RESTORATION OF A NOVA SCOTIA STREAM TO ENHANCE ATLANTIC SALMON PROVIDES FEW BENEFITS TO BENTHIC INVERTEBRATES

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ABSTRACT

Stream restoration is often undertaken with the goal of improving habitat for one focal species, most often a salmonid fish such as trout or salmon. Improvements in channel structure, especially the flushing of silt from sediments, should also benefit benthic invertebrate communities, but studies to date suggest substantial changes in benthic communities following restoration are not common. In a third-order Nova Scotia stream, we examined the effect of successful restoration to improve habitat for spawning Atlantic salmon on benthic invertebrate communities at sites where clogging of the bottom cobble with fine silt had been alleviated.

In a long-term comparison of two restored sites and two degraded sites, only six of 24 insect taxa showed increased population density five or seven years after restoration. In a second comparison of a comparatively undisturbed site against a newly restored site and a site restored eight years earlier, only three invertebrate taxa appeared to respond positively and consistently to restoration. In both studies there were no substantial changes in total invertebrate density, taxa richness, Simpson's diversity index or other community metrics over five years, except for a decline in the EPT/Chironomids ratio in the second study. Ordination of sites by correspondence analysis showed that, in both studies, benthic communities at unrestored control sites and restored sites were clearly different and did not become more similar through time. A long-term restructuring of the benthic community in the entire brook is suggested by the appearance of silt-intolerant shredders (Lepidostoma, Leuctra) among the most abundant members of the benthos in the second study, replacing silt-tolerant collectors (Tricorythodes, Optioservus) that dominated the earlier study.

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Habitat factors unaffected by in-stream restoration (frequent high discharge, lack of woody debris) limit benthic communities more than substratum quality.

Key Words: stream restoration; benthic invertebrates; sediments; silt tolerance; ordination

INTRODUCTION

In much of eastern North America and Europe, river restoration has been undertaken specifically to enhance populations of anadromous Atlantic salmon Salmo salar, an ecologically and economically important salmonid in decline throughout its range (Chaput 2012, Russell et al. 2012). River restoration to enhance Atlantic salmon spawning and rearing commonly involves putting back large woody debris (fallen logs, branches, tree root wads) that had historically been removed to improve drainage efficiency or facilitate driving logs (Crispin et al. 1993, Gore & Shields 1995, House & Boehne 1986, Muotka & Syrjänen 2007, Nagayama & Nakamura 2010). Because it is big, heavy and immobile, large woody debris redirects the flow of water and shapes the channel. Root wads of fallen bankside trees, for example, deflect current toward the centre of the channel and reduce bank erosion. Logs fallen across the channel act as check dams that impound water upstream and scour pools below. These alterations of the flow path create a more complex fluvial environment and contribute to reestablishing the natural riffle-pool sequence. In the absence of large wood, and abetted by channelization, stream channels tend to lose their pool-riffle sequence in favour of straight, homogenous reaches with uniformly mixed substrata and low habitat diversity (Crispin et al. 1993, Fausch & Northcote 1992).

Channel restoration for anadromous salmon may use in-stream structures intended to mimic the effect of natural fallen wood. Instream structures are especially useful in historically logged or farmed landscapes where riparian forests are too young to provide large woody debris naturally (Entrekin *et al.* 2008a,b, Muotka *et al.* 2002). A number of studies have demonstrated substantial increases in abundances of anadromous salmonids, or augmented spawning activity, in streams modified by in-stream structures (e.g., MacInnis *et al.* 2008, Pess *et al.* 2012), although this response is certainly not universal (Stewart *et al.* 2009). The effect of in-stream structures on other biota in the stream, in particular benthic invertebrates, has been less widely studied, despite that benthos are an integral part of stream ecosystems and a major component of the diet of salmonids (Syrjänen *et al.* 2011, Ward *et al.* 2009).

A change in the benthic invertebrate community following channel restoration would be expected because a greater diversity of habitats within the stream (pools, riffles, runs, bars, backwaters) should theoretically lead to a corresponding increase in biological diversity (Garcia *et al.* 2011, Sundermann *et al.* 2011a). Reduced bank erosion and complex currents created by in-stream structures should result in a lower proportion of silt and clays in the substratum as fine particles are flushed downstream or redistributed to sand bars (MacInnis *et al.* 2008). The removal of fine particles clogging interstices between larger sediments, especially in cobble and gravel, would create better micro-habitat for benthic invertebrates, as well as relieving other detrimental effects of siltation and high suspended sediment concentrations (Anderson *et al.* 1996, Cordone & Kelly 1951, Extence *et al.* 2013, Ryan 1991, Wood and Armitage 1999).

Nevertheless, the few studies to date have often shown no strong response of benthic invertebrate communities to river restoration for salmonids (Lepori et al. 2005, Schiff et al. 2011), a finding that extends to river restoration generally (Haase et al. 2013, Jähnig et al. 2009, 2010, Jähnig & Lorenz 2008, Palmer et al. 2010, Stranko et al. 2012, Sundermann et al. 2011a,b). Matthews et al. (2010) reviewed 46 cases of river restoration from 17 studies in U.K. and Europe, and found that the benthic community was less likely to show a positive response than any other indicator. Luohi et al. (2011) found that benthic invertebrate communities in Finnish streams barely changed from the degraded condition even 20 years after stream restoration for brown trout Salmo trutta. Conversely, Miller et al. (2010) performed a meta-analysis on 24 restoration studies and found that increasing habitat heterogeneity in stream channels generally increased species richness of benthic invertebrates, and that the largest and most consistent responses arose from adding large woody debris. Similarly, Muotka et al. (2002) and Muotka & Syrjänen (2007) found a steady increase in litter retention and numbers of two functional groups of benthic invertebrates (shredders and detritivores) up to eight years after restoration with large woody debris. At present then, we have no clear understanding of why benthic invertebrates respond to restoration in some rivers and not in others.

From 1992 to 2004, restoration works were carried out in Brierly Brook, a degraded tributary of West River in northern Nova Scotia, Canada, to rebuild the historical run of Atlantic salmon in the brook. Restoration concentrated on recreating the natural pool-riffle sequence in the brook, which had a very uniform channel, by installing artificial structures made of large woody debris (Andrus et al. 1988, Robison & Beschta 1990a, 1990b). Restoration increased the complexity of the stream channel and improved habitat for all freshwater life-stages of Atlantic salmon (Floyd et al. 2009). The number of Atlantic salmon redds in the brook increased dramatically after restoration began, from 43 in 1992 to 500-600 by 1996, and salmon preferred reaches with restoration structures to build redds (MacInnis et al. 2008). Sediments in restored reaches were substantially less embedded with fine particles only one year after in-stream structures were installed (Floyd et al. 2009). We hypothesized, therefore, that restoration would also lead to an increase in numbers and diversity of benthic invertebrates because of the improved habitat provided by silt-free sediments, and relief from the broader inhibitory effects of fine suspended solids. Unlike most previous studies, which have tested the effect of increasing habitat diversity on benthic invertebrates, the present work considered improvements in the quality of benthic habitats already present.

MATERIALS AND METHODS

Study Area

Brierly Brook, a 20-km-long, third-order stream (Fig 1) located west of Antigonish, Nova Scotia, (45° 36' N, 62° 04' W) is described fully elsewhere (Floyd *et al.* 2009, MacInnis et al. 2008,). The brook originates on Browns Mountain (elevation 350 m) and drains an area of 35 km². The brook flows through alluvial deposits of gravel and fine material (2–15 m thick) on top of unsorted glacial till (Davis & Browne 1996). The headwaters create a 6.5-km upper section (gradient 3.5%) surrounded by intermittently logged, Acadian mixed forest. The middle section (10.5-km, gradient 1.5%) flows through a mixed rural landscape of farmland, alder swale and new-growth forest. This section supports a thriving population of American beaver *Castor canadensis*, which have built at least 10 dams (Taylor *et al.* 2010).

The lower 2.5 km of the brook (gradient = 0.4%) flows through the urban landscape of Antigonish (population 5000), before

emptying into West River. Mean maximum monthly discharge in Brierly Brook is about 3.0 m³/s (April), but peak daily flows may be an order of magnitude greater (Town of Antigonish, unpublished data, 1983); mean minimum monthly discharge is 0.5 m^3 /s (July). The pH is typically circumneutral and conductivity averages 1140 μ S/cm (Floyd *et al.* 2009). All but the top 1.5 km of Brierly Brook are accessible to anadromous fishes, including brook trout *Salvelinus fontinalis*, brown trout and Atlantic salmon.

Restoration

Restoration of habitat for Atlantic salmon spawning and rearing in Brierly Brook primarily involved the use of two structures: digger logs and bank deflectors (MacInnis et al. 2008, Rutherford et al. 1994). The so-called digger logs are tree trunks laid across the stream channel in a manner simulating a fallen tree. The logs act as small dams, causing water and sediment to accumulate upstream (House & Boehne 1986, Wallace et al. 1995), and scouring a plunge pool downstream (Gurnell et al. 1995, Keller & Swanson 1979). Bank deflectors are triangles of logs, infilled with rock, built along the stream bank so that one log angles outward into the channel at 30°. Bank deflectors narrow the channel and deflect flow towards the opposite side of the stream, causing flows to converge and accelerate (Robison & Beschta 1990a,b). Along the near bank, the deflectors create back eddies where fine sediments accumulate, resulting in the formation of point bars just downstream from the deflector. Both these structures may decrease the embeddedness of the stream bottom by promoting currents that scour sands and silts around gravels and cobble on one side and deposit them in gravel bars on the other side.

Most of the severely degraded reaches in Brierly Brook (12.7 km of the brook, more than 60% of its length) were restored in a continuing effort from 1992 to 2004, beginning at the mouth. The placement of restoration structures, every 48 m in the middle and lower reaches, every 35 m in the upper 10 km of the brook, was intended to restore the natural pool–riffle sequence, which in most rivers leads to pools forming every five to seven bank-full river widths (Leopold 1994, Rosgen 1996). Deflectors and digger logs were most effective when used together. Crews placed deflectors on the upstream side of most digger logs, opposite the side of the stream where the pool was to be formed (see MacInnis *et al.* 2008 and Rutherford *et al.* 1994 for details).

Sampling and Analysis

This project incorporated two distinct data sets, from an extensive study (four sites along the brook) and an intensive study (three sites in one reach). The extensive study began in 1995. At each of two locations within the brook (one in the upper reach, one in the lowest reach) a newly restored treatment site was paired with a degraded site (negative control) upstream from it. Paired Sites A and B (downstream section), were 1.75 km apart, above and below the Town of Antigonish; sampling began three years after restoration at Site A (Fig 1). Sites C and D (upstream section) were 0.85 km apart and surrounded by young forest; Site C was restored in 1994, the year before sampling began. The downstream sites suffered from excess siltation, while the upstream sites had been scoured, in some places down to bedrock. The control sites were typical degraded sites and were not subject to any manipulation during the study.

At each site, a total of six benthic invertebrate samples (three from a riffle, three from a run) were collected every month from May through October in 1995, 1996, 1998 and 1999. As far as possible the same locations were sampled every year. Benthic invertebrate samples were collected using a Surber sampler (500 µm mesh), with a standard collection time of 2 min. Samples were returned to the laboratory in stream water within 1 hr and stored at 4°C for no more than 2 d. Invertebrates larger than 0.5 mm were sorted from sediments and debris and stored in 70% ethanol. All invertebrates were identified under a stereo dissecting microscope to the lowest practical taxonomic level, usually genus, and enumerated. Chironomidae were identified to the sub-family level. Taxonomy of this invertebrate collection was verified and updated in 2013 using more recent keys (Knopp & Cormier 1997, Merritt & Cummins 2008, Peckarsky *et al.* 1990, Stewart & Stark 1993, Wiggins, 2000), based on reference specimens.

The intensive study ran from 2003 to 2007 and used three sites within the low-gradient, middle section of the brook. This reach is highly channelized and surrounded by agricultural land with a narrow (0-10 m), early successional riparian zone. The surrounding vegetation is dominated by speckled alder (*Alnus incana*) with white spruce (*Picea abies*), trembling aspen (*Populus tremuloides*), large-toothed aspen (*Populus grandidentata*) and red maple (*Acer rubrum*). We divided the study site into three sections: the Old Restored Site, a 300-m section of stream that was restored using five digger logs in 1995; the New Restored Site, a 350-m section of stream that was restored in

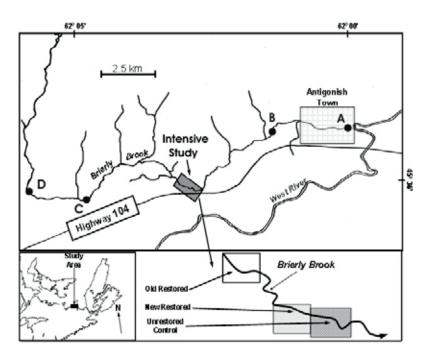


Fig 1 Map of Brierly Brook, northern Nova Scotia, Canada, showing locations of the sampling sites used in the extensive study (downstream: A, B; upstream: C, D) and in the intensive study.

August 2003 with five digger logs; and the (positive) Control Site, a 400-m section of largely intact brook that was untouched during the study (Fig 1). Apart from the Old Restored Site, which contained five artificial woody structures, before the study began there was almost no large woody debris anywhere in the study area. Several other reaches of Brierly Brook, outside the study area, were also restored over the study period (MacInnis *et al.* 2008).

Six replicate benthic invertebrate samples, three from riffles and three from runs, were collected with Surber samplers at each of the three sites in June 2003 (immediately before restoration structures were installed at the New Restored site), June 2005 (two years after restoration) and in early July 2007 (four years after restoration). Field and laboratory procedures were identical to those used in the extensive study, except that Chironomidae were identified only to family. (Genus-level identifications of Chironomidae are available for 2003 and 2005 from another study). Analysis of data from the extensive study relied on analysis of variance (ANOVA) on individual taxa (genera and insect orders) and a set of community metrics: total number of animals, total number of taxa, the sum of Ephemeroptera, Plecoptera and Trichoptera (EPT), the ratios EPT/(Chironomids +1) and EPT/total number, and Simpson's diversity index (Fore *et al.* 1996, Resh & Jackson 1993, Taylor & Bailey 1997). All variables except number of taxa, EPT/total, and Simpson's Index were transformed by log x+1 to correct for non-normality. Analysis began with the most abundant taxon and proceeded in order of abundance to the last taxon to constitute >2% of total numbers. Remaining taxa were too infrequent to make site differences discernable.

Because monthly Surber samples within the same year were probably not independent, data were analyzed by a repeated-measured ANOVA with Month as the subject factor, Year (1995-1999) as the within-subjects factor and Treatment (restored or control) and Location (upstream or downstream) as between-subjects factors. A change due to restoration would produce significant ($\alpha = 0.10$) main effects for Treatment or interactions of Treatment × Location (if upstream and downstream responded differently) or Treatment × Year (if differences emerged over time). Significant main effects for Year were taken to indicate temporal trends. This approach of repeated ANOVA for each taxon increases the risk of a Type I error (declaring a difference where none exists) beyond the nominal significance level of the test. However, despite the intensity of sampling, the power of the ANOVA was often low due to the low numbers and erratic distribution of the invertebrates; multiple tests increase the likelihood of detecting a difference. Moreover, in environmental monitoring, describing the nature, size and direction of effects, with allowance for uncertainty, is more useful than relying on strict hypothesis testing (Stewart-Oaten 1996, Muotka & Syrjänen 2007).

Overall differences in community structure among the four study sites were explored using Detrended Correspondence Analysis (DCA). Rare taxa, those collectively constituting <2% of total number at all sites in all years, and individually constituting 0.01-0.23% of total number, were omitted from this analysis. DCA used log-transformed data with down-weighting of less common taxa. DCA was applied separately to the downstream sites (Sites A and B) and the upstream sites (Sites C and D), grouping data by year, to see trends through

time. DCA was also applied to all four sites, grouped by site, to reveal spatial differences in community structure. For clarity, the centroids for each year or site were plotted in place of individual samples. Centroids were calculated as the means of the Axis 1 and Axis 2 co-ordinates for the samples in each group, with standard deviations indicating variation.

Analysis of data from the intensive study followed the same general procedure as for the extensive study, first using ANOVA (three-way, not repeated measures) on individual taxa and simple community metrics. All variables were log-transformed except total number of invertebrates. Preliminary inspection of the data suggested that differences were likely between riffles and runs, presumably because of the low gradient of this reach. Therefore, the ANOVA model included Habitat to partition this source of variation, along with Site, Year and Site × Year. A significant interaction would be expected if restoration of the New Restored site produced a change in the benthos in succeeding years. Detrended Correspondence Analysis was used to examine trends in community structure through space and time in the same manner as in the extensive study. Taxa collectively constituting < 2%of total numbers, and individually represented by fewer than seven individuals, were omitted from DCA. Analysis of Variance was done with Statistix 9.0 (Analytical Software, Tallahassee, Florida, U.S.A.); correspondence analysis used MVSP 3.12 (Kovach Computing Services, Pentraeth, Wales, UK).

RESULTS

Extensive study

A total of 30,528 invertebrates in 69 taxa were identified in the extensive study, among which 39 taxa constituted 98% of the total number. By far the most abundant organisms were chironomids of the subfamily Orthocladiinae, which constituted 19% of all animals collected. Over 50% of total number was contributed by that taxon and five others: *Hydropsyche* (Trichoptera), *Optioservus* (Coleoptera), Simuliidae (Diptera), *Heptagenia* and *Tricorythodes* (Ephemeroptera).

A total of 24 genera, families (Simuliidae) and sub-families (Orthocladiinae, Tanypodinae) were sufficiently abundant to analyze by ANOVA. The most consistent result among these analyses was a progressive change in abundance over the five years of the study

(Table 1). Five taxa, Orthocladiinae, *Hydropsyche*, *Optioservus*, *Caenis* and Simuliidae, steadily increased in numbers, while nine others declined. The declining taxa were predominantly mayflies (*Heptagenia*, *Ameletus*, *Hexagenia*, *Baetis*, *Cinygmula*, *Epeorus*), along with two Diptera (*Hexatoma*, *Bezzia*) and the cased caddisfly *Glossosoma*. *Heptagenia* declined to zero at Site C in 1999. Hence, over the five years of the study, the brook appeared to undergo a shift in conditions, and a corresponding shift in benthos abundances, independent of any response to restoration.

Twelve of 24 taxa examined showed a significant effect of restoration, or a significant interaction between restoration and time, or between restoration and upstream-downstream location (Table 1). Three-way interactions were rarely significant. Only five taxa revealed an unambiguous effect of restoration (treatment effect). Black flies (Simuliidae) were more abundant at restored sites than at degraded

| Table 1 | Summary of significant differences (P<0.10) detected by repeated-measures |
|---------|----------------------------------------------------------------------------------------|
| | ANOVA on the 23 most abundant genera, families (Simuliidae) or sub- |
| | families (Chironomidae) in Brierly Brook, 1995-1999. Values given are the |
| | significance levels of the F-values. Taxa are arranged from most to least |
| | abundant across all sites. Taxa which produced no significant differences ¹ |
| | are omitted. |

| Taxon | Treatment ² | Year | Treatment x Location ³ | Treatment × Year |
|------------------|------------------------|----------|--------------------------------------|---------------------|
| Orthocladiinae | | < 0.0001 | | |
| Hydropsyche | | 0.095 | | |
| Optioservus | | 0.047 | 0.0011 | |
| Simuliidae | 0.0016 | 0.002 | 0.0047 | 0.0009 |
| Heptagenia | | 0.007 | | |
| Tricorythodes | | | 0.091 | |
| Ameletus | | 0.032 | 0.064 | |
| Hexagenia | | 0.029 | | |
| Baetis | | 0.028 | | 0.033 |
| Glossosoma | 0.066 | 0.087 | | |
| Eurylophella | 0.063 | | < 0.0001 | |
| Paraleptophlebia | | | 0.044 | |
| Cinygmula | | 0.022 | | |
| Hexatoma | 0.027 | 0.023 | | |
| Beloneuria | 0.040 | | | |
| Psephenus | 0.011 | | 0.01 | |
| Epeorus | | 0.078 | | |
| Bezzia | | < 0.0001 | | |
| Caenis | 0.031 | 0 | 0.020 | 0.0062 |

¹ Serratella, Ephemerella, Haploperla, Dolophilodes, Tanypodinae

² Treatment = restored or degraded

³ Location = upstream or downstream

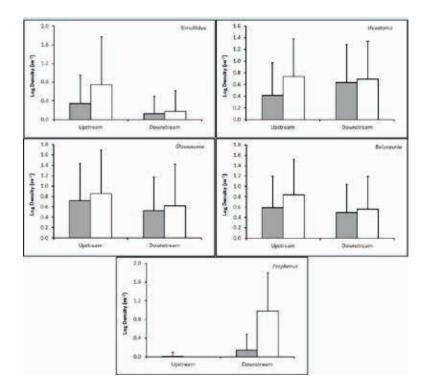


Fig 2 Mean abundances (log-transformed) of five taxa of benthic invertebrates that showed a consistent difference between restored sites (open columns) and control sites (filled columns) in the extensive study, 1995-1999. Values are means of six monthly samples, May-October, at each site over four years (n = 144). Error bars are standard deviations of log-transformed data.

control sites; the difference was greater at the upstream sites, and increased over the four years of the study (Fig 2). The caddisfly *Glossosoma*, the Dipteran *Hexatoma*, and the stonefly *Beloneuria* were all significantly more abundant at the restored sites. Beetle larvae of the genus *Psephenus* (water pennies) were substantially more abundant at the restored upstream site than at the control, although the beetle was nearly absent at both sites downstream (Fig 2).

The remaining seven taxa showed inconsistent and conflicting results. Abundances of the beetle *Optioservus*, (larvae), and the mayfly *Tricorythodes* were significantly greater at the degraded site upstream, but showed no difference downstream (Fig 3). The difference for *Tricorythodes* is barely detectable (Table 1). Two genera of mayfly, *Paraleptophlebia* and *Eurylophella*, were more abundant at the

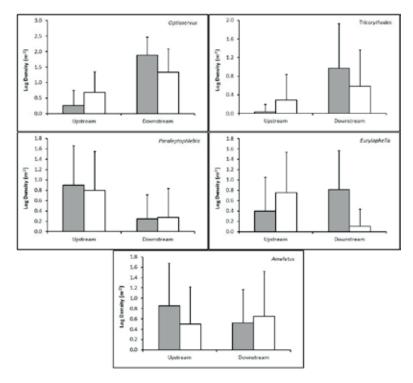


Fig 3 Mean abundances (log-transformed) of five taxa of benthic invertebrates that showed inconsistent differences between restored sites (open columns) and control sites (filled columns) in the extensive study, 1995-1999. Values are means of six monthly samples, May-October, at each site over four years (n = 144). Error bars are standard deviations of log-transformed data.

degraded control site than at the restored site upstream (*Eurylophella* by an order of magnitude), but more abundant at the restored site downstream. A third genus, *Ameletus*, showed the opposite pattern (Fig 3). Densities of *Baetis*, another mayfly, declined more rapidly over the five years of the study at control sites than at restored sites, creating a temporal transition from greater abundance at the control sites to greater abundances at the restored sites. Conversely, the mayfly *Caenis* was first observed at both downstream sites in 1998, and by 1999 it had become substantially more abundant at the degraded site, although absolute numbers remained low.

At a broader scale, none of the insect orders or community metrics evinced significant treatment main effects or treatment × year interactions. Ephemeroptera in general were more abundant at the control site upstream but at the restored site downstream (P = 0.054), reflecting the more common pattern among individual genera. This difference is reflected very weakly in EPT (P = 0.094) because Plecoptera and Tricoptera revealed no site differences. Diptera in general increased over time (P = 0.0012) along with Chironomidae (P = 0.0012), the numerically dominant component. The ratios EPT/Chironomidae and EPT/total were lower in 1998-1999 than in 1995-1996 (P<0.0001) but showed no response to restoration. Total number of invertebrates and total number of taxa both showed barely detectable treatment × location interactions (P = 0.074, 0.086) but the absolute differences are slight. Simpson's diversity index was high at all sites and was unaffected by restoration.

Detrended Correspondence Analyses resolved 18.5-22.5% of the variation on the first axis, 8.8-11.3% on the second axis and 5.9-7.2% on the third axis. The third axis generally re-iterated trends on the second axis. Community structure at the upstream sites (Fig 4A) and especially the downstream sites (Fig 4B) illustrates a clear temporal trend, probably related to the changing abundances of individual taxa noted above. In both reaches there was a clear separation between degraded control sites and restored sites, but no indication that the sites are diverging or converging through time. DCA on all four sites separated them into two groups of two (Fig 5). One group, however, contains a downstream control and an upstream restored site. Therefore, no effect of restoration can be inferred from this analysis.

Intensive Study

A total of 4076 invertebrates in 58 taxa were identified in the intensive study, among which 32 taxa constituted 98% of the total number. Again, over 50% of total numbers at all sites were represented by just five taxa: *Drunella*, *Ephemerella* (Ephemeroptera), Chironomidae, *Lepidostoma* (Trichoptera) and *Leuctra* (Plecoptera). Three of these taxa were not collected in the earlier, extensive study.

A total of 15 genera or families (Chironomidae, Simuliidae) were sufficiently abundant to analyze by ANOVA. Most taxa expressed large annual variations at all sites; differences among years were highly significant (P = 0.014 or less) for every taxon except *Hexatoma* (Diptera). Only Simuliidae produced an unambiguous difference among sites: abundance of black fly larvae was significantly greater at the Control site than at either restored site (P = 0.039).

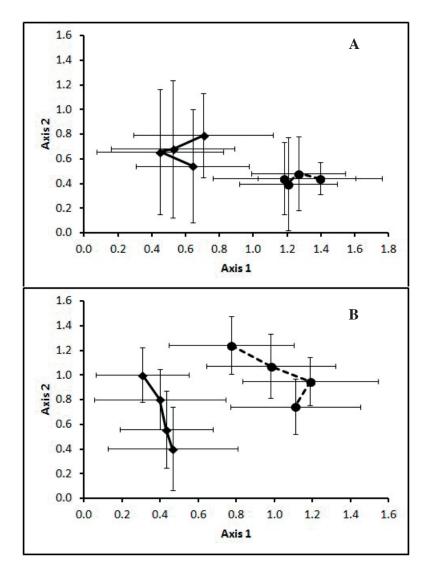


Fig 4 Results of detrended correspondence analysis of benthic invertebrate communities in Brierly Brook, 1995-1999 (extensive study). Each point represents the mean position (centroid) of 36 samples at each site in each year (six replicates in each of six months) on the first two axes of the ordination. Error bars are standard deviations. A: Upstream. B: Downstream. Diamonds = restored site; filled circles = negative (degraded) control site. Year 1999 is represented by right-most points on Axis 1 (A) or lowest point on Axis 2 (B).

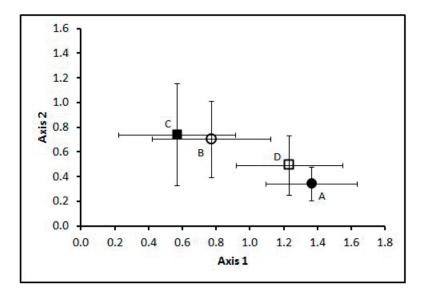


Fig 5 Results of detrended correspondence analysis of benthic invertebrate communities from all years 1995-1999 (extensive study). Each point represents the mean position (centroid) of 24 monthly means (each based on six replicates) over six months in each year, on the first two axes of the ordination. Error bars are standard deviations. Squares (C and D) = upstream sites; circles (A and B) = downstream sites. Filled symbols = restored sites; open symbols = negative (degraded) control sites.

Seven of 15 taxa revealed a significant interaction between Year and Site. *Baetis* was more abundant at the undisturbed Control site (Fig 6), and the difference grew larger from 2003 to 2007 (P = 0.072). Chironomidae did become more abundant at the New Restored site following restoration (P = 0.033), but no more so, and sometimes less, than at the other sites (Fig 6). Drunella, Epeorus (Ephemeroptera) and Hydropsyche (Trichoptera) differed erratically among sites and years (Fig 6), but showed no pattern consistent with a response to restoration (P = 0.065-0.0012). Neophylax (Trichoptera) was more abundant at both restored sites than at the undisturbed Control site in 2005 and 2007 (Fig 6), but showed no unique response to restoration at the New Restored site (P = 0.063). Finally, the leaf-shredding stonefly Leuctra was collected for the first time in 2003, and increased in abundance at all sites (Site, P = 0.043, Year \times Site, P=0.064) throughout the study, again without a consistent pattern among sites (not shown). Hence, the individual taxa provide

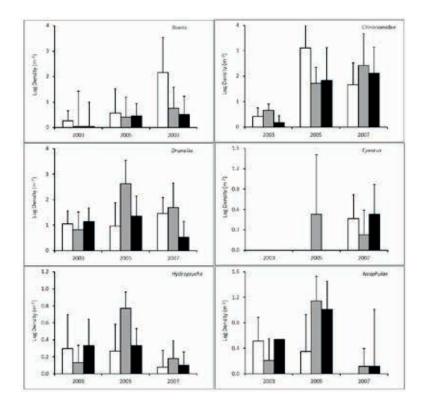


Fig 6 Mean abundances (log-transformed) of six taxa of benthic invertebrates that showed a significant Year × Site interaction, implying a response to restoration, among the undisturbed Control site (open columns), Old Restored site (grey columns) and New Restored Site (black columns) in the intensive study, 2003-2007. Values are means of six samples at each site in each year (n = 6). Error bars are standard deviations of log-transformed data.

only weak evidence that habitat restoration increased population densities in the intensive study.

Most of the 21 genera, tribes or sub-families of chironomids identified in 2003 and 2005 were too infrequent or varied in numbers too erratically to support any inferences. *Polypedilum*, found only in very low numbers at the Control site in 2003, appeared at the New Restored site, but not the Old Restored site, in 2005. *Tanytarsus*, present at the Old Restored and Control sites in 2003, was collected at the New Restored site in 2005. This result is at least consistent with a restoration effect, but numbers remained very low, averaging about one animal per sample. Although six of ten insect orders and community metrics evinced a significant difference through time (P = 0.059-0.0001), only Diptera produced a significant main effect for Site (P = 0.071). The abundance of Diptera increased from the New Restored site to the Old Restored site to the Control site (Fig 7), although the pattern is obscured by unequal annual variation (Year × Site, P = 0.052). This trend matches that expected from restoration, especially if the biotic response takes a long time. However, there was no meaningful increase in Diptera abundance at the New Restored site in 2005, and the number for 2007 is substantially lower than earlier.

None of the remaining insect orders, nor EPT, total number, total taxa richness or Simpson's Index, showed a significant response to restoration. The EPT/Chironomidae ratio produced a significant Site × Date interaction (P=0.0003), apparently because of large differences in abundance from year to year. The ratio did decline significantly at the New Restored site following restoration, implying a relative increase in the abundance of chironomids (Fig 7). A similar, but weaker Site × Date interaction for the EPT/Total ratio (P = 0.031) appears to arise from unequal annual changes in abundance among sites (not shown). The ratio declined (producing a more negative log-transformed ratio, implying relatively fewer EPT) after restoration at the New Restored site, although the difference was small.

Detrended Correspondence Analysis resolved 19.9% of total variance on the first axis, and 7.8% and 5.5% on the second and third axes. The first axis illustrates a change in community structure at all sites between 2003-2005 and 2007 (Fig 8). The trajectories for the New Restored and Old Restored sites are similar, and different from that of the Control site. Hence, while restoration appears to have changed benthos community structure at both restored sites in a similar way, there is no evidence that these sites are approaching the community structure at the undisturbed Control site.

DISCUSSION

Overall, the results of these two studies do not support a thesis that the restoration structures installed in Brierly Brook altered or augmented benthic invertebrate communities by improving benthic habitat. In the earlier, extensive study, only six of 24 genera appeared to respond positively to restoration; the greater number showed either

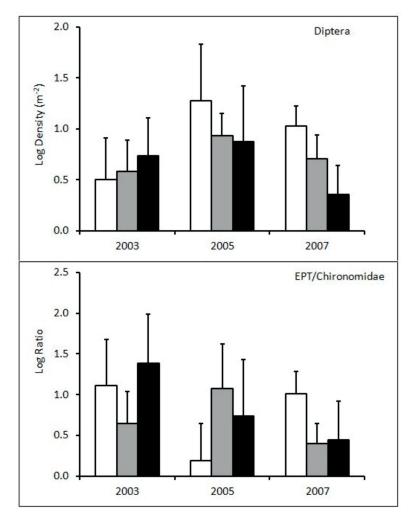


Fig 7 Mean abundances (log-transformed) of Diptera and the EPT/Chironomidae ratio at the undisturbed Control site (open columns), Old Restored site (grey columns) and New Restored Site (black columns) in the intensive study, 2003-2007. Values are means of six samples at each site in each year (n = 6). Error bars are standard deviations of log-transformed data.

conflicting results or no response at all. Responses by insect orders and broader community metrics were even weaker. In the intensive study, differences in abundance that could be generously attributed to restoration were found only for Simuliidae, *Baetis* and *Leuctra*, and the response for Simuliidae is opposite that observed in the earlier study. With the exception of the order Diptera, most insect orders

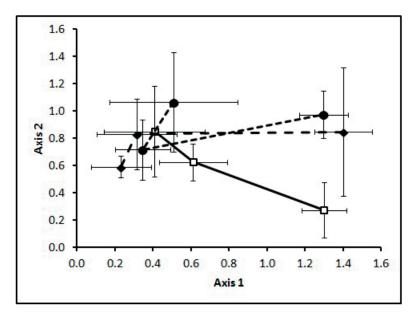


Fig 8 Results of detrended correspondence analysis of benthic invertebrate communities in Brierly Brook, 2003-2007 (intensive study). Each point represents the mean position (centroid) of six replicate samples, collected in each of 2003, 2005 and 2007, on the first two axes of the ordination. Error bars are standard deviations. Open squares = Control site; Diamonds = New Restored site; Circles = Old Restored site. Points for the year 2003 are on the left side of the Fig, those for 2007 are on the right.

and community metrics showed no marked response to restoration, or, in the case of EPT/Chironomids, changed in a direction usually taken as indicative of degradation (Hannaford & Resh 1995, Zweig & Rabeni 2001). These feeble responses were returned from an analytical approach deliberately biased toward finding significant differences. Separations of sites on correspondence analysis plots appear to reflect individual site characteristics rather than a coherent response to restoration. In both studies, benthic communities at degraded and restored sites were clearly different, but did not become more similar through time. Hence, while earlier work confirms that in-stream structures helped clear fine sediments from the substratum and therefore putatively improved benthic habitat, these changes had little or no effect on benthic invertebrate communities in Brierly Brook over at 12-year period.

In previous studies, four possible explanations have been offered for the absence of clear and positive effects of restoration on benthic invertebrates: (1) the effect is there but too subtle to be detected in the naturally high variability of benthic communities (Muotka & Syrjänen 2007); (2) full recovery takes a long time, perhaps decades (Haase et al. 2013, Jähnig & Lorenz 2008, Matthews *et al.* 2010, Muotka *et al.* 2002), longer than the duration of most studies; (3) source populations to provide colonists to the restored reach are missing because of widespread degradation or disconnection (Garcia *et al.* 2012, Lorenz & Feld 2013, Sundermann *et al.* 2011b) or (4) abundances of benthic invertebrates are limited by some other factor, unconnected to habitat restoration within the channel, such as pollution, nutrient supply, or riparian zone condition, (Entrekin *et al.* 2008a, 2009, Kail *et al.* 2012, Palmer *et al.* 2010).

In Brierly Brook, the first of these possibilities is unlikely because of the intensity and duration of the sampling, especially in the extensive study. While variability among sites was certainly high (coefficients of variation for insect genera at a site approach 100%), it seems unlikely that a restoration effect of any substantial magnitude would be missed by this analysis. Similarly, while both studies were of relatively short duration (five years), together they span 12 years, and finished 17 years after the first structures were installed in the brook. At least some movement of invertebrate communities toward the undisturbed condition should be evident in this much time (but see below).

Sundermann *et al.* (2011b) suggested that for restored rivers in Germany, the absence of an un-degraded source reach within a short distance was responsible for a lack of response in invertebrate populations. The restored reaches in Brierly Brook could be easily recolonized by invertebrate drift from the upper reach, which is forested and largely undisturbed. Moreover, Antigonish County is dense with streams and rivers that could provide colonizers. Fuchs & Statzner (1990) showed that recolonization after restoration disturbance was relatively rapid if a source community was located nearby, especially on the same stream. Therefore lack of colonizers cannot explain the absence of consistent, positive responses to restoration in Brierly Brook.

The fourth possibility, a factor external to the channel, seems most likely. In Brierly Brook, unstable substrata and poor litter retention are likely factors impeding recovery of the benthos. The brook carries abrupt high flows following rainstorms. Cobble and coarse gravel may be turned over too frequently by storm flows to support stable invertebrate communities. Lacking coarse woody debris, the brook also provides no impediment to high flows sweeping organic debris out of the system (Flores *et al.* 2011), depriving benthic invertebrates of an essential food source.

This possibility is supported by the unexpectedly low densities of invertebrates in Brierly Brook, and in other streams of northern Nova Scotia. Typical Surber samples in the intensive study, for example, contained <50 animals in total; numbers in individual taxa were commensurately lower. Some samples contained fewer than 10 individuals. By contrast, benthos densities in other regions of southern Canada are typically an order of magnitude greater (Taylor & Roff 1985, B. Taylor unpublished data). Ironically, these exceptionally low population densities, while probably a consequence of the historical disturbance to the steam and its valley, also impede our ability to detect improvements using standard sampling methods.

Nevertheless, the two studies together provide some evidence that the quality of stream habitat is improving. *Tricorythodes*, a silt-tolerant mayfly, and the silt-tolerant beetle *Optioservus* (Relyea *et al*. 2000) were among the five most abundant members of the invertebrate community in 1995-1999, and their numbers at the upstream sites remained high while other mayflies declined. *Caenis*, a second silt-tolerant mayfly (Extence *et al*. 2013), became established at the downstream sites at the same time. All three genera maintained higher densities at the degraded sites than at restored sites, suggesting some amelioration of siltation from the in-stream structures.

More importantly, neither Tricorythodes nor Caenis was captured anywhere during the intensive sampling in 2003-2007. This disappearance is unlikely to be a local site difference because the gradient in the middle reach is lower than elsewhere and substratum composition is similar. Instead, the later study recorded significant numbers of silt-intolerant Drunella (Relyea et al. 2000), along with Lepidostoma (a caddisfly) and Leuctra (a stonefly), both of which are leaf-litter shredders. These two genera are normally abundant in cool streams of northern Nova Scotia (MacDonald & Taylor 2008). Their appearance in Brierly Brook, and the disappearance of *Optioservus*, Caenis and Tricorythodes, suggest a declining influence of siltation as a controlling factor on the benthos and movement toward more normal community structure and improved energy retention. Hence, the brook as a whole may be moving toward a more stable condition, but there is no evidence that in-stream restoration structures were responsible for this trend.

Our results suggest there are narrow limits to the effectiveness of channel modifications aimed at restoring fluvial habitats in streams of this region. While the benefits of in-stream restoration to salmon spawning are unequivocal (Floyd et al. 2009, MacIinnis et al. 2008), benthic invertebrates appear to be limited by other factors, perhaps related to substratum stability and retention of leaf litter. In this respect our results accord with other studies that have reported absent or inconsistent effects of in-stream restoration on benthos communities (Lepori et al. 2005, Luohi et al. 2011, Matthews et al. 2010, Schiff et al. 2011). Is it fair to qualify these channel modifications as stream restoration then, or are they merely habitat improvements for one or a few fish species? This distinction is important because of the substantial amounts of money and effort, mostly by volunteers, directed toward stream restoration in the Maritimes. Benthic invertebrates are integral components of stream ecosystems and an important food source for salmonid fishes. Restoration works that do not improve conditions for benthos fall short of the goal of full ecosystem restoration, and may limit the benefits of improved spawning success, if young fish are food-limited. Research aimed at understanding the broader conditions limiting benthic communities in Maritime streams would therefore be of both theoretical and practical benefit.

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