TOWARDS A FUNCTIONAL UNDERSTANDING OF THE EFFECTS
OF SEDIMENT AGGRADATION ON STREAM FISH CONDITION

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ABSTRACT

Using both field and laboratory experiments, we evaluated mechanistic links among sediment aggradation, embeddedness and fish condition. In the field, we measured fish condition in three common stream and river species representing unique feeding guilds [creek chubs (surface and water column feeders), pumpkinseeds (omnivores) and white suckers (benthic invertivores)] over time across varying sedimentation levels. We continued this work in the laboratory with white suckers (benthic invertivores) and common shiners (surface and water column feeders), standardizing food amounts across degrees of sediment aggradation. In the field, pumpkinseeds – the species with the greatest foraging plasticity – showed no significant difference in condition across levels of sediment aggradation or time. Creek chubs and white suckers were affected by sediment level and time. White suckers – the most specialized forager – were most strongly affected, but exhibited the greatest loss of condition in least aggraded conditions. Laboratory data suggested that sedimentation and time spent in aggraded conditions were significant factors affecting common shiners, in spite of consistent food availability. Results varied across feeding guilds, indicating that opportunistic species that feed across the water column may be more resilient to sedimentation than more specialized trophic groups. However, all fish in the study experienced a loss of condition in aggraded environments over time, indicating that streams and rivers with extensive sediment aggradation are unlikely to support healthy fish assemblages. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: aggradation; embeddedness; fish condition; river; sediment; stream

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INTRODUCTION

Stream and river channel adjustment is increasingly recognized as an important factor affecting lotic fish communities (Shields et al., 1994; Sullivan et al., 2006). In particular, non-point source pollution in the form of sediment eroded from the landscape is pervasive (Nelson and Booth, 2002). Triggered by both natural and anthropogenic causes, increased sediment loads affect stream biological communities in a variety of ways. The effects of fine sediments on fish have been especially well documented (Bisson et al., 1992; Newcombe, 1994; Waters, 1995; Suttle et al., 2004). Increased turbidity and reduction of instream habitat heterogeneity are often cited as critical factors affecting fish community diversity, community structure and productivity (Berkman and Rabeni, 1987; Wood and Armitage, 1997; Mol and Ouboter, 2004). Increased coarse sediment supply has not received as much attention; yet it leads to channel aggradation, reduced flow capacity, flooding and channel instability (Nelson and Booth, 2002; Sullivan et al., 2004).

Localized bed aggradation resulting from both fine and coarse sediment in gravel-bed streams is a normal, transient phenomenon. However, human activities lead to myriad alterations in the morphology of stream and river ecosystems through various land-use practices (e.g. timber harvest, agriculture, urbanization, etc.) and habitat fragmentation (Schindler, 1987; Benke, 1990; Allan and Flecker, 1993; Seyedbaghiri, 1996; Booth and Jackson, 1997). Numerous investigations have shown that landscape alterations lead to increased peak flows and other changes in sedimentological and hydrologic regimes (Lull and Reinhart, 1972; Harr et al., 1975; Bormann and Likens, 1979; Hewlett and Doss, 1984; Swank and Crossly, 1988; Jones and Grant, 1996).

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These anthropogenic activities have drastically increased both the amount of sediment entering streams as well as its storage extent and duration, causing the topography of channel beds to undergo profound and lasting changes. Despite greater scientific attention to the interface between watershed land-use activities and aquatic conditions, and the widespread use of total maximum daily loads (TMDLs) in managing non-point source sediment pollution, the effects of sediment aggradation on stream and river fish communities is still not completely understood. This is particularly the case in larger streams and rivers, where experimental work presents significant challenges. This understanding is vital as land-use activities continue to cause increased sediment inputs across greater lengths of stream and river networks.

Although interruptions in the supply and/or availability of food resources are believed to constitute the principal influences of sedimentation on stream fish (Karr and Dudley, 1981; Berkman and Rabeni, 1987), the majority of analyses to date have focused on community structure. Considering functional feeding roles of stream fishes may yield important mechanistic insight into the topic. Functional feeding roles are diverse and relate to both the food consumed as well as to the primary foraging position [e.g. piscivores, benthic invertebrate feeder, surface and water column feeder, generalized invertebrate feeder, planktivore, herbivore–detritivore, omnivore, parasite (Horwitz, 1978)]. Feeding roles relate directly to resource partitioning of prey and habitat, which represents a critical mechanism in structuring and maintaining diverse fish assemblages (Baker and Ross, 1981; Moyle and Senanayake, 1984).

The purpose of the current study was to adopt a functional approach to explicitly test the effects of stream sediment aggradation on the condition of several common stream fishes representing key feeding guilds. We paid particular attention to the role of embeddedness and time spent in aggraded conditions and to potential threshold levels of sediment aggradation beyond which fish condition was impaired. We expected that fish condition would differ by feeding guild across varying levels of sediment aggradation. Specifically, we anticipated that fish introduced into aggraded environments would lose condition over time, diminishing most drastically in fish confined to areas with high levels of sediment aggradation and relying on more specialized feeding strategies.

METHODS

Our study included both field and laboratory components. We conducted field experiments in the Brown’s River, Vermont, from August through October 2003; and conducted laboratory experiments at the University of Vermont’s Rubenstein Ecosystem Science Laboratory from September through November 2004.

The Brown’s River Watershed is a mid-sized watershed in north-central Vermont. At the study reach, the river is a 4th order system, with a mean bankfull width of 30 m. Whereas water quality concerns in the region include stream instability and flooding, agricultural impacts, transportation infrastructure problems, dams, stormwater runoff and loss of forest and riparian zones (LCPB, 2004); sedimentation and habitat alteration are the primary threats to the watershed (VTDEC, 2001). The study site of our experiment was located in the lower third of the watershed. Along a 2000 m reach, we selected nine locations that represented three treatments determined by levels of sediment aggradation: three slightly aggraded, three moderately aggraded and three severely aggraded (Figure 1). Because a degree of sedimentation is a natural component of all alluvial stream systems, ‘slightly aggraded’ conditions represented our control treatment.

Having found a combination of both qualitative and quantitative techniques to be effective in measuring sedimentation relative to fish communities (see Sullivan et al., 2006), we determined degree of sediment aggradation by a combination of visual estimates, pebble counts and measurements of embeddedness. Visual estimates focused on field indicators (e.g. shallow pool depths, excessive sediment deposition, channel bed exposed during low flow periods, lateral migration of thalweg) as outlined by the regional geomorphic assessment protocols (see VTDEC, 2003). At each location, five representative transects were established at which pebble counts and embeddedness were recorded. At each location, pebble counts were conducted along each transect following Wolman’s (1954) method to estimate sediment size classes including $D_{50}$ and $D_{95}$ values; $D_{50}$ represents the median grain size and $D_{95}$ is the grain size at which 95% of the sample is finer. Following the Vermont Department of Conservation’s bioassessment protocols (VTDEC 2004), we measured the degree of embeddedness – the degree to which smaller particles surround or cover larger particles (Platts et al., 1983; Fitzpatrick et al., 1998) – by

haphazardly selecting 10 rocks in each location along each transect and determining the percent of the total surface area of the rock that was embedded.

In watersheds where sand is an important part of the annual sediment load, embeddedness is a measure of twofold importance. Firstly, it is an important streambed sediment indicator, frequently used as a target measurement in TMDL planning (USEPA, 1999). Secondly, the availability of interstitial space directly affects the feeding, refugia and reproduction of macroinvertebrates and fishes, and available area for periphyton (Lenat and Crawford, 1994; Waters, 1995; Merritt and Cummins, 1996). Embedded cobbles is but one of the ramifications of increased sediment aggradation.

At each site, we constructed an in-stream enclosure [7.5 m (length) × 3.5 m (width) × 1.2 m (height)] made from 6.35 mm netting and 1.8 m wooden stakes and situated to align with stream flow. The height of the enclosures was sufficient to project well above the water’s surface. Each enclosure contained a run/riffle area and a pool area (i.e. an area of faster flowing water and an area of slower flowing water). We did not cover the tops of the enclosures as we wanted natural riparian inputs into the enclosures to continue. Avian predators were discouraged by crisscrossed wires over the top and ‘scarecrows’ placed at each enclosure.

Turbidity (i.e. none, low, moderate, high – based on visual estimates) and amount of detritus (based on dried weight of collections of leaves and other coarse particulate organic matter at four representative locations within each enclosure) were measured. Number of large woody debris pieces >1.0 m × 0.1 m (Montgomery et al., 1995) were counted and bank vegetation and shade were visually estimated for each enclosure. Velocity was measured three times over the course of the field experiment (beginning, mid, end) in each enclosure at one point in pool habitat and one point in riffle habitat using a Marsh-McBirney® Flo-Mate 2000 (Frederick, MD, USA).

To avoid disturbing potential prey availability and/or colonization in and around the enclosure areas, we were unable to collect aquatic macroinvertebrates along the study reach. However, we did obtain an estimate of benthic aquatic macroinvertebrate food resources by collecting insects at three adjacent reaches that exhibited signs of channel aggradation. Because of the high resolution of geomorphic data needed to accurately categorize locations within reaches by degree of aggradation, these macroinvertebrate collections were only meant to yield composite estimates of invertebrate densities at similar reaches. In all, 18 samples were collected in both riffle and pool habitat using a Surber sampler with a 500 μm-mesh net by disturbing the substrate and scraping larger rocks for 90 s intervals. Samples were preserved in 70% ethanol and counted in the laboratory. Immediately following Run 1 of

Figure 1. Experimental design on Browns River, VT, USA. A, B and C (upstream to downstream) designate sets of enclosures, with the three levels of sediment aggradation treatment in each set represented by \( \bullet \) slight, \( \bigtriangleup \) moderate; and \( \square \) severe. This figure is available in colour online at wileyonlinelibrary.com
the enclosure experiment (see below), and again immediately before stocking with pumpkinseeds, macroinvertebrates were sampled in one corner in each of the treatment enclosures, minimizing substrate disruption as much as possible. Macroinvertebrates were counted (but not removed) from large sediment clasts, and the clasts were then carefully resituated in the same position in their respective enclosure.

Residents fish present in each enclosure area were collected prior to each experimental set using a Smith-Root® backpack electrofisher (Vancouver, WA, USA) and a 3 m × 2 m seine net, counted and removed from the area. We then captured adults of three common, ubiquitous stream species: creek chubs (*Semotilus atromaculatus* Mitchill), pumpkinseeds (*Lepomis gibbosus* Linnaeus) and white suckers (*Catostomus commersoni* Lacapede) in adjacent areas. Each of these species represents a unique feeding strategy. In the study region, adult creek chubs feed most commonly at the surface and in the water column on a variety of animal prey [i.e. surface and water column feeder (Horwitz, 1978; McMahon, 1982)]. Pumpkinseeds are typically omnivores that feed across the water column including on the benthos [i.e. generalist feeder (Halliwell et al., 1999)]. White suckers feed primarily on aquatic macroinvertebrates and are classified as benthic invertivores (Horwitz, 1978; Twomey et al., 1984) (Figure 2). To collect fish for the experiment, we used a 1.22 m × 12.19 m bag seine with 3.175 mm mesh weighted with lead-lines. In order to assess fish condition in naturally occurring wild populations in the larger study area, we used a combination of backpack electrofishing and seine netting to capture fish from each species from a suite of local rivers (including Browns River). These fish were measured (mm) and weighed (g).

Because white suckers and creek chubs are commonly found together yet employ unique and non-competitive foraging strategies, we put 40 white suckers and 12 creek chubs in each enclosure for a mean density of 4.2 fish m⁻³. We then conducted Run 1 of the river experiment for 4 weeks. Twenty-four days later – to allow for recolonization by invertebrates (Shaw and Richardson, 2001) – we put pumpkinseeds in the enclosures and began Run 2 of the field experiment. Pumpkinseeds were generally found in lower numbers in the watershed than either creek chubs or white suckers so we restricted the number of fish to nine individuals per enclosure. Because pumpkinseeds may compete for food and habitat with both creek chubs and white suckers, Run 2 of the experiment was conducted with pumpkinseeds alone to avoid potential interspecific competition. Although the fish density we used in the enclosures was generally higher than that observed before fish were removed (Table 1), we felt that our

Figure 2. Schematic representation of fish species and their associated feeding guilds used in the field (enclosure) and laboratory (tank) experiments, by Run #. This figure is available in colour online at wileyonlinelibrary.com
Table I. Characteristics of nine enclosures in Browns River, VT

| Set | Sed. Agg. level | $D_{50}$ (mm) - riffle | $D_{50}$ (mm) - pool | $D_{95}$ (mm) - riffle | $D_{95}$ (mm) - pool | % Shade | Vel (m s$^{-1}$) - riffle | Vel (m s$^{-1}$) - pool | % Emb - riffle | % Emb - pool | % LWD (% exposed) | Detritus (g) | Turbidity | Bank (% Veg) | Resident fish (#) |
|-----|----------------|------------------------|---------------------|-----------------------|---------------------|--------|------------------------|-----------------------|----------------|---------------|----------------|----------------|------------|-------------|--------------|-----------------|
| A   | Slight         | 8.90                   | 0.93                | 170.00                | 86.00               | 0–25   | 0.110                  | 0.035                  | 10             | 15            | 0             | 0.59         | None       | Yes (90)    | <30          |
|     | Mod.           | 2.20                   | 0.06                | 8.40                  | 0.06                | 25–50  | 0.600                  | −0.028                 | 70             | 70            | 3 (75)        | 3.70         | None       | Yes (50)    | <10          |
|     | Severe         | 1.50                   | 0.06                | 5.10                  | 0.87                | 0–25   | 0.128                  | 0.025                  | 100            | 100           | 3 (25)        | 5.86         | Low        | Yes (80)    | <10          |
| B   | Slight         | 2.60                   | 2.20                | 15.00                 | 22.00               | 0–25   | 0.245                  | 0.155                  | 40             | 35            | 0             | 1.85         | None       | Yes (100)   | <30          |
|     | Mod.           | 1.60                   | 1.00                | 12.00                 | 2.60                | 0–25   | 0.068                  | 0.035                  | 25             | 100           | 0             | 1.24         | Low        | Yes (60)    | <10          |
|     | Severe         | 2.40                   | 0.53                | 5.90                  | 5.20                | 25–50  | 0.253                  | −0.030                 | 85             | 100           | 0             | 0.04         | None       | No (n/a)    | <10          |
| C   | Slight         | 2.40                   | 0.56                | 38.00                 | 3.50                | 0–25   | 0.213                  | 0.075                  | 35             | 20            | 4 (75)        | 36.41        | Low        | Yes (30)    | <30          |
|     | Mod.           | 0.71                   | 0.66                | 6.70                  | 4.90                | 0–25   | 0.260                  | 0.090                  | 65             | 65            | 3 (50)        | 0.77         | None       | Yes (90)    | <10          |
|     | Severe         | 0.70                   | 0.57                | 3.70                  | 1.60                | 0–25   | 0.110                  | 0.048                  | 100            | 100           | 0             | 36.85        | Low        | No (n/a)    | <10          |

Sed. Agg. level (sediment aggradation level) refers to treatment, with three levels represented by ‘slight’, ‘moderate’ and ‘severe’. Vel, velocity; Emb, embeddedness; LWD, large woody debris. Bank refers to whether enclosure was adjacent to bank or not (% vegetation is the amount of vegetative cover on area of bank along enclosure).
experimental densities were appropriate given that natural densities of fish occurring in the larger study area (i.e. Browns River) exhibit variability, ranging from 1.1 to 17.4 fish m\(^{-3}\) (see Sullivan et al., 2006).

Fish were collected using the bag seine and all individuals were measured and weighed at 0, 7, 21 and 28 days for creek chubs and white suckers; and at 0, 7 and 14 days for pumpkinseeds (further measurements were precluded by a late season flooding event). A thunderstorm also interrupted data collection for pumpkinseeds on day 7 resulting in no measurements from ‘slight’ enclosures for Day 7.

We conducted the second phase of our experiment in a laboratory setting in order to directly test the role of sediment aggradation, while standardizing other factors. From streams in the region, we captured 90 common shiners (Luxilus cornutus Mitchill) and 35 white suckers for use as our study species. Because of the relatively small size of the tanks in the laboratory, instead of creek chubs, we opted to use smaller-bodied common shiners to represent surface and water column feeders (personal observation) (Figure 2). We placed all fish in holding tanks for 1 week to acclimate to temperature (22°C) and photoperiod (12 h). We placed nine oval rubber tanks (113.56 L, 73.7 cm × 48.3 cm) in a row on 1 m high tables, and designated three tanks as slightly aggraded, three as moderately aggraded and three as severely aggraded. From the same streams, we collected cobbles of roughly the same size that were covered by similar numbers of macroinvertebrates of the orders Ephemeroptera, Trichoptera and Diptera (\(\bar{x} = 62.1, \text{SD} = 19.0\)) and amount of periphyton (1/4–1/2 coverage). After filling the tanks with water, we arranged seven cobbles in each tank. In the slightly aggraded tanks, we poured 2.268 kg of coarse play sand (0.84 mm median diameter); in the moderately aggraded, we poured 4.536 kg of sand; and in the severely aggraded, 9.072 kg of sand. Thusly, cobbles were covered to varying degrees relative to amount of sand. We kept fish (nine common shiners and three white suckers per tank) in the tanks for 30 days, approaching a density similar to those in other investigations relating to sediment and fish growth (see Shaw and Richardson, 2001); we measured and weighed them to assess condition at 0, 10, 20 and 30 days. We replaced three cobbles with freshly collected (and colonized by macroinvertebrates) cobbles on days 10 and 20 to standardize food over time.

**Statistical analysis**

Indices are commonly used to assess the physiological status of fish (Copeland et al., 2008). Fulton’s Condition Factor, \(K\), is a commonly used measure of growth rate expressed by the equation \(K = W/L^3 \times 10^5\), where \(W\) is weight and \(L\) is length (Ricker, 1975). Despite debate relative to the appropriateness of \(K\) for some applications (Bolger and Connolly, 1989; Cone, 1989; Blackwell et al., 2000), we considered it to be an appropriate estimator of fish condition among single statistical representations of weight-length relationships for our study for the following reasons: \(K\) remains widely used to reflect the condition and nutritional status of individual fish across a range of habitats (Adams et al., 1992; Ribeiro et al., 2004; Iles and Rasmussen, 2005), \(K\) has been shown to vary due to location and environmental perturbation within a species and can be used to assess within population influences of environmental characteristics over time (Doyon et al., 1988; Ney, 1993; Fisher et al., 1996; Mills et al., 2000), and \(K\) has been applied to either our focal species themselves or closely related species (Freedman, 2005; Bist er, 2000; Neff and Cargnelli, 2004; Ribeiro et al., 2004). Additionally, \(b\) [slope of weight-length equation, \(\log_{10}(W) = a' + b \cdot \log_{10}(L)\)] from our experimental fish closely approached 3.0), thereby meeting \(K\)’s principal assumption of isometric growth (common shiner, 3.034; creek chub, 2.954; pumpkinseed, 2.882; white sucker, 2.920). Therefore, we used \(K\) to reflect growth rates of fish in our experiment. In assessing wild (i.e. uncaged) fish condition, only fish meeting certain length minima [common shiners and pumpkinseeds, >60 mm; creek chubs and white suckers >85 mm (McMahon, 1982; Trial et al., 1983; Twomey et al., 1984)] were assessed for condition, thereby excluding early age classes from the analysis. Given that fish that died during the course of the experiments represented the worst condition and the gravest potential effect of sedimentation, mortalities were assigned a 0.1 condition factor for statistical purposes.

Analysis of variance (ANOVA) followed by Tukey–Kramer honestly significant difference (HSD) (Tukey, 1953; Kramer, 1956) multiple comparison tests were used to test for differences in levels of embeddedness, flow velocities and detritus among the three treatment levels. We analysed substrate composition both between pools and riffles, and among composite measures (\(D_{50}\) and \(D_{95}\) values of pools and riffles combined) among treatments. Student’s \(t\)-tests were used to test for differences in mean \(D_{50}\) and \(D_{95}\) values between riffles and pools. ANOVA was also used to test for potential differences in mean \(D_{50}\) and \(D_{95}\) values among treatments.
Although we were quite successful in our recapture efforts, not every fish in a location was measured every time due to escapes, predation or our inability to find the fish. Individual fish in the enclosures (field) and tanks (laboratory) were not true replicates (pseudoreplication, Hurlbert, 1984) in our experiments. Enclosure or tank was the experimental unit and thus analysis was performed on the mean $K$ value for each enclosure or tank.

Differences in mean $K$ values were analysed using repeated measures ANOVA with sediment aggradation level as the main factor and set (i.e. three enclosure/tank replicate, hereafter ‘block’) as the blocking factor (fixed effects). Mean $K$ values for each species per enclosure/tank were used as the repeated measurements, followed by Tukey–Kramer HSD to test for pairwise differences in $K$ across time steps. We ensured that variances were homogeneous using Levene’s test and residual plots. $K$ values were log transformed to meet assumptions of normality. All statistical analyses were performed using JMP 7.0 Statistical Discovery Software (SAS Institute, Inc., Cary, NC) and utilized $\alpha = 0.05$.

RESULTS

Field enclosure experiments

Mean benthic macroinvertebrate density in the immediate vicinity of the enclosures was 125.6 individuals 100 cm$^{-2}$. After Run 1, macroinvertebrate density was markedly lower than in adjacent reaches, estimated at <32 individuals 100 cm$^{-2}$. However, by the end of the 24 day recolonization period, macroinvertebrate density had rebounded and was estimated at >100 individuals 100 cm$^{-2}$, approaching the density of the surrounding habitats.

Characteristics of each enclosure are outlined in Table I. Mean embeddedness levels were significantly different ($F = 64.52, p < 0.001, df = 8$) across treatments, with embeddedness of each level significantly different from the other two [slight – 25.42%, moderate – 65%, and severe – 97.5% (SD = 4.494%); $q^2 = 3.068, p < 0.05$ (Tukey–Kramer HSD test)]. Mean flow velocity in riffles was 0.22 m s$^{-1}$ (SD = 0.160 m s$^{-1}$) whereas in pools it was 0.045 m s$^{-1}$ (SD = 0.058 m s$^{-1}$). However, there was no significant difference in velocities of riffles ($F = 0.566, p = 0.595, df = 8$) and of pools ($F = 1.530, p = 0.291, df = 8$) among treatments. Mean $D_{50}$ values were 2.56 mm in riffle areas and 0.73 mm in pools and were significantly different from one another ($t = -3.041, p < 0.0078, df = 16$). Mean $D_{95}$ values were 2.63 mm in riffle and 1.73 mm in pools and were not significantly different from one another ($t = -1.538, p < 0.1436, df = 16$). Composite $D_{95}$ values (e.g. pool and riffle) were significantly different ($F = 8.986, p = 0.016, df = 8$), whereas composite $D_{50}$ values were only marginally different among treatments ($F = 4.379, p = 0.067, df = 8$) (Table I). Detrital mass did not differ among treatments ($F = 0.09, p = 0.920, df = 8$).

Both creek chub and white sucker condition ($K$) showed statistically significant differences in the ANOVA whole models ($p < 0.001$ for both, Table II), whereas the pumpkinseed model was only marginally significant ($p = 0.075$, Table II). In the effects tests, ‘day’ was the most significant source of variation relative to both creek chub ($p < 0.001$) and white sucker condition ($p < 0.0001$, Table III). ‘Sediment aggradation level’ was also significant in both the creek chub ($p = 0.008$) and white sucker models ($p = 0.002$, Table III). The interaction of time and sediment aggradation (‘day × sediment level’) was a significant factor ($p = 0.029$) in the creek chub model only (Table III).

Table II. Whole model ANOVA results for the field enclosure experiments

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>$F$-ratio</th>
<th>$p$-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Creek chub</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>17</td>
<td>32.6750</td>
<td>1.9221</td>
<td>13.58</td>
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<td>Error</td>
<td>18</td>
<td>2.5469</td>
<td>0.1415</td>
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<td></td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>13</td>
<td>0.0487</td>
<td>0.0037</td>
<td>2.63</td>
<td>0.0753</td>
</tr>
<tr>
<td>Error</td>
<td>9</td>
<td>0.0128</td>
<td>0.0014</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White sucker</td>
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</tr>
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<td>0.1734</td>
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</table>
Creek chub (Figure 3a), pumpkinseed (Figure 3b) and white sucker (Figure 3c) condition across treatments showed clear patterns of changes in condition over time. Creek chubs in slightly aggraded conditions experienced the least drastic loss of condition through Day 21, although their condition declined precipitously by Day 28. In contrast, white sucker condition across all sediment levels had declined to its lowest point by Day 21, and rebounded slightly by day 28 with fish experiencing the lowest condition in slightly aggraded conditions and the highest in moderately aggraded conditions. Pumpkinseed condition in moderate and severe treatments – reached its lowest point at day 7 and rebounded slightly by Day 14. White suckers and creek chubs experienced the greatest mortality, with the greatest number of mortalities occurring in the severe treatments. Conversely, pumpkinseeds experienced no mortalities during the course of the field experiment.

**Laboratory tank experiments**

Whole model ANOVAs for the tank experiments were significant for common shiner condition ($p = 0.0002$) but not for white sucker condition ($p = 0.3011$, Table IV) – in contrast to results of the enclosure experiments. ‘Day’ was the most influential factor on common shiner $K$, with ‘sediment aggradation’ and the interaction between time and sediment level both of importance (Table V).

Common shiner condition showed a strong pattern over time: a general decline from day 0 to 30 with a slight increase in condition in the moderate treatment at day 10 (Figure 4a). Shiners in the severe treatment tanks experienced the greatest loss of and lowest condition levels. White sucker condition responded in a more haphazard fashion (Figure 4b), although white sucker condition in the severe treatment was consistently the lowest over time. Common shiners experienced no mortalities in the tank experiments, whereas seven white suckers died over the course of the experiment.

Overall, results of the both the enclosure and tank experiments show a decline in fish condition across species from day 0 to the end of the experiments. However, the strengths of the relationships and the patterns differ among species and foraging guilds. Naturally occurring fish of the same species and age classes exhibited comparable condition factors to fish at day 0 (Table VI).

**DISCUSSION**

Sediment loading is widely considered the leading problem affecting stream and river ecosystems in the United States (USEPA, 1990; Sutherland *et al.*, 2002). Observational studies have shown that increased levels of sedimentation in stream channels have profound effects on fish communities (see Waters, 1995) including alterations in habitat (Allan *et al.*, 1997), community diversity and productivity (Dudgeon, 2000; Sullivan *et al.*, 2002).
2006) and the relative abundance of spawning guilds (Sutherland et al., 2002). However, the mechanisms responsible for these patterns are still not fully understood.

We used manipulative experiments to explore the specific relationship between impaired environmental conditions and fish condition, focusing on several common stream fish species that represented common feeding guilds. Because different species exhibit an array of ecological, behavioural, physiological and morphological adaptations to their respective habitats and feeding strategies (Karr et al., 1986; McCormick et al., 2000), we expected to observe variability in the response of each feeding guild used.

The enclosure experiments, set in a free-flowing river, tested fish responses with natural flow, water temperature and chemistry, photoperiod, drift and riparian inputs. Fish assemblage composition was manipulated and fish
movement was restricted. Of the altered factors, restricting fish movement might be the factor most expected to affect fish condition the greatest over time (Carmichael et al., 1984) given reductions in the availability of benthic macroinvertebrates and algae over time due to consumption. Therefore, we expected the omnivores and water column and surface feeders to capitalize on drift and allochthonous inputs of arthropods and leaves into the enclosures and exhibit greater resilience to sediment aggradation. The tank experiments were conducted to standardize elements over which we had limited or no control in the field: temperature, food quantity and accessibility, flow, water depth and other habitat characteristics (e.g. vegetation).

Of the three guilds used in the enclosure component of the experiment, opportunists, as represented by pumpkinseeds, were arguably the most resilient to sedimentation, exhibiting a mean loss in $K$ of only 0.105 (across

### Table IV. Whole model ANOVA results for the laboratory tank experiments

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>$F$-ratio</th>
<th>$p$-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common shiner</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>17</td>
<td>0.3347</td>
<td>0.0197</td>
<td>5.92</td>
<td>0.0002</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>0.0598</td>
<td>0.0033</td>
<td>5.92</td>
<td>0.0002</td>
</tr>
<tr>
<td>White sucker</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>17</td>
<td>1.5210</td>
<td>0.0895</td>
<td>1.28</td>
<td>0.3011</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>1.2534</td>
<td>0.0696</td>
<td>1.28</td>
<td>0.3011</td>
</tr>
</tbody>
</table>

### Table V. Effect tests from ANOVA models for the laboratory tank experiments

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>$F$-ratio</th>
<th>$p$-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common shiner</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sediment aggradation level</td>
<td>2</td>
<td>7.28</td>
<td>0.0048</td>
</tr>
<tr>
<td>Block</td>
<td>6</td>
<td>2.14</td>
<td>0.0982</td>
</tr>
<tr>
<td>Day</td>
<td>3</td>
<td>17.51</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Day × sediment level</td>
<td>6</td>
<td>3.46</td>
<td>0.0189</td>
</tr>
<tr>
<td>White sucker</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sediment aggradation level</td>
<td>2</td>
<td>0.68</td>
<td>0.5171</td>
</tr>
<tr>
<td>Block</td>
<td>6</td>
<td>1.59</td>
<td>0.2065</td>
</tr>
<tr>
<td>Day</td>
<td>3</td>
<td>1.7336</td>
<td>0.1960</td>
</tr>
<tr>
<td>Day × sediment level</td>
<td>6</td>
<td>0.95</td>
<td>0.4829</td>
</tr>
</tbody>
</table>
all three treatments) from the beginning to the end of the trial (Table III, Figure 3b), compared to mean losses of 0.831 in creek chubs and 0.655 in white suckers. Although the overall model was only marginally significant, ‘day’ appeared to be an influential factor. Because pumpkinseeds feed both at the surface and the bottom, and because they are opportunistic feeders, consuming aquatic invertebrate larvae, worms, larval salamanders, molluscs, small fish and occasionally pieces of aquatic plants (Werner, 1980; Deacon and Keast, 1987), it is unlikely that food depletion over time was the predominant factor in change of pumpkinseed condition. In fact, opportunistic feeding and high foraging plasticity have been cited as being related to spatial and temporal variations in pumpkinseed diet (Almeida et al., 2008). ‘Day’ effect results do suggest that pumpkinseeds initially lost condition due to confinement effects since both moderate and severe treatments lost condition. However, by Day 14, they had recovered substantial condition, particularly in slight treatment enclosures. K values in severe treatments were not as low as those in moderate sediment levels, perhaps because overhanging bank vegetation (Table I) at many of the

Figure 4. Time series plots showing (a) common shiner and (b) white sucker condition (K) in the laboratory tank experiments. Values represent mean K of the three replicates for each of the treatments/sediment levels (slight, moderate and severe). Error bars indicate one standard error above and below each group mean. Horizontal lines represent the mean of each group. This figure is available in colour online at wileyonlinelibrary.com
enclosures may have provided sufficient cover to offset the lack of in-stream habitat in highly aggraded conditions. Almeida et al. (2008) suggest that human-induced stream habitat alterations – including higher levels of silt and sand particles in the substrate – may be responsible for the establishment, abundance and high body condition of invasive pumpkinseeds in Spain (Elvira and Almodóvar, 2001).

Creek chubs and white suckers responded more severely. For both creek chubs and white suckers in the field enclosures, time of confinement (i.e. ‘day’) exerted the greatest influence on condition factor $K$ (Table III). In spite of unimpeded inputs of allochthonous food sources, it is likely that the variable ‘day’ captured not just time, but also decreasing availability of food and increasing confinement stress, leading to loss of condition. However, lack of benthic food might be expected to be common in aggraded reaches as a result of embedded cobbles and lack of suitable habitat for macroinvertebrates or sunlit space for periphyton, so benthic food paucity is also likely to be a critical factor for wild, unconfined fish living in aggraded streams. This supposition is supported by Sullivan (2004), who found that both creek chubs and white suckers exhibited the lowest condition in stream reaches characterized by significant vertical channel adjustment.

Another explanation for the ‘day’ effect in the field enclosures is lack of cover. The fundamental relationships between habitat structure and stream fishes are well documented (Gorman and Karr, 1978; Copp, 1989; Barbour and Stribling, 1991; Inoue and Nunokawa, 2002). Aggraded reaches are noted for lack of in-stream cover (Sullivan et al., 2004) – an important component in understanding the effects of increased sediment loads on stream fishes. This argument is particularly strong for creek chubs, for which ‘sediment aggradation level’ also influenced $K$ (Table III), particularly in slight treatments.

Unlike white suckers, the magnitude of the difference in creek chub $K$ among treatments differed over time (i.e. interaction effect), with an overall trend of least condition loss over the course of the experiment in slightly

<table>
<thead>
<tr>
<th>Species by day</th>
<th>Mean $K$</th>
<th>HSD</th>
<th>Mean $K$ (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Enclosure (field)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Creek chub</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 0</td>
<td>0.974</td>
<td>A</td>
<td>1.040 (0.150)</td>
</tr>
<tr>
<td>Day 7</td>
<td>0.757</td>
<td>A</td>
<td>(n = 72)</td>
</tr>
<tr>
<td>Day 21</td>
<td>0.315</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>Day 28</td>
<td>0.143</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 0</td>
<td>1.635</td>
<td>A</td>
<td>1.873 (0.200)</td>
</tr>
<tr>
<td>Day 7</td>
<td>1.493</td>
<td>B</td>
<td>(n = 46)</td>
</tr>
<tr>
<td>Day 14</td>
<td>1.530</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>White sucker</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Day 0</td>
<td>0.893</td>
<td>A</td>
<td>0.983 (0.155)</td>
</tr>
<tr>
<td>Day 7</td>
<td>0.231</td>
<td>B</td>
<td>(n = 72)</td>
</tr>
<tr>
<td>Day 21</td>
<td>0.135</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>Day 28</td>
<td>0.238</td>
<td>B</td>
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</tr>
<tr>
<td><strong>Tank (laboratory)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common shiner</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 0</td>
<td>0.834</td>
<td>A</td>
<td>0.978 (0.477)</td>
</tr>
<tr>
<td>Day 10</td>
<td>0.843</td>
<td>A</td>
<td>(n = 361)</td>
</tr>
<tr>
<td>Day 20</td>
<td>0.799</td>
<td>AB</td>
<td></td>
</tr>
<tr>
<td>Day 30</td>
<td>0.761</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>White sucker</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 0</td>
<td>0.870</td>
<td>A</td>
<td>0.983 (0.155)</td>
</tr>
<tr>
<td>Day 10</td>
<td>0.856</td>
<td>A</td>
<td>(n = 72)</td>
</tr>
<tr>
<td>Day 20</td>
<td>0.825</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td>Day 30</td>
<td>0.746</td>
<td>A</td>
<td></td>
</tr>
</tbody>
</table>

Table VI. Mean condition ($K$) across all treatments by species and time (where appropriate) of fish in the enclosures, tanks and natural settings (wild, uncaged). For enclosure and tanks, Tukey–Kramer HSD comparisons are presented for each species by day. Groups with same letter are not significantly different ($\alpha = 0.05$).
aggraded enclosures. Creek chubs are not known to be particularly sensitive (e.g. Danehy et al., 1998) to changes in physical habitat condition. Creek chubs have very small home ranges (Pflieger, 1997), and thus confinement may not have been inherently as stressful as with broader-ranging fish species. As a generalized carnivore, creek chubs are notably adaptable in diet (Pflieger, 1997), and would have taken advantage of food sources found in drift and at the water surface. These factors, alone and in combination, make our results somewhat surprising and suggest that sediment aggradation exerts indirect effects on water column and surface feeders.

Although common shiners responded more strongly to aggraded conditions, they shared a similar overall response pattern to creek chubs – their water column and surface feeder counterparts (Figures 3a and 4a). Our results suggest that aggraded bed conditions – those that obscure the gravel-rubble bottoms – significantly reduce common shiner K. Even slight levels of sedimentation in our tanks were associated with profound loss of condition (Figure 4a), indicating a high sensitivity to sediment aggradation. Common shiners feed on both plant material and insects (Fee, 1965; Moyle, 1973). In tanks designated ‘slight’ and ‘moderate’, periphyton and macroinvertebrates were significantly more exposed and accessible to fish (both on the benthos and in the water column) than in ‘severely aggraded’ tanks, yet this had no remediating effect on condition in common shiners. The ‘day × sediment level’ interaction suggests that the amount of time spent in highly aggraded conditions affects common shiner condition more strongly than an equal amount of time in less aggraded conditions.

White suckers are typically associated with the soft and finer substrates (Wehrly et al., 2003; Creque et al., 2005) generally found in pools. In spite of this substrate association, suckers exhibited a dramatic loss of condition after day 7 across all levels of sediment aggradation. Contrary to our hypothesis, white suckers experienced the lowest condition in slightly aggraded enclosures, where they would presumably have had the greatest access to preferred food sources including benthic invertebrate insects, crustaceans and snails (Werner, 1980). The cryptic coloration of white suckers and their ability to blend into the benthos might have mediated the potential stress responses from lack of cover in severely aggraded field enclosures. White sucker K in the laboratory tanks (where structure was standardized) tended to be greater in less aggraded tanks, lending support to this hypothesis.

In spite of significant effects of sedimentation, the effect of time was orders of magnitude stronger (Table II). Since white suckers do not forage throughout the water column (Figure 2), it is likely that reduction of benthic food sources (Swift-Miller et al., 1999) associated with time in the enclosures may have influenced white sucker condition more so than that of other species that were able to take greater advantage of allochthonous subsidies entering the stream and invertebrate drift in the water column. However, in contrast to the field enclosure experiment, white sucker condition in tanks was not associated with sediment aggradation level or time of confinement (Table V). Density differences among white suckers in the field enclosures and the tanks may have contributed to observed differences in condition. However, the contrasting enclosure and tank results more likely indicate that in an open system, there exist additional sources of stress associated with aggraded conditions that affect white sucker responses to sediment levels.

One such variable in the enclosure component of the experiment was the effect of predation stress from birds. Pumpkinseeds, creek chubs and white suckers are all preyed upon by a number of birds common in the area including herons, kingfishers and mergansers. Although measures were taken to deter birds from the enclosures themselves, there was still evidence of avian predators in the immediate vicinity, and the stress response to their presence is unknown. It would seem likely that fish in enclosures with the lowest sediment aggradation level – and, therefore, the greatest amount of available cover – would have suffered the least predator-induced stress.

For species of all feeding guilds, K values from all three treatments were markedly lower at the end of the experiments than at the outset. Whereas responses were fairly graded in the laboratory (Figure 4a,b), data from the field indicate possible threshold K responses (Figure 3a–c). In order to further tease out potential threshold patterns, additional data relating to turbidity regimes, hydraulic complexity, specific patterns of food availability and accessibility and external stressors would be needed.

CONCLUSIONS AND IMPLICATIONS

Aggraded conditions over time elicited a variety of responses in our focal fish species. Highly aggraded streams have little habitat structure, and consequently, important features related to trade-offs between foraging and predation such as velocity refuge, visual isolation and overhead cover (Fausch, 1993) are reduced or missing.
Stresses associated with lack of cover, exposure to predators, limited benthic food availability, turbidity and wide flow and temperature variability likely reduce the ecological performance of fish found in marginally aggraded habitats and may lead to behavioural changes and sublethal effects (Mesa et al., 1994). Newcombe and Jensen (1996) have shown that suspended sediment and turbid conditions negatively affect physiological, biochemical, histological and behavioural responses of aquatic biota. Our results indicate that some feeding guilds may be more vulnerable to effects of sediment aggradation than others. Benthic invertivores, although expected to be the most sensitive, may be more tolerant of higher sediment loads than conventional ‘bottom-up’ theory suggests. Opportunistic feeders, as represented by pumpkinseeds, appeared to be the most resilient, yet even the more plastic foraging strategies will likely be compromised given prolonged exposure.

If a stream is aggraded in a patchy distribution, and fish can avoid areas of severe sedimentation, then a sediment level capable of eliciting loss of condition in a caged experiment might not cause such an effect in a free population where fish can actively select alternative habitat. Evidence of this is provided by the higher condition of non-caged fish in regional streams than that of their caged counterparts (Table VI). However, if the extent and duration of sediment aggradation is such that there are no or limited unaffected areas, our results suggest that habitat damage (sensu Newcombe and Jensen, 1996) will have adverse effects on common stream species of different foraging strategies. Moreover, although we worked only with adult fish, sediment aggradation will likely have ill effects on multiple life stages (e.g. nest building, egg development and fry feeding).

Given the loss of condition across all three treatments relative to free-ranging fish (Table VI), experimental conditions likely played a role in observed K values. However, even wild, uncaged fish in severely aggraded reaches have access to patches of refugia, including additional structure and pockets of food. Given increasing sediment loads, these refugia will continue to diminish in distribution and extent, creating conditions not wholly unlike those of our experiment whereby fish movement is restricted not by mesh netting, but by expanses of aggraded streambed.

Streams and rivers are arguably sentinels and integrators of the effects of human activities on terrestrial as well as aquatic ecosystems (Williamson et al., 2008), largely because of the intricate linkages rivers share with their surrounding terrestrial landscapes. Understanding the responses of streams and rivers to changes in land use and cover that increase sediment inputs into the channel is critical for effective watershed management. Our findings underscore relationships between sedimentation and habitat loss and impairment, and link these directly to functional aspects of stream fishes in large streams and small rivers.

Sediment aggradation is a fundamental channel characteristic measured as part of many state and federal stream channel assessment protocols. Our results suggest that increased sediment aggradation associated with disturbed streams may essentially create aquatic ‘deserts’ of suboptimal and perhaps even unusable habitat. Managing the sediment loads associated with geomorphically unstable streams and preserving the connectivity of habitat along stream and river networks will be critical in managing and conserving fish populations. Finally, our work presents evidence that fish species representing common feeding guilds respond in unique ways to sediment aggradation levels over time, suggesting a particular need to recognize and protect those fish populations that are particularly susceptible to aggraded channels.

ACKNOWLEDGEMENTS

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