THE INFLUENCE OF CULVERTS ON SMALL STREAM FISH COMMUNITIES IN NORTHWESTERN ONTARIO

by

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ABSTRACT

Stream crossings may alter fish habitat and fragment lotic environments, which could alter fish movement in stream reaches and lead to changes in fish community structure and population dynamics at the local and riverscape level. The potential for point source disturbance impacts by culverts may be analogous to confluences and the hierarchal spatial arrangement of tributary junctions, which are known locations of increased biodiversity. There is currently limited information on habitat fragmentation and the cumulative effects that culverts might have at the local and landscape level on fish communities in northwestern Ontario. Forty-three culvert sites and seven confluence points on small cold water streams were selected across 10 watersheds northeast of Thunder Bay, Ontario to examine fish assemblages and community characteristics above and below culverts and confluence points, to: (1) determine the extent to which culverts block or impede the movement of fish; (2) to evaluate the relationships among patterns and responses of fish assemblages and functional groups to environmental variables and (3) compare the patterns of biological and physical disturbance between culverts and natural stream confluence points. Species richness, abundance, biomass and density were significantly lower below culverts compared to above ($p<0.05$). Conversely, there was no statistical difference when comparing fish demographics above and below confluence points. On average, there were fewer, but larger brook trout captured above culverts compared to below, suggesting that stronger swimming individuals were able to move through culverts. Although several environmental variables influence fish assemblages, the differences in habitat characteristics above and below culverts were marginal and unlikely to have a major affect in the structuring of fish communities, which suggests that difference in community assemblage above and below were the result of impeded movement. None of the culvert characteristics explained large amounts of variation in fish community above and below culverts. Although marginal, perched culverts and culverts not on stream bottom were most closely associated with differences in fish community above and below culverts. Upstream catchment area appeared to be the single most important environmental variable structuring fish communities across the study area. The results from my study support the hypothesis that culverts limit the movement of certain fish species. However, due to the combination of local and landscape environmental influences, it would be difficult to predict the long term impacts of culverts across multiple scales based on culvert characteristics alone.

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1.0 INTRODUCTION

Regional variation in climate, geomorphology, and hydrological regime provide the large-scale habitat template determining the range of life history traits found in stream fish assemblages (Resh *et al.* 1988; Fausch *et al.* 1994; Richards *et al.* 1996; Mensing *et al.* 1998; Sharma and Hillborn 2001; Brazner *et al.* 2005). Cummins (1974) suggested that streams and their surrounding terrestrial landscapes are functionally linked and fisheries scientists have since directed more research towards understanding these linkages with fish communities and populations at a broad variety of spatial and temporal scales (Vannote *et al.* 1980; Schlosser 1991; Fausch *et al.* 1994; Ward 1998; Wiens 2002; Wang *et al.* 2003; Brazner *et al.* 2005; Kocovsky and Carline 2006). Understanding the ecological linkages between regional, landscape and local-environmental variation and scale and how they influence ecological pathways including fish communities and stream habitat is essential in developing effective tools for assessing and addressing anthropogenic impairment and disturbance of aquatic ecosystems and for fisheries management. However, determining the quantitative function of any one particular variable or group of variables in explaining fish communities has proven quite difficult; primarily due to the interdependency of multiple scales (e.g. local, watershed, regional) and the stochastic nature of stream ecosystems (Benda *et al.* 1994a; Brazner *et al.* 2005).

Fish species abundance and distribution in headwater streams is highly influenced and structured by regional, landscape and local environmental variables. Variation in flow regime and natural and anthropogenic disturbance can affect the successional nature of stream habitat and thus have an effect on the permeability of potential upstream habitat for fish species (Vannote *et al.* 1980; Schlosser 1995a; Labbe and Fausch 2000; Schlosser and Kallemeyn 2000; Wang *et al.* 2003).

It was the recognition of the hierarchical structure and linkages between processes at the landscape scale and riverine components that formed Frissell *et al.*'s (1986) framework for stream habitat classification. Frissell *et al.*'s framework along with Schlosser's (1991) dynamic landscape model, which extended Vannote *et al.*'s (1980) river continuum concept, provides a theoretical basis for understanding fish-landscape research and how lotic (flowing-water) ecosystems are structured. The river continuum concept is based on the assumption that the physical structure of a river and its biological processes change in a gradual linear pattern, moving downstream through the watershed, most commonly associated with stream-order change. Based in part on the continuum concept, most riverine ecology in the past focused independently on understanding processes at the catchment scale (10^5-10^6m) such as landscape disturbance or channel dimensions or at the reach scale (10^1-10^3m) where most survey work and management takes place, with little attention focused on the intermediate segment scale (10^3-10^5m) where most lotic fish populations interact (Frissell *et al.* 1986). Interactions include movement to and from necessary habitat for refugia, spawning and feeding (Schlosser 1995b). Ward (1998) expanded on earlier theory by incorporating concepts of terrestrial landscape ecology in a "riverscape" approach to lotic ecology. More recently Fausch *et al.* (2002) proposed the need to focus research on the heterogeneous nature of stream habitat at intermediate spatial and temporal scales and the role of fish movement in linking habitat patches together through time. This approach bridges the gap between reach-scale and landscape-scale investigations and between research and conservation

(Kocovsky and Carline 2006). The riverscape approach requires an understanding of fish and their habitat in the context of the entire riverine landscape and its components, which includes biology, hydrology, geomorphology, water quality and connectivity. The riverscape concept also considers the ecological functions that occur at the watershed, intermediate and reach scales and links the important physical and biological processes in streams and their riparian zones at a scale relevant to natural and anthropogenic disturbance within the watershed (Fausch *et al.* 2002).

Natural disturbances such as storms, floods and fire within the watershed create spatial and temporal structure and variation in the habitat attributes of stream systems. Stream habitat heterogeneity occurs at varying spatial scales through geomorphic and hydrologic processes such as the transportation and deposition of organic and mineral materials (Resh *et al.* 1988; Reeves *et al.* 1995; Poff *et al.* 1997; Gomi *et al.* 2002.; Ward *et al.* 2002; Benda *et al.* 2004b). Through disturbance mechanisms, a spatial and temporal variety of habitat patches are created, which are important for fish species richness, populations and community dynamics (Schlosser 1982; Schlosser 1995b; Schlosser and Kallemeyn 2000). Fish assemblage structure (i.e. species richness, taxonomic composition and relative abundance pattern) is also strongly associated with habitat structure (Schlosser 1982; Poff and Allen 1995; Brazner *et al.* 2005).

Riverine ecologists have recognized the importance of spatial and temporal variation in the physical environment and how it can influence the growth, survival, immigration, and emigration of lotic fish species both directly and indirectly through the alteration of nutrient and organic cycling, production processes at lower trophic levels and resource and habitat use and availability (Schlosser 1991; Oberdorff *et al.* 2001).

Similar to how habitat patches create discontinuities in space, disturbances are capable of creating discontinuities in time and space and ultimately lend to the structuring of habitat patches within aquatic ecosystems (Benda *et al.* 2004b).

The process by which spatial arrangements of tributaries in a river network interact with stochastic watershed processes and ultimately influence the spatiotemporal pattern of habitat heterogeneity throughout a watershed was summarized by Benda *et al.*'s (2004b) '*network dynamics hypothesis*'. The hypothesis incorporates the theory behind both hierarchical habitat patch dynamics (Pringle *et al.* 1988; Townsend 1989, Wu and Loucks 1995; Poole 2002) and the application of landscape ecology to river systems (i.e. 'riverscapes') (Schlosser 1991; Rice *et al.* 2001; Fausch *et al.* 2002; Ward *et al.* 2002; Wiens 2002). Benda *et al.* (2004a,b) found that when a tributary enters a stream, there is an increase in nutrient and macroinvertebrate inputs and amplified channel disturbance regime at the confluence point. Reduced stream gradient upstream of confluence points may result in an increase in water volume, sediment and wood supply below confluence points. This punctuated disturbance regime at confluences ultimately increases environmental and habitat heterogeneity creating potential for higher biodiversity and ecosystem productivity in receiving streams (Kiffney and Richardson 2001; Rice *et al.* 2001; Wipfli and Gregovich 2002; Benda *et al.* 2004a,b).

Small headwater streams are closely linked to hillslopes and riparian forest, and are influential in regulating inputs of energy, nutrients and organic matter. These inputs contribute to downstream food webs and shape the structural characteristics of downstream habitat (Naiman and Latterell 2005). Headwater streams make up a substantial proportion of the stream length on the landscape and serve as habitat for macroinvertebrates, amphibians and fish (Meyer and Wallace 2001; Gomi *et al.* 2002). However, because headwater streams are small and numerous, their role is typically underestimated and inadequately managed compared to larger downstream systems (Gomi *et al.* 2002).

Variable movement (ranging behaviour) (Dingle 1996) within a heterogeneous lotic environment is essential to the survival of stream dwelling fish and to maintaining viable metapopulations (Schlosser 1991; Schlosser and Angermeier 1995; Fausch *et al.* 2002). Fish in small streams will move quickly and over relatively long distances when environmental conditions fall below certain requirement thresholds or in response to resource abundance and distribution along the riverscape (Gowan *et al.* 1994; Gowan and Fausch 1996; Curry *et al.* 2002; Gibson *et al.* 2004). Furthermore, in order for fish in small streams to move, conditions must become optimal, such as during increased discharge (Gowan and Fausch 1996; Mackereth and Armstrong 2001). Fish may also move for a variety of other reasons, including density-dependant interactions, resource availability, energetic requirements, predator avoidance, biotic and abiotic environmental conditions and for spawning (Gowan *et al.* 1994; Gowan and Fausch 1996; Belanger and Rodriguez 2002).

Spatial variation in fish communities stems from the interplay between historical barriers to dispersal which regulate regional distribution, and environmental constraints such as flow regime, water chemistry and predation which regulate small-scale distribution. Natural and anthropogenic barriers to upstream movement reduce connectivity within the watershed, thus affecting large-scale spatial habitat relationships which potentially influence stream fish population dynamics. These habitat relationships include habitat complementation, habitat supplementation, source-sink dynamics and neighbourhood effects (Dunning *et al.* 1992; Schlosser 1995b; Dingle 1996; Gowan and Fausch 1996; Fausch 2002). Habitat complementation refers to the spatial proximity of different resources or habitat types required by a species that are not substitutable, and are an important factor in determining population size and species persistence (Schlosser 1995b). Habitat supplementation occurs when food or habitat is substitutable and affects rate-dependant processes that influence fish population dynamics (Dunning *et al.* 1992). Source-sink dynamics deal with the spatial variation in juvenile production and mortality, rather than the spatial distribution of resources for individual organisms and also play an important role in determining population dynamics (Schlosser 1995b) Neighbourhood effect theory suggests that dispersers are more likely to move into adjacent than distant habitat patches and habitat patches with permeable versus impermeable boundaries (Schlosser 1995b). Restricted movement within the aquatic system will impact community and population dynamics by reducing the connectivity between spatially sub-divided populations and patches of suitable habitat within lifelong home ranges (Dingle 1996; Fausch *et al.* 2002). Restricted movement caused by barriers may also impede fish recolonization following disturbances, which, combined with demographic, environmental and genetic stochasticity, could cause local extinction, especially in small isolated populations (Shaffer 1981; Morita and Yamamoto 2002; Roghair *et al.* 2002; Angermeier *et al.* 2004).

In northwestern Ontario, native stream dwelling brook trout (*Salvelinus fontinalis* [Mitchill]) populations are widespread throughout coldwater boreal forest drainage networks and have evolved a strategy to survive under conditions that normally limit the distribution of other species (Scott and Crossman 1973; Mackereth and Armstrong 2001). Brook trout prefer summer stream temperatures at or below 20°C, are associated with streams where there are groundwater upwellings (Scott and Crossman 1973; Power 1980; Picard *et al.* 2003) and avoid warmer water temperatures (Cherry *et al.* 1977; Picard *et al.* 2003). Brook trout rely on access to and from small headwater streams for all parts of their life history and do not restrict their activity to small home ranges within streams (Shetter 1968; Gowan and Fausch 1996; Adams *et al.* 2000). Movement other than for reproduction can be associated with conditions becoming unsuitable (e.g. temperature), competition, and energetic requirements including foraging behaviour (Riley *et al.* 1992; Gowan and Fausch 1996; Adams *et al.* 2000; Gowan and Fausch 2002; Roghair *et al.* 2002).

Forestry is the primary land use in northwestern Ontario and has the potential to greatly impact lotic fishes and their habitat. Due to the extensive road networks associated with forestry operations and the topographic complexity of the Lake Superior Basin, many roads cross streams.

The initial local effects of forestry road construction and stream crossings on stream ecosystems in regards to water quality, sedimentation and the direct biological impacts on fish habitat downstream are well documented (Van Hassel *et al.* 1980; Trombulak and Frissell 2000; Spellerberg 2002). However, less is known regarding the consequences of roads on ecological functions and how they may fragment aquatic habitat by blocking or impeding the upstream movement of fish (Waters 1995; Warren and Pardew 1998; Wellman *et al.* 2000; Gibson *et al.* 2004). Because most streams in northwestern Ontario are small headwater tributaries of larger rivers it is often most time efficient and economically feasible for forest managers to install culverts at stream crossings, rather than bridges or bottomless arched culverts. Bridges and bottomless culverts generally help to maintain the ecological and physical integrity of the natural stream (Gibson *et al.* 2004). In Ontario the *Environmental Guidelines for Access Roads and Water Crossings* (OMNR 2001) lists a number of mandatory standards for planning, designing, constructing, maintaining and abandoning access roads or water crossings on Crown land in Ontario. The mandatory standards within the guidelines state that all applicable provincial (OMNR 1988) and federal legislation (Fisheries Act 1985) for water crossings must be considered and the prevention of harmful alteration, disruption or destruction of fish habitat, the obstruction of fish passage and the deposition of substances deleterious to fish must not occur. Although there are no specific standards for the type of crossing used at a site, the guidelines do provide best practice measures for different site conditions, primarily stream size, in order to comply with given legislation (Appendix I).

Culverts may fragment fish communities by directly blocking or temporarily impeding fish migration. Perched culverts are perhaps the most recognized form of barrier to fish movement and may impact certain species more than others depending on the stream depth below the culvert and fish jumping ability (Baker and Votapka 1990) . The degree to which a culvert is perched may vary depending on stream flow and thus may result in either a permanent or temporary barrier. Culvert gradients greater than 0.5% along with excessive water velocity in relation to fish swimming ability and size are also likely to block or impede the movement of certain species (Baker and Votapka 1990; Webb 1975; Motta *et al.* 1995; Warren and Pardew 1998; OMNR 2001). Unfortunately, most culvert guidelines (including those used in Ontario) base allowable culvert gradient and water velocity on the swimming ability of large adult fish rather than juveniles or smaller species. These factors combined with a lack of hydraulic roughness in the culvert may impede upstream movement (Baker and Votapka 1990). Ontario's guidelines also suggest that water depths of less than 20 cm in culverts can also pose movement problems especially for larger fish (Baker and Votapka 1990; OMNR 2001). If factors impede fish movement, it is likely that fish moving upstream are being delayed or stopped at the outlets of the culverts and may be vulnerable to avian, mammalian, and piscine predators (Gibson *et al.* 2004).

The hydraulic and physical conditions created by culverts may also constrain fish distribution and abundance. Warren and Pardew (1998) found that culverts had the highest mean velocities of five different crossing types and lowest fish passage (at constant fish size and water depth). Other potential barriers aside, water velocity and depth in culverts is likely to affect fish movement and thus assemblages on a seasonal basis. This may be particularly critical for migratory species, small fish and those with poor swimming ability. Because brook trout exhibit ranging behaviour and use small streams throughout there life history, they are vulnerable to habitat fragmentation and are therefore, valuable indicators when considering the impacts that culverts may have on fish communities. Due to high water velocities and altered stream flow, culverts may also impair ecosystem functions, and potentially alter the habitat structure in both up and downstream directions, either seasonally or on a permanent basis (Matthews *et al.* 1994; Warren and Pardew 1998; Angermeier *et al.* 2004).

The locally altered disturbance regime at a confluence is embedded within a larger pattern of disturbance frequencies and magnitudes that are continuously occurring throughout the watershed. The frequency and magnitude of these disturbances is mainly dictated by the hierarchical nature of branching river networks and the geomorphological landscape. It is possible that the local disturbance regime at culverts is analogous to that at confluences. Because of associated changes in the hydrology up and downstream of culverts and their position in the longitudinal flow of a riverine ecosystem, there is potential for an input of nutrients and sediment from adjacent roadways. There is also the possibility of changes in the amount of organic and inorganic material transported from upstream areas, depending on temporal variations in climate driven processes and the spatial distribution and geophysical characteristics of the materials in the upstream reach and the structural characteristics of the culvert. Because culverts could be creating these punctuations in the drainage network, it is possible that they are unnaturally and cumulatively altering and affecting the spatial distribution and availability of fish habitat and therefore fish communities.

Other jurisdictions, such as in the Pacific Northwest of the United States and British Columbia among others, have devoted a substantial amount of effort to understanding the effects of aquatic habitat fragmentation caused by culvert installations. Most guidelines and reports focus on the distribution and movement of anadromous salmonids. Unlike other jurisdictions, there has been little research into the larger implications of roads and stream crossings on fish communities in northwestern Ontario which has lead to the specific objectives to be addressed in this thesis:

1.1 *Objectives*

(1) Determine the extent to which culverts block or impede the movement of fish in small northwestern Ontario streams.

- If culverts block or impede the movement of stream fishes then I predict that local fish species richness, abundance, density, biomass and species diversity will be lower in reaches above culverts compared to below.
- Stream dwelling brook trout are good indicator species for evaluating movement impediments. The ability of brook trout to move through culverts is likely positively related to body size. Therefore if culverts impede brook trout movement then I would expect an increase in brook trout size, along with a decrease in relative abundance above compared to below culverts.
- Furthermore, if culverts block or impede fish movement, I predict that the magnitude of the difference in the fish community above relative to below the culverts will be positively associated with the degree of culvert impact measured as the extent of perching, height above stream bottom, and culvert gradient, length and diameter.
- If there are differences in fish relative abundance and assemblage characteristics above and below culverts, then I would postulate that under unrestricted conditions, such as at confluence sites, fish distribution and community structure would be more homogeneous throughout the sample reaches.

(2) Evaluate the general relationships among patterns and responses of fish assemblages and functional groups to local and landscape environmental variables.

- I predict that variation in the relative abundance of fish assemblages and assemblage characteristics above and below culverts and across all of the sites will be associated with a combination of landscape and local environmental variables and hydrological conditions.
- The degree of culvert impacts, including water velocity, culvert gradient and perched height are expected to account for variation in fish communities above and below culverts.
- I predict that differences in fish assemblages and functional groups above and below culverts will be associated with swimming ability; with upstream assemblages composed of stronger swimming species or larger individuals within a species relative to below culvert assemblages.

(3) Compare the patterns of biological and physical disturbance between culverts and natural stream confluence points.

- Based on riverine and hydrogeologic theory and retention properties, I expect to find increased organic and mineral material downstream of confluence points, thus increasing habitat heterogeneity.
- Depending on the interactions between surface and ground water upstream of confluences, tributaries may bring an influx of cold water to mainstreams, thus creating thermal refugia downstream of confluence points. Both of these disturbance mechanisms are likely to be similar along stream segments with road crossings and specifically those with culverts. Increasing water velocity in culverts may create scouring of the stream bed and carry material downstream. Logging roads are also known sources of sediment input to streams and can

contribute to the degradation of freshwater habitats and have detrimental impacts on aquatic biota (Reid and Dunne 1984; Kreutzweiser *et al.* 2005). Water runoff from roads to adjacent streams may affect downstream water temperature.

- Based on the hypothesis that confluences and culverts are creating similar disturbance regimes, I expect that downstream habitat composition would be similar at both types of sites. I expect that the downstream relative abundance of fish will be similar in reaches below culverts that are not barriers and below confluences.

2.0 GENERAL METHODS

2.1 Study Area

The study area is located northeast of Thunder Bay, Ontario, Canada (48°23′N 89°15′W) and encompasses sites on small streams with upstream catchment areas ranging from 1km^2- 33km^2, within the greater Kamnistiqua, Current, Mackenzie, Coldwater, Wolf, Black Sturgeon, Poshkokagan, Kabitotikwia and Nipigon River watersheds (Figure 1). All of these quaternary watersheds are part of the Lake Superior Basin, and drain into Lake Superior in Thunder Bay (Kamnistiqua, Current and Mackenzie River), Black Bay (Coldwater Creek, Wolf and Black Sturgeon River) and Nipigon Bay (Nipigon River), with the exception of the Poshkokagan and Kabitotikwia rivers which drain into Lake Nipigon (Figure1). Air temperature varies widely from a mean daily minimum between -20°C and -26°C in January to a mean daily maximum between 22°C and 25°C in July. Mean annual precipitation ranges between 700 and 850 mm (Environment Canada 2006).

The geological regions within the study area are the Superior highlands, Nipigon Plains and Thunder Bay Plains Ecoregions (Wickware and Rubec 1989). The Nipigon Plains Ecoregion is dominated by diabase bedrock formation. The principal surficial landforms are ground moraines and sandy glaciolacustrine plains. The surface relief consists of rolling and undulating hills with elevation ranging from 305-587 m (Wickware and Rubec 1989). The Thunder Bay Plains Ecoregion, situated along Lake Superior's north shore is composed primarily of diabase, greywacke, and shale bedrock formations (Wickware and Rubec 1989).

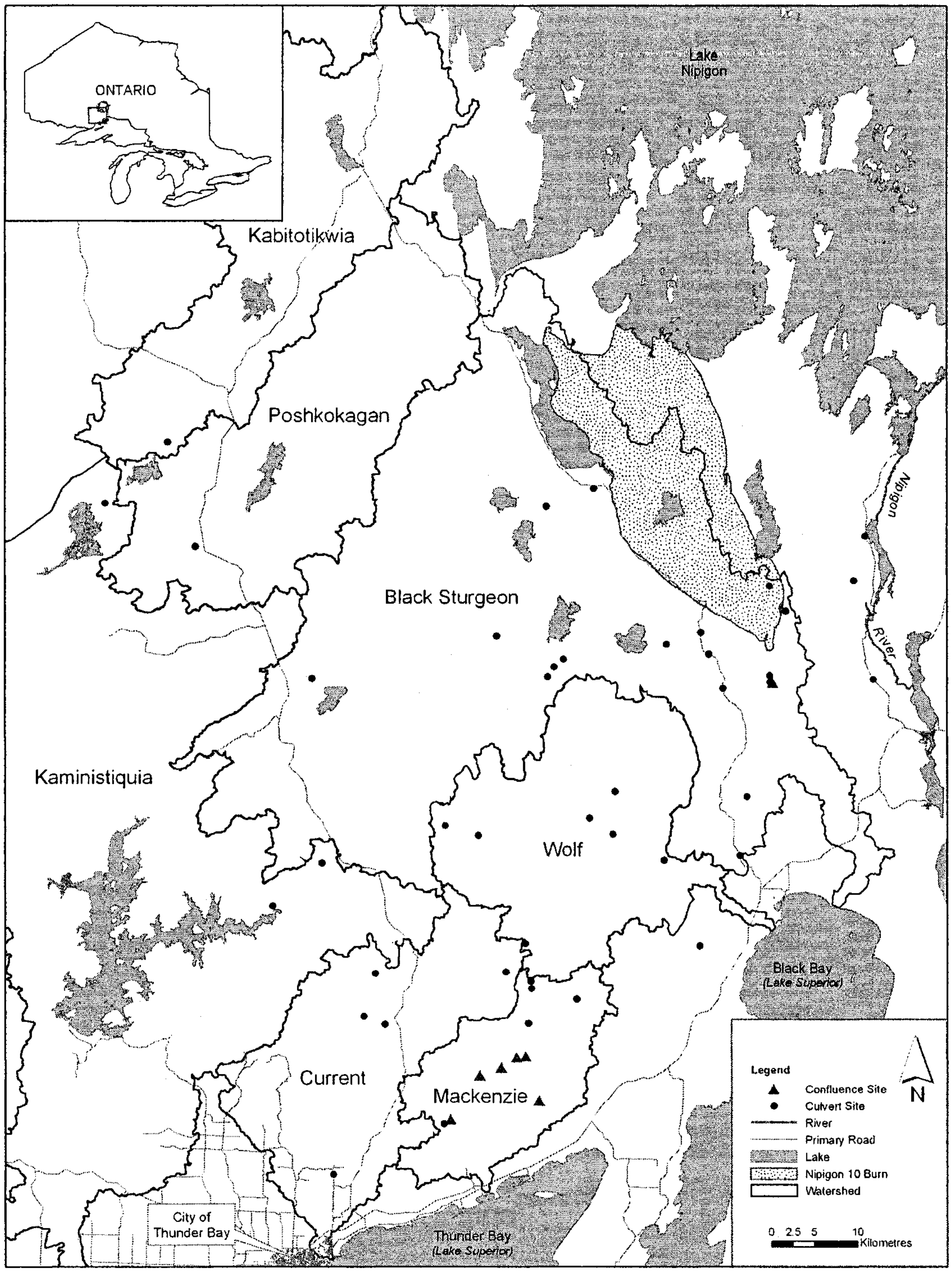

Figure 1. Study area, northeast of Thunder Bay, Ontario Canada.

The terrain is generally undulating with frequent steep to vertical slopes and rocky outcroppings with elevation ranging from 183-633 m (Wickware and Rubec 1989).

The Superior Highlands Ecoregion comprises a narrow corridor within the study area lying between Black Sturgeon Lake and Black Bay of Lake Superior. The bedrock is comprised of conglomerate and greywacke sedimentary rocks and diabase and granodiorite igneous rocks. Ground moraine and terminal moraines are the predominant surficial features in the region. The relief, like the other two ecoregions of the study area, is generally rolling and undulating with elevations ranging from 344-593 m (Wickware and Rubec 1989). The topography of the study area was formed primarily by glacial erosion and post-glacial sedimentation. Glacial action contributed various unconsolidated deposits to the present surface geology.

2.2 Site Selection and Sampling

Site selection began with the creation of a database of all of the forest access road stream crossings and confluences within the delineated watersheds in the study area using ARC/GIS software (version 9.1) (ESRI, Redlands, California). From the database of close to 2500 potential sites, approximately 500 sites were visited in person to determine their suitability for this study. I located 43 culvert sites and 7 confluences that met a standardized criteria in order to make comparisons within and between stream sizes and watersheds. The sites selected were assumed to be spatially independent, based on the fact that they were on separate tributaries and located in different sub-catchments. Watershed boundaries above each sampling site were delineated using a digital elevation model (25 m resolution) filled to eliminate sinks occurring in source elevation data (DEM version 1.1.0; Arcinfo Workstation Version 8.3). Provincial DEM data was provided by the Ontario Ministry of Natural Resources. Road density (m/km^2) was calculated from the DEM and used as a metric of landscape fragmentation. In order for a site to meet sampling criteria, it had to have at least 30 m of well defined stream channel below and above the culvert or confluence. A majority of the selected sites had enough continuous stream-channel to set up two 40 m reaches above and below. This reach length is approximately equal to 35 mean stream widths, depending on the complexity of the habitat and stream size. This distance typically encompasses three pool-riffle or two meander sequences (Leopold *et al.* 1964; Brazner *et al.* 2005) and ensures that the cumulative number of species captured has reached or exceeded an asymptotic level for the stream segment (Simonson and Lyons 1995). Unfortunately, several constraints including the proximity to wetlands, beaver ponds, dams, large pools, braided channels, geologic features and the complete absence of fish often voided potential sites or disallowed longer reach lengths, which limited the final number of sites used in the analysis.

Sampling was carried out from June through August when small streams in the study area are typically at or near base flow conditions. Each site survey included a one-pass electro-fishing survey conducted above and below the culvert or tributary; a habitat assessment, which both quantified and described the instream habitat structure and the riparian zone; stream discharge measurement; culvert measurements and road measurements and characteristics. Habitats were sampled the same day, or the day following electrofishing. Sampling procedures were identical at culvert and confluence sites, with the exceptions of culvert measurements.

2.3.1 Fish Assemblages

Fish were sampled by a three-person team using a single upstream pass with backpack electrofishing (Smith-Root, Inc. 1992, Model 15-B) gear along a reach. Before electrofishing, upstream and downstream ends of the survey reach were blocked using seine nets in order to prevent fish escape. Effort was made to thoroughly sample all habitats within a reach. At the end of each 40 m reach, all fish were identified, counted and batch weighed, except for brook trout which were weighed (g) and measured for total length (mm) individually and then released. Due the hybridization between northern redbelly dace (*Phoxinus eos*) and fincale dace (*Phoxinus neogaeus*), these species were collectively identified as *Phoxinus spp.* It was assumed that electrofishing sampled the entire size distribution of brook trout and all other species present.

The variability in fish community structure was assessed using species data summarized as species richness, species diversity (using Simpson's Diversity Index (1-*D*)), biomass (g/m^2), density (fish/m^2), and relative abundance (the abundance of a species (by any measure), divided by the total abundance of all species combined). Relative abundance is a dimensionless measure which helps to account for the relative change in species composition in response to differences in environmental factors. This approach tends to be more ecologically informative and comparable within and across streams with different fish densities (Brazner *et al.* 2005).

I also classified fish species in functional terms using a variety of autecological traits and guilds (Appendix II) that might be expected to respond to landscape and other environmental differences among streams (adapted from Poff and Allen 1995; Brazner *et al.* 2004). This approach is well suited to the comparison of taxonomically dissimilar assemblages and is the basis for much of comparative community ecology of stream fish. The functional perspective allows a more straightforward comparison of assemblages that are naturally dissimilar in taxonomy (Poff and Allen 1995). It is based on the theoretical expectation that species traits that promote local persistence will change along environmental gradients (Southwood 1977; Southwood 1988), thus perhaps giving rise to predictable rules of community composition (Poff and Allen 1995). Functional classifications were summarized as the proportion of fish within each class of a particular group at a given site.

2.3.2 Environmental Characteristics

Habitat variables (Appendix III.) including mean depth and wetted width were measured along transects perpendicular to stream flow, spaced 10 m apart along reaches below and above culverts and tributary junctions (Figure 2). Percent in-stream cover, substrate composition and over storey canopy closer was measured 5 m up and downstream of each transect (dashed line in Figure 2). Stream gradient (%) was measured using a clinometer every 10m in an upstream direction, to obtain a mean stream gradient along above and below stream reaches.

Water temperature was recorded above and below at the time of electrofishing. Temperature loggers were used to monitor temperature continuously at a subset of the sampling sites. Water temperature was recorded every four hours from May through October 2005 at five culvert and five confluence sites using temperature loggers mounted within 5 cm of the bottom of the stream at the middle of each reach, for a total of four loggers per site. (Onset Pendent Logger Onset Corp., Pocasset, Massachusetts). Water temperature was summarized as 7 and 21 day average maximums of continuously logged temperatures. Maximum averages represent periods with the highest average daily maximum temperatures based on calculations of all possible periods of 7 and 21 days during the study (Brazner *et al.* 2005).

Culvert characteristics including diameter, length, gradient, perched height, height above stream bottom, and plunge pool depth were measured at each site (Figure 3). Total stream discharge (m^3/s) was measured using a portable flow meter (Marsh-McBirney Inc., Flo-Mate model 2000) above and below culverts at the right-of-way which is defined as the cleared area along the road alignment which constrains the roadbed, ditches, road slopes and back slopes and below the tributary junction at confluence sites. A tape measure was placed perpendicular to the stream flow to form a transect and depth was recorded at 15 increments along each transect and velocity values were taken at 60% of the depth using the flow meter probe attached to a top-adjusting wading rod (Gallagher and Stevenson 1999).

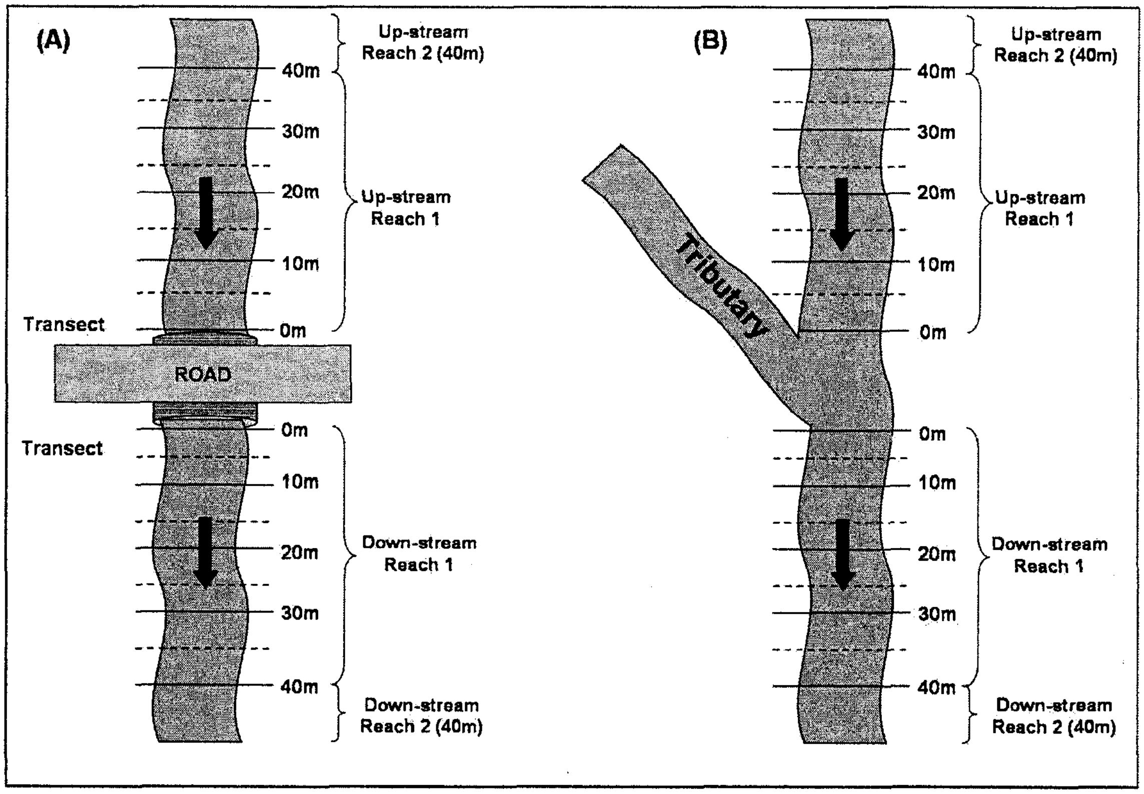

Figure 2. Site layout for culverts (A) and confluence (B) sites. Solid lines represent 10m segments, over which substrate composition was measured and dashed lines represent transects where water depth was measured.

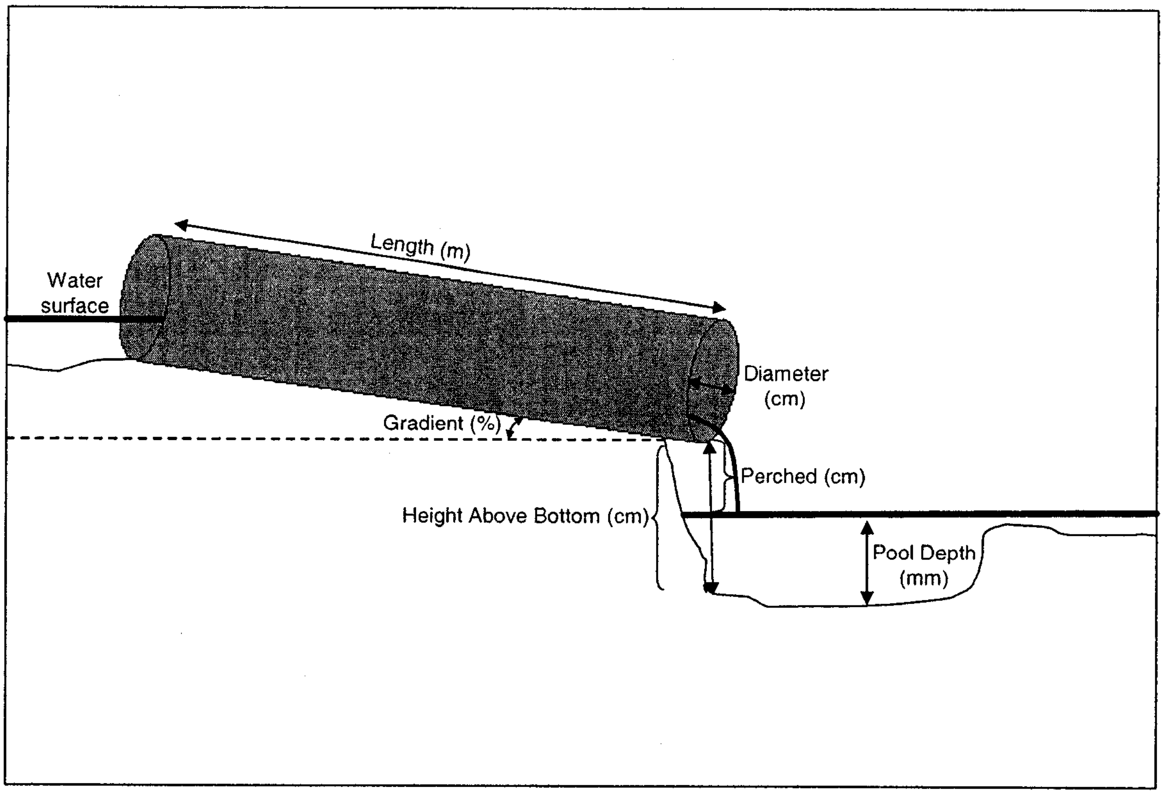

Figure 3. Schematic of culvert variables measured at each site.

2.4 Statistical Analysis Technique

2.4.1 Contrasting Above and Below

To evaluate differences in environmental characteristics and fish community structure above and below culverts and confluences I used a series of paired t-tests based on the differences between above and below at each site. The difference between parameter values above and below culverts was calculated by subtracting the values above from those below. The differences were summarized as high-low bar charts to illustrate the magnitude of difference above and below with respect to fish community structure and environmental variables. Positive values in the figures indicate that the measurement for the given variable was greater above compared to below and a negative value indicates that the measurement was higher below.

Linear regression was used to evaluate the degree of association between culvert variables and the magnitude of change in the difference in fish community structure between above and below culverts. Fish community structure metrics were regressed against culvert perched height, height above stream bottom, gradient, diameter and length.

2.4.2 Blocked Multiple Response Permutation Procedure

I used blocked multiple response permutation procedure (MRBP) to test the null hypothesis of no significant difference in overall species composition above and below culverts, using relative abundance data. The groups being compared were defined as above and below culverts and were blocked by site. A euclidean distance measure was used and an average distance function commensuration was applied to relativize the data, by equalizing the contribution of each variable to the distance function (McCune and Grace 2002).

MRBP is a non-parametric analogue of discriminant function analysis (DFA) suitable for paired-sample data that tests the null hypothesis of no significant difference between two or more groups (Zimmerman *et al.* 1985; McCune and Grace 2002). MRBP avoids many of the assumptions of DFA including distributional assumptions, which often make DFA inappropriate for certain types of ecological data (Zimmerman *et al.* 1985). MRBP is carried out by calculating the statistic delta (δ) which is the average distance between blocks within the treatments (groups). The expected delta is then calculated from the observed delta, by comparing it to a null distribution of deltas for all possible permutations of the samples into groups of equal size. A probability (p-value) of a delta smaller than the observed is calculated from the position of the observed deltas in the list of possible deltas and the associated test statistic T is calculated from a Pearson type III distribution derived from the probability. The greater the negative value of T is, the more the groups are separated. The p-value is useful for evaluating how likely it is that an observed difference is due to chance. The third statistic is the chance corrected within group agreement, denoted as A, which is calculated from the observed and expected deltas and measures the within-group homogeneity. If all items within a group are identical, then the observed delta = 0 and A = 1; conversely if the heterogeneity within the groups is equal to being expected by chance, then A = 0 (Zimmerman *et al.* 1985; McCune and Grace 2002).

2.4.3 Nonmetric Multidimensional Scaling Ordination

In order to assess the association between fish assemblages and watershed, and in-stream environmental gradients and help determine which environmental factors contributed the most to these associations, I employed a multivariate ordination procedure, nonmetric multidimensional scaling (NMS) using PC-ORD v.4 software (McCune and Grace 2002) to ordinate above and below stream segments in species space. NMS is a non-parametric, iterative ordination technique based on simple rank similarities among samples in the distance matrix and therefore avoids the assumptions of multivariate normality, common in other ordination methods and often violated by community data sets. NMS linearizes the relationship between environmental and species-based distances and effectively identifies responses to multiple environmental gradients without assuming linearity such as in principal components analysis or any underlying model of species response to gradients such as with correspondence analysis or canonical correspondence analysis (Kenkel and Orloci 1986; Faith *et al.* 1987; Brazner *et al.* 2005).

NMS analysis randomly positions the samples in an n-dimensional space, creating a distance matrix from the original n x p-dimensional main matrix where n is the number of rows, in this case sample sites and p is the number of columns, which in this case are species in the main matrix. This distance matrix is then refined using an iterative procedure that seeks a ranking and placement of n entities on k dimensions (axes) that minimize the stress of the k-dimensional solution. "Stress" is a measure of agreement between the dissimilarity (distance) in the original p-dimensional ordination space and distance in the reduced k-dimensional ordination space, where a stress value of zero indicates complete agreement (McCune and Grace 2002). NMS is unlike other ordination methods in that the number of axes is chosen in advance and the solution depends on the number of axes. Therefore the first axis of a three- dimensional solution may not correspond with the first axis of a two- or four- dimensional solution. In order to determine the appropriate number of axes for the ordination a general method is to calculate solutions for a number of dimensions, in this case axes one through six and then to plot stress against dimensionality (scree plot). Considering that stress is always lower in higher dimensional ordinations, the goal is then to select a number of axes beyond which reductions in stress are small.

Data were transformed (log n+1) to down-weigh the influence of abundant taxa and take into account rarer taxa as well. NMS analyses were run using the relative species abundance (($\log n + 1$) transformed) of 18 fish species above and below culverts, as well as the proportional abundance of fish in each functional group at a given site using PC-ORD v.4 autopilot mode (slow and thorough option) (McCune and Grace 2002), using Bray-Curtis dissimilarity as a distance measure to define sample ranks. Rainbow trout (*Oncorhynchus mykiss*) and Creek chub (*Semotilus atromaculatus*) were excluded from the analysis because they only occurred in small numbers at one site each. One through six dimensional solutions were calculated using random starting configurations, 40 runs with the real data and 50 runs with the randomized data. To evaluate the significance of the axes obtained from NMS runs, Monte Carlo permutation tests (100 simulations) were run to assess the probability that the sample scores in ordination space reflected a more accurate representation of the compositional similarity than could be obtained randomly ($p \leq 0.05$) (McCune and Grace 2002).

A Bray-Curtis distance measure was used as an after the fact means of calculating the proportion of variance represented by each of the three axes. Correlations between relative species abundance, environmental data, and the NMS axes were calculated as Kendall correlation to help assess which species and environmental variables may have the strongest influence on the differences among sites. Environmental variables and proportional abundances of fish functional groups that were most highly correlated with the ordination axes were plotted as vector overlays originating from the centre of the ordination plots, where the angle and length of the vectors reflect the direction and strength of the environmental variables (McCune and Grace 2002).

3.0 RESULTS

3.1 *Fish*

A total of 5920 individual fish comprising 20 species from nine families were captured at 43 culvert sites in 2004 (Table 1). Of all of the fish sampled 63.5% were captured downstream of culverts while 36.5% were captured upstream. Total relative abundance was greater below culverts compared to above (t= 2.729, df= 42, p= 0.009; Figure 4). Although total reach length above and below culverts did vary within and among sites (Appendix III), there was no statistically significant difference in reach length above and below culverts or confluence points. Species richness across all of the sites ranged from 0-10 species and was significantly higher below culverts, with an average of 3 species compared to above with an average of 2 (t= 3.875, df= 42, p<0.001; Figure 5). Species diversity did not differ significantly above and below culverts (Figure 6). Fish density averaged 0.86 fish/m^2 below culverts and 0.46 fish/m^2 above culverts (t= 2.936, df= 42, p= 0.005; Figure 7). Biomass below culverts averaged 1.27g/m^2 and 0.82g/m^2 above culverts (Figure 8). The mean values for each of the fish community metrics above and below culverts, along with the results from the transformed data paired t-test's, contrasting above and below are provided in Table 2.

Brook trout were caught at 14 of the 43 sites and on average, were generally more abundant and smaller below culverts compared to above. A higher total number of brook trout were captured below culverts (213 individuals) compared to above (144 individuals), and the average number of brook trout captured below culverts was 15.2 individuals and the average above culverts was 10.3 individuals, although the number caught among sites was quite variable (Figure 9).

Table 1. Summary of total fish captured at culvert sites during the summer of 2004.

Species	*Common name*	*Total catch*	*No. of sites*	*Total Down*	*Total Up*	*Range Down*	*Range Up*
Phoxinus spp.	Phoxinus	3284	29	1923	1361	0-305	0-211
Culaea inconstans	Brook stickleback	661	24	489	172	0-179	0-40
Margariscus margarita	Pearl dace	501	19	214	287	0-63	0-63
Salvelinus fontinalis	Brook trout	357	14	213	144	0-75	0-75
Rhinichthys atratulus	Longnose dace	229	9	211	18	0-119	0-5
Rhinichthys cataractae	Blacknose dace	191	4	173	18	0-153	0-17
Catostomus catostomus	Longnose sucker	183	3	162	21	0-157	0-18
Luxilus cornutus	Common shiner	142	11	99	43	0-29	0-19
Notropis hudsonius	Spottail shiner	110	2	57	53	0-48	0-27
Catostomus commersoni	White sucker	82	8	70	12	0-44	0-4
Notropis heterolepis	Blacknose shiner	54	9	48	6	0-21	0-5
Cottus cognatus	Slimy sculpin	44	5	42	2	0-18	0-1
Pimephales promelas	Fathead minnow	19	5	14	5	0-6	0-4
Esox lucius	Northern pike	19	5	11	8	0-5	0-4
Etheostoma exile	Iowa darter	12	6	10	2	0-5	0-2
Lota lota	Burbot	12	3	8	4	0-7	0-2
Umbra limi	Central mudminnow	10	1	7	3	0-7	0-3
Perca flavescens	Yellow perch	6	4	6	0	0-3	0
Semotilis atromaculatus	Creek chub	2	1	0	2	0-0	0-2
Oncorhynchus mykiss	Rainbow trout	2	1	2	0	0-2	0
Total		5,920	43	3,759	2,161		

Table 2. Paired t-test results contrasting log (n+1) transformed fish community and brook trout characteristics above and below culverts.

Fish	Mean Above	S.D. Above	Mean Below	S.D. Below	t	df	*p* (logn+1)
Relative Abundance	50.256	73.26	87.419	104.71	-2.729	42	<0.001
Species Richness	2.395	1.87	3.372	2.17	3.871	42	0.001
Species Diversity (1-*D*)	0.469	0.332	0.432	0.288	0.495	42	0.623
Fish Density (fish/m^2)	0.464	0.69	0.859	1.02	-2.936	42	0.001
Fish Biomass (g/m^2)	0.819	0.94	1.272	2.00	1.395	42	0.102
Brook Trout Abundance	12	20.66	17.417	22.63	1.448	11	0.175
Brook Trout Biomass	1.249	1.02	0.740	0.57	-1.871	9	0.089
Brook Trout Density	0.074	0.08	0.084	0.09	0.757	9	0.483
Brook Trout Mean Length (mm)	113.210	32.02	90.317	36.90	-3.321	9	0.007
Brook Trout Mean Weight (g)	37.414	41.63	19.819	23.57	-2.141	9	0.004

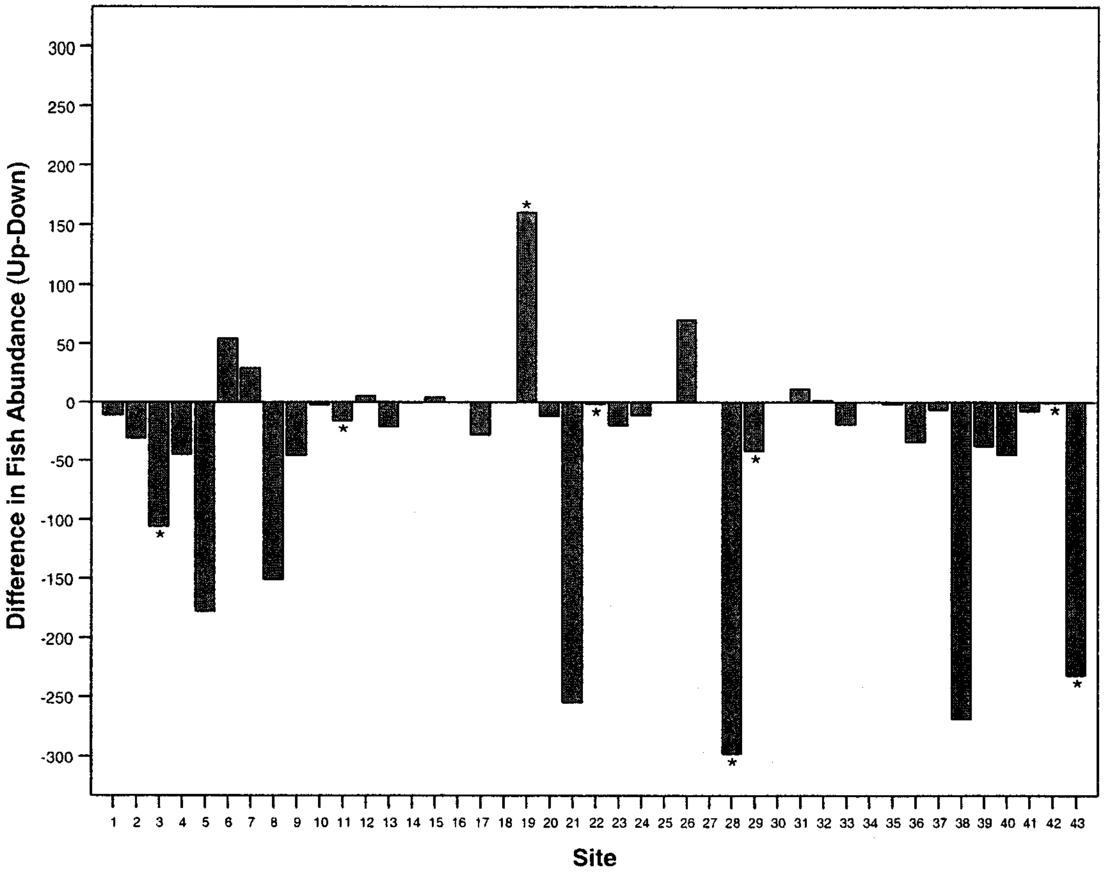

Figure 4. Difference in fish relative abundance calculated as the total relative fish abundance above culverts minus total relative abundance below culverts. Positive values indicate higher relative abundance above, while negative values indicate a higher relative abundance below. *= perched culverts.

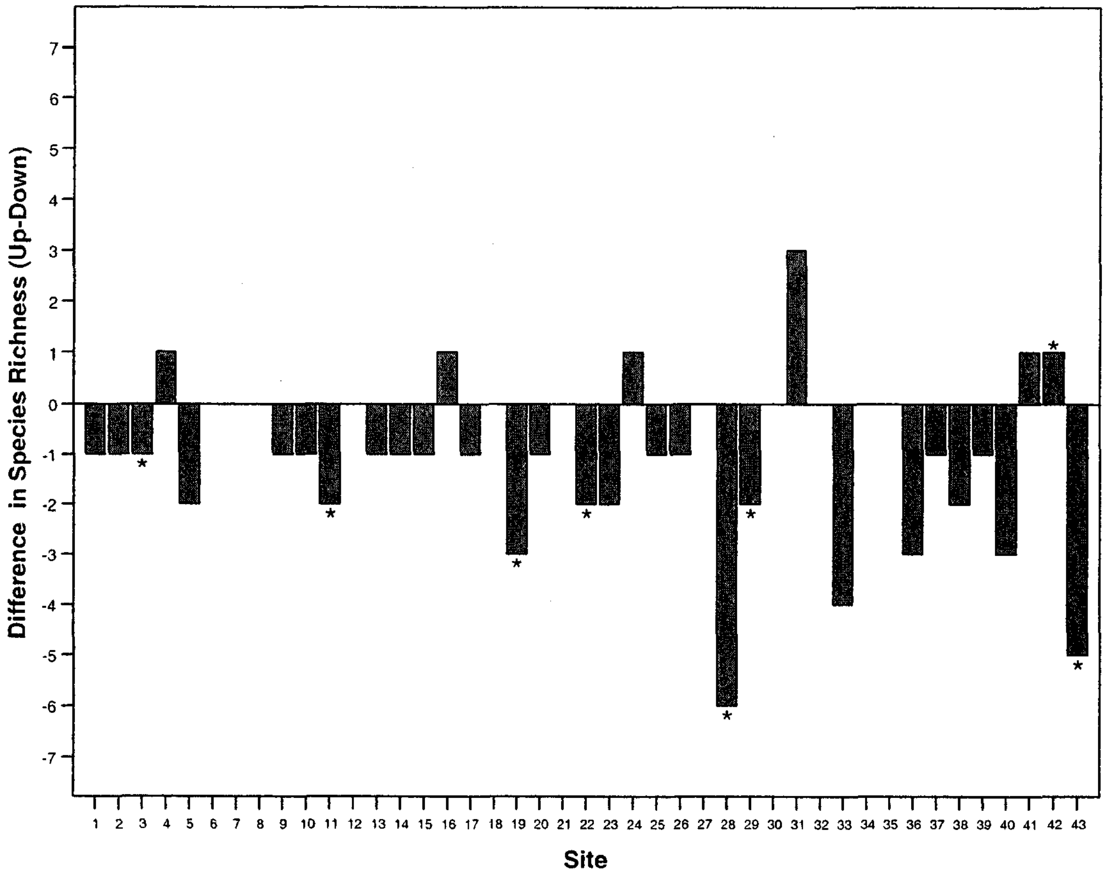

Figure 5. Difference in species richness calculated as the species richness above culverts minus species richness below culverts. Positive values indicate higher species richness above, while negative values indicate a higher species richness below. * = perched culverts.

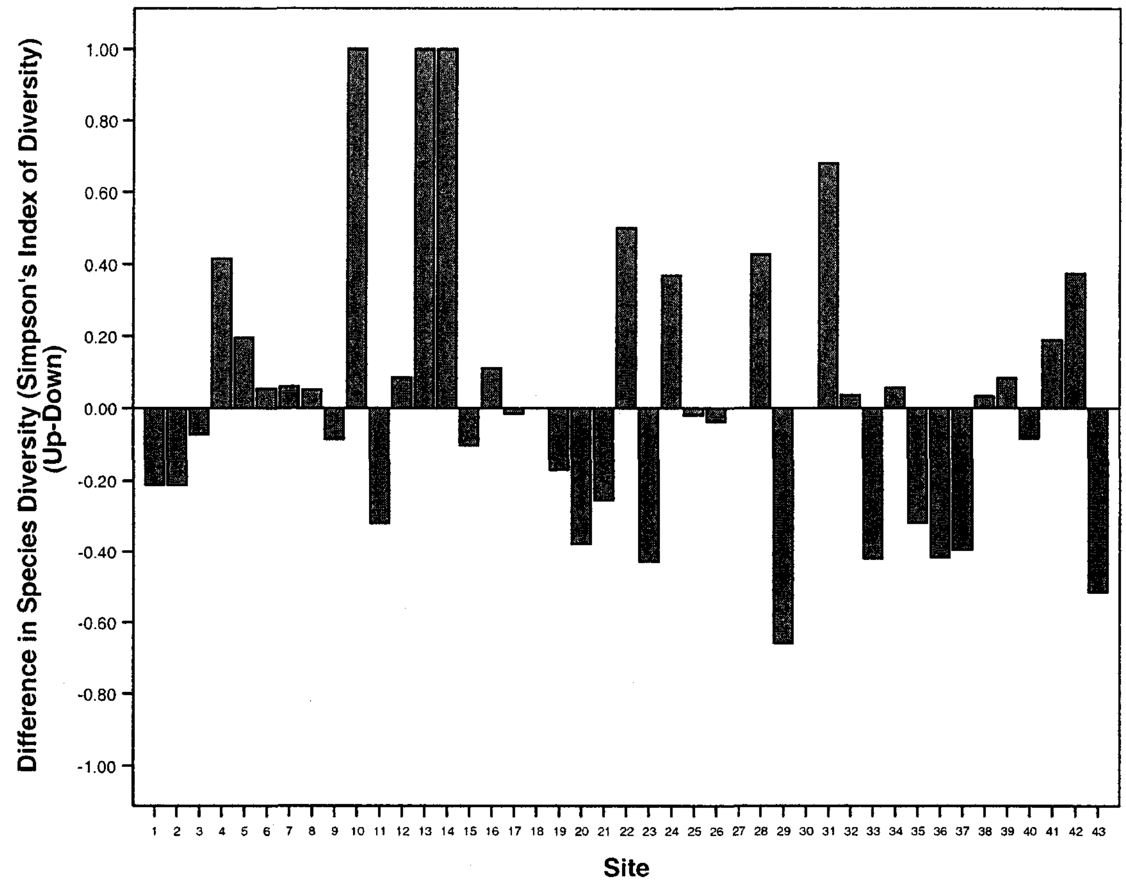

Figure 6. Difference in species diversity calculated as the Simpson's diversity index above culverts minus the diversity index below culverts. Positive values indicate higher species diversity above, while negative values indicate a higher species diversity below.

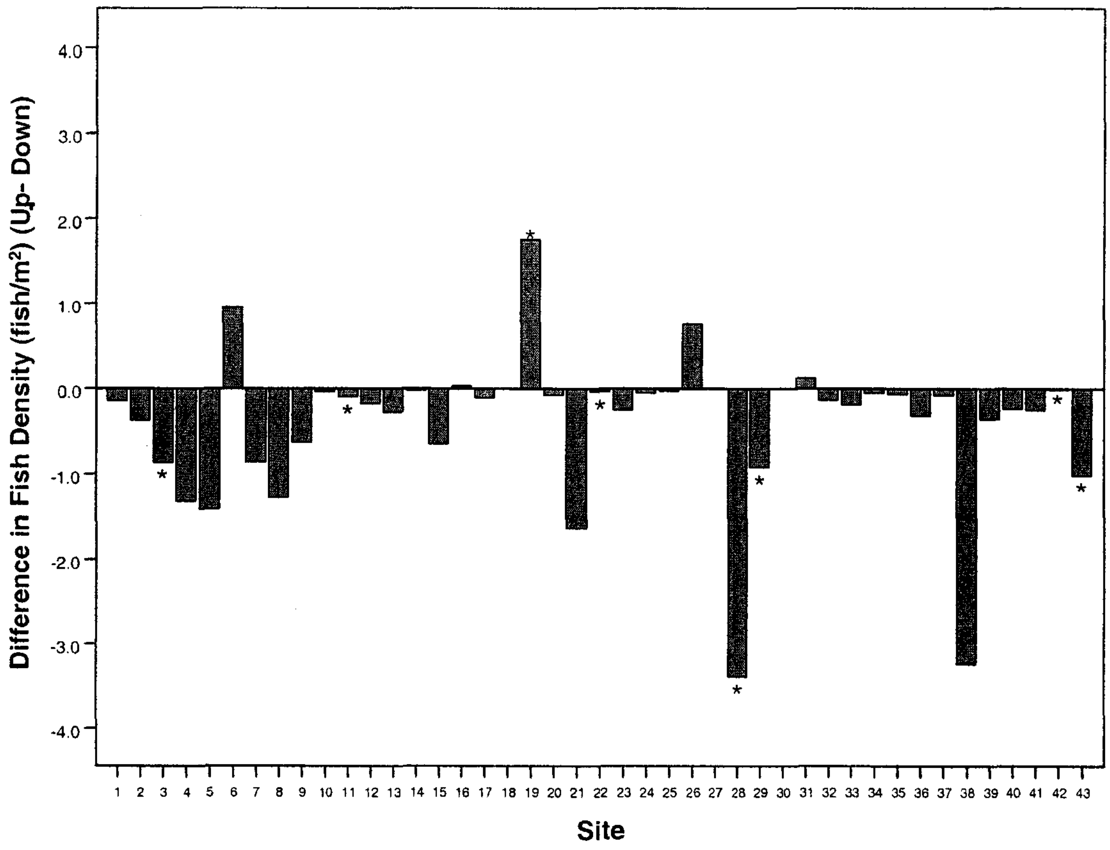

Figure 7. Difference in fish density (fish/m^2) calculated as the fish density above culverts minus fish density below culverts. Positive values indicate higher fish density above, while negative values indicate a higher fish density below. * = perched culverts.

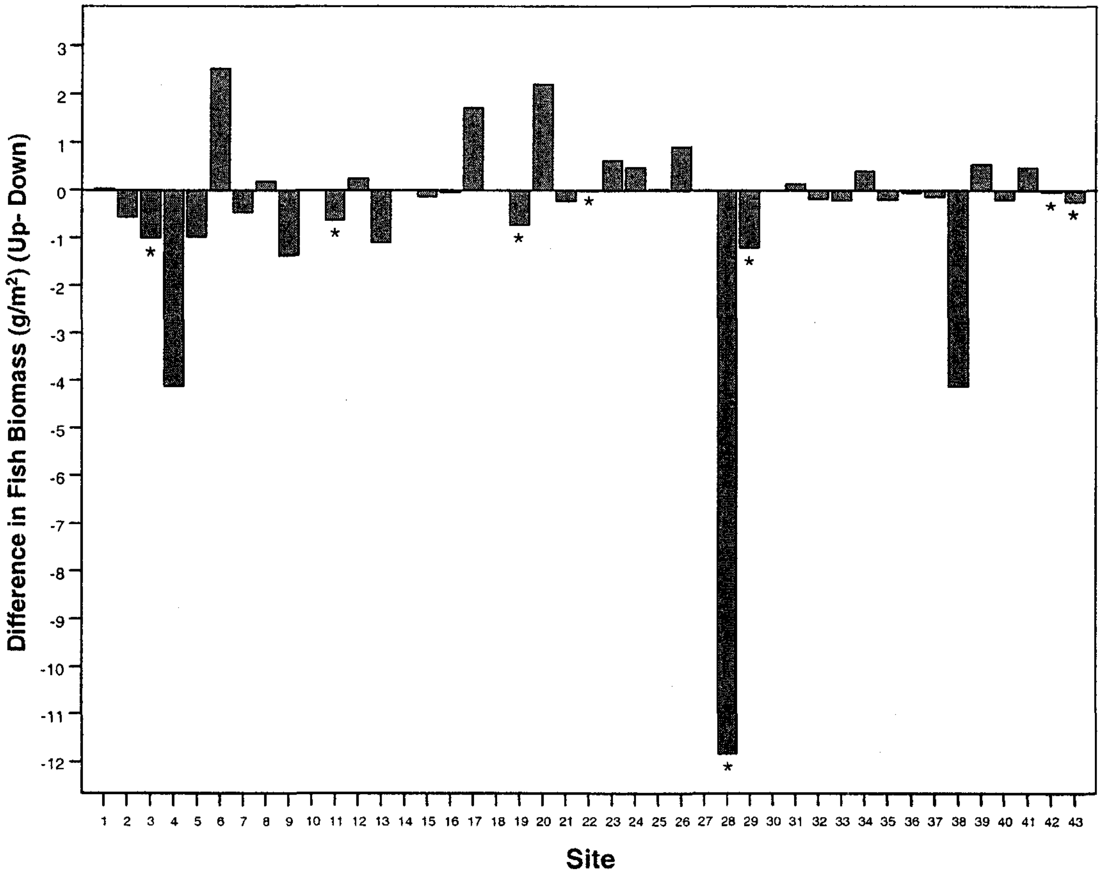

Figure 8. Difference in fish biomass (g/m^2) calculated as the fish biomass above culverts minus fish biomass below culverts. Positive values indicate higher fish biomass above, while negative values indicate a higher fish biomass below. *= perched culverts.

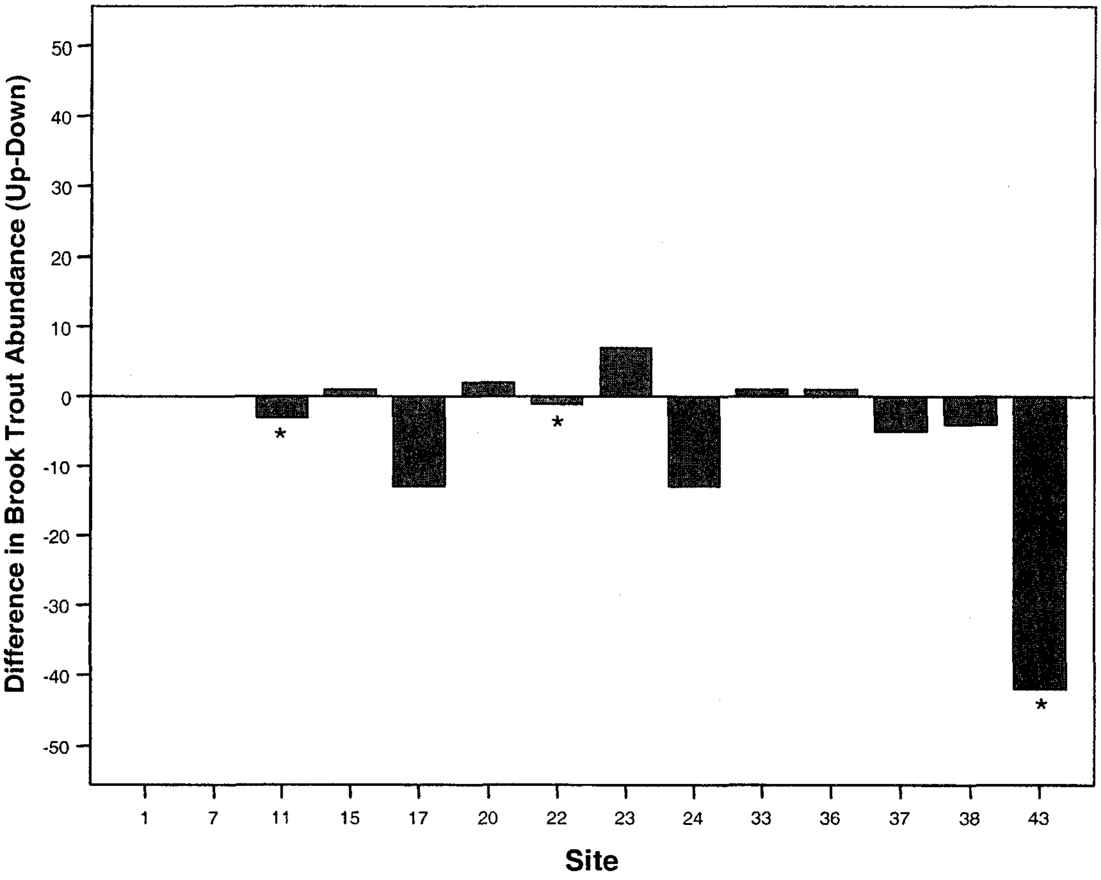

Figure 9. Difference in brook trout total abundance calculated as the abundance of brook trout above culverts minus the abundance of brook trout below culverts. Positive values indicate higher abundance above, while negative values indicate a higher abundance below. *= perched culverts.

The mean weight of brook trout caught in reaches above culverts, was 37.414g and 19.819g below ((log *n*+1) t= 3.504, df= 9, p= 0.007; Figure 10). The mean length of brook trout caught in reaches above culverts was 113.210mm and 90.137mm below ((log *n*+1) t=3.887, df= 9, p= 0.004; Figure 11). Brook trout biomass averaged 1.25g/m^2 above culverts and 0.74g/m^2 below culverts (Figure 12) and the average brook trout density was similar above and below culverts (0.074 fish/m^2 and 0.084 fish/m^2 respectively) (Figure 13).

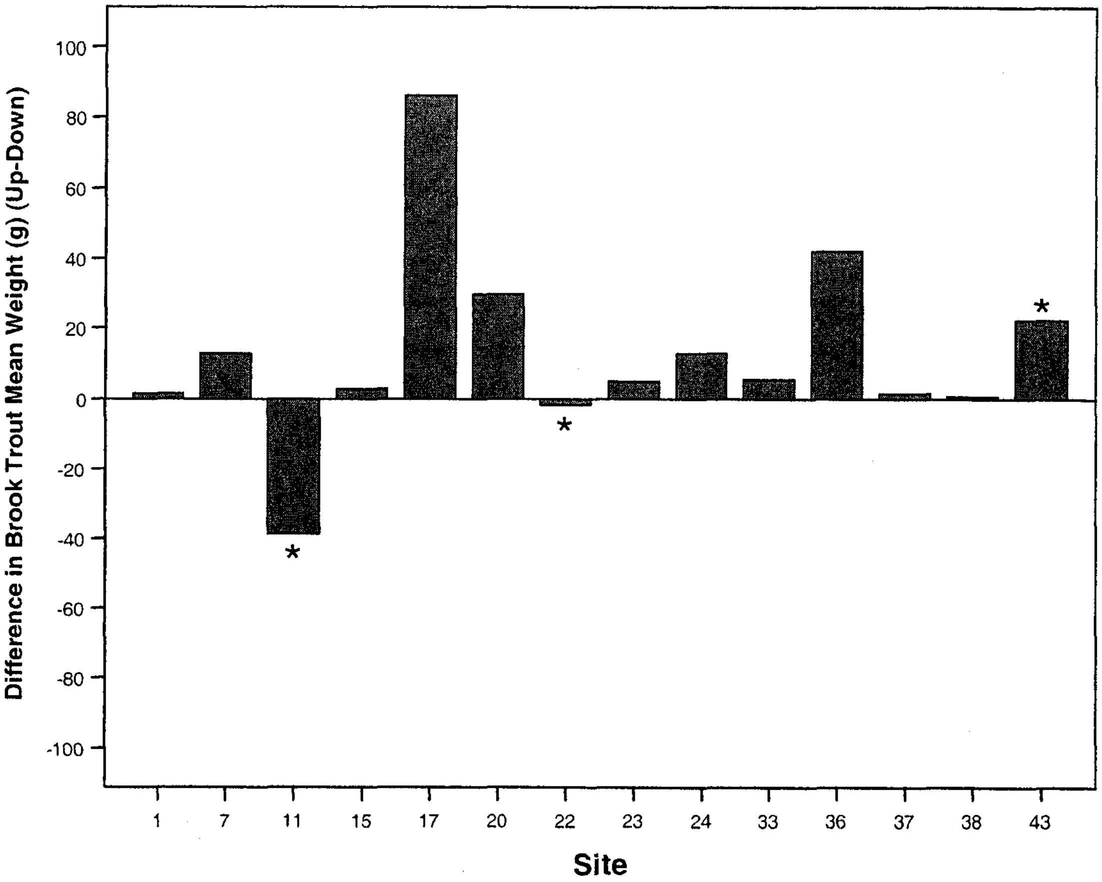

Figure 10. Difference in mean brook trout weight (g) calculated as the mean brook trout weight above culverts minus the mean brook trout weight below culverts. Positive values indicate higher mean weight above, while negative values indicate a higher mean weight below. *= perched culverts.

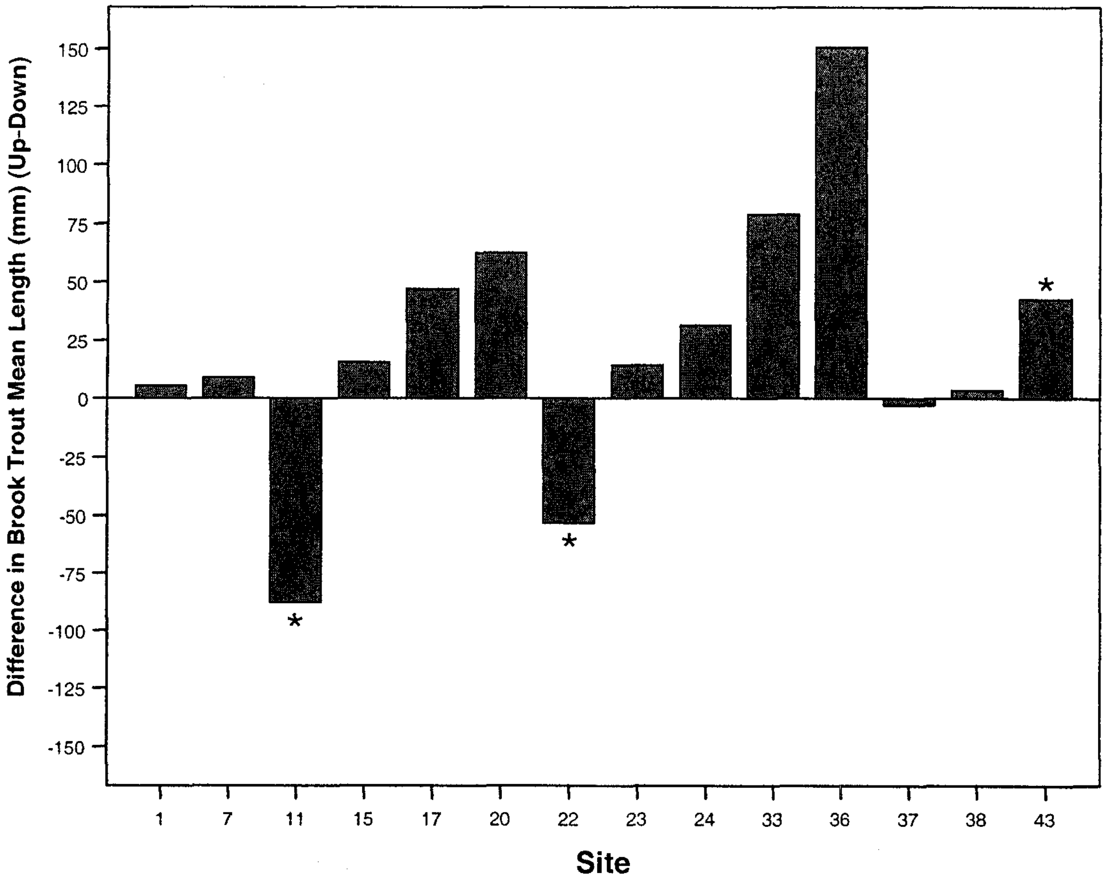

Figure 11. Difference in mean brook trout length (mm) calculated as the mean brook trout length above culverts minus the mean brook trout length below culverts. Positive values indicate higher mean length above, while negative values indicate a higher mean length below. *= perched culverts.

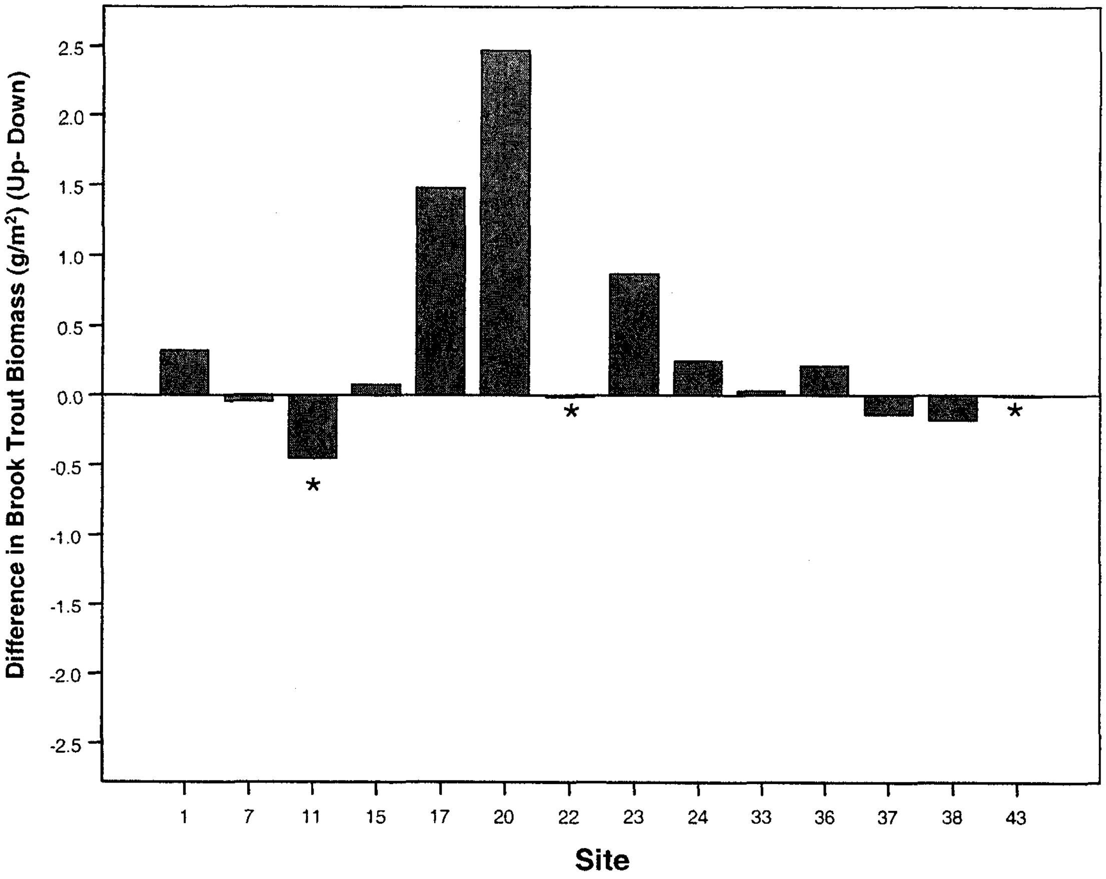

Figure 12. Difference in total brook trout biomass (g/m^2) calculated as the total brook trout biomass above culverts minus total brook trout biomass below culverts. Positive values indicate higher total biomass above, while negative values indicate a higher total biomass below. *= perched culverts.

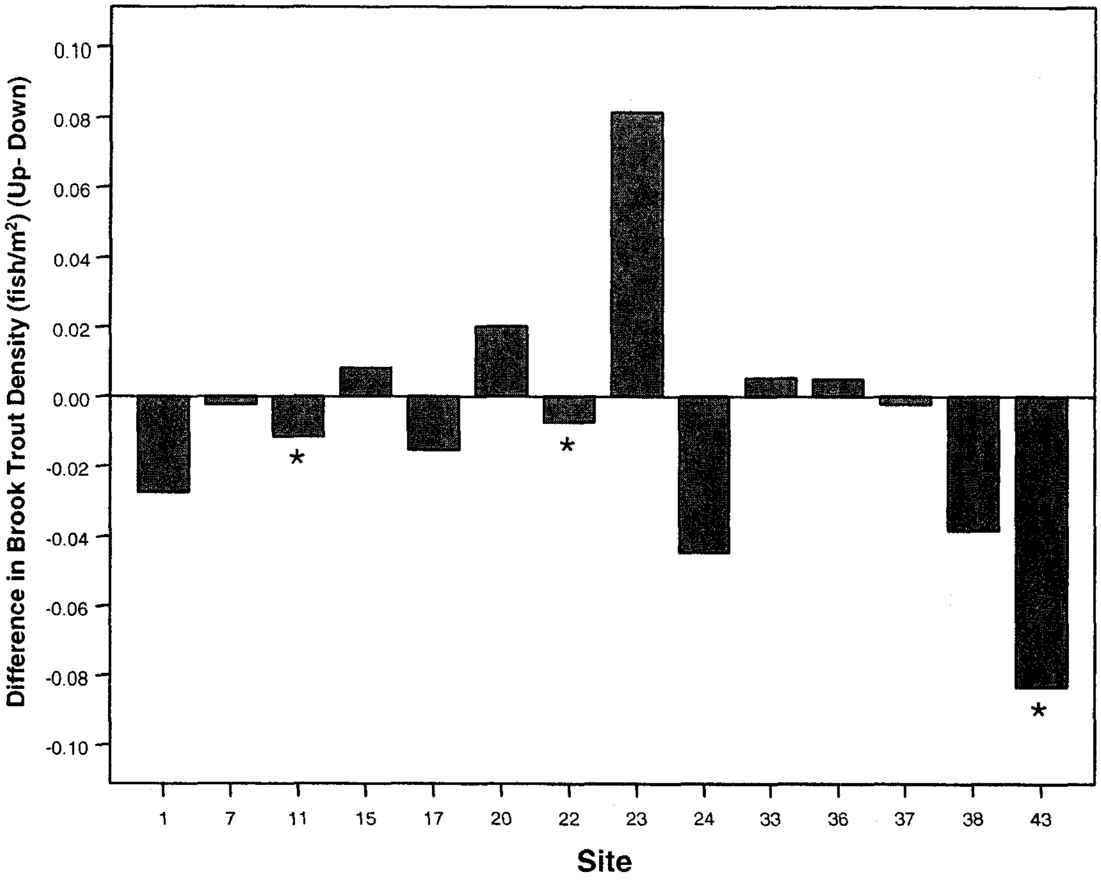

Figure 13. Difference in brook trout density (fish/m^2) calculated as the brook trout density above culverts minus brook trout density below culverts. Positive values indicate higher density above, while negative values indicate a higher density below. *= perched culverts.

3.2 *Culverts*

Of the 43 culverts sites sampled in 2004 (Appendix III), eight were perched at the time of sampling. Perched height ranged from 15 to 46 cm above the stream surface. Only one of the perched culvert sites did not have fish above the culvert. Other than the perched culverts, the outlets of 17 of the 43 culverts did not rest on stream bottom. The height above stream bottom for these culverts ranged from 4 to 42 cm and averaged 19cm. Culvert gradient ranged from less than 1 to 4.8%. Of the 43 culverts 19 had gradients less than 1%. In general there were very weak relationships between culvert variables and the magnitude of the difference in species richness, density and biomass above and below culverts.

When culvert variables were individually regressed against the difference in above and below culvert fish community characteristics at each site, perched height and height above stream bottom were the only two culvert variables that had statistically significant associations with any of the community characteristics. The magnitude of the difference in species richness between above and below tended to be greater for culverts with greater perched height (r^2= 0.151, p= 0.010; Figure 14a) and eight of the nine perched culverts had higher richness below culverts. The magnitude of the difference in species richness between above and below also tended to be greater for culverts with greater height above stream bottom (r^2= 0.129, p= 0.018; Figure 14b) but the relationship is very weak. Fish biomass and density had a weak but similar association with perched height and height above stream bottom (Figures 15 and 16). Culvert gradient, diameter and length had even weaker associations with species richness, biomass and density than perched height and height above stream bottom (Figures 17, 18 and 19). The tendency for higher species richness, density and biomass below culverts compared to above did not show a consistent relationship with any of the culvert variable in the regression model.

3.3 *Confluences*

The seven confluence sites sampled in 2005 yielded 2171 individual fish from five families and seven species (Table 3). Of all fish sampled 72.6% were captured downstream of the tributary junction and 27.36% were captured upstream. There was no statistically significant difference when comparing fish community structure above and below confluences (Figures 20-24). However, the low sample size underlying the confluence comparisons and the resulting lower statistical power may also contribute to the lack of differences upstream versus downstream. Unlike above and below culverts, there was no statistically significant difference in the mean relative abundance, richness, density or biomass of fish caught above and below confluence points. The lack of difference between above and below suggests that in the absence of a potential barrier, distribution is more continuous throughout sample reaches.

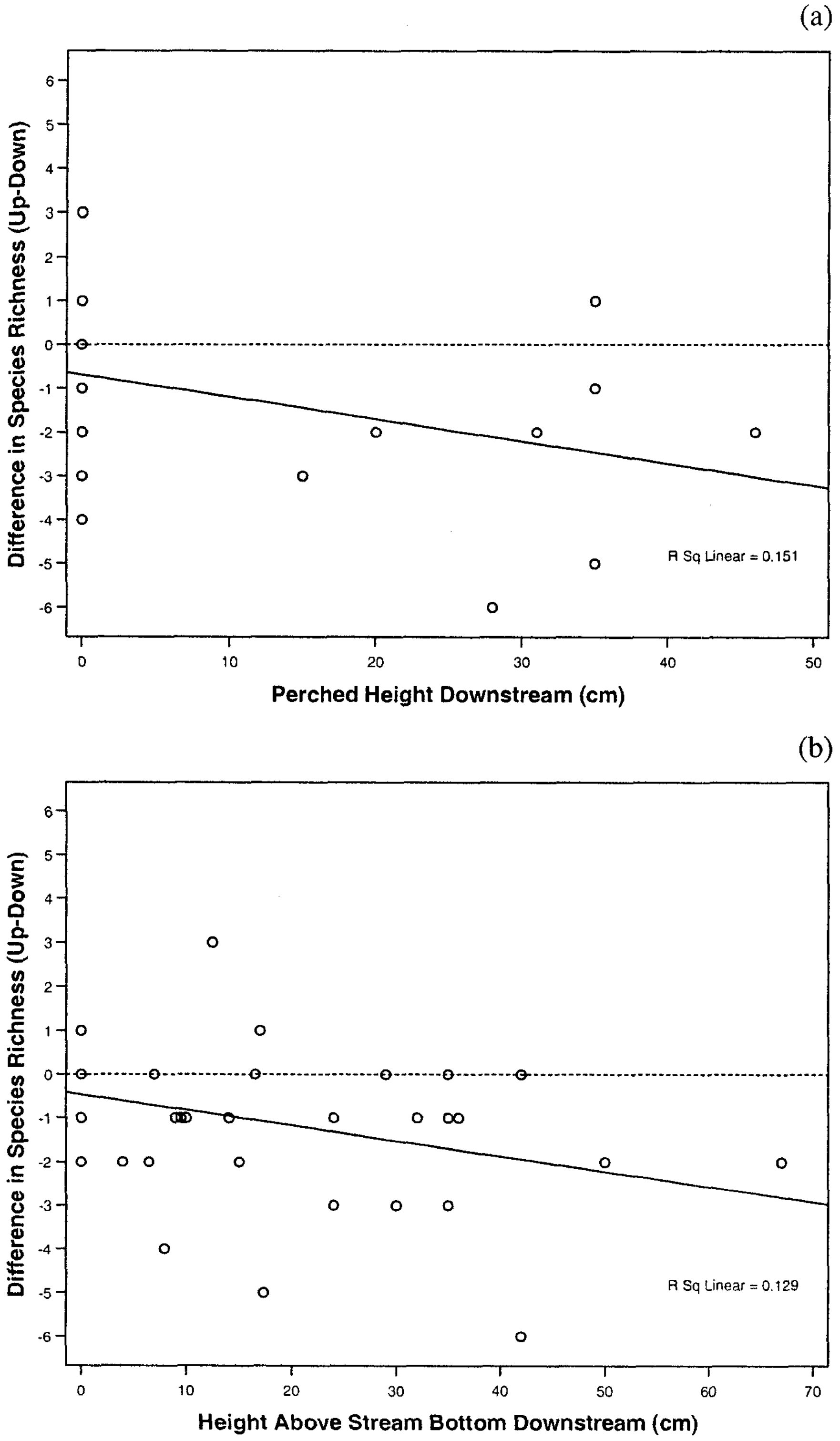

Figure 14. Difference in species richness above and below culverts regressed against (*a*) culvert perched height (cm) and (*b*) height above stream bottom (cm). Positive values indicate higher species richness above, while negative values indicate a higher species richness below.

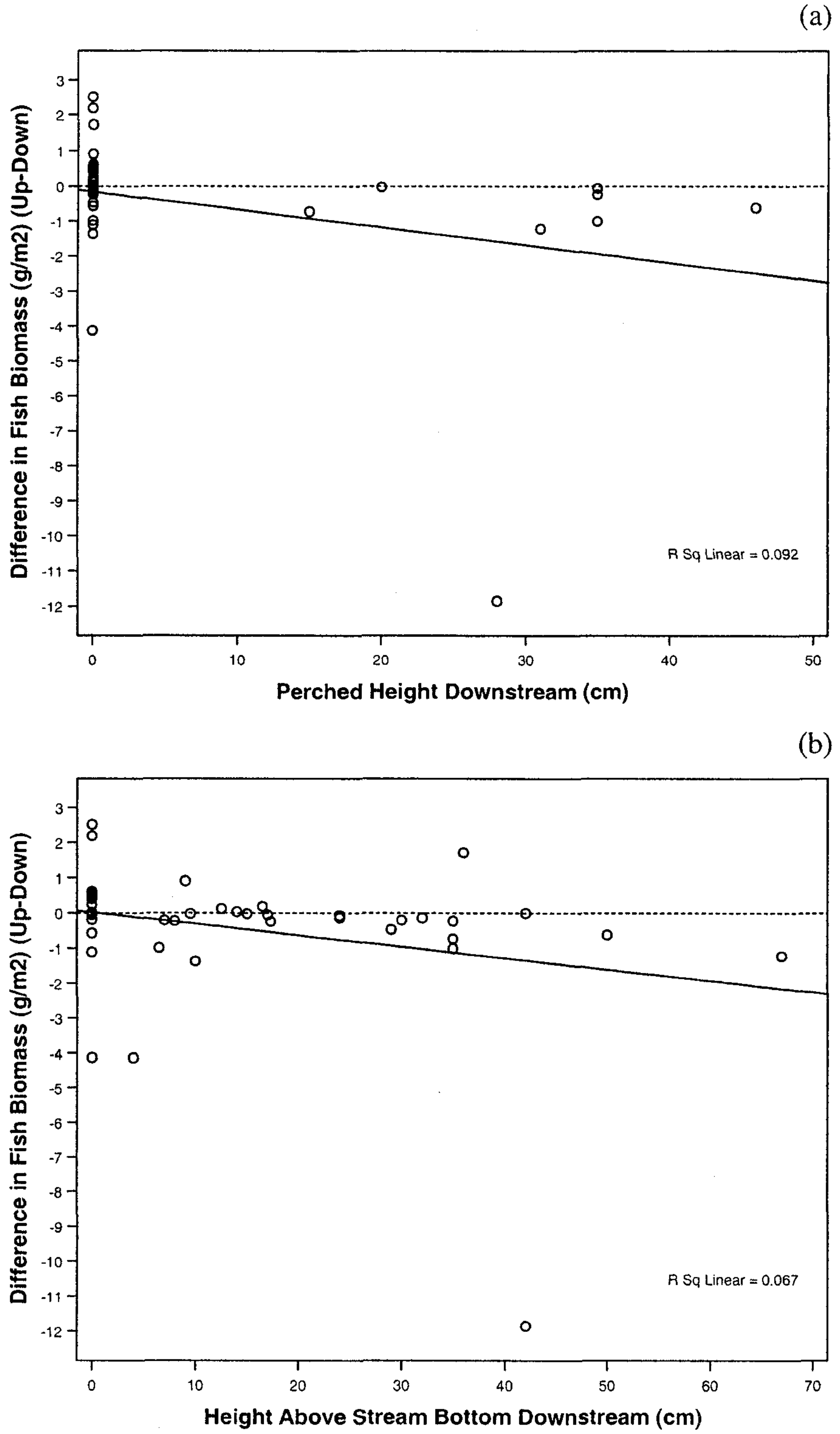

Figure 15. Difference in fish biomass (g/m^2) above and below culverts regressed against culvert (*a*) perched height (cm) and (b) height above stream bottom (cm). Positive values indicate higher biomass above, while negative values indicate higher biomass below.

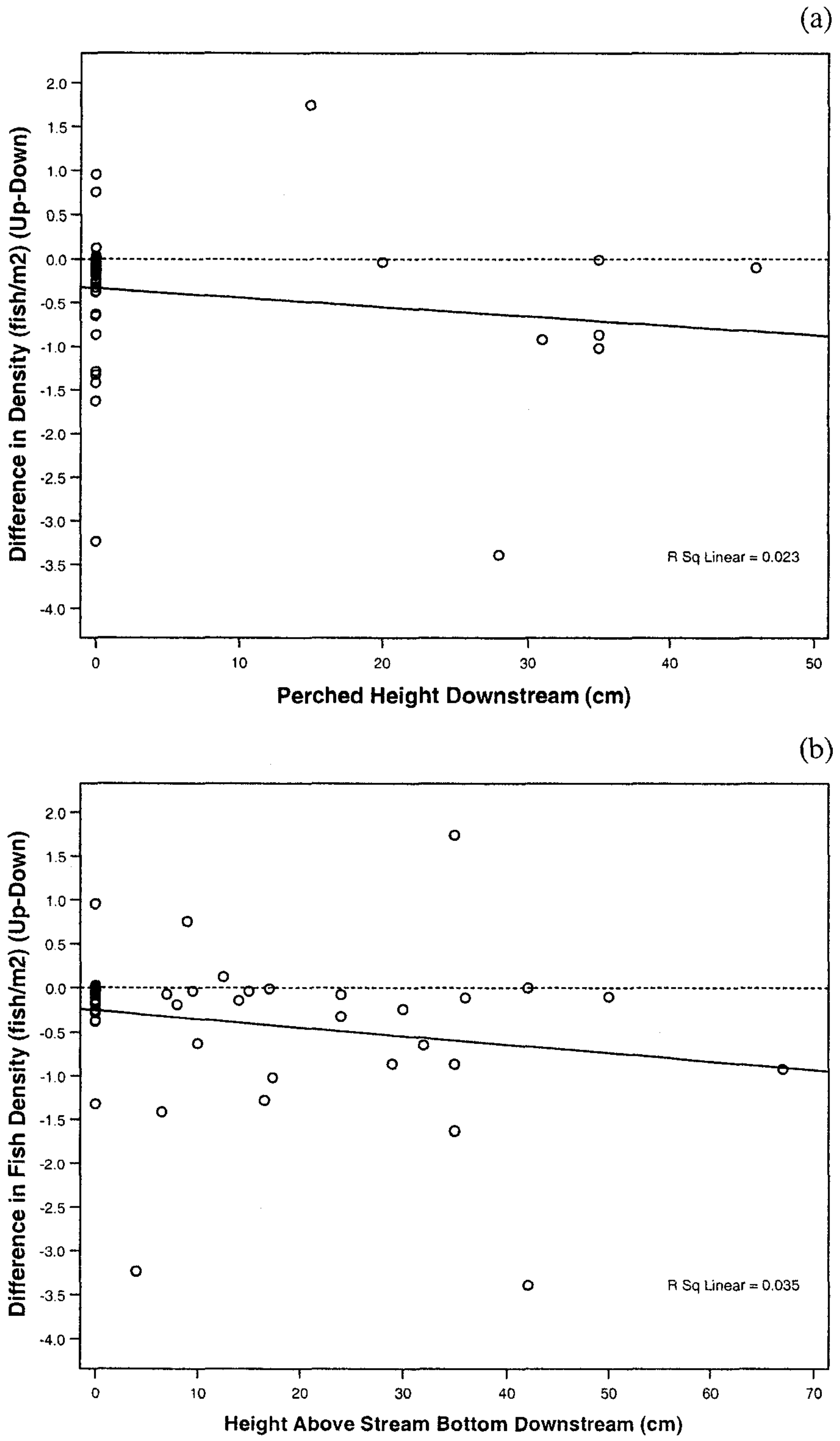

Figure 16. Difference in fish density (fish/m^2) above and below culverts regressed against (*a*) culvert perched height (cm) and (*b*) height above stream bottom (cm). Positive values indicate higher biomass above, while negative values indicate higher density below.

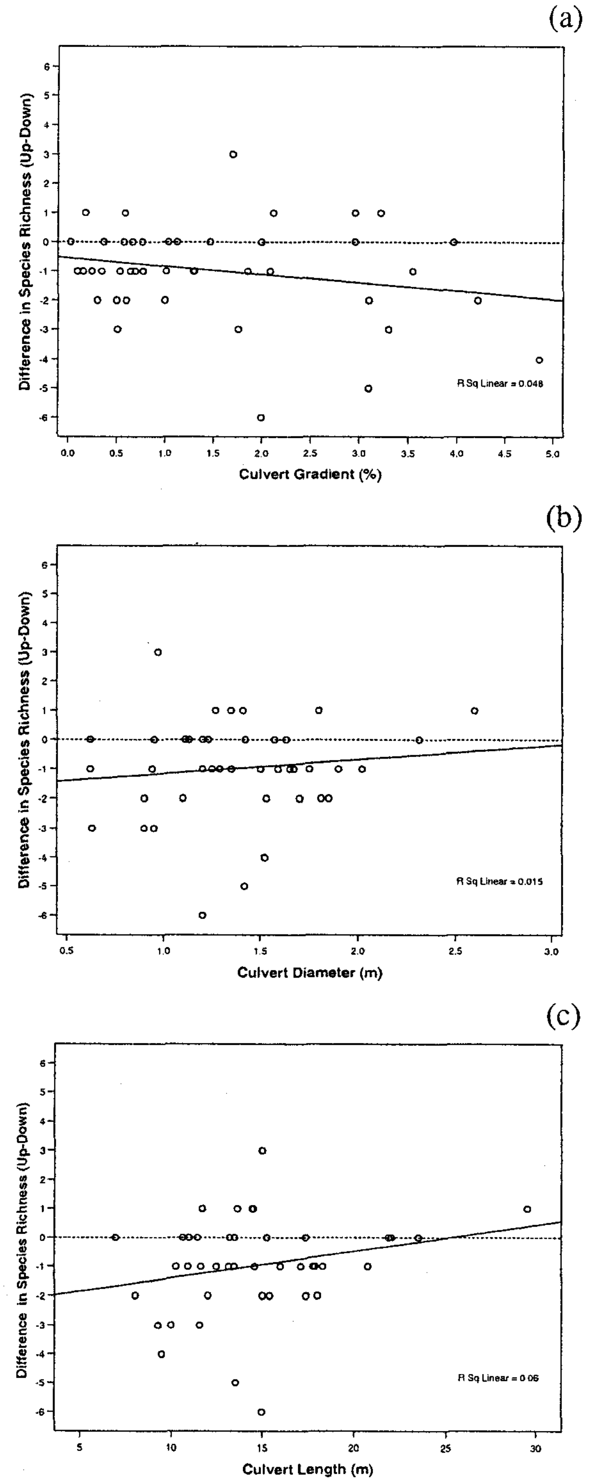

Figure 17. Difference in species richness above and below culverts regressed against culvert (*a*) gradient (%), (*b*) diameter (cm) and (*c*) length (m). Positive values indicate higher species richness above, while negative values indicate a higher species richness below.

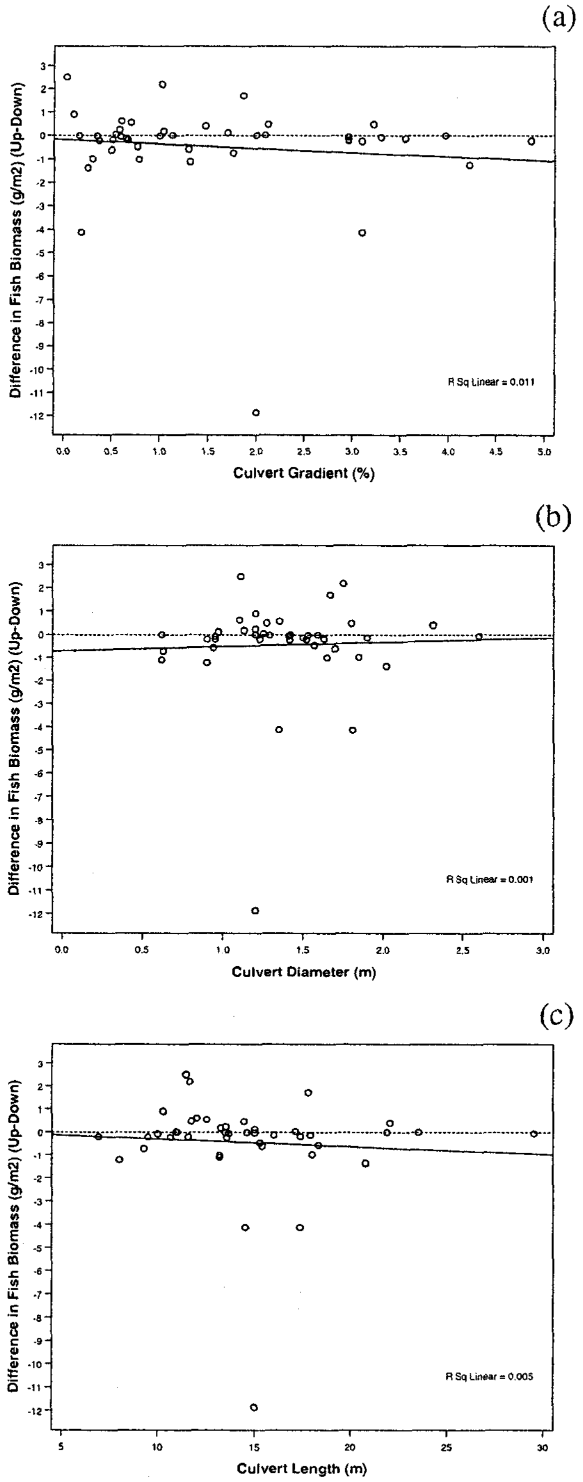

Figure 18. Difference in fish biomass (g/m^2) above and below culverts regressed against (*a*) culvert gradient (%), (*b*) diameter (cm) and (*c*) length (m). Positive values indicate higher biomass above, while negative values indicate higher biomass below.

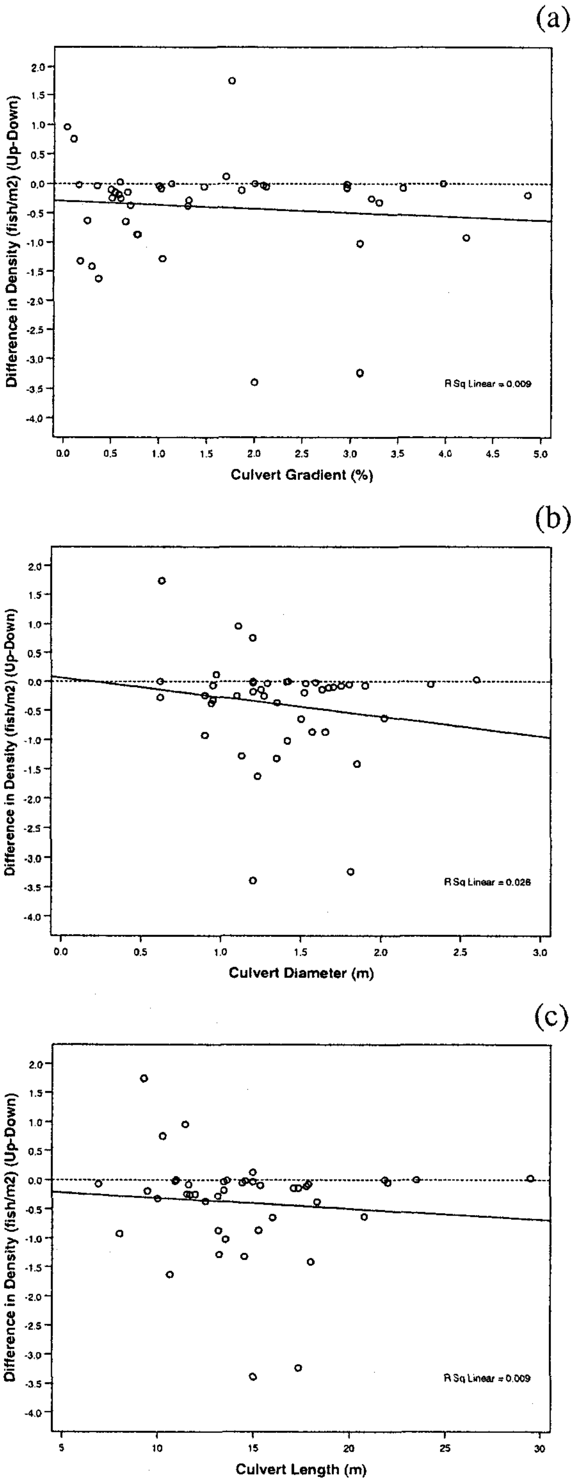

Figure 19. Difference in fish density (fish/m^2) above and below culverts regressed against (*a*) culvert gradient (%), (*b*) diameter (cm) and (*c*) length (m). Positive values indicate higher biomass above, while negative values indicate higher biomass below.

Table 3. Summary of total fish captured at confluence sites during the summer of 2005.

Species	Total Catch	No. of Sites	Total Down	Total Up	Range Down	Range up
Brook trout	111.00	4.00	85.00	26.00	0-41	0-14
Longnose sucker	1.00	1.00	1.00	0.00	0-1	0
Longnose dace	13.00	2.00	4.00	9.00	0-2	0-8
Pearl dace	13.00	2.00	4.00	9.00	0-3	0-9
Phoxinus	929.00	4.00	682.00	247.00	0-559	0-153
Brook stickleback	155.00	4.00	112.00	43.00	0-106	0-38
Slimy Sculpin	7.00	1.00	7.00	0.00	0-7	0

Table 4. Paired t-test results contrasting fish community characteristics above and below confluence points.

Fish	Mean Above	S.D. Above	Mean Below	S.D. Below	t	df	*p* (logn+1)
Relative Abundance	47.714	68.532	127.857	240.311	-1.215	6	0.180
Species Richness	1.857	1.069	2.429	1.512	-1.188	6	0.299
Species Diversity	0.253	0.277	0.222	0.241	0.267	6	0.779
Density (fish/m^2)	0.341	0.485	0.502	0.865	-1.008	6	0.335
Biomass (g/m^2)	0.568	0.510	0.960	0.816	-2.383	6	0.060

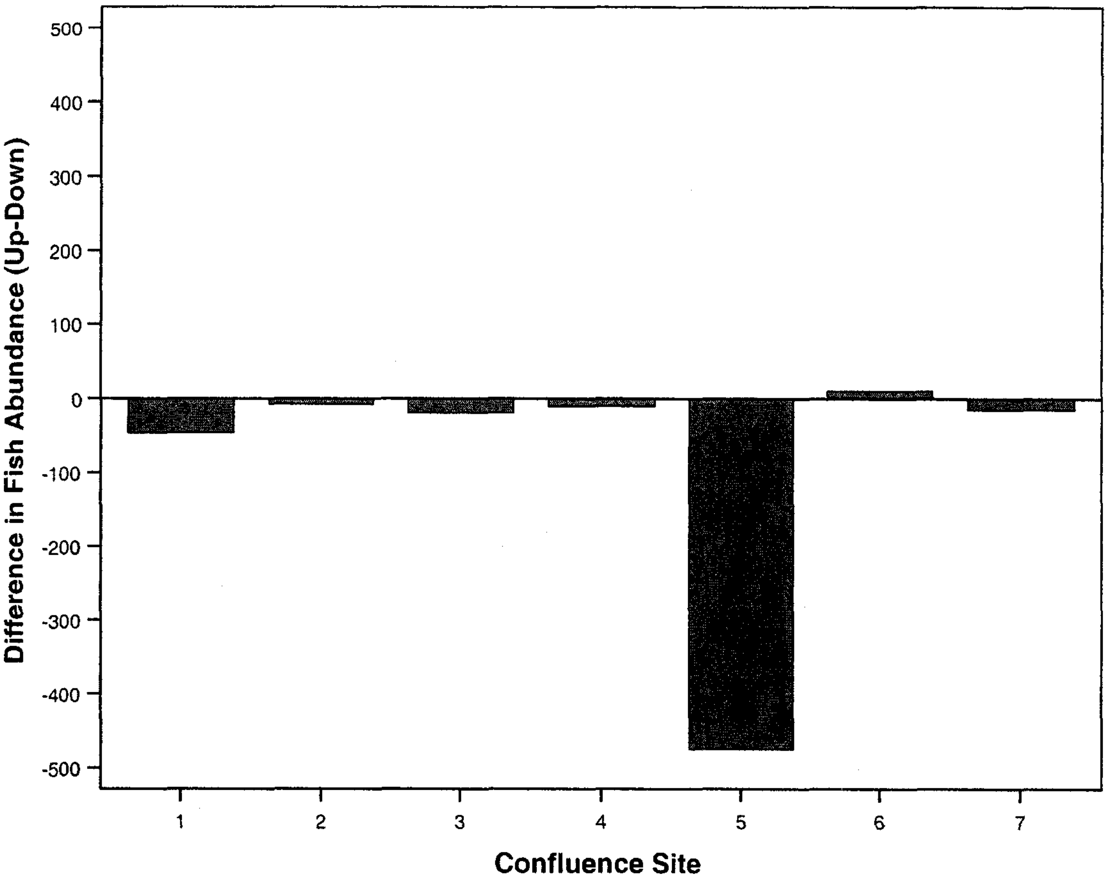

Figure 20. Difference in fish relative abundance calculated as the relative abundance above confluence points minus the relative abundance below confluence points. Positive values indicate higher relative abundance above, while negative values indicate a higher relative abundance below.

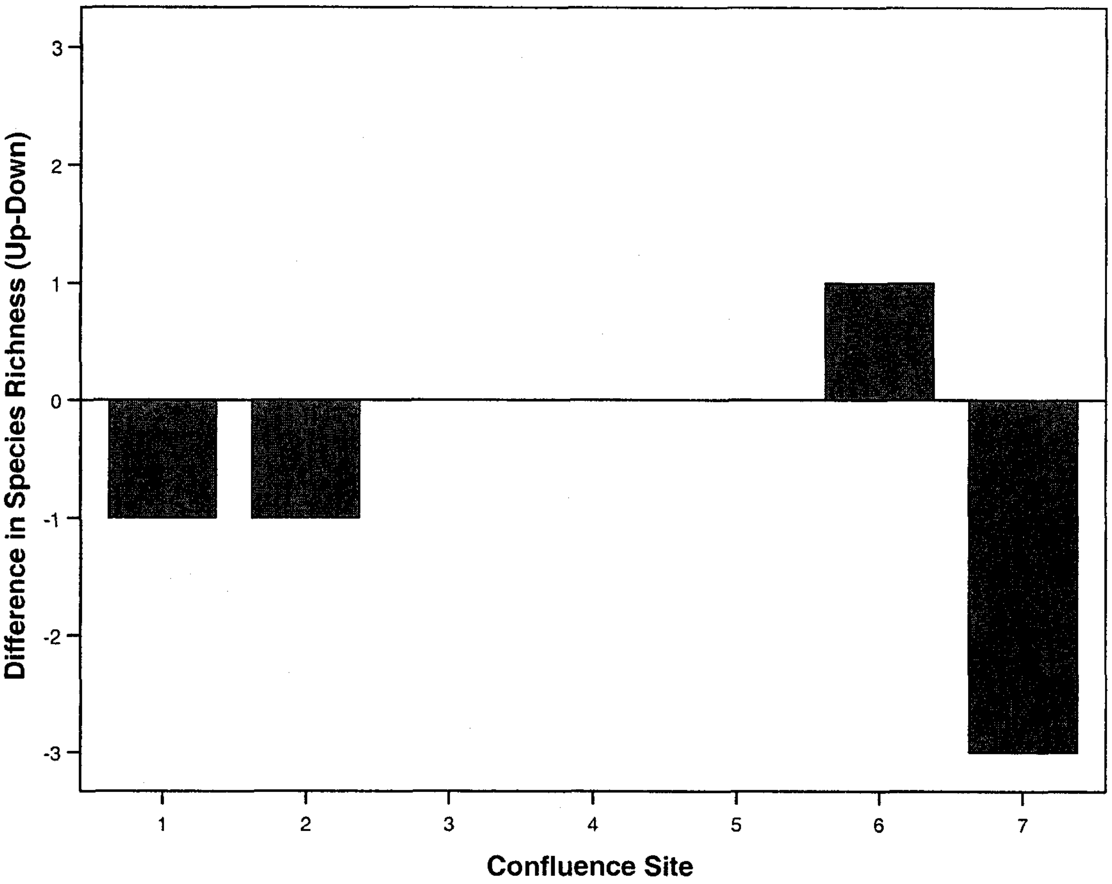

Figure 21. Difference in species richness calculated as the species richness above confluence points minus the species richness below confluence points. Positive values indicate higher species richness above, while negative values indicate a higher species richness below.

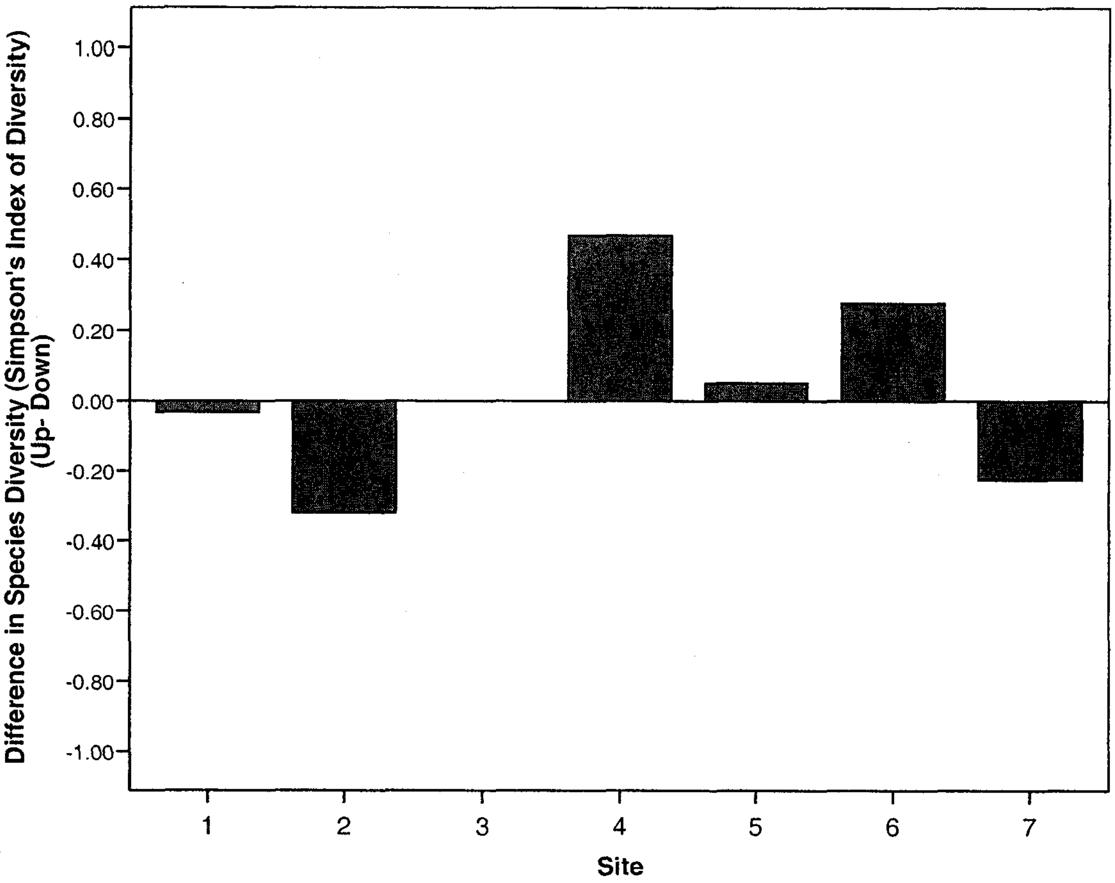

Figure 22. Difference in species diversity calculated as the Simpson's diversity index above confluence points minus the diversity index below confluence points. Positive values indicate higher species diversity above, while negative values indicate a higher species diversity below

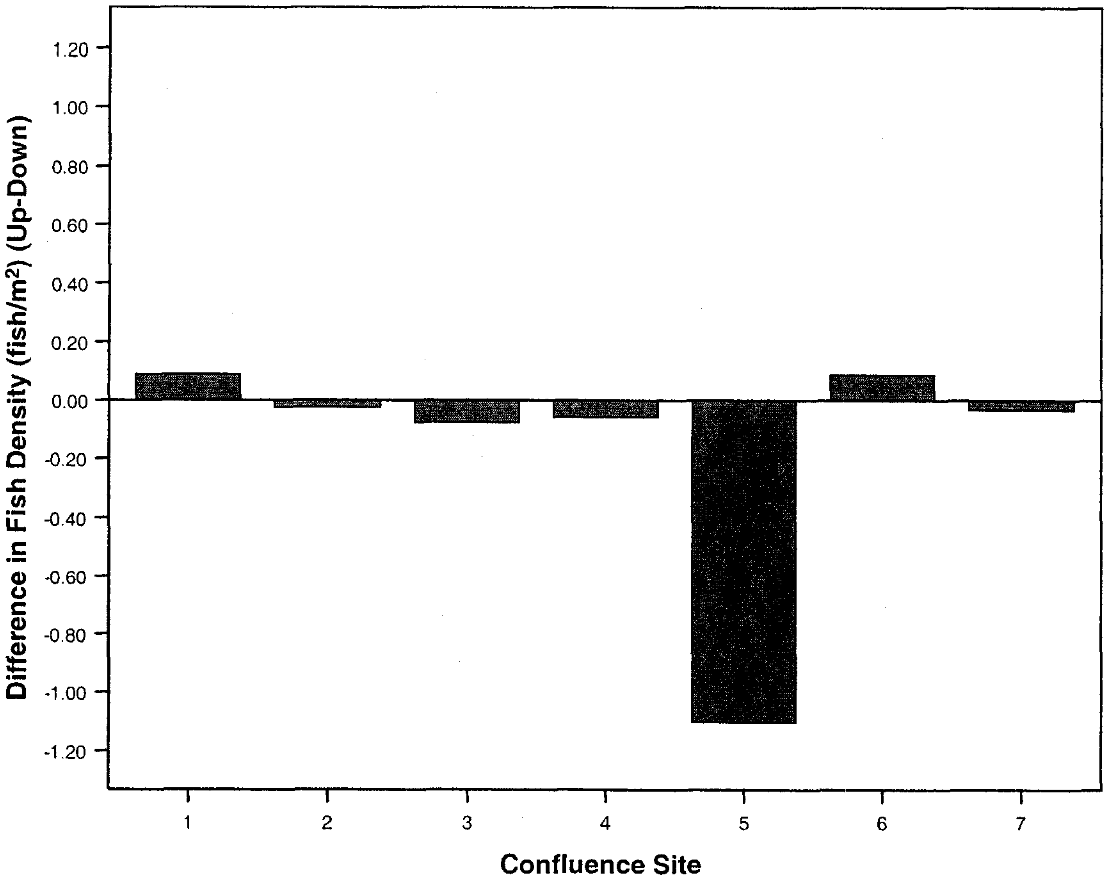

Figure 23. Difference in fish density calculated as the fish density above confluence points minus the fish density below confluence points. Positive values indicate higher fish density above, while negative values indicate a higher fish density below.

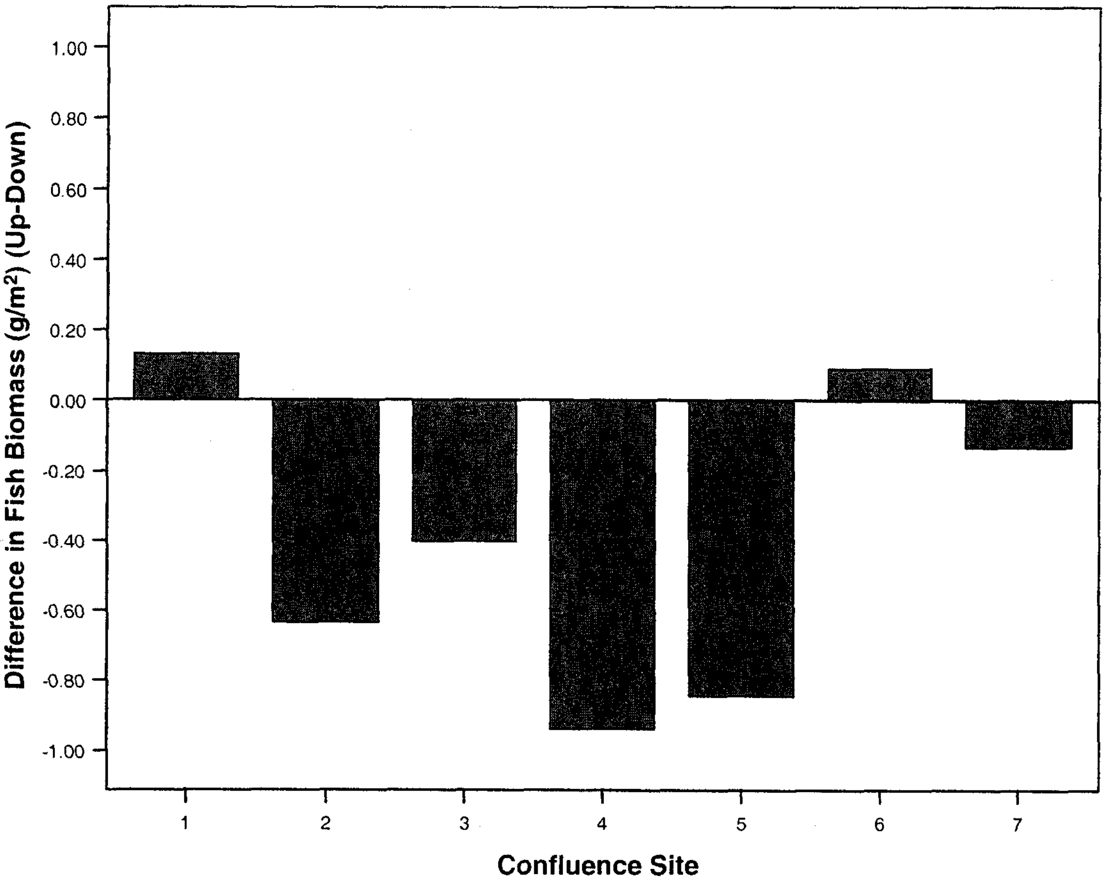

Figure 24. Difference in fish biomass calculated as the fish biomass above confluence points minus the fish biomass below confluence points. Positive values indicate higher fish biomass above, while negative values indicate a higher fish biomass below.

3.4 *Habitat*

Habitat characteristics above and below culverts and confluences differed very little. The only statistically significant difference in habitat was in the average substrate composition above and below culverts. Stream reaches above culverts tended to have a higher percentage of coarse substrate material. The percentage of large and small boulders was higher above culverts compared to below ($t=2.6$, $p= 0.014$; $t= 3.2$, $p=0.03$ respectively (Figure 25). Downstream reaches tended to have a higher percentage of large gravel ($t= -3.2$, $p=0.02$) and small gravel ($t= -3.39$, $p<0.01$) and a trend towards a fining of substrate materials below culverts compared to above (Figure 25). Conversely, there was no difference ($p<0.05$) in substrate composition above and below confluence points.

The average daily water temperature between May and October 2005 was lower in both reaches below culverts compared to sample reaches above culverts (ANOVA $F_{3, 3176} = 9.9$, $p< 0.001$; Figure 26). However there was no detectable difference in the daily average water temperature above and below confluence points during the summer of 2005 at confluence sites.

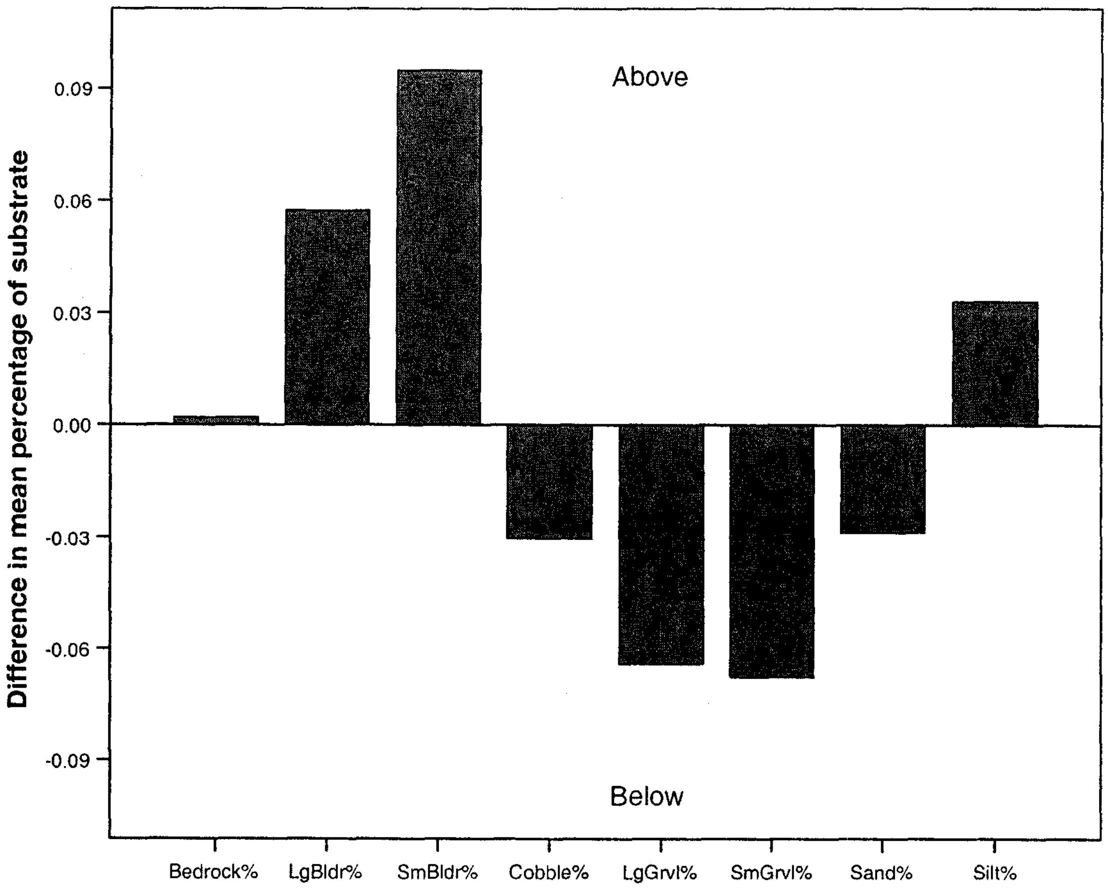

Figure 25. Difference between mean percentage of substrates above and below culverts. Positive values indicate higher mean percentage of substrate above, while negative values indicate a higher mean percentage of substrate below culverts.

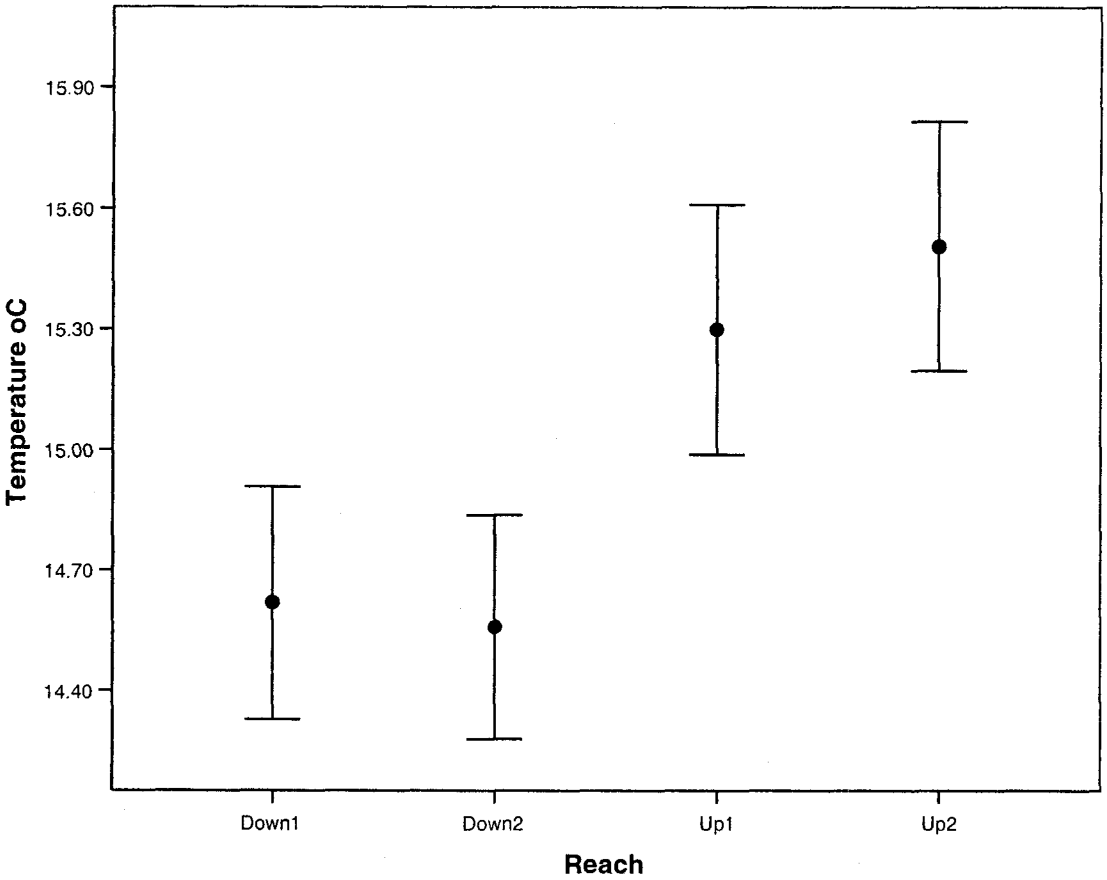

Figure 26. The average daily water temperature between May-October 2005 was lower in reaches below culverts compared to above (ANOVA $F_{3,3176} = 9.9$, $p < 0.05$). Error bars represent 95% confidence intervals around the mean.

3.6 *Fish Community Structure*

Analysis with MRBP indicated that overall fish community and functional group composition was significantly different above and below culverts (*T*= -2.7, p=0.022; and *T*= -2.1, p=0.031 respectively) when MRBP was used (Table 5 and 6). The *T* value is not particularly high for the either MRBP, and the low *A*-values indicate a great deal of heterogeneity in fish community composition and functional group composition within each of above and below treatment groups. Although differences in the overall community structure above and below culverts may exist, they are not particularly strong (Figure 27). Fish community composition was not statistically significant ($p<0.05$) above and below confluence points (Table 7 and Figure 28).

Table 5. Results of the MRBP testing the null hypothesis of no significant difference in community composition in reaches below and above culverts. N is the number blocks within each treatment. The observed delta is calculated from the data while the expected delta is derived from a null distribution. T is the MRBP test statistic, and A is the chance corrected within-group agreement. The MRBP was statistically significant at $p < 0.05$.

Treatment Groups	N	MRBP Statistics
Below Culvert	43	Observed Delta = 0.0017599207
Above Culvert	43	Expected Delta = 0.0017687724
		T = -2.7091378
		A = 0.00500446
		P = 0.02296723

Table 6. Results of the MRBP testing the null hypothesis of no significant difference in fish functional groups in reaches below and above culverts. N is the number blocks within each treatment. The observed delta is calculated from the data while the expected delta is derived from a null distribution. T is the MRBP test statistic, and A is the chance corrected within-group agreement. The MRBP was statistically significant at $p < 0.05$.

Treatment Groups	N	MRBP Statistics
Below Culvert	43	Observed Delta = 0.91460857E-03
Above Culvert	43	Expected Delta = 0.91797274E-03
		T = -2.1127003
		A = 0.00366478
		P = 0.03147935

Table 7. Results of the MRBP testing the null hypothesis of no significant difference in community composition in reaches below and above confluences. N is the number blocks within each treatment. The observed delta is calculated from the data while the expected delta is derived from a null distribution. T is the MRBP test statistic, and A is the chance corrected within-group agreement. The MRBP was not statistically significant when $p < 0.05$

Treatment Groups	N	MRBP Statistics
Below confluence	7	Observed Delta = 0.0206376
Above confluence	7	Expected Delta = 0.0205677
		T= 0.253177
		A= -0.003396
		P= 0.638

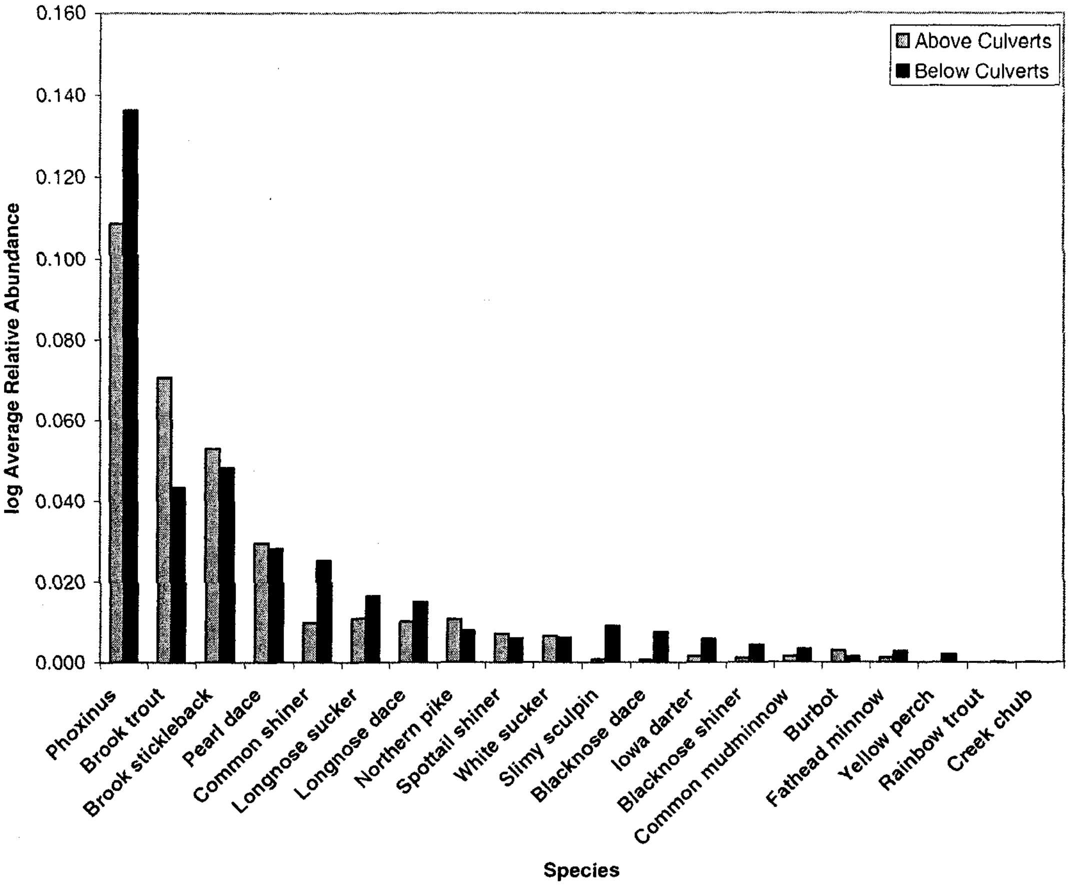

Figure 27. Average species relative abundance (log n+1) above and below culverts ranked from most common to rarest species.

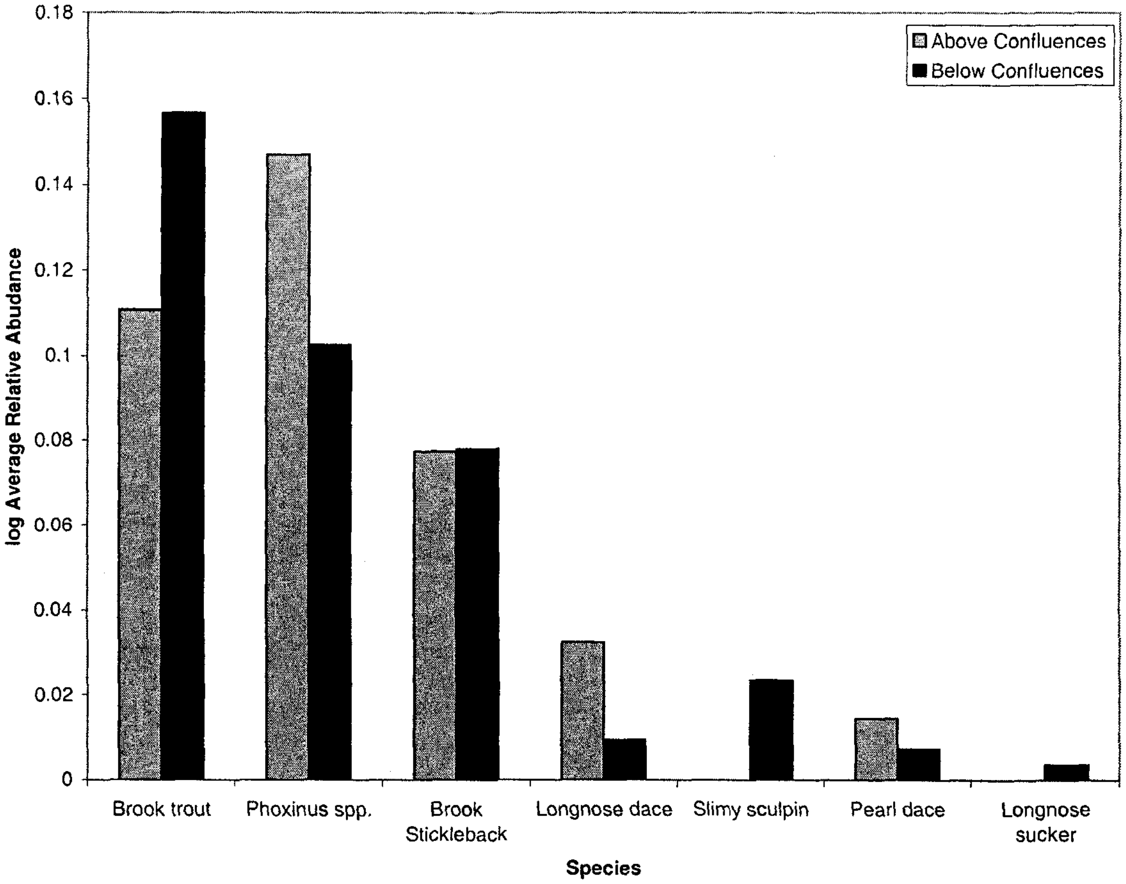

Figure 28. Average species relative abundance (log n+1) above and below confluence points ranked from most common to rarest species.

3.7 *Fish Community and Habitat Association*

The NMS for the species-based ordination identified a three-dimensional optimum solution with a final stress of 13.290 and had a significantly greater reduction in ordination stress than expected by chance (Monte Carlo permutation tests, $p<0.01$), indicating that the 3-dimensional solution provides an accurate representation of fish assemblage compositional dissimilarity among streams (Figures 29 and 30). The NMS solution was fairly strong and the percentage of ecological distance among sites accounted for by the first three ordination axes was 89%, indicating that the ordination did a good job of recovering the ecological complexity of the original distance matrix. Axis 1 accounts for 46% of the original ecological distance among sites in the ordination while axes 2 and 3 accounted for 22.2% and 21% of the variance respectively. Although the NMS solution separates fish communities fairly well, it fails to clearly distinguish between the overall differences in fish communities above and below culverts.

Environmental overlays (Figure 29) demonstrated that sites along the positive end of axis 1 (right hand side) were typically characterized by having a higher percentage of bank cover than sites along the negative end of the axis 1 (left hand side). The first axis was also associated with open canopy and percent silt, small boulder and large boulder substrates (Table 8). Sites along the negative end of axis 1 were characterized by having larger upstream catchment areas, higher total discharge, larger culvert diameters and lengths, wider mean stream width, and to a lesser extent, higher percent wood cover, greater stream area, higher percent cobble, greater culvert gradient and greater volume.

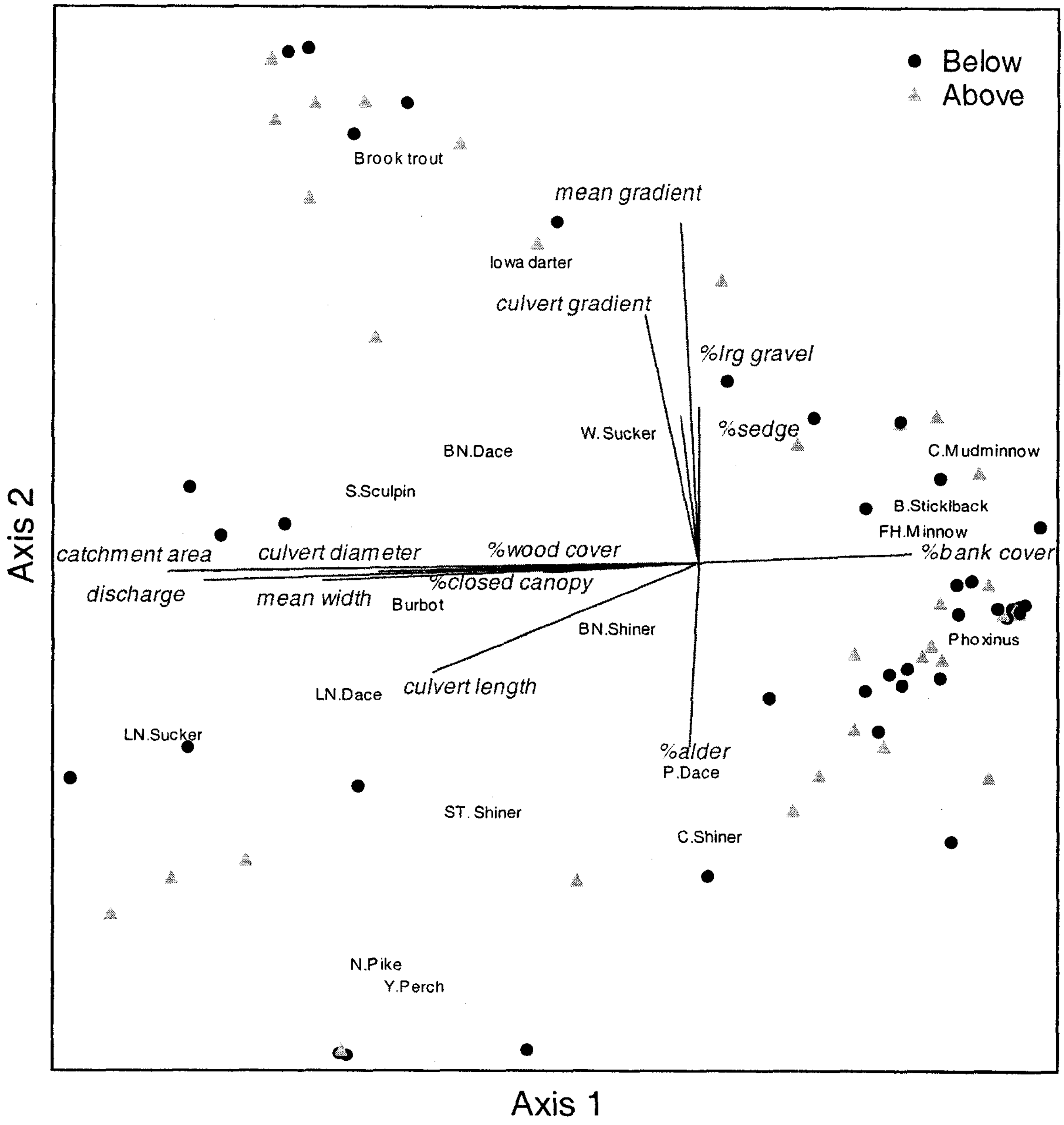

Figure 29. Plot of axis 1 versus axis 2 ordination of culvert sites in species space using nonmetric multidimensional scaling of log (n+1) relative fish abundance from sampling in 2004. The angle and length of vectors radiating from centroid of the ordination reflect the correlation ($r \geq 0.25$) between ordination scores and environmental variables. The interspersion of up and downstream reaches is an indication that culverts do not have a systematic structuring effect on fish community composition.

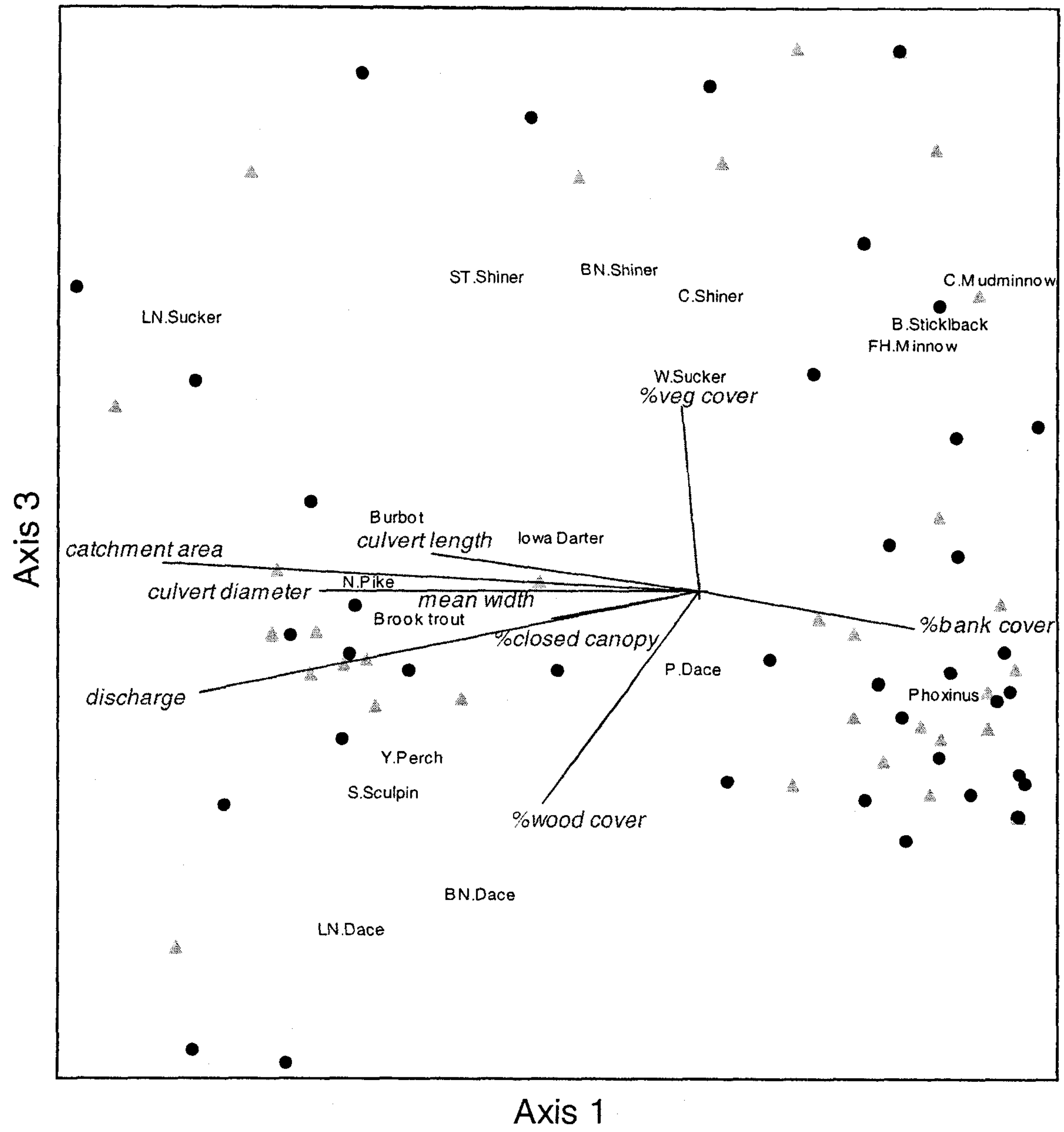

Figure 30. Plot of axis 1 versus axis 3 ordination of culvert sites in species space using nonmetric multidimensional scaling of log(n+1) relative fish abundance from sampling in 2004. The angle and length of vectors radiating from centroid of the ordination reflect the correlation ($r \geq 0.25$) between ordination scores and environmental variables. The interspersion of up and downstream reaches is an indication that culverts do not have a systematic structuring effect on fish community composition.

Table 8. Axis loadings for each environmental variable and Kendall correlation between ordination axes one through three.

Environmental Variables	Axis1	Axis1-tau	Axis2	Axis2-tau	Axis3	Axis3-tau
Catchment area	0.217	-0.319	0.002	0.119	0.012	0.013
Road density	0.000	-0.041	0.046	-0.174	0.008	-0.026
Reach length	0.006	0.063	0.039	0.204	0.001	-0.012
Mean width	0.126	-0.208	0.005	-0.096	0.001	0.045
Mean depth	0.002	-0.019	0	-0.038	0.015	-0.051
Mean gradient	0.01	-0.079	0.134	0.31	0.002	0.004
Temperature	0.019	-0.16	0.03	-0.168	0.007	0.042
Area	0.06	-0.118	0.003	0.014	0.001	0.055
Volume	0.024	-0.114	0.006	-0.027	0.006	-0.002
Bedrock	0.001	0.11	0	-0.009	0.023	-0.183
Large boulder	0.011	0.034	0.001	0.015	0.001	0.063
Small boulder	0.01	0.02	0.001	0.011	0.006	0.035
Cobble	0.048	-0.126	0.004	0.1	0.004	0.066
Large gravel	0.001	-0.061	0.062	0.177	0	0.029
Small gravel	0	0.026	0	0.116	0.001	-0.028
Sand	0.03	-0.082	0.009	-0.042	0.001	-0.067
Silt	0.028	0.153	0.022	-0.033	0.025	-0.06
Alder	0.005	-0.047	0.071	-0.177	0.001	0.008
Sedge	0.008	-0.058	0.059	0.189	0.01	0.139
Shrub	0.002	-0.057	0	0.02	0.001	-0.055
Upland	0.03	0.071	0.002	-0.006	0.007	-0.05
Bank cover	0.081	0.15	0.002	0.088	0.013	-0.115
Vegetation cover	0.007	-0.04	0	0.021	0.076	0.18
Wood cover	0.066	-0.162	0.002	-0.028	0.081	-0.127
Open canopy	0.005	0.093	0.059	0.074	0.017	0.09
Partial canopy	0.005	0.023	0.045	-0.019	0.004	-0.044
Closed canopy	0.06	-0.186	0.002	-0.165	0.013	-0.012
Total discharge	0.194	-0.253	0.009	0.002	0.042	-0.214
Average velocity	0.025	-0.094	0.042	0.137	0.038	-0.096
Perched height	0.005	-0.07	0.002	0.055	0.027	0.14
Height above bottom	0.003	-0.077	0.002	0.036	0.002	0.016
Culvert diameter	0.158	-0.249	0.005	0.015	0.002	0.055
Culvert length	0.124	-0.23	0.045	-0.06	0.022	0.154
Culvert gradient	0.03	-0.105	0.105	0.268	0.003	0.073
Water depth in culvert	0.002	-0.031	0.009	-0.135	0.001	-0.013
Plunge pool depth	0.006	-0.11	0.001	-0.027	0.004	0.015

Since total discharge, culvert diameter and length and mean stream width are correlated with upstream catchment area, they may not be contributing unique information to the ordination and it is therefore difficult to determine their relative importance. *Phoxinus sp.*, brook stickleback, central mud-minnow and fathead minnow were most common at sites positively correlated with axis 1 (smaller streams). Brook trout, longnose sucker, northern pike, longnose dace and slimy sculpin were associated with sites that were negatively correlated with axis 1 (large streams) (Table 9).

The sites on the positive end of the second axis (Figure 29) (towards the top) are characterized by higher mean stream and culvert gradient and a higher mean percentage of large gravel and percent sedge meadow riparian and to a lesser extent, average water velocity. Counter intuitive to the species associated with the positive end of the second axis; the strong association of sedge meadow is likely the result of a small number of outlier sites that had a high percentage of sedge meadow and many individuals not typically associated with sedge meadow site types. The negative end of axis two (towards the bottom) was typified by sites with a high percentage of alder riparian areas and to a lesser extent, higher road density, and a higher percentage of silt and sand substrate (Table 8). The second NMS axis most strongly separated brook trout communities from northern pike and cyprinid communities (Figure 29). The relative abundance of brook trout explained the highest proportion of variance of any of the three axes from the NMS and had the strongest correlation with any of the axes (Table 9). Species most positively associated with the second axis included brook trout, white sucker, blacknose dace, iowa darter and slimy sculpin.

Table 9. Axis loadings for each species and non-parametric Kendall correlations between the relative abundance of each species at each site and site scores for NMS axis one to three.

Species	Label in Plot	Axis1	Axis1-tau	Axis2	Axis2-tau	Axis3	Axis3-tau
Brook trout	Brook trout	.318	-.417	.685	.604	.007	.038
Northern Pike	N.Pike	.108	-.245	.219	-.385	.000	-.038
Central Mudminnow	C. Mudminnow	.024	.155	.002	.099	.028	.158
Longnose sucker	LN.Dace	.174	-.312	.029	-.163	.061	.216
White Sucker	W.Sucker	.003	-.074	0.25	.083	.089	.190
Common Shiner	C.Shiner	.000	-.035	.122	-.275	.139	.229
Blacknose shiner	BN.Shiner	.010	-0.84	.006	-.115	.106	.061
Spottail shiner	ST.Shiner	.031	-.089	.046	-.245	.071	.082
Fathead minnow	FH.Minnow	.022	.060	.001	.029	.066	.149
Blacknose dace	BN.Dace	.027	-.119	.006	.134	.065	-.147
Longnose dace	LN.Dace	.105	-.119	.021	-.110	.138	-.332
Pearl dace	P.Dace	.004	-.109	.168	-.289	.044	-.163
Phoxinus sp.	Phoxinus	.658	.695	.066	-.100	.218	-.158
Burbot	Burbot	.051	-.203	.002	-.195	.001	.107
Brook Stickleback	B.Sticklback	.145	.294	.013	.095	.420	.388
Yellow perch	Y.Perch	.023	-.138	.057	-.214	.011	-.172
Iowa Darter	Iowa darter	.011	-.085	.041	.067	.001	-.082
Slimy Sculpin	S.Sculpin	.061	-.246	.003	.047	.035	-.074

The fish species that most strongly characterized conditions associated with the lower end of the second axis included northern pike, pearl dace, yellow perch, common shiner and spottail shiner.

The separation of fish communities along the third axis (Figure 30) may be associated with a higher percentage of instream vegetation cover at sites positively related to the axis versus sites along the lower end which had a higher percentage of woody debris suitable for fish cover. Other environmental variables are difficult to interpret mainly due to the low amount of variation among sites explained by this axis and the low correlation between the axis and most variables (Table 8). The third axis, which accounted for the least variation among sites, represented a gradient of sites high in brook stickleback and *Phoxinus sp.* along the upper end of the axis, to sites high in longnose dace along the lower end (Figure 30).

All three NMS axes were interpretable from the functional perspective. Sites located on the lower end of the first axis were characterized by fish communities typical of rock spawning benthic invertivores or piscivores that had low silt tolerances and cold water requirements (Figure 31). The functional requirements of the fish at sites located along the lower end of the first axis reflect the association with larger catchment areas that have higher mean discharge and larger mean stream widths (Figure 31). Fish associated with sites positively correlated to the first axis were generally silt tolerant, omnivores and general invertivores that spawn in vegetation and cavities. These communities are more typical of warmer, low gradient streams with smaller upstream catchment areas (Table 10).

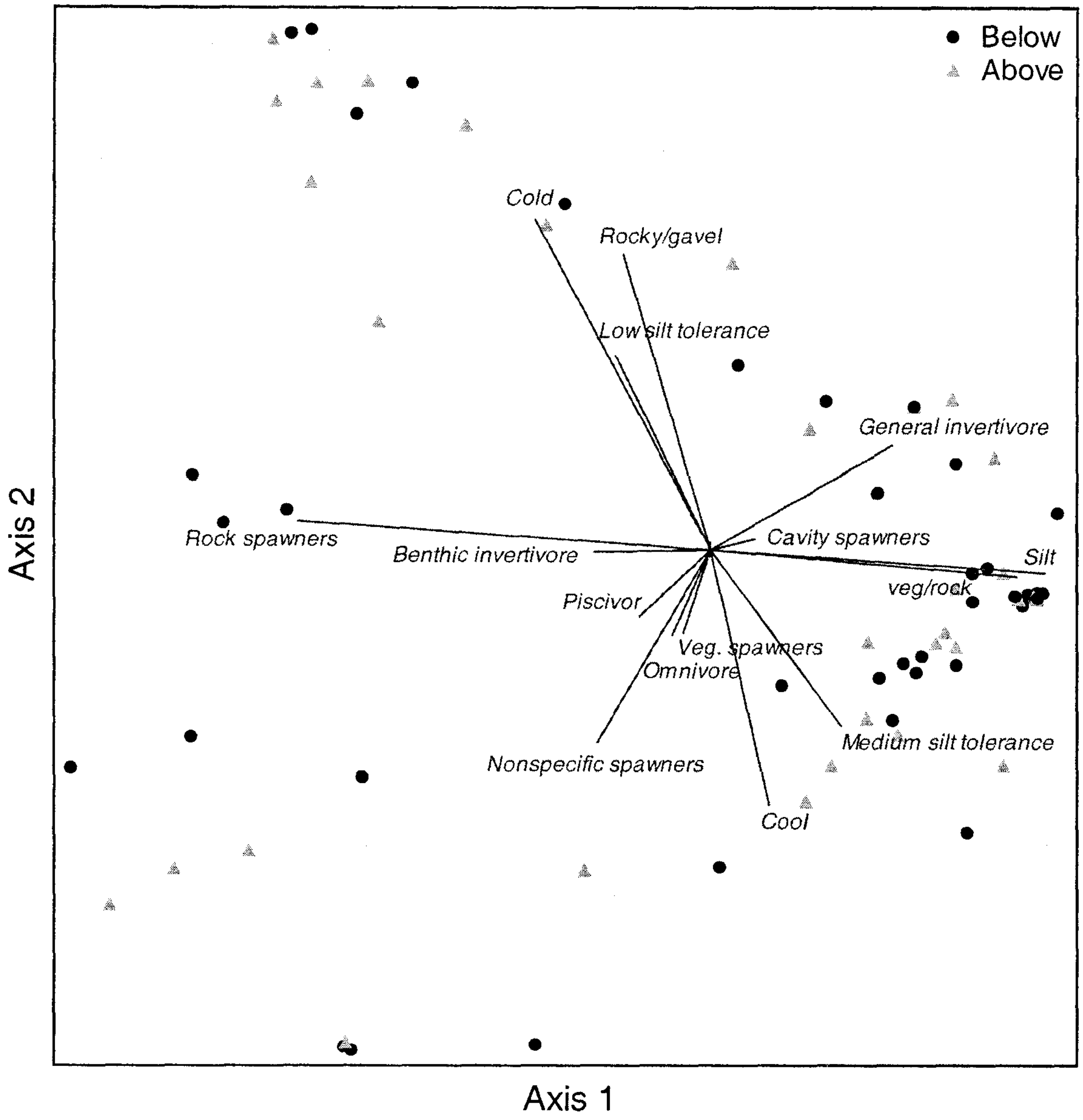

Figure 31. NMS ordination of culvert sites with proportional abundance of fish functional groups as overlay vectors. The angle and length of vectors radiating from centroid of the ordination reflect the correlation ($r \geq 0.25$) between ordination scores and functional group abundance. Plot of axis 1 versus axis 2.

Table 10. Axis loading and Kendall correlation between fish functional groups and ordination axes one through three.

Functional Groups	Axis1	Axis1-tau	Axis2	Axis2-tau	Axis3	Axis3-tau
Omnivore	0.074	-0.158	0.168	-0.314	0.043	0.012
General invertivores	0.353	0.41	0.203	0.28	0.061	-0.106
Benthic invertivores	0.227	-0.303	0.003	0.037	0.033	0.157
Piscivores	0.138	-0.352	0.132	-0.343	0	0.002
Rocky /gravel substrate	0.17	-0.287	0.578	0.552	0.037	0.294
Silt substrate	0.649	0.691	0.046	-0.07	0.22	-0.422
Non-specific substrate	0.222	-0.385	0.38	-0.509	0.108	0.141
Rock spawners	0.803	-0.731	0.059	-0.02	0.002	0.133
Vegetation spawners	0.052	-0.144	0.165	-0.296	0.005	0.039
Vegetation / rock spawners	0.598	0.659	0.054	-0.089	0.258	-0.467
Sand spawners	0.01	-0.084	0.006	-0.115	0.106	0.061
Cavity spawners	0.085	0.188	0.02	0.13	0.368	0.313
High silt tolerance	0.001	-0.028	0.024	0.144	0.015	0.125
Medium silt tolerance	0.254	0.381	0.348	-0.415	0.079	-0.336
Low silt tolerance	0.186	-0.318	0.38	0.421	0.05	0.283
Warm water	0.029	0.211	0.004	0.068	0.438	0.415
Cool water	0.114	0.219	0.499	-0.537	0.165	-0.392
Cold water	0.344	-0.445	0.645	0.575	0.014	0.003

Fish communities at sites located on the upper end of the second axis tended to be silt intolerant, general invertivores associated with rocky gravel substrate and cold water streams. While species on the lower end of the second axis tended to be associated with cool water, had a moderate tolerance to silt, had non-specific substrate preferences and tended to be piscivorous or omnivorous and vegetation spawners (Figure 31).

Functional characters associated with fishes from sites along the upper end of the third axis included warm water, cavity and sand spawners that generally have non-specific substrate requirements. Communities along the lower end tended to include cool to cold water, vegetation/ rock spawning species (Figure 32; Table 10).

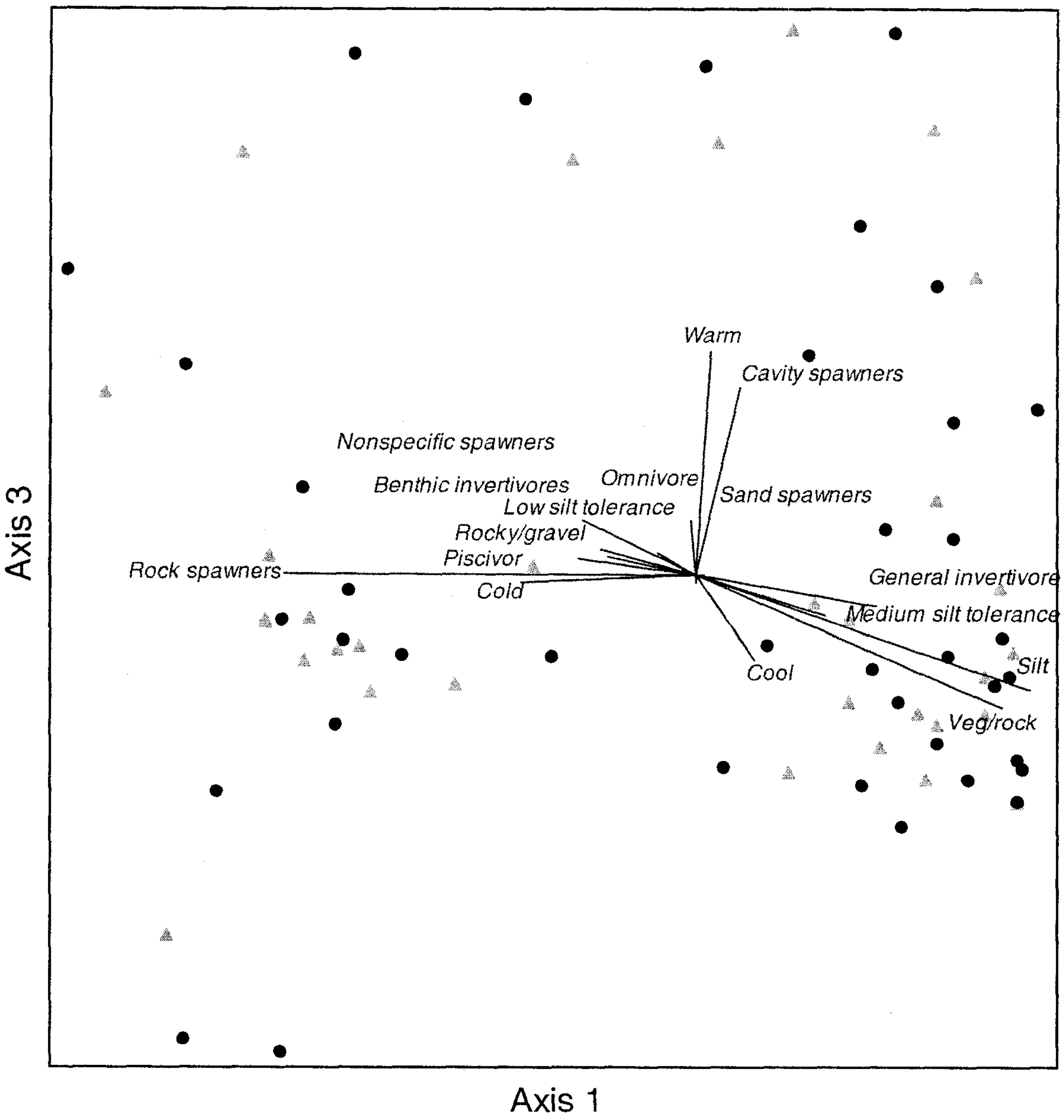

Figure 32. Ordination of culvert sites with proportional abundance of fish functional groups as overlay vectors. The angle and length of vectors radiating from centroid of the ordination reflect the correlation ($r \geq 0.25$) between ordination scores and functional group abundance. Plot of axis 1 versus axis 3.

4.0 DISCUSSION

Culverts are widely regarded as a threat to the structure and connectivity of stream fish habitat. My study clearly indicates that fish communities above culverts differ from those below. Relative fish abundance, species richness, biomass, and density were consistently higher below culverts compared to above. However, the fact that fish were present above all but five culverts means that the culverts are likely acting as filters to movement rather than completely blocking it.

Relative fish abundance, species richness, density and biomass were consistently lower in reaches above culverts compared to below, despite the site to site variation that existed in the magnitude of the difference. These results, in combination with the lack of a significant difference in the relative fish abundance, species richness, density and biomass above and below confluence points were an indication that culverts may be limiting the movement of fish from below culverts to reaches above culverts. With the exception of two of the perched culverts, the magnitude of differences in the relative fish abundance, richness, density and biomass was greater below perched culverts than above. The pattern of consistently more fish, higher diversity, density and biomass below culverts must not be construed as an indication that culverts are always barriers to fish movement, but rather, that they likely contribute to the variability in the distribution of the fish along stream reaches adjacent to culverts. The combination of a culvert's physical characteristics and the stream condition, along with the particular fish community assemblage will determine whether a culvert will restrict fish movement and alter the community structure.

Small streams often require recolonization following harsh winter or summer conditions and the density of source populations can also affect movement and recolonization rates (Sheldon and Meffe 1995). The pattern of consistently fewer fish and lower total biomass and density above culverts compared to below, across multiple watersheds and hyrdrogeomorphic regions may also be an indication that limited re-colonization is taking place above culverts over time. Studies by Sheldon and Meffe (1995) and Lonzarich *et al.* (1998) on the recovery of fish assemblages from experimentally defaunated streams reinforced the notion that stream fishes are highly mobile and that spatially restricted episodic disturbances are likely to produce short term impacts on fish assemblages. These impacts may become more severe under conditions of chronic disturbance or for populations of rare species or locally adapted genomes.

Species richness typically increases with increasing stream size and has been linked to ecosystem complexity as predicted by the river continuum concept (Gorman and Karr 1978; Vannote *et al.* 1980; Schlosser 1991; Robinson and Rand 2005). Small population sizes and spatial constraints often associated with isolation and fragmented habitats can lead to a loss of recolonization potential, reduced life history and habitat diversity, decreased individual movement and increased extinction risks through demographic and environmental variation (Fritz 1979; Rieman *et al.* 1993; Dunham *et al.* 1997; Hilderbrand and Kershner 2000; Fahrig 2001). Similarly, the loss of connectivity and immigration among populations and the amount of time that they are disconnected may substantially shorten the time to extinction. The more spatially restricted populations become, the greater the chance that a required habitat component is insufficient or missing for a life history stage (Dunning *et al.* 1992) or the physical space necessary to maintain a given population size no longer exists (Hilderbrand and Kershner 2000).

Source-sink relationships which deal with spatial variation in the production of juveniles can be important for long term stability of populations (Pulliam 1988; Dunning *et al.* 1992; Schlosser 1995a; Schlosser 1998). It is possible that the lower species biomass and overall relative fish abundance in stream segments above culverts is an indication of source-sink dynamics where local recruitment above culverts from downstream sources is not sufficient to maintain the population. This is especially likely if culverts create cumulative spatial and temporal variation in and along stream habitats, locally and throughout the watershed. The relationship between source populations and sinks is particularly critical for metapopulation-nodes which are spatially separated from the remainder of the population. Due to the hierarchical nature of stream networks, source populations in depauperate headwater streams most often exist in larger downstream habitats or refugia. The number of species and density increases with upstream catchment area, as well as from beaver ponds which can be reproductive sources for lotic fish assemblages (Ward and Blaustein 1994; Schlosser 1995a; Taylor 1997; Mackereth 2005 pers.comm.; Parker 2006).

Although the aim of this study was not to examine the rate of extinction or species persistence in isolated communities above and below culverts, evidence here and from the literature suggests that fragmentation in conjunction with a multiple other factors including environmental and demographic stochasticity can lead to reduced abundance, density and species and ultimately the local extinction of certain species over time (Rieman *et al.* 1993; Dunham *et al.* 1997; Hilderbrand and Kershner 2000). If multiple factors act consecutively or simultaneously and are difficult to detect, factors associated with local extinctions may need to be considered on a case specific basis (Dunham *et al.* 1997). Culverts may have a stronger effect on biota, fish populations and fish communities in specific watersheds, but show a weak overall effect in an analysis such as this, where many stream habitats affected by a variety of factors functioning at different scales are compared (Fausch *et al.* 1994).

Although more brook trout were captured below culverts than above, the average weight, length and biomass of brook trout captured above culverts was greater. These results were consistent with my hypothesis that if culverts affected brook trout movement, then I would find larger individuals above culverts compared to below. Assuming that there were limited upstream population sources, my results would suggest that culverts are acting as a filter to the movement of smaller individuals. Based on my results, culverts in general may not be permanent barriers to larger and thus stronger swimming brook trout. However, the difference in brook trout relative abundance, biomass, and density was greater below the three culverts that were perched and mean weight and length were higher below two of the three culverts that were perched. Due to the small sample size of sites with perched culverts and brook trout, I was unable to definitely conclude whether perched culverts would have an effect on brook trout movement.

The fact that brook trout were fewer in number and typically larger in weight and length above culverts compared to below suggests that larger fish with stronger swimming and jumping ability may be capable of ascending culverts (Poulin and Argent 1997, Warren and Pardew 1998). Gowan and Fausch (1996) found that brook trout that moved the most in high elevation streams in Colorado tended to be longer in length, but in poorer condition than the general population. Movement of brook trout in their study was highest during the fall spawning period and near the end of spring runoff as discharge approached baseflow, when instream conditions (depth and velocity necessary for good foraging opportunities) would start to become unsuitable (Gowan *et al.* 1994). It is most likely that if brook trout in my study area were to move through culverts, it would occur during a relatively short time period when water levels and velocity were neither too high nor too low. In the event that suitable flow regime does not coincide with critical times for brook trout movement, culverts would become barriers that restrict the movement of smaller, weaker swimmers. This scenario is applicable to other stream dwelling fish that exhibit ranging behaviour necessary to carry out their life history. Due to seasonal stochasticity in stream flow and the ranging behaviour of stream fishes, the patterns in abundance, richness, density and biomass above and below culverts has the potential to vary throughout the ice-free year and over the long term.

The higher relative abundance, species richness, density and biomass of fish below culverts compared to above and the more uniform distribution of fish at confluence sites is evidence that culverts may be having an impact on fish movement. The magnitude of difference between above and below culvert fish community suggests that the physical characteristics of culverts may be affecting species richness, relative abundance, density and biomass and the size distribution of larger species such as brook trout. Furthermore, the positive association between the magnitude of difference in fish community below culverts and culvert variables is evidence that the physical characteristics of culverts may be associated with the higher abundance, diversity, density and biomass below compared to above culverts. The associations between the magnitudes of difference of culvert impacts on community structure further supports my first objective of determining the extent to which culverts block or impede fish movement. Higher perched height and height above stream bottom was associated with a greater magnitude in difference between species richness below culverts. The negative correlation between perched height and height above stream bottom with species richness was the only statistically significant regression model and explained more variation in the data than any of the other culvert variables. These results in particular are consistent with my hypothesis that as the degree of the impact increases; the more fish community structure will differ above and below culverts. The difference between above and below biomass and density was not as closely associated with perched height and height above stream bottom as species richness. Culvert gradient, diameter and length all had marginal associations with fish community structure; however figures 16-18 were included to illustrate that there was an association between the difference above and below culverts and the selected culvert variables. Site to site variability was great due to the influence of a large number of environmental variables. However, the weak but consistent trend between fish communities and culvert variables generally supports the hypothesis that culverts effect fish movement.

Warren and Pardew (1998) found that culverts had the highest mean velocity and the lowest fish passage of four different crossing types examined in a study in Arkansas. Although I did not explicitly measure water velocity in culverts, the combination of other culvert variables including gradient and perched height along with velocity likely have an effect on fish communities and their ability to ascend culverts on a seasonal basis.

Alteration of stream flow at culverts and high variability in total stream discharge and velocity typical of headwater streams in the study area may temporarily limit the movement of all fish species at certain times of year. When conditions become optimal culverts may only limit the dispersal of selected species.

Variability in environmental characteristics at local and landscape scales is expected to influence both fish assemblages and the potential influence of disturbance factors such as culverts. The second objective of this thesis was to evaluate the general relationships among patterns and responses of fish assemblages and functional groups to local and landscape environmental variables. I found that culverts in combination with a suite of local and regional environmental variables structure fish community composition and species diversity distributed along stream segments above and below culverts. Fish assemblage structure and functional group composition differed significantly above and below culverts, suggesting that culverts were a critical variable in describing variation in fish communities along stream segments. Similar to other studies, patterns in fish assemblage and species richness in my study were influenced by a number of local and landscape scale environmental variables that were potentially confounding covariates (Cumming 2004; Grenouillet *et al.* 2004; Brazner *et al.* 2005).

My results illustrate the complexity in isolating the specific culvert variables necessary for predicting whether culverts are definable barriers to fish movement and how they might influence the structuring of fish assemblages along stream segments above and below culverts. Quantifying the relative importance of any one particular environmental variable was difficult, due to strong correlations that typically existed among them. The strength of the interdependency between the variables can also vary from region to region and was a likely source of variation in my data set (Minshall *et al.* 1983; Brazner *et al.* 2005). Despite not being able to isolate a given suite of variables that could predict fish community above and below culverts, I was still able to explain a number of important relationships among landscape, habitat, culvert and fish assemblage characteristics, which allowed me to successfully meet the majority of my objectives.

My results supported a number of linkages between landscape, habitat and biota. The ability to separate fish assemblages in the study area both taxonomically and functionally along environmental gradients ultimately supported my second objective. Despite not clearly separating above and below culvert fish assemblages in ordination space, there was a detectable difference in the relative abundance of species above and below culverts, which I would have expected to show up in the ordination. The lack of complete overlap of the above and below site markers in the ordination plots suggests that minor differences in species relative abundance exist at the site level. The dissimilarity in community assemblage above and below culverts is likely small and not detectable over the short time frame of this study and the relatively small number of sites across several watersheds and hyrdrogeomorphic regions with varying degrees of anthropogenic landscape disturbance. Unlike macroinvertebrates and phytobenthos assemblage patterns which seem to be more under the control of local factors such as instream habitat and substrate (Richards *et al.* 1997; Sponseller *et al.* 2001), fish assemblages seem to be more strongly influenced by watershed and landscape factors (Brazner *et al.* 2005). Studies have also highlighted the fact that important fish habitat is strongly influenced by the geology and land use in the watersheds (Richards *et al.* 1996; Grenouillet *et al.* 2004; Brazner *et al.* 2005).

As a consequence of the strong correlations between some of the environmental variables, culvert variables were weak predictors of fish community assemblages using NMS. It is possible that culvert characteristics, and the conditions that they create, could have a greater influence on fish assemblage both at a taxonomic and functional level then my results suggest. My results suggest that other environmental variables may be overriding the effects that culverts might be having on fish assemblages in small headwater streams. Brazner *et al.* (2005) found that environmental factors played an important role in structuring patterns in fish assemblages while others are confounded by variables that are closely related. Likewise, several variables in my analysis were closely associated with one another and are surrogates of stream size, which explains a large proportion of variation in the data. Variables related to hydraulic regime, such as stream discharge, channel dimensions and culvert diameter are highly influenced by upstream catchment area and geomorphological composition and land use (Richards *et al.* 1996; Maridet *et al.* 1998). Similar to other studies, these results suggest that upstream catchment area is a reasonable latent variable capable of explaining the complex interactions of several hydrological variables (Grenouillet *et al.* 2004; Parker 2006). My results are also consistent with those of many other studies concluding that stream size was the most important factor influencing fish species composition (Matthews and Robinson 1988; Grenouillet *et al.* 2004). In light of this, one would expect that differences in species composition above and below culverts would be the result of impeded movement through the culvert. Of the culvert variables least confounded with other environmental variables, culvert gradient and length accounted for the most variation in species composition and were the most highly correlated with any of the axes in the ordination. Yet, neither variable explains differences in above and below culvert relative fish abundance. Higher culvert gradient tended to be associated with brook trout, sculpin, darter and white sucker communities and functionally linked with cold water, silt intolerant species that prefer rocky gravel substrate. However, this pattern was likely more of an artifact of higher stream gradient than culvert gradient. I expected that perched height, height above stream bottom and water depth in culverts would play more of role in determining fish assemblages than they proved to in this analysis. Their lack of detectable influence on fish community structure in the NMS was likely due to a limited number of sites that were perched and the fact that sampling took place during baseflow when the water depth in culverts was similar across all of the sites.

The percentage of bank, wood, and vegetation cover, large gravel and riparian type were all relatively important local environmental variables driving the patterns in fish assemblage that I observed. Despite their importance in contributing to the structuring of fish assemblages and functional groups, they did differ statistically above and below culverts. The trend towards finer substrates such as large gravel and small gravel below culverts, compared to the higher percentage of large and small boulders above culverts in conjunction with no differences along stream reaches at confluence sites, is an indication that culverts are potentially influencing the local habitat structure at a very small scale. Increased water velocity at the outlet of culverts combined with increased streambed scouring and bank erosion above and below culverts could likely result in the transport of fine substrate material downstream (Baker and Votapka 1990). The transport of road sediment into adjacent streams is also well documented (Kreutzweiser *et al.* 2005). However, there was no indication that the difference in substrate type above and below culverts was sufficient to alter fish assemblage structure. In fact, based on what I have found local habitat differences above and below culverts are relatively minor and fish assemblage differences appear to be mainly due to movement.

There are a number of other factors, such as water chemistry and culvert age that were not quantified in this study but may play an important role in structuring fish communities and their distribution above and below culverts. Roads are recognized point sources of contaminants and nutrients, that tend to become more concentrated downstream. Runoff from roads may therefore lead to changes in the natural solute dynamics in streams and alter conductivity and pH which have an affect on fish community composition (Trombulak and Frissell 2000). Due to the limited number of available sites, I was unable to control for the age of culvert installations. As culverts age and roadways deteriorate, they are likely to become more of a potential barrier to fish movement. It is possible that these factors may contribute to variability in fish communities above and below culverts and among sites and should be considered in future research.

Contrary to what I expected, the mean daily water temperature was significantly lower in reaches below culverts and showed no significant difference above and below tributary junctions at confluence sites. Water temperature is among the most important variables determining the metabolic health of fish and is highly interrelated with hydrological regime, forest cover, and land use (Schlosser 1991). Theoretically, water temperature should generally increase as it moves downstream away from groundwater upwellings and is exposed to radiant heat. The mean daily water temperature below culverts was nearly a degree celsius colder than above culverts. One possible explanation for the lower water temperatures below culverts, though not examined in this project, is the result of hyporheic exchange. It is possible that surface water is being constrained at the culvert and forced into the interstitial pore space along the stream bottom, known as the hyporheic zone and mixing with typically cooler groundwater, only to return to the surface further downstream as colder water than upstream of the culvert (Brunke and Gonser 1997; Parker 2006). Water temperature was negligible as an exploratory variable in the ordination mainly due to the fact that there was no statistically significant difference in the single water temperature reading taken above and below all of the culverts in 2004. Like other variables closely related to hydrologic regime, water temperature at this scale is likely overshadowed and could be explained using upstream catchment area. Again, this begs the question of appropriate scale for studying changes in fish assemblage.

Although I did not explicitly examine the different landscape descriptors used in recent studies (Brazner *et al.* 2005; Smith and Kraft 2005) I found that neither road density nor any single local descriptor, with the exception of upstream catchment area could consistently explain the variation in community composition across multiple landscapes let alone above and below culverts. A descriptor's ability to explain variation with accuracy is likely a function of its range of variation, which typically increases with the area encompassed (Wiens 1989; Angermeier and Winston 1999), as well as the biota's sensitivity to changes in the descriptor. Because several of the small-scale variables measured in this study often vary throughout the day, season or year (i.e. temperature, water depth, vegetation cover, and canopy cover), efficient sampling must reflect these temporal changes that affect stream dwelling fish species. For this reason, detecting changes in fish assemblage and functional structure above and below culverts or confluences in our study area would require a much finer scale that would look at assemblages over time and at distinctly different scales (Cumming 2004; Lamouroux *et al.* 2006).

My results provide evidence that culverts affect fish communities as a whole across the landscape. The relative abundance of individual species above and below culverts is likely influenced by spatial and temporal site specific conditions, the location of the culvert within the watershed and the number of road crossings and natural barriers both downstream and upstream. In order to determine the impacts of culverts on fish assemblages at the landscape scale within a watershed, a more comprehensive and long-term inventory of culverts and natural barriers would need to be conducted. In order to maintain the biological integrity of this region and others, I believe it is important that an attempt be made to understand the response of fish assemblages to forest access road construction, culvert installation, and logging rather than simply the response of single species or particular populations (Brazner *et al.* 2005).

From a management perspective, my results suggest that it is necessary for fisheries managers and forest planners to understand the species structure and functional character of fish assemblages and their relationship to the landscape features and the disturbance occurring on it, in order properly assess watershed conditions. Several jurisdictions currently have guidelines and legislation regulating stream crossings in order to maintain fish passage. However, anecdotal evidence and results from this project suggest that as culverts age and receive little or no maintenance, they move away from their ability to allow fish passage and become more likely to alter the fish community and the distribution of species along stream gradients. Due to the difficulty in predicting the long term impacts on fish assemblages caused by culverts, let alone logging or land alterations, managers should work towards maintaining connectivity within watersheds. Connectivity can be attained by limiting the number of circular culverts used within a watershed, accountability for culvert maintenance and by carefully planning road construction.

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APPENDIX I

Common water crossings on forest access roads in Ontario (OMNR draft guidelines 2001).

Site Conditions	*Structure Type*	*Design Considerations*
Large Crossing: -Drainage Area >50sq.km -Flow >25m3/sec -Water Width > 10m -Water Depth > 1.5m	**-Bridge** • OMNR permanent bridge • Modular truss bridge • Temporary steel bridge	-Single or multispans -Possible instream abutment or pier -Channel morphology & stability -Permanent or temporary -Need crib or pile bridge foundation
Small Crossing: -Riffle with gravel, cobble, or larger substrate -Streambed slope < 3.5% -Bedrock or unmovable boulders -Shallow fast water	**-Bridge** **-Arch culvert (< 20' span)** **-Embedded Round Culvert** • Set 20%-40% of diameter below substrate • Natural substrate fills into pipe • Channel width in pipe = natural • Culvert diameter 1.25 times the bankfull channel width • Install on flat gradient	-Clear span normal water width -Permanent or temporary -Need crib or pile bridge foundation -Pre-construction testing to confirm embedment is recommended. If embedment is not possible, change to bridge or arch culvert.
Small Crossing: -Substrate is gravel, sand or finer -Stream Slope < 0.5% -Quiet flow velocity (no surface ripples)	**-Normal Round Culvert** • Set 10% of diameter below streambed • Install on flat gradient	-Size design for flood flows -Channel morphology & stability -Pipe alignment in stream -Quality installation & backfill

APPENDIX II

Functional classification of captured species

Species	Family	Common Name	Trophic Guild	Substrate Preference	Spawning Substrate Preference	Silt Tolerance	Thermal Guild
Catostomus catostomus	Catostomidae	Longnose sucker	B	N	LI	M	CL
Catostomus commersoni	Catostomidae	White Sucker	B	N	LI	H	CL
Phoxinus spp.	Cyprinidae	Phoxinus	G	SI	PL	M	CL
Margariscus margarita	Cyprinidae	Pearl dace	G	N	LI	M	CL
Rhinichthys atratulus	Cyprinidae	Longnose dace	O	R	LI	L	CL
Rhinichthys cataractae	Cyprinidae	Blacknose dace	B	R	LI	H	CL
Luxilus cornutus	Cyprinidae	Common Shiner	O	N	LI	M	CL
Notropis hudsonius	Cyprinidae	Fathead minnow	O	N	LI	M	CL
Notropis heterolepis	Cyprinidae	Blacknose shiner	O	N	PS	L	CL
Pimephales promelas	Cyprinidae	Fathead minnow	O	SI	SP	H	W
Semotilis atromaculatus	Cyprinidae	Creek chub	O	R	LI	H	CL
Cottus cognatus	Cottidae	Slimy sculpin	B	N	SP	L	CD
Esox lucius	Esocidae	Northern Pike	PI	N	PH	L	CL
Lota lota	Gadidae	Burbot	PI	R	LI	M	CL
Culaea inconstans	Gasterosteidae	Brook Stickleback	G	R	SP	L	W
Perca flavescens	Percidae	Yellow perch	PI	N	PL	M	CL
Etheostoma exile	Percidae	Iowa Darter	G	SI	PL	L	CL
Salvelinus fontinalis	Salmonidae	Brook trout	G	R	LI	L	CD
Oncorhynchus mykiss	Salmonidae	Rainbow trout	PI	R	LI	L	CD
Umbra limi	Umbridae	Central mudminnow	B	SI	PH	H	CL

Note: Trophic guilds: O= Omnivore, G= general invertivore, B= benthic invertivore, PI= Piscivore (adapted from Brazner *et al.* 2004 after Poff and War 1995 (Poff, N.L., and J.D. Allen. 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. Ecology 76: 606-627).
General substrate preference: R= rock/gravel, SI= silt, N= non-specific
Spawning substrate: PH= phytophils (vegetation spawners), PL= phytolithophils (vegetation/rock spawners), PS= psammophils (sand spawners), LI= lithophils (rock spawners), SP= speleophils (cavity spawners) (Categories are from Balon 1975 in Brazner *et al.* 2004)
Silt tolerance: H= high tolerance, M= medium tolerance, L= low tolerance, Thermal guild: CD= cold (10-17°C), CL= cool (18-26°C), W= warm (>27°C)

APPENDIX III

Mean and range of in-stream habitat, riparian, culvert and watershed conditions

	Down			Up		
Environmental Variable	Mean	Minimum	Maximum	Mean	Minimum	Maximum
In-stream habitat variables						
Mean Width (m)	2.72	1.21	5.56	2.58	1.04	5.48
Mean Depth (m)	0.18	0.07	0.49	0.19	0.07	0.47
Temperature (^oC)	13.48	6.00	19.60	13.48	6.00	19.60
Area (m^2)	202.75	76.00	444.80	172.12	70.40	370.50
Volume (m^3)	37.42	8.81	213.01	32.59	9.82	115.35
Total Discharge (m^3/s)	0.04	0.00	0.22	0.04	0.00	0.28
Average Velocity (m/s)	0.11	0.00	0.40	0.11	0.00	0.24
Substrate (%)						
Bedrock	0.03	0.00	0.44	0.03	0.00	0.58
Large Boulder	0.06	0.00	0.63	0.12	0.00	0.56
Small Boulder	0.19	0.00	0.74	0.29	0.00	0.83
Cobble	0.18	0.00	0.79	0.15	0.00	0.58
Large Gravel	0.14	0.00	0.39	0.07	0.00	0.41
Small Gravel	0.12	0.00	0.44	0.05	0.00	0.28
Sand	0.16	0.00	0.88	0.13	0.00	0.88
Silt	0.13	0.00	0.73	0.16	0.00	0.94
Riparian vegetation (%)						
Alder	0.51	0.00	1.00	0.47	0.00	1.00
Sedge	0.13	0.00	1.00	0.05	0.00	0.88
Shrub	0.07	0.00	0.44	0.12	0.00	0.75
Upland	0.29	0.00	1.00	0.33	0.00	1.00
Fish cover (%)						
Bank Cover	0.33	0.00	0.58	0.33	0.00	0.75
Vegetation Cover	0.22	0.00	0.61	0.22	0.00	0.67
Wood Cover	0.42	0.06	0.88	0.44	0.14	0.88
Canopy closer (%)						
Open Canopy	0.23	0.00	1.00	0.17	0.00	1.00
Partial Canopy	0.72	0.00	1.00	0.77	0.00	1.00
Closed Canopy	0.05	0.00	0.50	0.07	0.00	1.00
Culvert Measurements						
Perched Height (m)	0.06	0.00	0.46	0.01	0.00	0.62
Height Above Stream Bottom (m)	0.15	0.00	0.67	0.07	0.00	0.43
Culvert Diameter (m)	1.38	0.62	2.60	1.38	0.62	2.60
Culvert Length (m)	14.61	6.94	29.52	14.61	6.94	29.52
Culvert Gradient (%)	1.48	0.00	4.86	1.48	0.00	4.86
Water Depth in Culvert	0.15	0.00	0.46	0.19	0.00	2.80
Plunge pool Depth	0.34	0.00	0.96	0.19	0.00	0.42
Watershed Variables						
Catchment Area (km^2)	6.39	0.17	32.26	6.39	0.17	32.26
Channel Gradient (%)	0.50	0.18	1.11	0.52	0.18	0.89
Road Density (m/km^2)	1155.78	12.53	3742.57	1155.78	12.53	3742.57