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SOME EFFECTS OF RIPARIAN HABITAT ALTERATION ON LOTIC INVERTEBRATE ECOLOGY

By

Roger Malcolm Strand

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ABSTRACT

SOME EFFECTS OF RIPARIAN HABITAT ALTERATION ON LOTIC INVERTEBRATE ECOLOGY

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Three studies were conducted to determine the effects of allogenic alteration of riparian habitat on benthic invertebrate ecology.

Study 1. Community abundance, richness, and diversity were monitored during two radically different landscape alterations which occurred simultaneously in a northern Michigan watershed. This three-year study incorporated analyses of introduced substrata samples taken from an upstream forested reach undergoing the transition from unrestricted flow to beaver pond and from a perennially overgrazed pasture reach experiencing the initial effects of cattle exclusion. Beaver colonization and cattle exclusion both resulted in initial abundance increases. Recovery from overgrazing led to increased diversity while disturbance by beaver resulted in decreased diversity. Impoundment produced large changes in community structure and functional composition. In contrast, cattle exclusion did not meaningfully affect community composition. Disturbance by beaver fostered increased abundance of broadly distributed habitat generalists while recovering and undisturbed habitat harbored less common taxa with specialized habitat requirements. The forest reach supported many taxa not found in the overgrazed pasture reach, but the pasture reach contained few taxa not found in the forest reach. Therefore, losses of forest reaches that result from human activities may have relatively large impacts on watershed biodiversity.

Study 2. The initial response by predacious stonefly nymphs (*Paragnetina media*) to intense sedimentation was examined in field trials with chambers designed to give nymphs the choice to stay or reposition in response to sediment additions. The results indicate that the often posited immediate-escape response to the onset of intense sedimentation may not be commonly enacted by stonefly nymphs or perhaps by other relatively immobile, lotic insects.

Study 3. Net-spinning caddisflies often thrive in the heavily sedimented waters of midwestern agricultural catchments despite the presumed costs of sedimentation-induced net fouling. A laboratory experiment was conducted to determine whether larval growth and survival of *Hydropsyche betteni* and *Ceratopsyche sparna* are affected by intense, episodic sedimentation. Larvae of both species suffered increased mortality in sedimentation treatments relative to controls and taxa were differentially affected as *H. betteni* significantly outperformed *C. sparna*. Sedimentation did not, however, alter the relative growth rate of either species.

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1

BENTHIC INVERTEBRATE ECOLOGY IN AMERICA'S PASTURE- AND RANGELAND STREAMS

> Erosion eats into our hills like a contagion, and floods bring down the loosened soil upon our valleys like a scourge. Water, soil, animals, and plants - the very fabric of prosperity - react to destroy each other and us. Science can and must unravel those reactions, and government must enforce the findings of science (Leopold 1923).

Seventy-three years have passed since Aldo Leopold issued this advisory to future ranchers, ecologists, and policy makers and today almost one-half of Earth's terrestrial space is grazed by domestic animals (Goude 1994). After more than a century of large-scale grazing in the United States, overgrazed pastures and range have become common features on the rural landscape (Fleischner 1994, Wissmar et al. 1994, Waters 1995). Cattle grazing is by far the most common way to use land the American west, where more than seventy percent of the landscape is grazed. Most of this land is held in public trust and as evidence of ever-increasing habitat damage mounts, policy makers are being pressured by scientists and concerned citizens to restrict grazing in particularily sensitive habitats (Armour 1991, 1994; Fleischner 1994).

There is general agreement among range managers and ecologists that many currently grazed habitats, for example alpine meadows (Kondolf 1994), can not sustain conflicting societal demands for maximized cattle production and optimized water- and wildlife-habitat quality (Fleischner 1994, Li et al. 1994, Brown and McDonald 1995, Mosely et al. 1993). Despite this reality, grazing on public lands continues with little regulatory recognition of differential habitat sensitivity, even as restoration costs often far outweigh fiscal inputs from grazing fees (Minshall 1989, Fleischner 1994, Kondolf 1994).

It is well-established that habitat types vary in nature and magnitude of response to cattle grazing (Milchunas and Lavenroth 1993, Li et al. 1994). For example, plant species richness in grasslands within the historic range of bison often increases with cattle grazing intensity, whereas introduction and intensification of cattle grazing in grasslands outside of the historical range of bison or other large herbivores is known to cause plant richness to sharply decline (Milchunas and Lavenroth 1993, Hofstede 1995).

Cattle, unlike bison, spend a disproportionate amount of time feeding and wallowing in streams. This universal intensification, particularily during hot weather, renders riparian areas in all grazed habitat types especially vulnerable to overgrazing (Kauffman and Krueger 1984, Resh et al. 1988, Armour et al. 1991, 1994, Platts 1991, Fleischner 1994, Waters 1995). Most of the concern over grazing-induced riparian and instream habitat damage has been centered on the consequent reductions of game-fish production that typically occur in heavily grazed catchments (Armour et al. 1991, 1994, Fleischner 1994). There is still, therefore, much left to learn about grazing effects on the numerically (Hynes 1970) and often energetically dominant animals (Waters 1984) that comprise lotic invertebrate communities.

This chapter provides an overview of cattle-grazing effects on instream and riparian-zone habitat that are known or suspected to affect benthic invertebrate ecology. Subsequent chapters include an analysis of management-induced recovery of a perennially overgrazed, northern-Michigan stream and two studies conducted to fill voids in understanding of grazing-induced sedimentation effects on aquatic insect behavior, growth, and survival.

General effects of livestock grazing on stream ecology

Overgrazing is a contemptuous term that remains undefined by range managers (Fleischner 1994), but has nonetheless been determined to be the cause a variety of negative effects in aquatic ecosystems (Minshall et al. 1989, Fleischner 1994, Waters 1995) (Figure 1). Overgrazing (*sensu* Leopold 1923) in riparian areas is indicated by total vegetative denudation along banks and channels which results in increased erosion (Kauffman et al. 1983 b, Gamougoun et al. 1984), sedimentation, eutrophication (Odion et al. 1988, Waters 1995), and thermal regime variation (Li et al. 1994) (Figure 1). Benthic invertebrates are sensitive to fluctuations in all of these environmental characteristics both directly through modification of physiological processes (Hynes 1966, 1970; Sweeny 1993) and indirectly through alteration of substrata characteristics (Kauffman and Krueger 1984, Waters 1995).

Effects of riparian vegetation transformation

Intense grazing pressure in riparian forests results in drastically diminished tree regeneration in aging pastures. This process typically ultimates in transformation of vegetative community from forest to grassland (Fausch and Bramblett 1991, Li et al. 1994). The consequently reduced inputs of abscised leaves and woody debris to streams causes the elimination food and shelter for a diverse array of benthic invertebrates (Merritt and Cummins 1996) and fish (Hynes 1970). Stream structural and biogeochemical characteristics are also altered by reduction of debris-dam habitat as habitat heterogeneity is lessened (Sedell 1990), and important sites for carbon (Meyer et al. 1988) and phosphorus dynamics (Munn 1989) are eliminated.

The structural changes associated with riparian-zone denudation may also remove cues necessary for habitat recognization by aerial adult aquatic insects on mate-location or dispersion flights. The shift in dominance between two black fly species was demonstrated by Timm (1994) to be an example of this type of differential habitat selectivity by ovipositing females. After timber was cleared from a reach of a Rhine River tributary, the opportunistic *Simulium ornatum* rapidly displaced *S. vernum* as the dominant black fly in the stream. There were no changes in substrata, water chemistry, or resource availability to account for the differences. However these species do behave differently when seeking oviposition sites. *Simulium vernum* prefers shaded riffles for egg deposition, whereas *S. ornatum* only oviposits in riffle exposed to full sun. Because many other aquatic insects use physical cues when seeking oviposition sites (Wallace and Anderson 1996), it is probable that discovery awaits other such direct effects of grazing-mediated riparian transformation on benthic community composition.

Effects of increased erosion

Bank sediments exposed by overgrazing erode into overland flow following spates and rapid snowmelt. These processes immediately elevate concentrations of suspended solids (Waters 1995), nitrogen, and phosphorus (Mosely et al. 1993) and eventually blanket stream beds with deposited sediments (Waters 1995). Substrata burial can be lethal to benthic invertebrates in extremely high levels (Thomas 1985) or in sensitive life stages such as immobile pupae (Rutherford and Mackay 1986).

Benthic invertebrate communities often experience functional and taxonomic changes in response to persistent sedimentation. Typical transitions feature the replacement of animals that require solid substrata with those that thrive in thick deposits of soft substrata (Nuttall and Bielby 1973, Quinn et al. 1992, Waters 1995). For example, Strand and Merritt (Chapter 2) found that the relative proportional abundance of filter-feeders to omnivorous gatherers, a measure of particulate transport versus deposition and of the availability of solid substrata (Merritt and Cummins 1996), was far greater in an undisturbed reach of a northern Michigan stream than it was in an overgrazed reach.

Habitat simplification through substrata burial also is likely to reduce hyporheic-zone quality. This sub-flow region is saturated with a mixture stream and ground water and is inhabited a variety of invertebrates, some of which are hyporheic endemics and others that forage and seek refuge from disturbance in hyporheic habitat (Williams 1984, Meyer et al. 1988, Dahm and Valett 1996). As the habitat of occasional and permanent hyporheic residents is vanquished by interstitial filling, biogeochemical activity at nutrient upwelling sites is also diminished (Grimm et al. 1991, Findlay 1995, Dahm and Valett 1996, Grimm 1996). This process imposes limits on stream metabolism through alteration of nutrient cycling rates (Grimm and Fisher 1984). Grazing-induced hyporheic burial is expected to be particularily destructive to the benthic ecology of temporary streams where population persistence for many invertebrates is dependant upon the survival of individuals that wait out no-flow periods in damp, subchannel interstitial spaces (Fisher and Gray 1983).

Effects of excrement input

Due to the periodic threat of bacterial pollution of drinking water, cattle excrement input to streams, perhaps more than any other grazing-related problem, concerns to humans who live downstream from grazed riparian areas. High loads of excrement input are also suspected to impose direct threats to aquatic life. Foremost among these is the potential of nutrient enrichment to affect instream biogeochemical processes (Mosely et al. 1993, Harris et al 1994).

In seasonally grazed streams, eutrophication that results from waste-mediated fertilization, principally through increased phosphorous loading (Allen et al. 1982, Mosely et al. 1993), can drastically reduce dissolved oxygen concentration (Harris et al. 1994) and increase algal and macrophyte production (Fleischner 1994). Persistent fertilization and selective herbivory by cows often result in the formation of dense instream accumulations of unpalatable plants such as *Cladophora glommerata* (Armour et al. 1991, 1994, Matthews et al. 1994), a widespread filamentous green alga, mats of which typically contain few, if any, benthic macroinvertebrates (personal observation). Substrata domination and benthic shading that result from the presence of thick algal growths may also reduce benthic secondary productivity by limiting the establishment of the more readily foraged-on five-kingdom amalgam known as biofilm or periphyton which coats most exposed substrata (Cummins 1973, Lamberti and Feminella 1996).

Extremely high levels of excrement input in seasonally grazed streams may act to further slow instream secondary productivity through ammonia toxicity to invertebrates and fish. Although ammonia levels rarely exceed the tolerance threshold of most pasture-stream inhabitants (Overcash et al. 1983), particularily sensitive organisms may be displaced due to chronic, ammonia-induced damage to gill membranes (Hazel et al. 1979, DeGraeve et al. 1980). Acute ammonia toxicity (1.2-8 mg/l) (Hazel et al. 1979, DeGraeve et al. 1980) is also a potential problem associated with heavy grazing, especially during dry, hot weather when stream flow is low and cattle wallow to alleviate heat stress.

Effects of thermal regime alteration

Although cattle grazing does not universally cause pronounced elevations in stream temperature (Li et al. 1994), thermal regimes are known to vary more in grazed than in ungrazed streams (Kauffman and Krueger 1984). Li et al. (1994) reported that insolation increased with increasing grazing activity as did algal and invertebrate biomass. These conditions combined to render grazed habitat less amenable to trout as increased temperature caused a decline in the ratio of trout to invertebrate biomass. This relationship has been detected elsewhere and has been in part attributed to direct heat stress to trout (Platts and Rinne 1985, Platts and Nelson 1989, Minshall et. al. 1989) and partly to elevated temperature-mediated increases in the abundance of less-preferred invertebrate prey (Tait et al. 1994).

Sweeny (1993) documented 2 to 4°C increases attributable to clearing of northeastern U.S. forest streams. This increase may seem trivial when compared to daily and seasonal temperature fluctuations in terrestrial realms; however, in the relatively constant lotic thermal environments, 2-4°C can be a large-enough difference to affect the physiology and alter distributions of sensitive species (Sweeny and Vannote 1986).

In streams where grazing elevates insolation, consequent restrictions on intolerant species and concurrent increases in secondary production by thermally insensitive species (Murphy and Hall 1981, Murphy et al. 1981, Hawkins et al. 1983, Bilby and Bisson 1987) are therefore expected to result in changes in benthic community composition and bioenergetics.

Riparian-forest clearing may also affect the metabolism and reproduction of aerial adult aquatic insects through thermal regime alteration. Tree removal eliminates shaded resting structure which is utilized extensively, and perhaps required by, adult aquatic insects. Most holometabolous aquatic insects rely on resources stored during the larval period to complete their life cycles (Sweeny 1993). Therefore, resource conservation prior to reproduction may have positive effects on fecundity. Reduction or elimination of cool, humid resting habitat could thus limit the reproductive potential of sensitive species.

Aldo Leopold warned us long ago that overgrazing of livestock can negatively affect ecological processes in pastured watersheds. Although there is still relatively little known about the specific effects of grazing on lotic animals, it is certain that the physical impacts of grazing and trampling can combine to alter channel hydrology, vegetative composition, and nutrient-retention capacity. The ultimate synergy of these effects produces simplified lotic ecosystems, less buffered from climatic disturbance, undergoing heightened stream-water losses of nutrients. This distressing scenario is far too common in American watersheds where short-term economic gains are commonly sought despite the glaring portent of ecological calamity.

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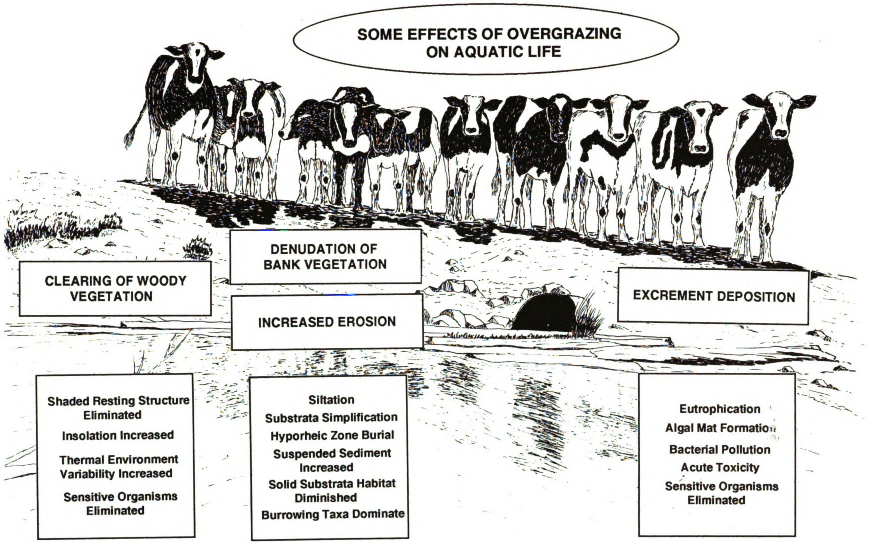

Figure 1. Some effects on lotic ecology of grazing cattle in small-stream riparian zones.

2

BENTHIC INVERTEBRATE RESPONSE TO CATTLE EXCLUSION AND BEAVER COLONIZATION IN A SMALL, MICHIGAN STREAM

Abstract. Benthic invertebrate community abundance, richness, and diversity were monitored during two radically different landscape alterations which occurred simultaneously in a northern Michigan watershed. This three-year study incorporated analyses of introduced substrata samples taken from an upstream forested reach undergoing the transition from unrestricted flow to beaver pond and from a perennially overgrazed pasture reach experiencing the initial effects of cattle exclusion. Prior to habitat alteration, abundance was higher and diversity was lower in grazed sites. Taxonomic richness was similar between reaches, but the forest reach had a higher proportion of endemic taxa which produced substantial inter-reach differences in the proportions of taxa from each functional-feeding guild. Beaver colonization and cattle exclusion both resulted in initial abundance increases. Recovery from overgrazing led to increased diversity while disturbance by beaver resulted in decreased diversity. Impoundment produced large changes in community structure and functional composition. In contrast, cattle exclusion did not meaningfully affect community composition. Disturbance by beaver fostered increased abundance of broadly distributed habitat generalists while recovering and undisturbed habitat harbored less common taxa with specialized habitat requirements. The forest reach supported many taxa not found in the overgrazed pasture reach, but the pasture reach contained few taxa not found in the forest reach. Therefore, losses of forest reaches that result from human activities may have relatively large impacts on watershed biodiversity.

OVERVIEW

In 1989, legislation was adopted to combat the problem of overgrazing of Michigan's headwater riparian areas. The program provided farmers with an 80% savings on wells, improvements to stream crossings, and fence to exclude cattle. Carlson Creek was one of four upper-peninsula streams selected for these restoration measures before the program was discontinued in 1992. During the winter of 1990-1991 the pasture-land owner, the Michigan Department of Natural Resources, and the U.S. Soil Conservation Service reached an agreement to restore the channel by fencing cattle out before the 1992 pasturing season. We were allowed to analyze the response of the stream invertebrate community to these restoration efforts.

During 1991, cattle had unrestricted access to the pasture reach of Carlson Creek and instream and near-bank conditions were degraded by years of trampling and wallowing (Figure 1). In stark contrast, the upstream forest reach was relatively undisturbed (Figure 2). Two 20-m long sites in the forest reach and two in the pasture reach, were selected for analysis through the final year of lower-riparian grazing and the first and second years of recovery. Forest-reach sites were to serve as comparative analogues to pre-grazing conditions during the first year of the study and as a presumably static habitat relative to the pasture reach. However, in June of 1992, beaver colonized the upstream reach forming a pond that eventually extended to include both "reference" sites at the same time at which cattle were excluded from the pasture reach. This serendipitous action presented the unique opportunity to simultaneously examine radically different riparian-habitat alterations occurring along contiguous reaches.

The primary objective of the study was to characterize the responses of forest- and pasture-reach benthic invertebrate communities to beaver impoundment and cattle exclusion in an attempt to assess the effects on lotic ecology of the onset of, and recovery from, landscape disturbances.

INTRODUCTION

Livestock grazing effects on benthic invertebrate ecology

Chapter 1 provides an overview of the effects of livestock grazing on stream-dwelling benthic invertebrates. In general, the effects of cattle grazing in riparian areas have been determined to be ecologically negative (e.g. Leopold 1923, 1946, Tarzwell 1938, Resh et al. 1988, Armour et al. 1991, 1994, Fleischner 1994, Waters 1995). However, there is disagreement among range managers concerning the severity of the likely consequences of current practices (e.g. Fleischner 1994, Brown and McDonald 1995). Most of the concern over the repercussions of grazing-induced riparian and instream habitat alteration has been centered on consequent reduction of game-fish production (Armour et al. 1991, 1994). There is, therefore, much left to learn about grazing effects on the numerically (Hynes 1970) and often energetically dominant (Waters 1984) animals that comprise lotic benthic invertebrate communities.

When cattle are allowed unrestricted access to streams, they tend to spend disproportionate amount of time feeding and wallowing in or near water (Van Vuren 1982, Kauffman and Krueger 1984, Fleischner 1994). Grazing in riparian areas is known to modify lotic biotic processes through alterations of insolation level, substrata characteristics, and flow regime (Minshall et al. 1989, Armour et al. 1991, 1994, Fleischner 1994, Waters 1995). By eliminating vegetative cover (Kauffman et al. 1983 a, Platts and Nelson 1985 a, Odion et al. 1988), grazing livestock at high densities results in increased rates of erosion (Kauffman et al. 1989, Gamougoun et al. 1984), sedimentation, eutrophication (Odion et al. 1988, Waters 1995), and thermal regime variation (Li et al. 1994). Alterations of all of these physical parameters are known to affect benthic invertebrates through substrata transformation (Kauffman and Krueger 1984, Waters 1995) and modification of physiological processes (Sweeny 1993).

Habitat restoration through cattle exclusion is a well-established way to improve standing stocks of benthic invertebrates and fish (Peters 1962, Bjorn 1973, Armour et al. 1991, 1994, Waters 1995). In perhaps the first study conducted to quantify the efficacy of stream improvements which include cattle exclusion, Tarzwell (1938) demonstrated that invertebrate production and trout growth rate in southwestern U.S. streams were greatly enhanced during the eighteen months that followed exclusion. Several other exclusion studies followed (e.g. VanVelson 1979, Stuber 1985) and like that of Tarzwell (1938), the primary emphasis was on characterizing trout response. In all of these cases exclusion proved to be a successful way to improve fish production.

The effects of beaver activity on benthic invertebrate ecology

Virtually all habitats on earth are controlled to some extent by organisms whose activities are influential in determining community composition and biogeochemical properties (Holling 1992, Jones et al. 1994). The ecological consequences of cattle grazing well demonstrate the human capacity to modify lotic environments. As allogenic engineers, organisms that alter their environment and control the flow of resources to other organisms (Jones et al. 1994), humans are rivaled in lotic ecosystems only by beaver (*Castor canadensis*) (Naiman et al. 1986, 1988).

The cyclical colonization pattern that typifies beaver inhabitation of a watershed initiates with woody vegetation removal during pond formation and ultimates in sedge and littoral vegetation domination early in the post-abandonment phase (Hammerson 1994). Like other successional processes in terrestrial plant communities, such as those initiated by forest-to-pasture transformation, beaver colonization results in altered rates of secondary productivity and decomposition through transportation and transmogrification of the products of primary producers (Huston 1994).

Damming-induced flow-rate reductions and depth increases activate a typical lotic-to-lentic habitat transformation. However, due to beaver-induced modification of substrata characteristics, the resultant pond is quite unlike other lentic habitats (Naiman et al. 1988). Beaver feeding and construction activity typically result in the formation of thick deposits of augmented woody material (Naiman et al. 1986). Wallace and Benke (1984) detected high levels of invertebrate production in these accumulations, primarily as a result of increases in larval midge abundance (Diptera: Chironomidae). These omnivores are also suspected to benefit from often large inputs of organic material that result from defecation by waterfowl, fish, and other animals attracted to beaver ponds (Hammerson 1994). Although invertebrate secondary productivity can be elevated by organic inputs associated with pond formation, community functional diversity typically declines as a result of elimination of filter-feeders, biofilm scrapers, and herbivores (Naiman et al 1986).

Beaver activity can also strongly affect habitat conditions immediately downstream from impoundments by entraining silt and modulating flow (Naiman et al. 1986, Hammerson 1994). For example, the clean gravel substrata critical to the success of an endangered beetle species (*Brychius hungerfordi*, Coleoptera: Halplidae) is set up and maintained in its type locality by a series of beaver impoundments. Much of the current rarity of this beetle is believed to be attributable to the replacement of beaver by humans as the principal engineer of northern Michigan streams (Strand and Spangler 1994).

Disturbance, perturbation, and recovery

The level of disruption of biotic processes exacted by localized fluctuations in abiotic conditions is indicative of community resistance to landscape alteration-mediated stress (*sensu* Underwood 1989). Organismal response to abiotic stress is believed to be dependent to a large degree upon historical disturbance regime. Events with extreme consequences to biota are commonly differentiated from those of lesser impact with the terms "disturbance" and "perturbation" respectively (Huston 1994).

There is strong evidence of a fundamental trade-off between relative resistance and resilience to temporally isolated episodes of stress (Hutchinson 1953, Connell 1978, Huston 1979, 1994). Hutchinson (1951, 1953) described those organisms that are relatively easily displaced by perturbation, but able to quickly colonize newly disturbed habitat, as "fugitives" due also to their apparent inability to persist once conditions are stabilized. The relative proportions of fugitive species and high resistance, long-term occupants, or "occupiers," are reflective of a habitat's relative position on a stress gradient from mild perturbation to catastrophic disturbance. Maximum species richness is expected in habitats that sustain moderately frequent stress episodes of intermediate intensity because conditions in these habitats allow for the persistence of populations of fugitive- and occupier species (Hutchinson 1953, Connell 1978, Huston 1979, 1994).

The relative novelty of a stress event is believed to be more important than its magnitude in determining resultant effects on biota. If stress frequency, regardless of intensity, is maintained at a high level over a long period of time, then it is expected that the organisms that comprise the affected community have in common a relatively high resistance and resilience to that type of stress, or perturbation. Perturbations are therefore, not expected to exact lasting changes to community composition. However, if an event is uncommon and intense enough to cause the elimination of organisms to proceed at a rate greater than that at which they are able to accumulate, then it is assumed that the effect of the stressor, or disturbance, will directly alter community structure and can, if severe enough, have lasting consequences (Hutchinson 1953, Huston 1994).

Within this theoretical construct, benthic invertebrate dynamics in Carlson Creek from 1991 to 1993 are considered the result of the onset of disturbance by beaver in the forest reach and recovery in the pasture reach from initial land-clearing disturbance and subsequent decades of overgrazing-generated perturbation.

Site description

Carlson Creek slowly flows from Kaks Lake, a small undeveloped lake in Michigan's upper peninsula to an impoundment of the Taquamenon River two miles downstream. Riparian characteristics change dramatically along its course from climax forest, to cattle pasture, bog, and ultimately to marsh.

1991

Table 1 contrasts pre-alteration forest- and pasture-reach substrata particle size and chemical compositional characteristics as well as selected stream water properties. From Kaks lake, Carlson Creek flowed at a rate of 0.3 m/second over 3 km of mixed-hardwood riparian forest. In this forest reach, Carlson Creek was shallow (less than 40 cm) and unevenly shaded. Open stretches were characterized by *Typha* and other typically lentic littoral-zone vegetation; closed zones support little or no instream vegetation (Figure 2A). The predominant substrata in the forest reach was wood and mixed gravel and cobble with underlying sand.

Riparian vegetation in the pasture reach consisted of patches of tag alder (*Alnus* sp.) along a short grass and exposed soil course. Habitat condition varied from a 8 m-wide channel cutting through cattle congregation sites at about 0.7 m/ second to slower flow spread out over a 15 m-wide channel coursing around dense clumps of sedge (Figure 1 A). The predominant substrata was up to 25 cm of silt overlying gravel and cobbles. Cattle were allowed to graze through the forest that demarcates the downstream pasture boundary. The stream spread out in this reach to a width of about 30 m. It then flowed slowly through a *Typha* marsh for approximately 1.5 km to a large impoundment of the Taquamenon River created to improve waterfowl habitat.

1992-1993

Beaver moved into the forest reach during June, 1992 and built a dam downstream from both sites. Consequently, flow slowed and stream depth and width increased dramatically (Figures 2, 3). During the same time period, a fence was constructed to exclude cattle below the high-water mark of the pasture reach. Inter-reach responses of riparian and instream landscape alteration are depicted in Figures 1 and 2.

METHODS

Invertebrate sampling

In order to collect the most taxonomically representative set of samples possible without destroying benthic habitat, a combination of artificial substrata types (rocks, wood, leaf packs) and drift nets were used to sample benthic invertebrates.

Rocks

The invertebrate fauna of rocks was sampled by introducing similarily sized and textured field stones (mean area ≈ 0.283 m2) allowing approximately 30 days for the establishment of biofilm and subsequent invertebrate colonization. In preliminary studies, a one month colonization period was sufficient for invertebrate colonization yet brief enough to avoid total burial. Rock size was determined by wrapping cobbles in foil, weighing the foil, and extrapolating foil area from a predetermined relationship between foil area and mass. Rock samples were taken during July, August, and September, 1991-1993 from two pasture and two forest sites. A total of 155 rock samples were collected.

Wood

Pieces of cottonwood bark (≈ 0.175 m2), selected for its relatively uniform and rough texture, were anchored to the streambed and collected after approximately 30 days. Area was determined with the same procedure described for rocks. Wood samples were taken during September and November, 1991-1993. A total of 108 wood samples were collected.

Leaves

Four-gram, white oak (*Quercus alba*) leaf packs, selected for their intermediate breakdown time (Petersen and Cummins 1974), were secured to bricks and placed in erosional zones facing upstream to simulate natural debris dams (as recommended by Merritt et al 1979). Packs were removed from streams after 31 days in 1991 and 44 days in 1992. The dramatic reduction in beaver pond size that occurred following a dam break in 1993 destroyed year three samples. A total of 51 leaf packs were collected.

Invertebrate drift

Drift was monitored with 1-m long, 0.5-m wide, and 0.5-mm diameter mesh drift nets positioned vertically. Four nets were placed in riffle areas in one forest site and two pasture sites. Nets were set before dusk and pulled the following morning as recommended by Waters (1972). Animals collected with drift nets were used only for taxonomic information due to difficulty in interpreting forest-reach drift catches during beaver-pond formation. Drift samples were taken monthly from July to September, 1991-1992. A total 59 drift samples were collected.

Analyses of richness and abundance

Invertebrate samples from the entire study included a total of 35,667 individuals representing 99 taxa (Appendices 1, 2). Whenever possible, insects were identified to genus using keys in Merritt and Cummins (1996 a); non-insect invertebrates were identified to class or lower. Abundance and richness as used here refer to total number of individuals or taxa corrected for substrata area and colonization period. Therefore values express relative rate of colonization as well as community variety and abundance.

Community diversity

The hierarchical richness index procedure (HRI) (French 1995) combines measurements of taxonomic richness and abundance into a single term that describes, in the case of the studies presented here, the variety and abundance of benthic invertebrate inhabitants of stream reaches undergoing differential disturbance pressure. The HRI procedure is defined by the equation:

$$HRI = \sum (s_i \times i)$$

where i are group ranks (the most abundant group rank = 1, secondmost = 2, and so on) and s_i are within group scores (mean abundances), such that all $s_i \geq s_{i+1}$ (French 1995).

Functional- feeding guilds

Although not strictly defining for most species, benthic invertebrates typically belong to one of six primary functional feeding-guilds: filterers, gatherers, scrapers, predators, herbivores, and shredders (Cummins 1973, 1980). Estimates of proportional abundance, biomass, and richness of these groups in benthic communities have been shown to be demonstrative of lotic habitat condition (Merritt and Cummins 1996 a, b). Abundance, as used in functional feeding group analyses here refers to total number of individuals collected with each substrate type.

Tolerance indices

Benthic invertebrates have widely varying tolerances to ecological disturbance (Resh et al 1988) and anthropogenic pollutants (Rosenberg and Resh 1996). Once these tolerances are established, it becomes possible to rank organisms by their relative tolerance index values. Analyses of benthic invertebrate community tolerance index values can then be used to assess past and present habitat conditions (Hilsenhoff 1988, Resh and Jackson 1993, Resh et al. 1996). The family-level tolerance index of Resh et al (1996), a compilation of past values presented in Hisenhoff (1988), and Lenat (1993), was used to assess relative tolerance of Carlson Creek benthos undergoing beaver impoundment and cattle exclusion (Table 2).

Depth, flow, and dissolved oxygen

Depth and flow-rate measurements were taken at each sampling date. Depth was measured in the middle of the channel at each site the position at which substrates were placed. Flow rate was measured by determining the rate at which a fishing float travel over 2 m of channel. Baseline dissolved oxygen concentration was determined with a portable DO meter at each site on September 17-20, 1991.

Substrata sediment composition

Sediment core samples were taken on July 21, 1991 with an 30 cm-long, 5 cm-diameter, PVC cylinder driven 20 cm into the substratum, covered from below and removed. Particle size- and chemical composition of these was determined by the Michigan State University Plant Nutrient Laboratory (see Table 1).

Suspended sediments

Monthly water samples were taken from July to September, 1991-1993 by submerging a 0.5-l, glass jars into the stream from one forest-reach and one pasture-reach site. Samples were vacuum filtered through a preweighed, 0.4 micron, polycarbonate filter which was then dried and weighed on a microbalance to determine suspended solid mass.

Statistical analyses

Community characteristics (abundance, richness, and diversity) were analyzed with an ANOVA model that included reach (forest vs pasture), year (three years for rock and wood, two years for leaves), and site nested within reach (two sites per reach). Reach, year, and site were treated as fixed effects. Abundance and richness data were log-transformed to correct for heterogeneity of variance. Least squares means comparisons made at each level of reach and year are used to estimate the relative strength of treatment effects.

The proportional representation of different functional-feeding guilds (filterers, gatherers, scrapers, predators, and herbivores) was analyzed with a contingency analysis (CATMOD procedure, SAS 1990) that tested for effects of reach (forest vs pasture), year (three years for rock and wood, two years for leaves), and the interaction between reach and year. In all cases, the null hypothesis was that the proportion of individuals representing each feeding guild did not differ across treatments. Shredders were excluded from these analyses due to their low frequency of occurrence.

Two-by-two chi-square tests were used to analyze responses of populations and feeding guilds to landscape alteration (calculations follow Dowdy and Wearden 1991). Three null hypotheses were tested: (1) the probability that taxa would persist, disappear, or appear from 1991 to 1993 was independent of reach and tolerance index, (2) changes from 1991 to 1993 in the number of taxa were the same in forest and pasture reaches, and (3) the probability that taxa from the forest reach also occurred in the pasture reach equalled the probability that taxa from the pasture reach also occurred in the forest reach.

RESULTS

Baseline comparisons: undisturbed vs overgrazed reaches

Measurements of abiotic characteristics in the forest and pasture reaches indicate that substrata chemical composition, particle-size array, water temperature, dissolved oxygen concentration, and suspended solid concentration were similar between reaches during 1991 (Table 1, Figure 4). However, these contiguous reaches had obviously different riparian characteristics (Figures 1, 2) which apparently had strong effects on benthic invertebrate community composition (Appendices 1, 2).

During the summer pasturing season, invertebrate abundance was far greater in forest-reach rock samples than it was on pasture-reach rocks (back-transformed least squares means = 12.2 vs 7.5 inds./m^2, $t = 2.67$, $p = 0.0086$) (Table 3, Figure 5). However, abundance on wood samples (collected after cattle had been removed) was similar between reaches, suggesting perhaps that autumn conditions were more similar between reaches than was the case when cattle were present. Leaf-pack samples, which were taken late in the fall, reveal a more abundant forest-reach invertebrate community (back-transformed least squares means 3.4 vs 1.6 inds./ day, least squares means $t = 2.40$, $p = 0.021$) (Table 3, Figure 5) primarily due to the presence of larval black-fly (***Prosimulium***, Diptera: Simuliidae) densities which were 13 times greater in the forest reach than in the pasture reach.

Taxonomic richness and community diversity (HRI) were similar in undisturbed and overgrazed reaches during 1991(Figure 5). However, community composition and reach-specific endemism, varied considerably between reaches. Forty-five percent of the taxa collected in 1991 from the forest reach were endemics, whereas all but 14% of taxa collected in the pasture reach occurred in both reaches ($x^2 = 8.79$, $p \leq 0.01$, Appendices 1, 2).

Although richness and diversity were similar between reaches, reach-specific endemism differences directed substantial inter-reach differences in the proportion of taxa representing different functional-feeding guilds (Table 4; Figures 6, 7). Gatherers were much more abundant in pasture reach rock and leaf-pack samples relative to forest-reach samples, but were similar in wood samples. There was little difference in filterer abundance on rocks, but they were more abundant in forest-reach wood and leaf-pack samples as winter-developing populations of *Prosimulium* were far more abundant in forest-reach, particularily in leaf-pack samples (Figures 6, 7). The relative proportion of filterers to gatherers, a measure of particulate organic matter in transport versus deposition (Merritt and Cummins 1996 b), was greater in the forest reach on rocks (0.23 vs 0.11), wood (0.16 vs 0.04), and leaf packs (2.47 vs 0.06). This upstream-downstream relationship, indicates that riparian-zone grazing affected the ratio of erosional to depositional benthic habitat in Carlson Creek. Biofilm scrapers were more abundant in the forest-reach than in the pasture reach on rock (2.36 vs 1.99 inds./m^2), wood (6.36 vs 1.83 inds./m^2) and leaf-pack samples (0.07 vs 0.03 inds./day) due principally to differential abundances of heptageniid mayfly nymphs (Ephemeroptera: Heptageneiidae). The relative proportion of predators to other groups, an estimate of predator-prey ratio (Merritt and Cummins 1996 b), was more than two-fold higher in forest-reach rock samples than it was in pasture-reach rock samples (20 vs 10% of total abundance). This was largely due to the presence of five predator taxa found only in the forest reach (Appendices 1, 2). The proportion of predators to other groups was similar between reaches on wood samples and lower in leaf-pack samples (Figures 6, 7).

General effects of beaver impoundment and cattle exclusion

Figures 1 and 2 depict the transition of the forest-reach from free flow in 1991 to impoundment by 1993. Increased depth and reduced flow were accompanied by a change in substrata from mixed fine-mineral composition (Table 1, Figure 3) supporting a variety of macrophytes to a benthic habitat consisting principally of beaver-masticated wood material with little rooted vegetation. Cattle exclusion actuated rapid recolonization by plants on previously barren banks and channel. Depth and flow remained constant and suspended solids increased from 1991-1993 (Figures 1-4).

The effects of landscape alteration on abundance

Beaver activity resulted in a large increase in abundance from 1991 to 1992 in rock and wood samples (Table 4, Figure 5). These responses were largely the result of combined abundance increases in non-Tanypodinae Chironomidae (Chironomidae hereafter) which increased 38% on rocks and 41% on wood; Tanypodinae Chironomidae which increased 7% on rocks and 20% on wood; and Hirudinea which experienced increases of 14% on rocks and 6% on wood. In leaf-pack samples, abundance losses (largely *Prosimulium*), overwhelmed the effect of Chironomidae increases leaving no net effect of the first stage of impoundment. Abundance decreased markedly during the second year of beaver activity on both rock and wood samples (Figure 5). In general, those taxa that experienced proportional increases from 1991 to 1992, decreased from 1992 to 1993. Chironomidae abundance decreased by 59% on rocks and 66% wood, Tanypodinae decreased by 17% on rocks and 33% on wood, and Hirudinea populations declined by 23 % on rocks.

As was the case in the free-flow to impoundment transition, relaxation of instream and stream-bank trampling in the pasture reach resulted in large abundance increases during the first season of restoration (Table 3, Figure 5). Abundance increased more than 17-fold on rocks (back-transformed least squares means ≈ 8 vs 138 inds./m^2 in 1991 and 1992 respectively, $t = 8.28$, $p = 0.0001$), tenfold on wood (≈ 40 vs 400 inds./m^2, $t = 7.56$, $p = 0.0001$), and two-fold in leaf packs (≈2 vs 4 animals per day, $t = 3.66$, $p = 0.0007$). These effects were largely attributable to Chironomidae abundance increases (75, 67, 56% of total increases on rocks, wood, and leaf packs respectively). From 1992 to 1993, abundance decreased somewhat on rock samples and considerably on wood samples (back-transformed least squares means ≈ 400 vs 137 inds/m^2, $t = 4.19$, $p = 0.0001$). However, despite these declines, there remained a significant overall increase on both rocks (≈8 vs 66 inds./m^2, $t = 7.39$, $p = 0.0001$) and wood (from ≈ 40 to 140 inds./m^2, $t = 4.18$, $p = 0.0001$) as a result of large increases from 1991 to 1992

(Table 3, Figure 5).

Abundance increased at least temporarily with both environmental changes largely as a result of concurrent Chironomidae increases in forest and pasture reaches. Although abundance patterns were similar between reaches in rock and wood samples, the effect of cattle exclusion was far greater and less transient than that of beaver impoundment (Figure 5). Abundance changed from being higher in 1991 in the undisturbed forest reach, to being far lower than that in pasture reach by 1993 on rocks (back-transformed least squares means ≈ 16.5 vs 66 inds./m2, $t = 2.99$, $p = 0.003$) and somewhat lower on wood (≈ 52 vs 60 inds./m2, $t = 3.56$, $p = 0.0006$) (Figure 5).

Effects of landscape alteration on richness

Taxonomic richness changed little on rocks and leaf packs during the first year of beaver activity, but increased considerably on rocks by 1993. This effect was largely the result of increases in occurrence of all of the relatively few taxa present in 1993, for the total number of taxa actually declined markedly as a result of beaver activity (Appendix 1). Beaver impoundment also strongly affected taxonomic richness on wood samples, but the pattern was different from that detected with rock samples (Figure 5). Richness increased from 1991 to 1992 primarily as a result of the difference between taxon additions (23 taxa comprising 18% of 1992 abundance) and eliminations (12 taxa comprising 46% of 1991 abundance). This increase was followed by a sharp decrease in 1993, which was largely accounted for by 1993 taxa eliminations (Appendix 1). The total number of taxa in all samples combined decreased sharply from 54 taxa prior to impoundment to 29 and 21 taxa in the subsequent two years. This decline occurred in all trophic guilds (Appendix 1), but was most pronounced in taxa that require relatively silt-free, solid substrata (reductions of 78, 60, and 62% of filterers, scrapers, and predators respectively) (Figure 6).

In contrast to the effects of impoundment on richness, cattle exclusion resulted in taxonomic richness increases, particularily in rock samples (Table 3, Figure 5). Although richness changed little on wood and leaf-pack samples, richness in all substrate types combined increased from 41 to 59 taxa after one year of cattle exclusion, then returned to 42 by 1993 (Appendix 2). Beaver impoundment had a much greater overall effect on richness than did cattle exclusion. While richness declined steadily during pond formation, the net effect of cattle exclusion on richness was the addition of just one taxon ($x2 = 8.40$, $p < 0.001$; 1991-1993 totals = 54, 29, and 21 in forest-reach samples and 41, 59, and 42 in pasture-reach samples). Response to cattle exclusion and beaver impoundment included taxa that persisted, disappeared, and appeared in differing proportions between reaches ($x2 = 15.62$, $p = 0.004$). Compared to cattle exclusion, beaver impoundment resulted in more disappearance (48 vs 9%), less persistence (16 vs 32%), and less appearance (35 vs 59%) from 1991 to 1993 (total taxa = 69 and 66 for forest- and pasture-reach respectively).

Tolerance index values varied little between reaches or years (all means between 4.2 and 5.6), organismal response to changing landscapes was detected in an analysis of the effects of habitat alteration in general (impoundment and exclusion combined). Taxa assigned low tolerance index values (TI = 1-5), compared those with high values (TI = 6-10), were less likely to persist (19 vs 37%), more likely to disappear (53 vs 34 %), and equally likely to appear following perturbation ($x2 = 4.93$, $p = 0.085$).

The effects of landscape alteration on community diversity

Diversity, as estimated with the HRI procedure, increased on wood samples over the first year of beaver activity (Figure 2) (least means squares, $t = 5.74$, $p = 0.0001$) then returned to near free-flow levels by 1993. The same trend was evident in rock samples although high variance resulted in insignificant differences from 1991 to 1992. As was the case overall, leaf pack samples indicate that beaver activity had no detectable effect on diversity (Table 3, Figure 5).

Community diversity increased with cattle exclusion but showed only transient changes with beaver impoundment. Prior to beaver activity and cattle exclusion, forest-reach diversity was similar to that in the pasture-reach in rock and wood samples (Figure 1). By 1993, however, HRI values indicate that diversity was much higher in the pasture reach relative to the impounded forest-reach on these substrates. This was both the result of declines experienced in the forest reach and strong, positive effects of pasture-reach restoration.

Effects of landscape alteration on functional-feeding groups

Differential declines in richness and overall increases in abundance attributable to the lotic-to-lentic transition produced strong treatment effects on proportional abundance of functional-feeding guilds (Table 4, Figures 6, 7). The general pattern of this transition was that scraping and filtering taxa were replaced by collector-gatherers able to exploit vast deposits of organic material that form as a result of beaver feeding activity and impoundment of fine particulates (Naiman et al. 1986, Hammerson 1994).

In free-flowing conditions, filter feeders comprised 12, 8, and 64% of invertebrates collected from rock, wood, and leaf-pack samples respectively. Filterer abundance then declined sharply from 1992-1993 (to 3, 2, and 31 %) as beaver activity slowed flow (Figure 4) and buried substrata. The 1993 beaver pond community as sampled with rocks was devoid of filterers; wood samples were composed of just 2% filterers which were zooplankton that do not require current to facilitate filter-feeding (Figure 6, Appendix 1).

The proportion of gatherers to other taxa increased on all substrata. On rocks and wood, increases were primarily as a result of Chironomidae dynamics. The proportion of Chironomidae on forest rocks increased from 10% of the community in 1991 to 31% in 1992 and up again in 1993 to 52% of the total community. On wood, Chironomidae accounted for 19% of the total abundance in 1991, then increased to 43% in 1992 and dropped to 27% in 1993. The proportional abundance of gatherers on leaf packs increased as a result of an 11% increases in chironomid abundance from 1991 to 1992 (Figure 6).

Biofilm scrapers declined as a proportion of the community from 1991 to 1992 (Figure 3). On rocks, *Stenacron*, *Stenonema*, *Macdunnoa*, *Arthroplea* (all Ephemeroptera: Heptageniidae) and *Helicopsyche* (Trichoptera: Helicopsychidae) declined dramatically while *Nixe* (Heptageniidae) and Gastropoda populations experienced proportional increases. Gastropoda and *Stenacron* population increases influenced an overall scraper abundance increase on wood samples as a result of impoundment. By 1993, *Stenonema* and *Stenacron* were the only scrapers collected from the then fully formed pond (Figure 6, Appendix 1).

Stream-to-pond transition caused the replacement invertebrate predators adapted for lotic existence with those that typically inhabit standing water. Proportional increases of predators from 1991 to 1992 on rocks (Figure 6) were primarily the result of changes in Tanypodinae abundance which comprised 3% of the community in 1991 and increased to 6% by 1992, and Hirudinea which increased from 4% to 11% from 1991 to 1992. Tanypodinae abundance dynamics also strongly influenced the relative abundance of predators on wood samples which increased from 13 to 21%. The proportion of predators changed little on leaf packs from 1991 to 1992 as decreases in *Oecetis* (Trichoptera: Leptoceridae) and *Hemerodromia* (Diptera: Empididae) were directly offset by additions of *Chauliodes* (Megaloptera: Corydalidae) and *Nyctiophylax* (Trichoptera: Polycentropodidae) (Appendix 1). Although predator abundance generally increased with beaver activity, predator richness declined sharply (Appendix 1) largely as a result of local elimination of lotic specialists. On rocks, *Nyctiophylax*, *Polycentropus* (Trichoptera: Polycentropodidae), *Nigronia* (Megaloptera: Corydalidae), and *Probezzia* (Diptera: Ceratopogonidae) were eliminated. *Hemerodromia* (Diptera: Empididae) disappeared from all substrata. Leaf-pack samples indicated that *Isoperla* (Plecoptera: Perlodide) also abandoned the forest reach as beaver activity proceeded (Appendix 1).

The strong effects of cattle exclusion on abundance were disproportionally distributed between functional-feeding guilds, but not to the same degree as they were as a result of beaver impoundment (Figures 5-7). Filterers decreased gradually on rocks due to reductions of fingernail clams (Sphaeriidae) and net-spinning caddis larvae (*Cheumatopsyche*) and increased on wood as a result of increases in Shaeriidae and *Hydropsyche,* thus producing little overall functional change. Filterers increased in numbers on leaf-packs largely as a result of proportional increases in *Prosimulim* which increased from 14 to 50 % of total abundance. At the catchment level (forest and pasture reaches combined), increases in the pasture compensated for upstream declines that resulted from impoundment.

Collector-gatherer response to cattle exclusion were largely attributable to Chironomidae abundance dynamics. Gatherers increased in relative proportion on wood and leaf packs from 1991 to 1992 and decreased on wood from 1992 to 1993. On rocks, gatherer abundance and taxonomic composition changed little from 1991 to 1993 (Figure 7, Appendix 2). The ratio of filterer and gatherer proportional abundances, a measure of relative levels of transport and deposition of particulate organic matter (Merritt and Cummins 1996 b), was greater in the forest reach on rocks (0.23 vs 0.12), wood (0.16 vs 0.044), and leaf packs (2.47 vs 0.06). This upstream-downstream relationship, typical of comparisons made between low- and mid-order streams (Merritt and Cummins 1996 b), indicates that pasturing may have affected the relative amounts of erosional and depositional benthic habitat in Carlson Creek.

The proportion of predators to other taxa changed little from 1991 to 1993 on rocks and decreased on wood despite increases in all predacious taxa present (with the exception of *Hemerodromia* which decreased slightly on wood). Therefore, it was the concurrent large increases in other taxa (principally Tanypodinae) that drove observed differences in predator proportions between years. In contrast to this pattern, predator decreases on leaf packs were the result of large decreases experienced in populations of Hirudinea and *Hemerodromia.*

The lotic to lentic transition that resulted from beaver activity had a far greater effect on invertebrate community functional composition than did pasture-reach restoration efforts (Figures 6, 7). This is perhaps the result of differential levels of landscape transformation, for relaxation of trampling did not affect channel characteristics nearly as much as did beaver impoundment (Figure 3, 4).

DISCUSSION

The onset of beaver-mediated disturbance and recovery from overgrazing in Carlson Creek generated pronounced abundance increases in response to both landscape alterations. These increases were largely the result of concurrent large increases in chironomid midge populations and therefore exemplified the commonly observed early dominance of post-alteration communities by small, rapidly developing generalists (e.g. Nuttall and Bielby 1973, Wallace and Gurtz 1986). In a manner suggestive of a delayed density-dependant response, abundance declined from 1992 highs by 1993 in both forest- and pasture reaches (Figure 5). The principal inter-reach difference between compensatory responses was that, from 1991 to 1993, abundance increased in the pasture-reach and decreased in the forest-reach.

Similarities in inter-reach patterns of response to beaver impoundment and cattle exclusion could be evidence of inter-annual abundance patterns within the catchment (forest and pasture reaches combined) and therefore not the result of concurrent landscape alterations. However, community richness- and compositional changes varied considerably between reaches and thus evidence very different landscape-alteration processes.

During 1991, differing riparian characteristics were reflected in the feeding ecology of reach-specific endemic taxa. Forest-reach endemics included four taxa that consume coarse particulate organic material (*Mystacides*, *Taeniopteryx*, *Acentria*, Isopoda) and no strictly fine-particle feeders. The opposite relationship was detected in the pasture reach where endemics included two fine-particle feeders (*Ameletus* and *Hexagenia*) and no large-particle specialists (Appendices 1, 2). This invertebrate taxonomic distribution reflects the expected pattern in particle size composition when moving from tributary to mouth, or as is apparent in Figure 1, from areas of dense to sparse allochthonous vegetation (Vanotte et al. 1980, Merritt and Cummins 1996 b).

Prior to disturbance by beaver, the forest-reach benthic community was richer, more diverse, and more evenly distributed across functional-feeding guilds than was the pasture-reach community. This resulted in large inter-reach differences in feeding-guild richness. In the pre-impoundment forest reach, filterer-, predator-, and shredder richness estimates were greater; gatherer richness was lower; and scrapers and herbivores were proportionally similar between reaches. These relationships shifted entirely as beaver activity progressed and cattle exclusion was initiated. By 1993, all forest-reach functional-feeding guilds were less rich than their pasture counterparts due to the combined net effect of richness decreases in response to impoundment and richness increases in response to habitat restoration.

Although the effects of beaver impoundment on abundance, richness, and diversity were more transient than those of cattle exclusion, lotic-to-lentic transition directed considerably more substantial functional changes in the invertebrate community than did restoration efforts. Unlike the strong effects of impoundment, relaxation of trampling perturbation did not cause lasting changes in the functional structure of the benthic communities (Figures 6, 7). Restoration could, however, have potentially lasting effects on reach-level bioenergetics as a result of the general pattern of increases in abundance, richness, and diversity from 1991 to 1993 (Figure 5).

The benthic invertebrate community response to impoundment of the forest reach typified well-established effects of beaver disturbance. Beaver pond formation typically results in replacement taxa that depend on flow to deliver food, scrape biofilm from solid substrata, or cling to vascular hydrophytes with taxa adapted to exploit vast accumulations of entrained allochthonous organic material.(Naiman et al. 1986, 1988). Therefore, because the sampling program was clearly sensitive to changes caused by beaver, the effects detected in response to excluding cattle from Carlson Creek may allow a broadening of scope of inference to include restoration efforts undertaken elsewhere.

Fencing and bank stabilization efforts were endeavored principally to enhance substrata and water quality in effort to slow erosion and re-establish the pasture reach as a brook trout (*Salvelinus fontinalus*) nursery. Benthic invertebrate standing stocks increased on all substrata in response to exclusion. It is therefore reasonable to assume that insectivorous fish may have also benefitted from enhanced food resources. However, because increases were predominantly in taxa that burrow into soft sediment, high levels of deposition and transport (Figure 4) were still indicated by 1993 which would undoubtedly limit brook trout redd success (Waters 1995).

Inter-reach and inter-year habitat differences were evidenced by visual inspection and detection of significant invertebrate responses to disturbance and recovery (Tables 5, 6; Figures 1, 2, 5). However, despite obvious physical change in both reaches, tolerance index values varied little between reaches or throughout landscape alterations. Published benthic invertebrate tolerance values were therefore arguably insensitive to stress induced by livestock grazing and beaver activity in Carlson Creek. However, at the catchment level (forest and pasture reaches combined), tolerance index values indicated relative resistance and resilience to the effects of changing environments. Low-tolerance to perturbation was associated with relative inability to persist, higher likelihood of disappearance, and equal ability to appear following perturbation. This pattern would, in recently (or continually) disturbed reaches, result in a higher proportion of high-tolerance taxa than would be expected in relatively stable habitat. The data therefore indicate that although mean TI values were not responsive to the effects of beaver activity or cattle exclusion, it seems that the tolerance index may be useful in assessing an organism's relative resilience to changing physical conditions.

As was the case in a study conducted by Reed et al. (1994) in three Australian streams undergoing different levels of livestock grazing, functional-feeding group composition in Carlson Creek was the most illustrative of initial habitat condition (undisturbed vs overgrazed) and thus potentially the best on-site method of determining habitat condition in grazed streams. Community response to habitat restoration was, however, best characterized by changes in diversity as estimated with the hierarchical richness procedure (Figure 5).

The relative contributions of local and regional processes on richness reveals that local (reach-level) spatial heterogeneity contributed immensely to regional (catchment-level) richness in Carlson Creek. Prior to beaver colonization and cattle exclusion, reach-specific endemism was far more common in the free-flowing forest reach than it was in the overgrazed pasture reach. However, by the second year of impoundment and restoration, the opposite relationship was detected as most beaver-pond inhabitants could be found in both reaches. Disturbances by beaver and cattle therefore facilitated the establishment of communities rich in habitat generalists and conversely, undisturbed and recovering conditions encouraged the establishment of habitat specialists. Catchment-level biodiversity was thus enhanced through maintenance and augmentation of landscape heterogeneity, a phenomenon expected to ensure maximum stability in agricultural ecosystems (Tilman 1996).

SUMMARY

(1). Beaver colonization and cattle exclusion both resulted in initial abundance increases in chironomid midge populations, thus exemplifying the commonly observed dominance of post-alteration communities by small, rapidly developing ecological generalists.
(2). Recovery from overgrazing led to increased community diversity while disturbance by beaver impoundment resulted in decreased diversity.
(3). Impoundment by beaver produced very large changes in community structure and functional composition. In contrast, recovery from cattle-grazing disturbance did not meaningfully affect community composition.
(4). Disturbance by beaver fostered increased abundance of broadly distributed habitat generalists while recovering and undisturbed habitat harbored less common taxa with specialized habitat requirements.
(5). The forest reach supported many taxa not found in the overgrazed pasture reach,

but the pasture reach contained few taxa not found in the forest reach. Therefore, losses of forest reaches that result from human activities have relatively large impacts on watershed biodiversity.

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Table 1. Baseline abiotic data collected from forest- and pasture-reach sites during 1991. Values indicate means ± 1 se.

	FOREST	PASTURE
Substrata		
% Sand	48.4 ± 4	49.4 ± 27
% Silt	11.7 ± 1	15.7 ± 11
% Clay	39.9 ± 5	34.9 ± 16
pH	8.4 ± 0.4	8.55 ± 0.05
CEC (me/100g)	20.4 ± 1.45	18.4 ± 4.2
P (ppm)	10.5 ± 0.5	23 ± 18
K (ppm)	108 ± 27	77.5 ± 32.5
Ca (ppm)	3452 ± 262	3141 ± 668
Mg (ppm)	340 ± 10	297 ± 93
Na (ppm)	260 ± 59	212.5 ± 72.5
NH_4 (ppm)	2.25 ± 0.05	2.45 ± 0.75
NO_3 (ppm)	2 ± 1	3.5 ± 2.3
H_2O		
Temp. (° C)	19.4 ± 1.8	15.7 ± 0.8
DO (mg/l)	7.85 ± 0.17	8.3 ± 0.24

Table 2. Carlson Creek invertebrate tolerance-index values (from Resh et al 1996).
* = values estimated for this study.

COLLEMBOLA*	4	TRICHOPTERA		COLEOPTERA	
PLECOPTERA		Brachycentridae	1	Dytiscidae*	7
Taeniopterygidae	2	Glossosomatidae	0	Elmidae	4
Perlodidae	2	Helicopsyche	3	Gyrinidae	7
		Hydropsychidae	4	Haliplidae*	4
EPHEMEROPTERA		Hydroptilidae	4		
Baetidae	4	Lepidostomatidae	1		
Caenidae	7	Leptoceridae	4	DIPTERA	
Ephemerellidae	1	Limnephilidae	4	Ceratopogonidae	6
Ephemeridae	4	Polycentropodidae	6	Chaoboridae	3
Heptageniidae	4	Psychomyiidae	2	Chironomidae	6
Leptophlebiidae	2			Dixidae	4
Siphloneuridae	7			Empididae	6
				Simuliidae	6
ODONATA		MEGALOPTERA		Tipulidae	3
Calopterygidae	5	Corydalidae	0		
Coenagrionidae	9	Sialidae	4	AMPHIPODA	4
Cordulegastridae	3			ISOPODA	8
Gomphidae	1	LEPIDOPTERA		ACARI	4
Lestidae	9	Noctuidae*	5	GASTROPODA	7
Libellulidae	9	Pyralidae	5	CNIDARIA*	3
				NEMATOMORPHA	10
				NEMATODA	10
				HIRUDINEA	10
				OLIGOCHAETA	10

Table 3. ANOVA results comparing invertebrate community characteristics as estimated with rock, wood, and leaf-pack samples (see Figure 1).

ROCKS		Log (Abundance)		Log (Richness)		HRI	
Source	df	MS	F	MS	F	MS	F
Reach	1	1.122	5.242 *	1.492	12.277 ***	182353.9	19.837 ***
Year	2	8.129	37.996 ****	8.075	66.429 ****	175408.2	19.081 ****
Reach x Year	2	2.375	11.092 ****	0.458	3.771 *	106644.7	11.601 ****
Site (Reach)	2	0.298	1.391	0.228	1.876	1033.4	0.112
Site x Year (Reach)	4	0.367	1.716	0.173	1.426	6203.4	0.675
Error	137	0.214		0.122		9192.8	
WOOD							
Reach	1	1.172	10.198 ***	0.194	4.257 *	2472.4	9.348 ***
Year	2	6.411	55.773 ****	1.309	28.787 ****	16075.0	60.777 ****
Reach x Year	2	0.353	3.072 †	0.234	5.136 **	980.8	3.709 *
Site (Reach)	2	0.268	2.333	0.179	3.930 *	565.4	2.138
Site x Year (Reach)	4	0.146	1.267	0.017	0.369	138.2	0.522
Error	92	0.115		0.045		264.5	
LEAVES							
Reach	1	0.040	0.323	0.000	0.000	0.5	0.058
Year	1	0.291	2.340	0.174	6.555 ***	6.3	0.807
Reach x Year	1	1.656	13.305 ****	0.069	2.606	74.1	9.563 **
Site (Reach)	2	1.624	13.051 ****	0.209	3.937 *	72.8	9.359 ***
Site x Year (Reach)	2	0.613	4.926 *	0.132	2.489	37.2	4.788 *
Error	43	0.124		1.396		7.8	

† $P < 0.10$, * $P < 0. 05$, ** $P < 0.01$, *** $P < 0.001$, **** $P< 0.0001$

Table 4. Contingency analyses testing whether the proportion of animals representing different functional feeding groups varied between reaches in rock, wood, and leaf-pack samples (see Figures 2, 3).

	ROCKS		WOOD		LEAVES	
	df	x^2	df	x^2	df	x^2
Reach	4	109.12***	4	125.09***	4	3.42
Year	8	262.44***	8	272.42***	4	117.30***
Reach x Year	8	77.38***	8	129.36***	4	22.09***

*** $p < 0.001$

Figure 1. The pasture reach of Carlson Creek in (A) 1991, (B) 1992, and (C) 1993.

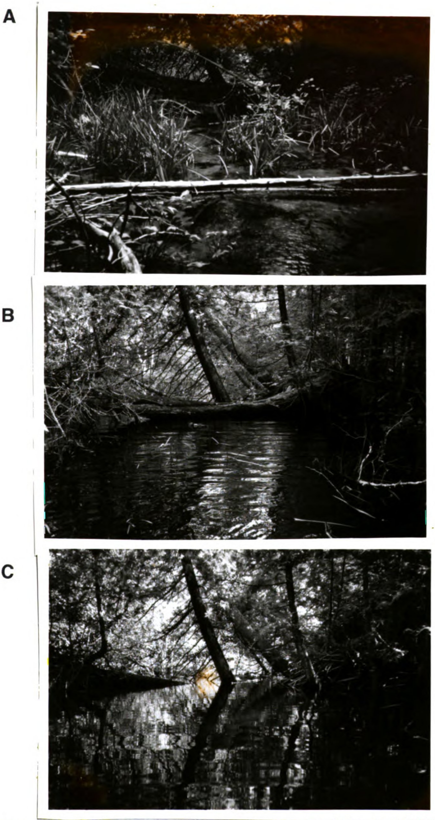

Figure 2. The forest reach of Carlson Creek in (A) 1991, (B) 1992, and (C) 1993.

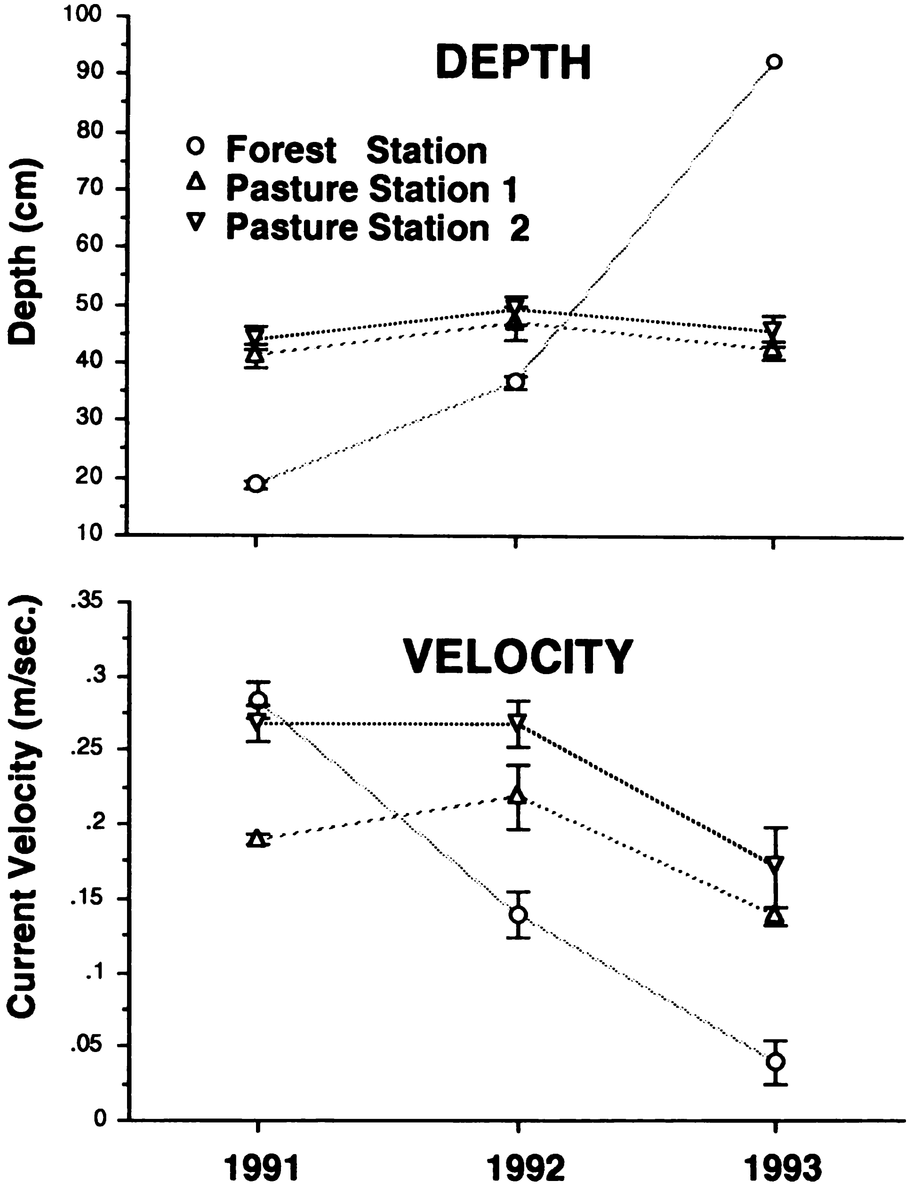

Figure 3. Mean depth and flow rate ± 1 se in one forest-reach and two pasture-reach stations. Measurements taken during July, August, and September, 1991-1993.

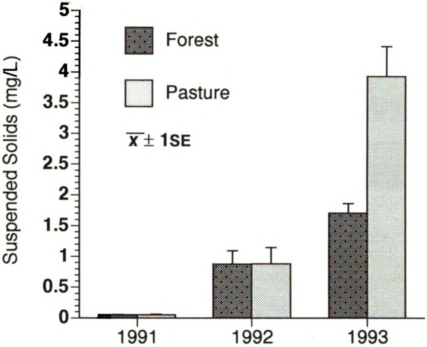

Figure 4. Suspended solid concentration from forest- and pasture-reach water sampless taken monthly, July-September, 1991-1993.

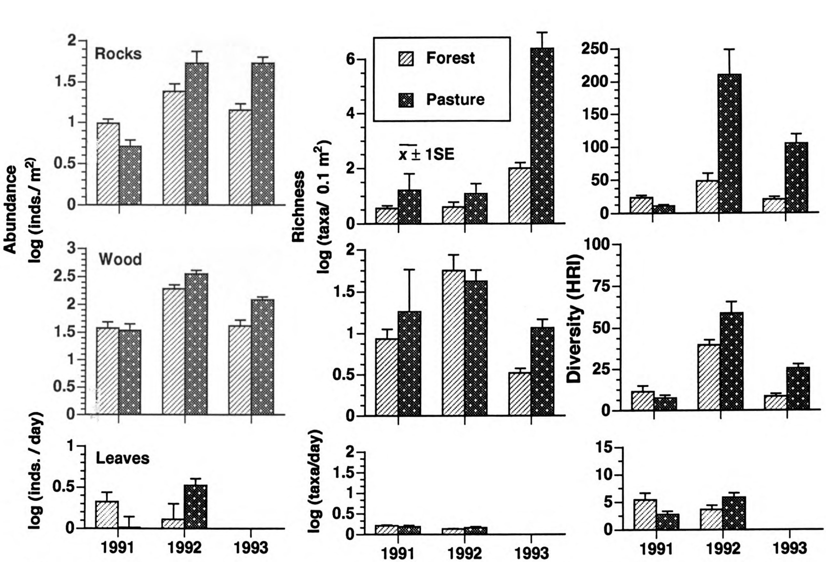

Figure 5. Mean invertebrate abundance, richness, and diversity in rock, wood, and leaf-pack samples.

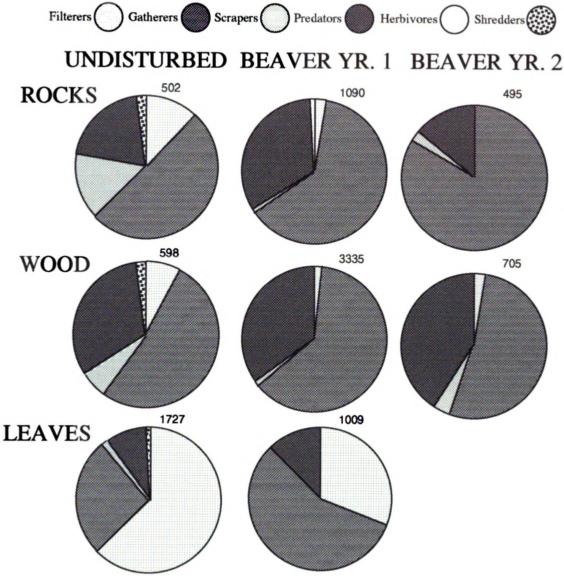

Figure 6. Community functional-feeding group composition in forest-reach samples. Values indicate total number of animals collected. Functional-feeding groups that comprised less than 1 % of total are not represented on pie-charts. These are: 3 herbivores in 1992 wood samples and 5 scrapers in 1992 leaf-packs.

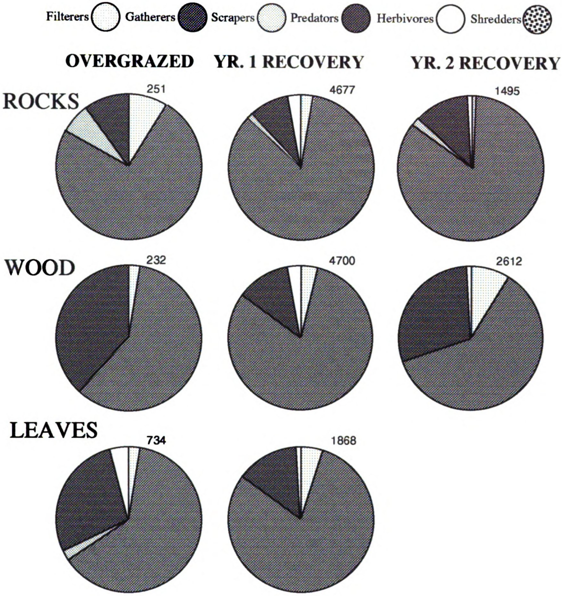

Figure 7. Community functional-feeding group composition in pasture-reach samples. Values indicate total number of animals collected. Groups that comprised less than 1% of total count are not represented on pie-charts. These are: 2, 9, and 9 scrapers in 1991-1993 wood samples respectively; 1 herbivore in 1991 wood samples; and 6 scrapers in 1991 leaf-pack samples.

APPENDIX 1

Appendix 1. Forest-reach taxa organized by feeding guild and year of collection. Letters after taxa names indicate sample type(s) from which animals were collected: R=rock; W=wood; L=leaf packs; D=drift.

FEEDING GUILD	1991 UNDISTURBED	1992 BEAVER IN	1993 BEAVER YR. 2
FILTERERS	*Arthroplea* R *Brachycentrus* L *Ceratopsyche* R W *Cheumatopsyche* R L D *Hydropsyche* R W L D *Neureclipsis* W D *Prosimulium* W L D Bivalvia R W D Cladocera D	*Ceratopsyche* D *Cheumatopsyche* R W L D *Hydropsyche* R W D *Prosimulium* R W L D *Neureclipsis* W D Bivalvia R *Hydra* R L D Cladocera W L D Copepoda D	Cladocera W Copepoda W
GATHERERS	*Podura* D *Baetis* R W L D *Caenis* R W D *Paraleptophlebia* L D *Mystacides* R *Psychomyia* R W *Dubiraphia* W *Macronychus* W L D *Optioservus* L *Stenelmis* R Chironomidae R W L D Nematoda R L Acari R W D	*Podura* R W D *Baetis* R W L D *Caenis* R W *Ephemerella* R W *Paraleptophlebia* W L D *Mystacides* W *Dubiraphia* W D *Macronychus* W D *Optioservus* W *Stenelmis* W L Chironomidae R W L D Nematoda R Acari R W D	*Podura* R *Caenis* W *Ephemerella* W *Paraleptophlebia* W *Optioservus* W Chironomidae R W *Dixella* W Oligochaeta R Acari R
SCRAPERS	*Macdunnoa* R *Stenacron* R D *Stenonema* R W L D *Helicopsyche* R D Gastropoda R D	*Nixe* R *Stenacron* R W L D *Stenonema* R W L D *Helicopsyche* R Gastropoda R W	*Stenacron* W *Stenonema* W
PREDATORS	*Amphiagrion* D *Argia* D *Boyeria* R D *Chromagrion* D *Cordulegaster* R *Calopteryx* R L D *Promogomphus* D *Isoperla* L *Nigronia* R *Nyctiophylax* R *Oecetis* R L D *Polycentropus* R *Chaoborus* D Tanypodinae R W L D *Dicranota* W *Probezzia* R *Hemerodromia* W L Hirudinea R W	*Argia* D *Calopteryx* W *Isoperla* L *Boyeria* W *Chauliodes* L *Nigronia* R *Sialis* R *Oecetis* R W D *Nyctiophylax* R W L *Polycentropus* R W *Dineutis* D Tanypodinae R W L D *Hemerodromia* R W L D Hirudinea R W D Nematomorpha R W	*Argia* W *Sialis* W *Oecetis* W *Probezzia* W Tanypodinae R W Hirudinea R W Nematomorpha W
HERBIVORES		*Hydroptila* R W *Oxythira* W *Peltodytes* D	
SHREDDERS	*Taeniopteryx* W *Hydatophylax* D *Lepidostoma* R L D *Pycnopsyche* R W *Acentria* D *Tipula* D Amphipoda D Isopoda L	*Taeniopteryx* L *Lepidostoma* R D *Pycnopsyche* R *Trianodes* W D Amphipoda R W D	Amphipoda W

Appendix 2. Forest-reach taxa organized by feeding guild and year of collection. Letters after taxa names indicate sample type (s) from which animals were collected: R=rock; W=wood; L=leaf packs; D=drift.

APPENDIX 2

FEEDING GUILD	1991 OVERGRAZED	1992 CATTLE EXCLUDED	1993 RECOVERY YR. 2
FILTERERS	*Cheumatopsyche* R W D *Hydropsyche* R L *Neureclipsis* D *Prosimulium* R L D Bivalvia R W L D	*Brachycentrus* R *Ceratopsyche* R W L D *Cheumatopsyche* R W L D *Hydropsyche* R W L D *Neureclipsis* W D *Prosimulium* W L D Bivalvia R W D *Hydra* D Cladocera R L D Copepoda D *Daphnia* R D	*Brachycentrus* W *Cheumatopsyche* R W *Hydropsyche* W Simuliidae R Bivalvia R *Hydra* R W
GATHERERS	Collembola W Ameletus D *Baetis* R W L D *Caenis* R L D *Ephemerella* W *Paraleptophlebia* L *Hexagenia* R Siphloneuridae R *Psychomyia* R *Dubiraphia* R L *Macronychus* W D *Optioservus* L D *Stenelmis* W *Dixella* L D Chironomidae R W L D Nematoda R W L D Oligochaeta L Acari W	Collembola L D *Podura* D *Baetis* R W L D *Caenis* R W L D *Ephemerella* R D *Paraleptophlebia* R W L D *Psychomyia* R W D *Dubiraphia* R L D *Macronychus* W D *Stenelmis* R W D *Dixella* R D Chironomidae R W L D *Antocha* D Nematoda R W L D Oligochaeta R Acari R W L D Copepoda R W	*Podura* R *Baetis* R W *Caenis* R W *Paraleptophlebia* R W *Mystacides* W *Psychomyia* R W *Dubiraphia* R W *Macronychus* W *Optioservus* R W *Stenelmis* R W Chironomidae R W Nematoda R W Acari R W Copepoda W
SCRAPERS	*Pseudocloeon* R *Stenacron* R L D *Stenonema* R L D *Glossosoma* D Gastropoda D	*Heptagenia* R *Nixe* R *Stenacron* R D *Stenonema* R W L D Psphenidae D *Helicopsyche* R W Neophylax W *Neophylax* W Gastropoda D	*Stenacron* R W *Stenonema* R *Helicopsyche R W*
PREDATORS	*Calopteryx* D *Polycentropus* W L Dytiscidae L D Tanypodinae R W L D *Probezzia* D *Hemerodromia* R W L D Hirudinea R L D	*Aeschna* D *Calopteryx* D Corixidae D *Nigronia* D *Oecetis* R W D *Nyctiophylax* L *Polycentropus* W D *Agabus* D *Dineutis* D Tanypodinae R W L D *Dicranota* R *Hexatoma* R *Hemerodromia* R W L D Hirudinea R W L D Nematomorpha R W	*Boyeria* R W *Calopteryx* W *Oecetis* R *Polycentropus* W *Dineutis* R Tanypodinae R W *Limnophora* R *Hemerodromia* R W Nematomorpha W Hirudinea R W
HERBIVORES	*Hydroptila* W L	*Hydroptila* R W L D *Oxythira* R W L D *Paraponyx* W *Haliplus* R *Peltodytes D*	*Hydroptila* R W *Oxythira* W *Paraponyx* R W *Petrophila* R
SHREDDERS	*Lepidostoma* D *Pycnopsyche* L D *Grensia* D *Hydatophylax* L *Tipula* D Amphipoda L D	*Lepidostoma* D *Pycnopsyche* R W L D *Nectopsyche* R L *Trianodes* R D *Hydatophylax* D Tipulidae R Amphipoda R W L D Decapoda R Isopoda D	*Lepidostoma* R W *Pycnopsyche* R *Hydatophylax* W Amphipoda R W

3

THE BEHAVIORAL RESPONSE OF THE STONEFLY *PARAGNETINA MEDIA* (PLECOPTERA: PERLIDAE) TO THE ONSET OF INTENSE SEDIMENTATION

Abstract. The initial response by *Paragnetina media* (Plecoptera: Perlidae) nymphs to increased suspended sediment concentration was examined in field trials with chambers designed to give nymphs the choice to stay or reposition in response to experimental sediment additions. The results indicate that the often posited immediate-escape response to the onset of intense sedimentation may not be commonly enacted by stonefly nymphs or perhaps other relatively immobile, lotic insects.

INTRODUCTION

What do stream-dwelling animals do when they experience rapid increases in suspended sediment concentration? The answer to this question is fundamental to understanding the effects of the massive amount of sediment entering flowing water globally as a result of human activities (Waters 1995). However, except for the notable exception of several widely studied Salmonidae species (e.g. Tagert 1984, Reiser and White 1988), little is known about how, or if, high concentrations of suspended sediments affect aquatic organisms (Cordone and Kelly 1961, Reiser and White 1988, Servizi and Martens 1991, 1992, Waters 1995).

The enhancement of suspended sediment levels associated with human agricultural, silvicultural, and industrial activities is widely suspected to force benthic invertebrates to flee impacted habitats (e.g. Hynes 1973, Newbury 1984, Williams and Feltmate 1992), however, virtually no empirical evidence has been presented to support this contention (Waters 1995). Extreme sedimentation events such as those that follow heavy rains in overgrazed river-bottom land (Tarzwell 1938), reservoir flushing (Gray and Ward 1982), road construction (Ogbeibu and Victor 1989), and riparian zone clear-cuts (Webster et al. 1992) definitely have the effect of removing benthic invertebrates. However, in most cases it is not known whether these responses were instantaneous reactions to stress created by elevated suspended solid concentrations or an eventuality associated with habitat degradation (Waters 1995).

Several field experiments have been conducted to determine the direct effects of heavy sedimentation on benthic invertebrate behavior (Brunskill et al. 1973, Rosenberg and Snow 1975 a, b, Rosenberg and Wiens 1978, Culp et al. 1986). For example, Rosenberg and Wiens (1978) observed that introducing unsorted bank sediments to a Northwest Territories river caused a marked increase in drifting invertebrates five hours after the episode. They concluded that sediment addition at 30 mg/ l initially "strips" benthos from substrata and that the most sensitive and most exposed organisms leave first. However, because samples were not taken immediately after sediment addition, initial stripping was not actually measured. After pouring sand into riffles of a British Columbia stream, Culp et. al (1986) also cited unmeasured scouring effects of saltating sediment particles as the causative factor of, in this case, instantaneous drift of invertebrates that inhabit stone surfaces.

One technical problem common to traditional field studies of invertebrate response to sedimentation is that specific drift-initiating factors remain undetectable with standard drift-monitoring techniques (Waters 1995). After producing and analyzing data such as that reviewed above, White and Gammon (1977) concluded that sedimentation-mediated drift may not be a consequence of stress caused by sediment (i.e. catastrophic drift) but rather to light-attenuation-induced behavioral drift (*sensu* Waters 1972, Müller 1974). Therefore, drift in response to rapid increases in suspended solid concentration may be interpreted as a response to local overpopulation or resource scarcity (density-dependent drift) that would not necessarily result in negative effects on benthic communities (Waters 1995).

The primary objective of this study was to determine if nymphs of the relatively immobile, predacious stonefly *Paragnetina media* (Plecoptera: Perlidae) would immediately reposition in response to the onset of intense sedimentation. Exposure to sediments was limited to a brief period of time in order to focus on assessing the immediate, direct effects of sedimentation on stonefly behavior such as integument scouring and gill fouling.

METHODS

Stoneflies

Paragnetina media (Walker) nymphs are common inhabitants in eastern U. S. streams (Frison 1935, Stewart and Stark 1988). Characteristically associated with fast-flowing streams, their flattened body shape and gripping tarsal claws allow nymphs to crawl over relatively silt-free substrata and through accumulations of allochthonous debris in search of a wide variety of invertebrate prey (Stewart and Harper 1996).

In mid-Michigan, *P. media* nymphs hatch from early summer-laid eggs and reach maturity by the spring of their second year (Heiman and Knight 1970). Tightly synchronous emergence (late May in mid-Michigan) enhances the probability of mating success of these weak-flying, short-lived adults (Feltmate and Pointing 1986) and consequently allows determination of nymphal age due to the great disparity in size when age classes overlap (Heiman and Knight 1970). Species determination was made with keys in Stewart and Stark (1988). Stoneflies in the autumn of their second year were used in experiments; they were collected and trials were conducted in a riffle of a second-order, mid-Michigan pasture stream that flowed over cobble and gravel substrata (Prairie Creek, Ionia Co., MI; 43°N, 85°W).

Experimental procedure

Nymphs were collected with soft forceps and placed into a pan of aerated stream water that contained a small stone for them to cling to. When six nymphs were collected (five for one set of trials), the stone (with clinging nymphs) was removed and placed into a sedimentation-response chamber (Figure 1). *Paragnetina media* nymphs are relatively sessile once a position is established (Felmate and Pointing 1986). This allowed for trials to get underway before a move unrelated to the treatment was likely to be attempted (approximately 10 seconds after introduction).

Sedimentation-response chambers are compartmentalized, 2-mm thick plastic boxes with 1 mm-diameter mesh walls (Figure 1). Chambers were designed to provide nymphs with four options in response to exposure to a sediment and water slurry delivered directly into the chamber from an upstream reservoir. Response options include (1) maintain position in the (220 x 85 x 35 mm) overlying compartment (= stayed); (2) move down through 20 x 5 mm slots to a like-sized underlying chamber (=down); (3) move upstream into a 200-mm long, 0.5-mm diameter, mesh net (= upstream); and (4) move downstream into a into 200-mm long, 0.5 mm mesh net (= downstream) (see Table 1, Figure 2).

The sediment-delivery system is composed of a 23 l, plastic pale fitted with 3 m of 40-mm diameter, plastic tube through which the sediment and water slurry (or just water for control trials) is delivered to a chamber from an upstream position. When the sediment and water slurry (or water in control trials) had completely passed through the chamber (approximately 2 minutes after the onset of a trial), it was disconnected from the sediment-delivery system and removed from the stream. Nymphs were then collected from the nets and compartments and preserved in 70% ethanol. Trials were conducted on 19 September, 1993 and 23 September, 1994. A total of eight sediment and nine control trials were conducted.

Sediments

A slurry consisting of a 1.5 l container of bank sediments and 23 l of stream water produced a level of sedimentation downstream from chambers that was similar to that measured during a heavy spate in Prairie Creek (24 mg/l on 15 September, 1993); a level that is known to produce negative, yet sublethal effects on benthic invertebrates (Newcombe and MacDonald 1991). The actual suspended sediment level in chambers was approximately ≈ 56 mg/l as determined with a a Hach 2100 A NTU meter and a known mg/l : NTU relationship. Trials were conducted on days when the stream was running relatively clear of suspended sediments. Therefore, control trials were conducted with low-sediment (> 1 mg/l) water samples. Sediment particle-size and chemical composition was determined by the Michigan State University Plant and Soil Nutrient Laboratory (Table 2).

Statistical analysis

A single-factor, repeated-measures ANOVA model was used to test the effects of the two treatments on behavioral response. Response alternatives include maintaining position, moving below the main compartment, moving upstream, or downstream (see Table 1).

RESULTS

Results presented in Figure 2 indicate that *P. media* nymphs do not immediately flee habitat in response to intense sedimentation. Nymphs were expected to reposition at a higher frequency in sedimentation trials, however they actually moved less in sediment trials than in controls (mean % ≈ 70.8 vs 50.7) (ANOVA: $P > 0.053$, Table 1, Figure 2). There were no significant differences between repositioning options within trials or between treatments (Table 1, Figure 2).

DISCUSSION

The experimental population of mid-Michigan *P. media* nymphs were apparently resistant to, or experimental conditions did not reproduce, gill-fouling (Hynes 1970) and integument shearing effects (Culp et al. 1986) believed to be associated with high levels of bank sediment in flow. Perhaps frequent exposure in the recent past has led to the establishment of the tendency to maintain position during high-sedimentation episodes due to the commonality of such incidents in the pastured experimental stream reach. The selective pressure against enacting movements unrelated to resource acquisition is likely reinforced in Prairie Creek by selection against relocation during daylight hours due to heightened risk of being eaten by visual-feeding insectivorous fish (Waters 1972). This pattern was also detected in unquantified preliminary trials conducted by *Cheumatopsyche* and *Hydropsyche* larvae (Trichoptera: Hydropsychidae) in a Minnesota stream with thriving insectivorous fish populations.

The relatively immobile *P. media*, may have also acquired a position-maintenance strategy early in its evolutionary history. In order for an organism to successfully colonize a novel habitat, it must be able to respond to its most severe conditions. Almost universally, the behavior to deal with novel stress such as that which seemingly accompanies habitat shifts and rapidly changing environments, must be expressed prior to morphological adaptation (Mayr 1982). For example, protoplecopterns, terrestrially adapted animals believed to have secondarily invaded aquatic habitats some 300 mya

(Imms 1957, Illes 1965, Ross 1965), had to maintain position while exposed to high levels of flow and sedimentation events prior to acquiring lotic adaptations such as streamlined morphology and gripping tarsal claws (Wooten 1972). Therefore, throughout their history, *P. media* nymphs and their direct progenitors may have evolved a strategy of position maintenance in response to episodes of intense sedimentation.

Evidence presented here indicates that one species with limited mobility, relatively long development time, and patchily distributed resources is more likely to endure sedimentation rather than attempt to avoid the stress of exposure by attempting to reposition. It is clear that benthic invertebrates do not respond to anthropogenic sedimentation in a consistent manner, thus reinforcing the exigency for clarification the roles of phylogeny, morphology, and regional ecology in influencing invertebrate behavioral response to the widespread problem of anthropogenic sedimentation in streams.

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Table 1. ANOVA results comparing the number of stonefly nymphs that selected each behavioral option (see Figure 2).

		STAYED		DOWN		UPSTREAM		DOWNSTREAM	
Source	df	MS	F	MS	F	MS	F	MS	F
Sed. Level	1	1709.68	4.427 †	0.079	1.931	0.013	3.529	0.000	0.007
Error	15	386.16		0.041		0.004		0.003	

† P= 0.053

Table 2. Particle-size distribution and chemical composition of bank sediments used in sedimentation treatments.

Soil Type: Loam, pH 7.1

Mineral Component: 70.7%	Organic Component: 29.3%		
45.8 % Sand	Na	258	ppm
32.7 % Silt	Cl	620	ppm
21.4 % Clay	NO3	5.4	ppm
	NH4	74.7	ppm

Figure 1. A sedimentation-response chamber.

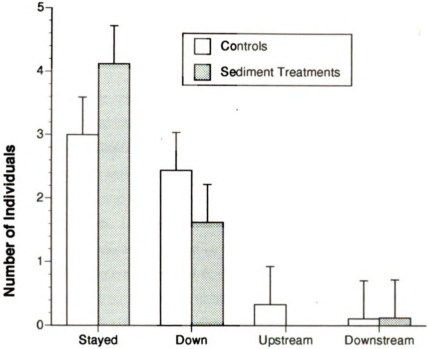

Figure 2. Mean number of stoneflies (± 1 se) that chose each behavioral option in 9 control and 8 sedimentation trials.

4

EFFECTS OF EPISODIC SEDIMENTATION ON THE NET-SPINNING CADDISFLIES *HYDROPSYCHE BETTENI* AND *CERATOPSYCHE SPARNA* (TRICHOPTERA: HYDROPSYCHIDAE)

Abstract. Net-spinning caddisflies often thrive in the heavily sedimented waters of midwestern agricultural catchments despite the presumed costs of sedimentation-induced gill- and net-fouling. We conducted a laboratory experiment to determine whether larval growth and survival of two mid-Michigan Hydropsychidae species (*Hydropsyche betteni* and *Ceratopsyche sparna*) are affected by daily exposure to high levels of sedimentation. Larvae of both species had a decreased likelihood of survival in sedimentation treatments relative to controls and taxa were differentially affected as *H. betteni* significantly outperformed *C. sparna*. Sedimentation did not alter the relative growth rate of either species although slight losses by *H. betteni* and gains by *C. sparna* produced significant differences in relative growth rates between species.

INTRODUCTION

Sedimentation to North American streams, most of which is human generated (Waters 1995), is widely believed to harm stream-dwelling organisms through the effects of increased deposition and transport of sediments (Newcombe and MacDonald 1991, Waters 1995). High levels of sediment deposition and suspension have been demonstrated to negatively affect several game-fish species (principally salmonids) by burying eggs and fouling gills (Newcombe and MacDonald 1991; Sevizi and Martens 1991, 1992; MacDonald and Newcombe 1993; Waters 1995). The situation is not as clear, however, for the often numerically (Hynes 1970) and energetically dominant (Waters 1984) animals that comprise benthic invertebrate communities. In fact, the abundance of many benthic invertebrates typically increases in response to heavy sedimentation (Hamilton 1961, Hynes 1966, Gammon 1970, Learner et al. 1971, Nuttall and Bielby 1973, Waters 1995).

Invertebrate abundance increases that result from high levels of sediment deposition are typically experienced by relatively small, burrowing species adapted to exploit deposits of fine-particulate organic material. The conditions that favor these burrowing organisms often result in the exclusion of species that require solid substrata. Loss of the relatively large animals that inhabit exposed benthic habitat often results in overall invertebrate biomass declines (Waters 1995). Further biomass reductions also typically follow exclusion of exposed-substrata inhabitants as a result of secondary productivity declines in insectivorous fish populations (Tait et al. 1994).

Extremely high levels of sedimentation that result from acute disturbances, such as streambed-suction mining (Thomas 1985), riparian clearcutting (Webster et al. 1992), and road construction (King and Ball 1967) commonly have large, but impermanent effects on benthic communities. However, there is of yet only limited understanding of the effects of chronic sedimentation at levels moderate enough to increase suspended-solid concentration but preclude total habitat transformation through substrata burial (Waters 1995).

In this study, a presumably agricultural-pollution tolerant species (*Hydropsyche betteni*) and a relatively intolerant species (*Ceratopsyche sparna*) (as determined by Schmude and Hilsenhoff 1986) were exposed to daily episodes of heavy sedimentation to determine: (1) whether larval growth and survivorship are affected by episodic sedimentation (Fleischner 1994, Waters 1995), and (2) whether taxa would perform differentially as predicted by present distribution patterns (Ross 1944, Schmude and Hilsenhoff 1986).

Effects of sedimentation on filter-feeders

Invertebrate species are known to be differentially affected by fluctuations in suspended sediment concentration. For example, Culp et al. (1986) found that sedimentation-mediated drift response was most pronounced in invertebrates that inhabit exposed substrata surfaces. Invertebrates are also expected to differ in response to suspended sediments as a result of relative exposure as dictated by feeding strategy. Due to their near uniform reliance on the availability of stable substrata, filter-feeding invertebrates are suspected to be particularily sensitive to suspended-sediment increases (Hynes 1973). However, little evidence has been presented in support of this widely held view (Waters 1995).

Filter feeders that utilize morphological filtration structures are apparently particularily sensitive to suspended sediment increases. For example, unionid clams (Aldridge et al. 1987), and cladocerans (McCabe and O'Brien 1983) are known to experience feeding limitation when exposed to high levels of suspended sediment. However, filter feeders that utilize external structures such as hydropsychid nets may not be as hindered by high levels of suspended sediment as are those that feed with anatomical filtration structures.

Some Hydropsychidae species occupy both high- and low-sediment environments and are therefore potentially unaffected by moderate to heavy sedimentation (Schmude and Hilsenhoff 1986). Learner et al. (1971) reported that *Hydropsyche pellucidula* larvae in clean reaches of a U.K. stream were much larger than conspecifics in a reach receiving suspended solids from coal-mining operations. They concluded that development was delayed by sedimentation. However, because this hypothesis was not, and has not been tested (Waters 1995), it remains unknown if larvae in high-sedimentation environments grow, survive, and reproduce at rates similar to those in optimal habitat such as the low-sediment environment below many impoundments (Fremling 1960).

Hydropsychidae nets trap sediment as well as a wide array of potential food items (Wallace and Sherberger 1974, 1975, Wallace and Merritt 1980). It thus seems probable that as sedimentation increases, nets require more maintenance and frequent replacement. The result of higher net-maintenance costs may be the expenditure of energy that would otherwise be used for respiration and growth. In addition, because silk production requires expenditure of lipid reserves critical to adult reproductive success (Wallace and Malas 1976, Petersson and Hasselrot 1994), more-frequent net replacement may affect caddisfly fitness.

METHODS

Microcosms

Four 45-l aquaria were fitted with stream-flow simulators (BioQuip Products, Pasadena, CA) and surface-sanitized with 70% ethanol. A 10 x 10 x 40 cm, split-face concrete block, 5 g of ponderosa pine needles (used for retreat construction), 2 Kg aquarium sand, 1 Kg gravel, and 8.5 l stream water were added to each tank. All substrata were autoclave sterilized. An air compressor was used to generate flow. Water was allowed to circulate for 10 days prior to larval hydropsychid introduction in order to allow time for the current to create nearly uniform bed morphology between tanks.

Caddisflies

Final-instar (=fifth instar) *Hydropsyche betteni* and *Ceratopsyche sparna* (as determined by keys in Schmude and Hilsenhoff 1986) were collected from rocks removed from two second-order streams that flow through a combination of mid-Michigan agricultural and residential land (*H. betteni*: 21 November, 1994, Prairie Creek, Ionia Co., 43°N, 85°W; *C. sparna* 19 November,1994, Flint River, Lapierre, Co., 43°N, 83° 15'W). Larvae were allowed to acclimate to tank temperature (mean = 20°C) from field-collection temperatures of (5°C) before they were introduced into tanks. Net-spinning activity of both species has been determined to be maximal in 20°C water (Fuller and Mackay 1980). Twenty-five individuals of each species were added to each tank.

Larvae were fed a daily diet comprised of 0.5 g powdered Tetra Min™ staple food and 0.1 g Red Jungle Brand™ Micro-food. Larvae of both species were observed feeding on this diet. Feeding was continued for two days following termination of sedimentation episodes to allow the passage of inorganic material so as to avoid nonfood items from affecting final weights.

Surviving larvae were placed in 1.5 ml vials, stored at -20°C, thawed, identified, cleansed of debris for 1 minute in a sonic cleaner, dried for 24 hours at 65°C, and weighed on a microbalance. Relative growth rate of each larva was determined with the equation:

RGR = (ln final mass - ln mean initial mass)/ time (days in captivity)

Mean initial mass values were derived from measurements of a representative sample of each taxa (*H. betteni* n=24, *C. sparna* n=21) which were frozen upon collection to be dried and weighed with the experimental animals.

Sediments

Sediment additions were initiated on 26 November, 1996 after all larvae had positioned themselves and constructed retreats. Sediment was collected from a bank deposit near the *H. betteni* collection site. Sediments were autoclave sterilized for one hour, thoroughly dried at 65°C, and sieved through a 0.6 mm-mesh sieve. Particle size array and chemical composition were determined by the Michigan State University Plant Nutrient Laboratory (see Table 1).

Two tanks were randomly chosen to receive daily sedimentation. Each day (16 total), 11 g of sediment were added to experimental microcosms. The initial turbidity (mean = 23 nephelometric turbidity units (NTU)) is considered to be sufficient, if sustained, to cause adverse, but sub-lethal effects on benthic invertebrates such as reduced growth or forced abandonment (Newcombe and MacDonald 1991, MacDonald and Newcombe 1993).

Suspended-solid level was measured with a Hach 2100 A NTU meter. NTU measurements were taken before each trial and several times throughout the first three hours after the onset of trials, after which levels in sediment-treatment tanks approximated those in control tanks (Figure 1).

Abiotic conditions

Measurements of water temperature and pH were taken daily. These parameters did not vary between tanks more than the level of accuracy of the meters (± 1°C, 0.5 pH) (mean temperature = 20.8°C, mean pH = 8.5). Current velocity was calibrated between tanks with a digital flow meter and was set to generate moderately turbid flow that did not sweep away larvae crawling on exposed substrata. Velocity 5 cm above retreats was ≈5 cm/second.

Statistical analyses

An ANOVA model was used to test the full interaction of the effects of species (two species), tank (4 tanks), and sediment level (two levels) on relative growth rate (see Table 2). Survival-rate data were analyzed with a contingency analysis model (CATMOD procedure, SAS 1990) that tested the same interaction of effects (see Table 3). Survivorship data were analyzed with and without pupae. The addition of pupae to the analysis of survivorship did not meaningfully affect treatment effects (Appendix 1) and is therefore excluded from reported values.

RESULTS

Relative growth rate

Sediment treatments had no effect on the relative growth rate of either species (Table 2, Figure 2). On average, *C. sparna* grew and *H. betteni* lost mass in sediment treatments and controls (*C. sparna*: 0.061 vs 0.059 mg dry mass gained per day and *H. betteni*: 0.061 vs 0.024 mg dry mass lost per day in control and sediment treatments respectively) (Figure 2). This interspecific difference is highly significant (Table 2).

Survival

Both species suffered higher mortality in sediment treatments than in controls, and as was the case in relative growth rate measurements, taxa were differentially affected (Table 3, Figure 3). In contrast to the interspecific trend detected in relative growth rates, *H. betteni* vastly outperformed *C. sparna* (Table 3, Figure 3). There was no intraspecific, inter-tank variation with the exception of *H. betteni* in control tanks which differed by only one survivor.

Individuals of each species pupated in both treatments (n = 2 *H. betteni*, 3 *C. sparna*) prior to completion of the trial. One pupa of undetermined species was consumed by accidentally introduced, larval Chironomidae (*Eukiefferiella* sp.), a phenomenon also observed in microcosms by Rutherford (1986) and in nature by Rutherford and Mackay (1986).

DISCUSSION

Intraspecific effects

Sediments were added at a level predicted to cause sub-lethal effects such as reduced growth or behavioral avoidance (*sensu* Newcombe and MacDonald 1991). However, although the mode of action is unclear, sediment treatments were lethal to a proportion of experimental populations of both species (Table 3, Figure 3). The two most-often posited deadly effects of high levels of sedimentation are critically lowered resilience to suspended solids and enhanced lethality caused by substrata burial (Waters 1995). Entrainment in thick deposits of sediment is known to be lethal to benthic invertebrates, but only when heavy sedimentation is prolonged enough to completely bury substrata (Thomas 1985) or when immobile forms like hydropsychid pupae are buried and ultimately suffocate (Rutherford and Mackay 1986). Either scenario occurring in a microcosm can be interpreted as representative of potentially negative effects on natural populations, but certainly not as absolutely lethal ones in habitats where successful behavioral avoidance is possible.

It is also possible that each microcosm could, perhaps because of spatial limitation, only support 22 - 23 *H. betteni* and 10 *C. sparna* (as in control tanks) and, through habitat denudation, sediment treatments reduced capacity to 15 *H. betteni* and 8 *C. sparna* (as in both sediment tanks). Habitat simplification through substrata burial is known to cause eventual declines in benthic invertebrate populations (e.g. Tarzwell 1938, Hamilton 1961, Nuttall and Bielby 1973); but as insects were stocked at a small fraction of field densities and many retreats were exposed and unoccupied at the termination of the 16-day experiment, burial seems unlikely to have been the only cause of larval death.

Relative growth rates were similar intraspecifically and across treatments suggesting that surviving larvae were apparently unaffected by sedimentation (Table 2, Figure 2). Nets were observed to be clogged with sediment after exposure and were cleaned or replaced prior to the onset of the next trial. It seems reasonable, therefore, to presume that conditions in the sediment-treatment tanks required higher net maintenance costs relative to those in controls . However, because sediment treatments had no effect on relative growth rates (Figure 2), net maintenance costs over 16 days were probably negligible for survivors of sediment treatments. The possibility does exists that younger larvae would have responded differently due their typically higher growth rates (Cudney and Wallace 1980, Mackay 1979, 1984) and net-spinning activity (Fuller and Mackay 1980). However, other indirect measurements of growth rate have revealed that final-instar hydropsychids do gain mass (Cuffney and Minshall 1981).

Interspecific effects

The expectation that *H. betteni* are more tolerant to sediment treatments than *C. sparna* (Schmude and Hilsenhoff 1986) was not corroborated by interspecific comparisons of relative growth rate and survivorship. Survivorship data suggest that larval mid-Michigan *H. betteni* are more manipulation-resistant than *C. sparna*, which may indicate higher general resistance which is also evidenced by their distribution in Wisconsin (Schmude and Hilsenhoff 1986). However, although captivity was more lethal for *C. sparna* larvae overall, survivors actually fared better than the average *H. betteni* larva which experienced mass loss.

The overall higher mortality incurred by experimental *C. sparna* populations could also have been in some way influenced by interspecific interactions, perhaps competition for high-quality retreat sites. Hydropsychid battles over retreat sites are common, and not surprisingly, the odds of intruder victory typically favor larger combatants (Jannsson and Vuoristo 1979). Therefore, because final-instar *H. betteni* are more than three times larger than final-instar *C. sparna* (Figure 2), the higher probability of winning battles over retreats may have influenced mortality in the spatially limited microcosm environments.

In his excellent review of the effects of sedimentation in streams, Waters (1995: 60) proclaimed that "on the basis of current knowledge, the direct effect of suspended sediment upon benthic invertebrates does not appear to be a significant influence upon stream invertebrate communities." Results from this study, as well as those presented in Chapter 3, indicate that some benthic invertebrates are sensitive to, and potentially harmed by, high levels of sediment in suspension. Although the effects of sedimentation on invertebrate community composition are typically more the result of sediment deposition than transport, additional stress inflicted on benthos by elevated suspended sediment levels may impose chronic, low-level stress and therefore have indirect effects upon invertebrate communities. Given the enormity of the problem, it is conceivable that almost every lotic invertebrate population has been exposed to sedimentation that resulted from human activities. It seems certain, therefore, that widespread and chronic sedimentation-enhancing activities such as overgrazing of cattle in small stream riparian areas, have in aggregate, immense ecological consequences.

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Table 1. Particle-size distribution and chemical composition of bank sediments used in sedimentation treatments.

Soil Type: Loam, pH 7.1

Mineral Component: 70.7%	Organic Component: 29.3%		
45.8 % Sand	Na	258	ppm
32.7 % Silt	Cl	620	ppm
21.4 % Clay	NO3	5.4	ppm
	NH4	74.7	ppm

Table 2. ANOVA results comparing relative growth rates of *Hydropsyche betteni* and *Certaopsyche sparna* in two sediment treatments and two controls (see Figure 2).

Source	df	MS	F	P
Species	1	0.011	80.900	0.0001
Sed. Level	1	0.000	0.051	0.8221
Species x Sed. Level	1	0.000	0.291	0.5907
Tank (Sed. Level)	2	0.000	0.295	0.7452
Species x Tank (Sed. Level)	2	0.000	1.968	0.1449
Error	103	0.000		

Table 3. Contingency analyses testing whether *Hydropsyche betteni* and *Ceratopsyche sparna* survival differed in sediment treatments and controls (two tanks each) (see Figure 3).

Source	df	x^2	P
Species	1	29.24	0.000
Sed. Level	1	9.54	0.002
Species x Sed. Level	1	4.38	0.036
Tank (Sed. Level)	2	0.16	0.923
Species x Tank (Sed. Level)	2	0.16	0.923

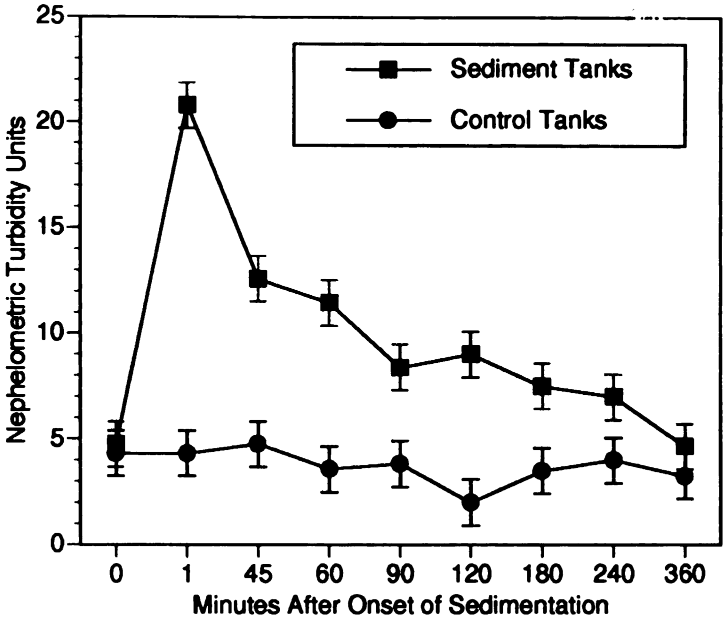

Figure 1. Mean NTU ± 1 se in two sediment- treatment and two control tanks.

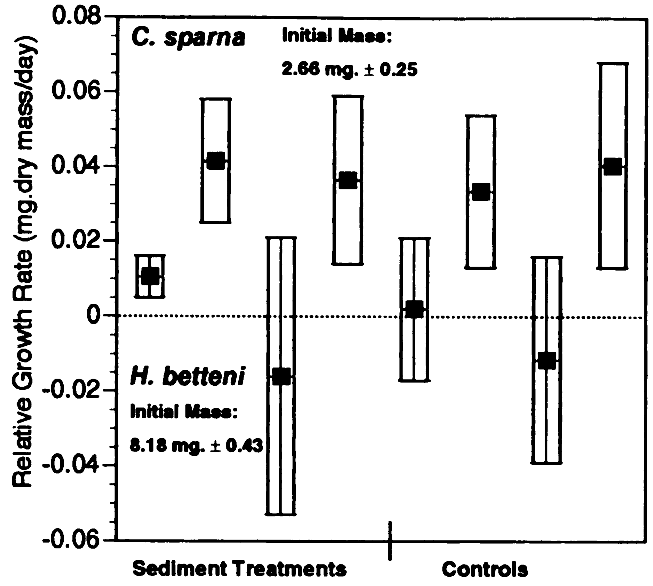

Figure 2. Box plots of mean RGR ± 1 SE of *Hydropsyche betteni* and *Ceratopsyche sparna* in two sedimented and two control tanks. Mean pre-trial dry mass (± 1 se) indicate relative size of fifth-instar *H. betteni* (n=24) and *C. sparna* (n=21).

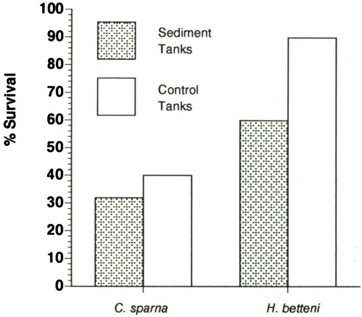

Figure. 3. Mean survivorship of larval *Ceratopsyche sparna* and *Hydropsyche betteni* in two sedimented and two control tanks. Standard error = 0.000 for all but *H. betteni* control which is 0.020.

Appendix 1. Contingency analyses testing whether *Hydropsyche betteni* and *Ceratopsyche sparna* survival differed in sediment treatments and controls with pupae included (see Table 3).

Source	df	x^2	P
Species	1	34.84	0.001
Sed. Level	1	6.76	0.000
Species x Sed. Level	1	3.86	0.049
Tank (Sed. Level)	2	0.32	0.850
Species x Tank (Sed. Level)	2	0.32	0.850

APPENDIX 1

APPENDIX 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1996-8

Title of thesis or dissertation (or other research projects):

Some effects of riparian habitat alteration on lotic invertebrate ecology

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name (s) (typed)

Roger Malcolm Strand

Date 17 September, 1996

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original:	Include as Appendix 1 in ribbon copy of thesis or dissertation.
Copies:	Included as Appendix 1 in copies of thesis or dissertation. Museum(s) files. Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX 1.1

APPENDIX 1.1

Voucher Specimen Data

Page 1 of 1 Pages

Number of:	Museum where deposited	Entomology Museum, Michigan State University (MSU)
	Other	
	Adults ♂	
	Adults ♀	
	Pupae	
	Nymphs	3 (P.media)
	Larvae	4 (C.sparna), 5 (H.betteni)
	Eggs	

Species or other taxon	Label data for specimens collected or used and deposited
Paragnetina media (Walker)	MI: Ionia Co.,Prairie Creek, 43°N, 85°W, 22-xi-1994
Ceratopsyche sparna (Ross)	MI: Lapeer Co., Flint River 43°N, 83° 15'W, 19-xi-1994
Hydropsyche betteni Ross	MI: Ionia Co.,Prairie Creek, 43°N, 85°W, 22-xi-1994

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Roger Malcolm Strand

Date 17 September, 1996

Voucher No. 1996-8

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

17 Sept 1996

Date