	0.097
	Depth	-1.36	6.32	-0.21	0.830
	Bridge $\times$ upstream	1.13	1.43	0.79	0.428
	Reference $\times$ upstream	0.31	1.31	0.23	0.816

SE, standard error. The intercept of each model represents fish counts for downstream, culverted streams; variable coefficients then represent their relationship to the intercept. Individual stream-level effects were accounted for by including it as a random intercept term in each model. Differences in area sampled between stream reaches were accounted for by including an offset ( $\log m^2$ , excluding richness) in each model. Because wetted stream width and water depth were associated with stream type (Table S4) and influenced fish response metrics (Table S2), they were included as fixed effects to account for their variation.



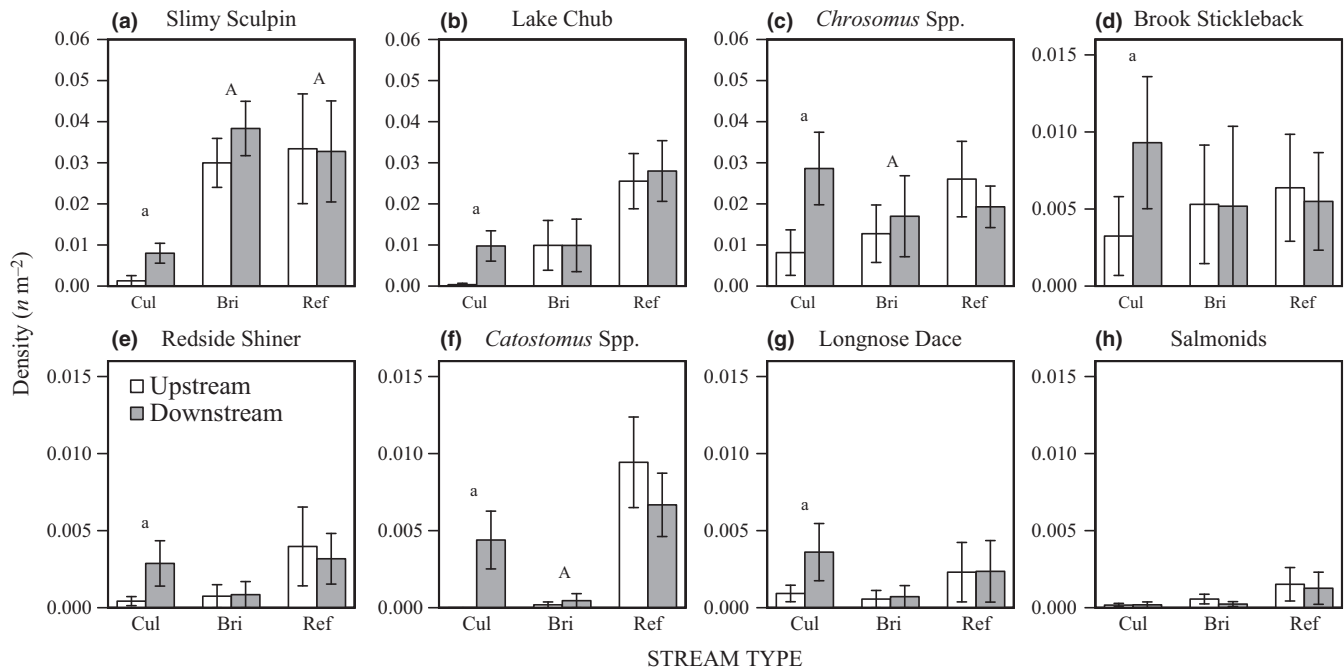
**Fig. 3** Barplot of fish community metrics of (a) fish density ( $n\ m^{-2}$ ) and (b) species richness across stream types and upstream and downstream locations (mean  $\pm$  SE). Sample sizes for stream types are as follows: culvert,  $N = 11$ ; bridge,  $N = 11$ ; reference,  $N = 11$ . Cul, culverted streams; Bri, bridged streams; Ref, reference streams. Significant differences across stream types are identified by lower case by 'A' above bars, while significant differences between upstream and downstream reaches within streams are identified with lower case 'a'.

## Discussion

### Crossing effects on physicochemical habitat characteristics

Culverted streams in our study were associated with significantly higher percent fines, water temperature, water depth and turbidity, and lower dissolved oxygen and water velocity. These observations are generally consistent with previous studies (Wellman, Combs &

Cook, 2000; Park *et al.*, 2008; MacPherson *et al.*, 2012). In particular, our findings support Wellman *et al.* (2000) and MacPherson *et al.* (2012) in that sediment accumulation and water depth were greater in streams with culverts than in bridged or reference streams. This is consistent with Favaro *et al.* (2014) who found larger sediment sizes to be associated with reference streams as compared with culverted streams. The study also



**Fig. 4** Density (mean  $\pm$  SE) of (a) Slimy Sculpin, (b) Lake Chub, (c) *Chrosomus* spp. (i.e. Northern Redbelly Dace, Finescale Dace, and their hybrid), (d) Brook Stickleback, (e) Redside Shiner, (f) *Catostomus* Spp., (g) Longnose Dace, (h) salmonids (i.e. Arctic Grayling, Bull Trout, Mountain Whitefish) by stream type and location. Sample sizes for stream types are as follows: culvert,  $N = 11$ ; bridge,  $N = 11$ ; reference,  $N = 11$ . Cul, culverted streams; Bri, bridged streams; Ref, reference streams. Significant differences across stream types are identified by lower case by 'A' above bars, while significant differences between upstream and downstream reaches within streams are identified with lower case 'a'.

showed a marked difference in upstream as compared with downstream habitats in culverted streams. Given our study sampling design (300-m stream reaches buffered from stream crossings by 25 m) and the low gradient nature of streams in the study region, this suggests culverts may be acting as constrictions causing upstream backwater effects. Stream channel constriction is often observed where culverts are present (Belford & Gould, 1989; Macdonald & Davies, 2007; MacPherson *et al.*, 2012) and can cause hydrological modifications which in turn alter geomorphological properties of streams (Gordon *et al.*, 2013). In our study streams, culverts may be constricting the downstream movement of water and abiotic materials, thus causing higher water depths and subsequent increases in pool habitat with concomitant decreases in riffle and run habitat. Higher upstream temperatures on culverted streams may then be the result of increased pool habitat and water depth, as similarly observed by MacPherson *et al.* (2012).

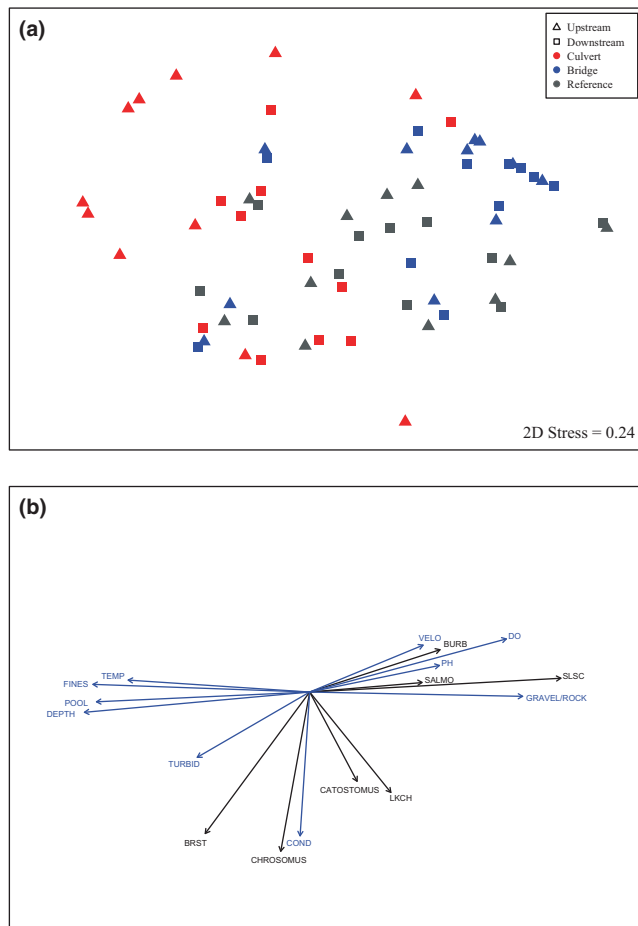
While all lotic systems contain natural levels of sediment, road–stream crossing sites are often significant point-source locations for erosion and sedimentation (Ottburg & Blank, 2015). Culverted and bridged streams had elevated turbidity levels, and bridged streams had

**Table 2** Results from two-way permutation multivariate analysis of variance (PERMANOVA) testing the effects of stream type, location and the interaction of stream type and location on Bray–Curtis dissimilarity of species assemblages. Boldface indicates significance at  $\alpha = 0.05$

Variable	d.f.	Sums. Sqs	F value	R <sup>2</sup>	P (perm)
Stream type	2	2.87	5.80	0.16	<b>0.008</b>
Location	1	0.27	1.11	0.02	<b>0.006</b>
Stream type $\times$ location	2	0.55	1.11	0.03	<b>0.011</b>
Residuals	58	14.34		0.80	

PERMANOVA model included a strata variable for stream to account for random stream to stream variation.

more fines in downstream versus upstream reaches. This suggests significant sediment input from erosional processes occurring at the crossing road surface and stream bank. Indeed, evidence of erosion was documented at all but one culverted stream, and all but two bridged streams (B. Maitland, pers. observation). These observations are consistent with numerous studies examining the impact of resource roads and stream crossings on sediment loading (Spillios, 1999; Lachance *et al.*, 2008; Thomaz, Vestena & Scharrón, 2013; Wang, Edwards



**Fig. 5** Non-metric multidimensional scaling (NMDS) ordination based on species density in 66 stream reaches and relationships with physicochemical habitat variables, total fish density and individual species. The stress level signifies the accuracy of the ordination for representing original dissimilarities in two dimensions. (a) Study streams are displayed with different colours. Upstream reaches are displayed with a triangle symbol and downstream reaches with square symbols. (b) Physicochemical habitat variables and fish species ( $P \leq 0.05$  based on 10 000 permutations) are displayed as vectors indicating the strength and direction of maximal correlations to the NMDS configuration. Vectors are distinguished by their colours; physicochemical habitat characteristics (blue) and fish (black). Note: Species abbreviations are as follows: SALMO = Arctic Grayling, Bull Trout and Mountain Whitefish; CHROSOMUS = Northern Redbelly Dace, Finescale Dace, Northern Redbelly Dace X Finescale Dace; BRST = Brook Stickleback; LKCH = Lake Chub; CATOSTOMUS = White Sucker, Longnose Sucker; SLSC = Slimy Sculpin; BURB = Burbot.

& Wood, 2013). While stream banks adjacent to crossings will, overtime, become re-vegetated and stabilise, heavy rain and flooding can destabilise banks and facilitate erosional processes (Chapman *et al.*, 2014). As increases in suspended and deposited sediments can have serious negative impacts on stream fishes (e.g. feeding behaviour, spawning success, species richness;

Chapman *et al.*, 2014), determining the tolerances of different species of fish to sediment loads associated with logging and oil and gas development is a high-priority research need (Boyce & Poesch, 2014), and should be examined broadly across the boreal region. Further, our results provide evidence that bridges may not be acting as ecologically benign structures as previously postulated (Warren & Pardew, 1998; Pluym, Eggleston & Levine, 2008). By considering a reference stream condition, this study is able to show that bridges, along with culverts, are acting as significant point-source locations for sediment delivery into boreal streams. While data concerning stream conditions prior to stream crossing installation is unavailable, these findings together with numerous other studies (e.g. Spillios, 1999; Lachance *et al.*, 2008; MacPherson *et al.*, 2012) support the contention that stream crossings – and culverts in particular – can alter fish habitat at the whole- and within-stream scale as compared with nearby reference streams through changes to habitat structure, hydrology and water quality, factors which can influence where fish occur (Gorman & Karr, 1978).

#### Crossing effects on stream fish communities

After accounting for physical differences in habitat that affect fish responses, we found evidence of fragmentation effects as species richness and Slimy Sculpin, *Chrosomus* and *Catostomus* densities varied in response to stream type. These results are consistent with previous research that has demonstrated alterations in local abundances and species richness in relation to stream crossing structures (Nislow *et al.*, 2011; Perkin & Gido, 2012). Perkin & Gido (2012), for instance, found reduced species richness in fish communities isolated by stream crossings compared with those which maintained connectivity with the surrounding stream network. Our results are also consistent with research that has found reductions in species-specific densities as an effect of stream crossings (MacPherson *et al.*, 2012; Favaro *et al.*, 2014). Slimy Sculpin densities were on average 6 times higher in our reference streams than in culverted streams. Similarly, Favaro *et al.* (2014) found densities of Coastrange Sculpin (*Cottus aleuticus*) and Prickly Sculpin (*Cottus asper*) to be on average 90 times higher in reference streams than in culverted streams, and MacPherson *et al.* (2012) found that whereas 69% of their reference sites had Spoonhead Sculpin, only 12% of their culverted sites similarly did. This information demonstrates that both species richness and the densities of species differ among stream types. Furthermore, our results support



the contention that sculpin are an effective indicator taxon for alterations to stream connectivity (Favaro *et al.*, 2014) given their benthic habit and weak swimming abilities (Nelson & Paetz, 1992; Lemoine, Bodensteiner & Tierney, 2014). Conversely, Northern Redside Dace and Finescale Dace densities were positively associated with culverted streams in the study area. Species in the genus *Chrosomus* prefer slow, warm water streams and are commonly found over fine substrata (Nelson & Paetz, 1992). As culverted streams in our study were characterised by deeper, warmer water with high levels of fine sediment, fragmentation effects on *Chrosomus* species may be buffered by their ability to tolerate habitat of reduced quality.

Local abundance and species richness should typically be depressed in the presence of a barrier to immigration (i.e. movement), and thus, local reductions in these metrics may be appropriate proxies for fragmentation (Nislow *et al.*, 2011). On average, total fish density and species richness, and densities of Slimy Sculpin, Lake Chub, *Chrosomus* spp., Brook Stickleback, Redside Shiner, Longnose Dace and catostomids were significantly reduced in upstream relative to downstream habitats in streams crossed by culverts. These findings support observations showing reduced upstream fish abundances and species richness as compared with downstream habitats on streams crossed by culverts (Warren & Pardew, 1998; Wheeler, Angermeier & Rosenberger, 2005; Nislow *et al.*, 2011), particularly for small-bodied, non-game stream fish (MacPherson *et al.*, 2012; Perkin & Gido, 2012; Favaro *et al.*, 2014). Causes for the impediment of fish movement are related to physical factors including steep culvert slope and excess water velocity (Belford & Gould, 1989; Burford *et al.*, 2009; MacPherson *et al.*, 2012) or perching of the culvert above the water surface (Mueller *et al.*, 2008; Burford *et al.*, 2009; Norman *et al.*, 2009; MacPherson *et al.*, 2012). These factors are exacerbated for weak-swimming stream fish commonly found throughout lowland boreal and foothills streams (e.g. cottids, cyprinids and catostomids). Of the 11 culverts examined in this study, eight were categorised as complete barriers, two as partial barriers and one as completely passable (AESRD, 2014; Table S2). Culverts in our study constricted stream channel width and increased instantaneous stream velocities at the crossing outlet (mean =  $0.39 \text{ m s}^{-1} \pm 0.4 \text{ SD}$ ). Excessive water velocities, in addition to physically inhibiting fish movement (Warren & Pardew, 1998; Macdonald & Davies, 2007), can also lead to the development of large outwash scour pools and hanging culverts over time (Park *et al.*, 2008). Outlet drop heights averaged 0.22 m ( $\pm 0.26 \text{ SD}$ )

for culverts in our study. MacPherson *et al.* (2012) found that hang heights as small as 0.16 m (mean,  $\pm 0.24 \text{ SD}$ ) may be complete barriers to upstream movement of Burbot, and partial barriers to Spoonhead Sculpin, catostomids and cyprinids. In our culverted streams, Burbot were never observed, catostomids were observed in eight streams and only once found in upstream habitats, and Slimy Sculpin found in seven streams and only once in upstream habitats. Accordingly, our results suggest that culverts are impeding upstream movement of non-game fish in boreal watersheds, possibly to the point of upstream extirpation. Multi-year studies that follow fish communities in habitats above culverts are warranted to further address the hypothesis that upstream extirpations are the result of stochastic environmental events (e.g. drought, flood, ice scour) combined with reduced or completely eliminated upstream immigration from downstream source populations (Eisenhour & Floyd, 2013).

While we provide an expanded view of stream crossing effects on freshwater fish communities in boreal streams, there are a few caveats. This study was of a large-scale, comparative design in which stream type was not randomly assigned to streams due to the non-random placement of culverts and bridges on the landscape. Thus, the effect of stream crossing configuration within the stream network could not be evaluated (Chelgren & Dunham, 2014). This is a common problem in stream crossing studies which investigate ecological patterns rather than their underlying mechanisms (Levin, 1992; Favaro *et al.*, 2014). Herein, we attempted to control for landscape and habitat-level differences in site selection and analyses, but unmeasured variables may have confounding effects on our observations of stream type effect. The fact that this study was carried out during summer low flow may have also influenced upstream fish densities as culvert passability for particular fish species has been shown to change relative to stream discharge (Bouska & Paukert, 2010; Mahlum *et al.*, 2014). Future studies should accordingly incorporate temporal scales into analyses to account for changes in culvert passability throughout the year. Finally, incorporating capture probability of fish into analyses of stream crossing effects may help further elucidate impact by accounting for species-specific differences in capture efficiencies (Neufeld *et al.* 2015).

#### *Cumulative effects on boreal watersheds*

There is presently a limited amount of published literature on the effects of natural resource development on

aquatic ecosystems in Canada's boreal forest (Kreutzweiser *et al.*, 2013), although trends suggest principal impacts from industrial resource development results from increased fine sediment loads (Anderson, 1996; Ripley *et al.*, 2005; Browne, 2007; Scrimgeour *et al.*, 2008) or malfunctioning culverts (Browne, 2007; Park *et al.*, 2008; MacPherson *et al.*, 2012; Torterotot *et al.*, 2014). Collectively, our results support the hypothesis that the effects of culverts at the whole-stream scale are the result of fragmentation effects from stream-wide extirpations and within-stream effects likely the result of inhibited movement within streams. It is possible, however, that multiple mechanisms (i.e. habitat degradation and fragmentation) are working synergistically and exacerbating the effects of stream crossings on boreal streams. Modifications to streams from the presence of crossing structures may be reducing habitat quality, thus leading to lower fish densities and altered communities. For example, shifts in habitat (e.g. lotic to lentic nature, temperature regime, increased fines) often favour generalist species over more specialised, sensitive ones and can lead to species extirpations and biotic homogenisation (Rahel, 2000; Roberts, 2001; Poff *et al.*, 2007).

The cumulative effects of natural resource development and additional stressors – such as natural abiotic stressors, climate change and forest pests – also remain largely unknown for the boreal region (Kreutzweiser *et al.*, 2013). For example, salvage logging in response to mountain pine beetle infestation and spread is expected to increase watershed disturbance in forested watersheds of western Canada (Redding *et al.*, 2008), thereby exacerbating sediment loading (Chamberlin, Harr & Everest, 1991). It was subsequently found in Alberta that infestation rates were too low to cause significant impacts to aquatic systems; however, this conclusion could not be substantiated by habitat or fish abundance data because these data do not exist for vast portions of the province (Weiss, 2011). Given the vulnerable nature of northern fishes to resource development (Reist *et al.*, 2006), this poses serious concerns for long-term persistence and biodiversity maintenance of freshwater fish populations in boreal forest watersheds. With expanded development expected in much of North America's boreal forest (Schindler & Lee, 2010), mitigation measures which limit impacts from stream crossings are needed to ensure proper ecosystem function in freshwater systems. This is particularly important given the general lack of consistent monitoring across remote northern environments (Weiss, 2011; Brandt *et al.*, 2013). To this end, this study provides a baseline to which remediation actions within our study watershed can be compared to validate

the efficacy of stream crossing remediation to restore connectivity for fish populations.

In conclusion, this study shows that culverted streams in Canada's boreal forest have higher levels of fine sediments, increased stream temperatures and water depth and less coarse rocky substratum as compared with bridged and reference streams. Culverted streams were associated with lower sculpin densities and higher *Chrosomus* spp. densities, evidence of whole-stream scale fragmentation effects. These effects were also pronounced within streams, where the majority of fish species exhibited significantly lower densities in upstream as compared to downstream habitats. Broadly, these results have negative implications for populations of stream-resident and potadromous species in the boreal forest region, including salmonids, cyprinids and catostomids. Given our findings in the context of recent research, the widespread and growing distribution of culverts on the boreal landscape (Prévost *et al.*, 2002; Park *et al.*, 2008; Miller, 2012; Januchowski-Hartley *et al.*, 2013), and increasing rate of natural resource exploitation across the boreal region (Kreutzweiser *et al.*, 2013), we conjecture that alterations to fluvial stream systems associated with stream crossings may be driving changes in stream fish communities, potentially at a very large scale. This is likely facilitated by the cumulative effects of habitat connectivity loss, alterations to instream habitat and other stressors. Regional studies such as this can fill gaps in our understanding of how anthropogenic features interact with freshwater environments and guide adaptive ecosystem management and land-use planning (Carlson, Wells & Jacobson, 2015) by identifying fragmentation hotspots where remediation and conservation dollars should be focussed to ensure the greatest ecological return on remediation dollar invested.

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### Supporting Information

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

**Table S1.** Selected physicochemical habitat characteristics in upstream (U) and downstream (D) reaches of study streams in the Simonette watershed in west-central Alberta, Canada, summer 2013.

**Table S2.** Physical characteristics and fish passability rating of stream crossings examined in the Simonette watershed of west-central Alberta, Canada, summer 2013.

**Table S3.** Species collected in 66 stream reaches in the Simonette watershed of west-central Alberta, Canada, summer 2013.

**Table S4.** Parameter estimates for linear mixed effect models (LMEs) investigating variation in physical habitat characteristics across stream type (culvert versus bridge versus reference), stream location (upstream versus downstream), and the interaction of stream type and location. Boldface indicates significance at  $\alpha = 0.05$ .

**Table S5.** Parameter estimates for linear mixed effect models (LMEs) investigating variation in chemical habitat characteristics across stream type (culvert versus bridge versus reference), stream location (upstream versus downstream), and the interaction between stream type and location. Boldface indicates significance at  $\alpha = 0.05$ .

**Table S6.** Coefficient estimates from generalized linear mixed models (GLMMs) investigating variation in fish response metrics as a function of physical habitat characteristics. Boldface indicates significance at  $\alpha = 0.05$ .

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