# *The Serial Discontinuity Concept and other Factors affecting the Diversity and Abundance of Ephemeroptera (Mayflies) in the Green River*

**by Tristan Leong**

## ABSTRACT

Modern society is vitally linked to its water resources for direct consumption as well as transportation, agriculture, recreation, and power generation. As a result, most major rivers in the United States have been impounded by human-made dams, which alter a river's dynamic natural processes, also called "natural flow regime." Changes to a river's natural flow regime may dramatically affect its geologic integrity, biotic community, and ecosystem function.

Consequently, many have proposed guidelines to assist river conservation and restoration efforts to reproduce a river's natural dynamic character. (Poff et. al1997) Still others such as Stanford and Ward (2001) suggest that riverine processes and function will eventually recover downstream from a point of disturbance with the natural addition of tributary inputs, as described by their Serial Discontinuity Concept. A major contention to this argument however is that, rivers are characteristically dynamic entities, influenced by many factors, and rarely exist entirely within the framework of either the SDC or other ecological theories we describe. Consequently, ecologists and geomorphologists such as Stanford and Ward, are constantly updating their theories in order to "better describe" the functioning of these dynamic river ecosystems.

While the Serial Discontinuity Concept has been discredited in some cases (Powell et. al 2005), it may help provide the framework for accurately describing some riverrine phenomena, such as the assessment of lower level invertebrate communities. For example, when examining aquatic communities such as those found in the Green River of Utah and Colorado, Stanford and Ward described downstream trending improvements found by Mark Vinson (2001), which showed an increased aquatic invertebrate diversity downstream from a major impoundment. This dataset appears to show a strong association with the SDC theory because aquatic invertebrate communities replenish diversity downstream. It is the purpose of this paper to closely analyze this dataset in order to examine the original SDC as it pertains to predictions concerning the effects on aquatic invertebrate communities. In doing so, this paper focuses on how aquatic

invertebrates can be used as measures of biotic change, with specific emphasis on Green River mayflies.

## INTRODUCTION: WHY MAYFLIES & THE GREEN RIVER?

For the past 40 years, the Flaming Gorge Dam has dramatically altered the environment of the Green River Utah. This once highly seasonal tributary to the greater Colorado River is now greatly impeded by this dam, which has caused a precipitous decline in many species of native fish, insects, and remarkable alteration in its riparian community. Nowhere is this more evident than in the reach from the immediate tail-waters below Flaming Gorge Dam to Brown's Park, where the aquatic invertebrate community has been radically changed, resulting in a marked reduction of the diversity of insects, specifically mayflies. Possible reasons for this dramatic decline in the diversity of the aquatic invertebrate community include 1) habitat alteration and loss 2) loss of important food inputs, 3) increased competition from amphipods and New Zealand Mudsnails, 4) increased predation risk by non-native trout, and lastly 5) other anthropogenic water management issues not related to the dam operation, such as the poisoning of the river in the mid 1960's by the Utah Fish and Game. Because the Green River has had an established long-term invertebrate dataset, studying the effects of regulation on its aquatic community provides an excellent opportunity for further study. But why use mayflies exclusively for this analysis?

Mayflies are an important order of insects for biomonitoring, or "the systematic use of living organisms and their responses to determine the quality of the aquatic environment." (Merrit & Cummins 1996) Many biotic indices use mayflies as a key indicator species, such as those described in Hilsenhoff (1988) in determining the degree of organic pollution or disturbance. Due to their biology, mayflies generally require cool, clean, well-oxygenated water to move over their gills in order to respire, and are therefore considered reasonable indicators of the relative amount of dissolved oxygen in a system.

For the Green River, however this aspect is less important due to its desert environment, where dissolved oxygen would be ordinarily low because the higher water temperature, relative to non-desert streams, would decrease oxygen carrying capacity, and because the river consistently dried during long periods of drought and small influxes of water. Ironically with the advent of the dam, there is now a higher dissolved oxygen concentration in the river's water due to the Flaming Gorge's ability to supersaturate oxygen in the system, though surprisingly this change seemed to have little effect on mayfly diversity or abundance.

The Green River mayfly ecology has been well studied. Originally described by Edmunds and Musser in 1960 as "extremely plentiful, with 30 species, and one of the most diverse assemblages worldwide," the Green appears to have one of the most robust records in the United States for mayflies and aquatic invertebrate assemblages' pre- and post-construction of a dam. Therefore, in assessing the relative ability of the Green River to restore its biotic community downstream of Flaming Gorge dam, one can use mayflies as a fairly accurate proxy measure for the aquatic invertebrate community because A) they are well studied for the Green River system, B) they are found throughout the system, C) they have well understood responses to disturbances, more so than most other aquatic insects, and D) they are key components in most well-known biotic indices. Before we move on to the analysis however, we must look into other reasons that may have affected the current assemblage of mayflies present in the river, along with understanding a little about their life history.

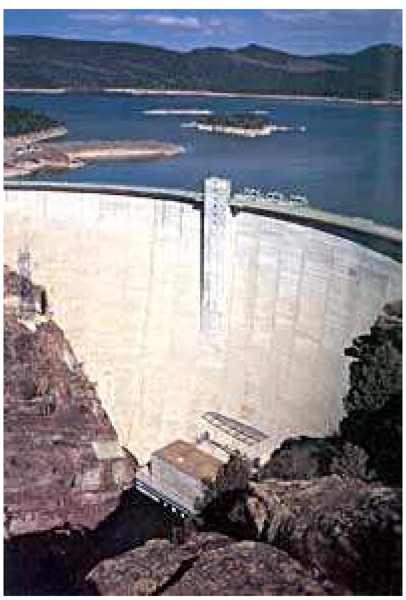

**Figure 1**. Flaming Gorge Dam on the Green River
www.wildlife.utah.gov/fishing/flaming_gorge.html

## MAYFLY LIFE HISTORY

All mayflies belong to the order of insects: Ephemeroptera, of which there are 19 families recognized throughout the world. Mayflies are described as hemimetabolous insects, in that the larvae undergo a metamorphosis which lacks a pupal stage. They can be distinguished in both juvenile and adults forms by either possessing three tails at the end of the abdomen (occasionally they may only have two tails), having only one claw at the end of their tarsi, or by the presence of gills on their abdomen (larvae only). Adults have two pairs of wings, with their hind wings reduced.

The beginning of the mayfly lifecycle starts with female mayflies, which deposit eggs on the water's surface, drop clusters of eggs from the air, and in some cases crawl back under that water to attach eggs to the substrate (Merritt & Cummins 1996). The eggs often mature after a few weeks, though a number of species are known to delay hatching, or be dependent on specific water temperatures for egg development (Edmunds & Waltz 1996). After hatching, the larvae grow for as short as 14 days to up to 3-4 years to adulthood, depending upon the habitat. Most species develop within a year's time. As they grow, larval mayflies must molt or "shed their outer skin." Mayflies are known to go through many instars or "developmental cycles" between molting.

Generally, mayfly larvae feed by collecting or scraping algae and detritus from the substrate, though some feed on aquatic macrophytes and a small percentage may occasionally prey upon other small organisms (Lawler 2006). Mayflies as a whole exhibit a wide variation in dietary preferences. Thus, in order to better understand mayfly food-web relationships, ecologists now use the "functional feeding group" approach, which merely attempts to classify organisms (especially insects) to their role in processing fine or coarse organic matter. These functional feeding groups depend highly on the individual family of mayflies to which they belong, as many exhibit various feeding strategies and habitat preferences (Figure3).

As the larvae develop, the later instars begin to take on similar characteristics to their adult forms. Sexual organs may develop, along with wings or wing pads that will eventually enable the insect to leave the aquatic medium and complete its lifecycle. When the conditions are favorable, the larvae swim, float, or crawl to the surface of the water where they break free of their larval exoskeleton, unfold their wings, and fly away. At this point in its lifecycle, the mayflies are referred to as subimagos.

Subimagos are an intermediary stage in the adult lifecycle. For the most part subimagos are sexually immature, though some species of mayflies exhibit female reproduction at the subimago stage (Lawler 2006). Differentiating between the two adult stages, the subimago and sexually mature imago, is fairly easy to identify as subimagos will appear darker, due to the hydrofuge hairs that cover their body and enable them to float more readily on the water's surface during their emergence. Additionally, subimago males may sometimes lack the proper placement of their sexual organs on their abdomen. After hatching from the water's surface subimagos find a suitable place to molt once more into the final stage of their lifecycle, the sexually mature imago.

Imago males after molting cluster together in swarms usually at sunrise or sunset to grasp onto imago females and reproduce. Once mated, females lay their eggs, and the adults die quite soon afterwards. The adult stage of the mayfly lifecycle is very short and can last for as little as a few hours to a couple of weeks (Edmunds & Waltz). Because of this shortened adult lifecycle, mayfly adults do not eat and lack mouthparts to feed.

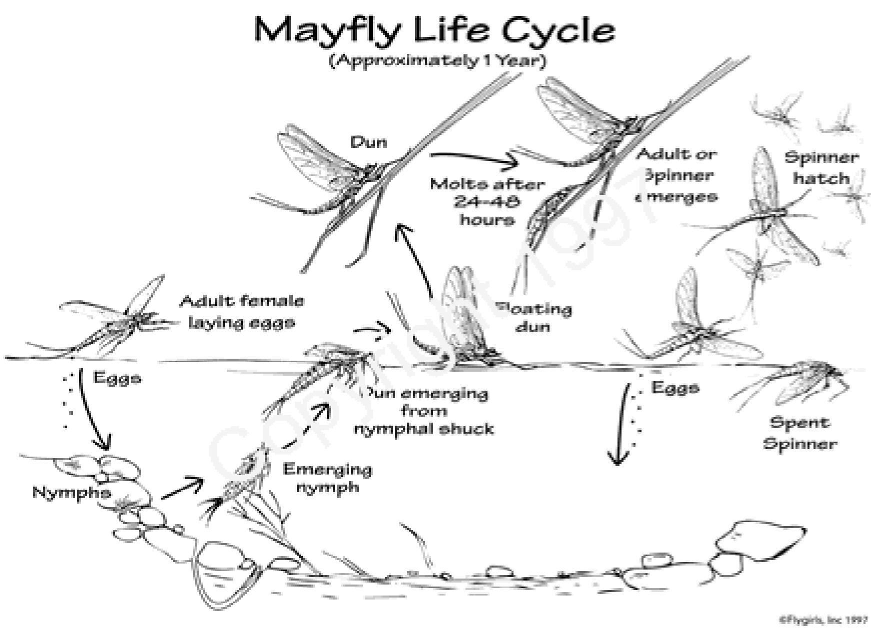


**Figure 2**. Mayfly Lifecycle
http://www.flytyingtools.com/webpages/mayflyArt.htm

| Taxa (Number of species in parentheses) | Habitat | Habit | Trophic |
|---|---|---|---|
| Acanthametropodidae | Lotic depositional (large rivers) | Swimmers, Clingers | Predators (engulfers) |
| Baetidae | Generally lotic erosional and depositional | Generally swimmers and clingers | Collectors, scrapers, gatherers |
| Heptageniidae | Lotic and Lentic erosional | Clingers | Scrapers & gatherers |
| Ephemerellidae | Lotic erosional, some depositional, a few in lentic vascular hydrophytes | Clingers, some sprawlers, and swimmers | Generally collectors of detritus, some scrapers, few shredders |

**Figure 3**. Ecological Data for Mayflies of North America (as reproduced from Merrit and Cummins 1996)

## PRE-DAM MAYFLY FAUNA

Prior to dam construction, the section now directly downstream of Flaming Gorge Dam supported a diverse and abundant mayfly fauna, which was adapted to the highly variable hydrology typical of Rocky Mountain Rivers. (Vinson 2001) Samples by previous studies suggest this section of the Green River was taxonomically rich, with over "30 species of mayflies collected at a single site (Edmunds & Musser 1969)." According to studies done by Edmunds (1969), Sessions (1963), Dibble (1967), Musser (1980), Pearson (1980) and others, and re-evaluated by Vinson, it is believed twenty five genera of mayflies once inhabited the reach between Red Creek and the dam. These genera include those listed in Figure 4 (see below). According to Vinson, this extreme diversity in mayflies for such a small area suggests that the Green River above Red Creek may even have supported a higher mayfly species richness, when compared to other mid-order, high-flux desert streams. Unfortunately, few pre-dam quantitative samples were collected to verify this theory.

| Taxa | Time period | | | |
|---|---|---|---|---|
| | <1962 | 1963–1967 | 1977–1981 | 1981–1999† |
| Ephemeroptera | | | | |
| Ameletidae | | | | |
| *Ameletus* | | | | DRC |
| Ametropodidae | | | | |
| *Ametropus albrighti* | U+D | | | |
| Baetidae | | | | |
| *Baetis* | U+D | U+D | U+D | U+D |
| *B. insignificans* | URC | | | |
| *B. tricaudatus* | | | | U+D |
| *Callibaetis* | U+D | | | |
| *Camelobaetidius warreni* | URC | | U+D | |
| *Cloeon* | | | | DRC |
| Caenidae | | | | |
| *Brachycercus* | U+D | | | |
| *Caenis* | URC | | DRC | |
| Ephemerellidae | | | | |
| *Attenella* | | | | DRC |
| *Drunella* | | | | DRC |
| *D. doddsi* | | | | DRC |
| *D. grandis* | | | | DRC |
| *D. spinifera* | | | | DRC |
| *Ephemerella* | | | | DRC |
| *E. grandis* | | | | DRC |
| *E. inermis* | U+D | | U+D | U+D |
| *E. infrequens* | | | | DRC |
| *Serratella levis* | | | | DRC |
| Ephemeridae | URC | URC | | |
| *Ephemera* | URC | | | |
| *Hexagenia limbata* | | | | DRC |
| *Pentagenia* | URC | | | |
| Heptageniidae | URC | U+D | | |
| *Cinygmula* | | | | DRC |
| *Epeorus* | | | | U+D |
| *E. albertae* | URC | | | |
| *E. longimanus* | | | | URC |
| *Heptagenia* | | | URC | DRC |
| *H. elegantula* | U+D | | | |
| *H. limbata* | URC | | | |
| *Rhithrogena* | | | U+D | DRC |
| *R. robusta* | | | | DRC |
| *R. undulata* | U+D | DRC | | |
| Isonychiidae | | | | |
| *Isonychia sicca campestris* | U+D | | | |
| Leptophlebiidae | | | | |
| *Choroterpes albiannulata* | U+D | | | |
| *Leptophlebia gavastella* | U+D | | | |
| *Paraleptophlebia* | | URC | DRC | DRC |
| *Traverella albertana* | U+D | | | DRC |
| Oligoneuriidae | | | | |
| *Lachlania powelli* | U+D | | | |
| Polymitarcyidae | | | | |
| *Ephoron album* | U+D | | | DRC |
| Pseudironidae | | | | |
| *Pseudiron* | U+D | | | |
| Siphlonuridae | | | | |
| *Siphlonurus* | URC | | | |
| Tricorythidae | | | | |
| *Leptohyphes* | | | | DRC |
| *Tricorythodes minutus* | U+D | DRC | DRC | U+D |

**Figure 4**. Historic Mayfly Abundance on the Green River (from Vinson 2001)

## POST-DAM CONDITIONS

Once completed, Flaming Gorge Dam affected the hydrology of the Green River nearly overnight. Daily discharge declined significantly ranging from >300cubic meters/sec maximum daily flows to less then 140cubic meters/sec, and increasing minimum flows to 20cubic meters/sec from <10cubic meters/sec with no yearly consistency (Vinson 2001). Yearly flooding occurring most often during mid-June associated with snow-melt runoff, ceased almost entirely (Schmidt 2006). Average water temperatures below the dam dropped, were typically cooler throughout the year, and varied little with maximums reaching the range of 8-10°C and minimums reaching. 3-4.5°C (Vinson 2001). Daily sediment transport and bed particle movements declined (Schmidt 2006). As a result, fine sediment deposits were all but eliminated from this reach of the river, and the clarity of the water increased, allowing the establishment of the bryophyte *Amblystegium,* and the green algae *Chara* and *Cladophora* on top of most of the substrate (Vinson 2001). (See Figure 5 below)

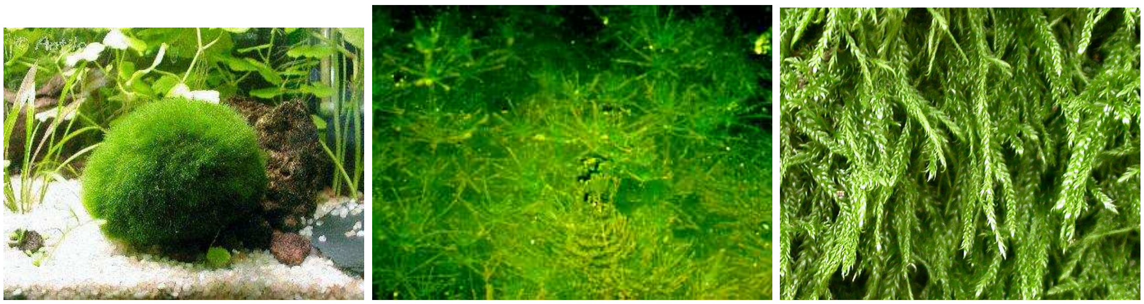

**Figure 5**. Established bryophytes and green algae of the Green River.

| Cladophora- Green Algae | Chara- Green Algae | Amblystegium- Bryophyte |
|---|---|---|
| www.antilo.com | www.okstate.edu | www.waarneming.nl |

In response to all of these dramatic changes, mayflies and other aquatic invertebrates began to decline in diversity and relative abundance below the dam, which is discussed in the section below. This perturbation of the Green River tail-water environment following the Dam's closure is characteristic of the types of deleterious effects dams can have on aquatic ecosystem. Data for the system shows a decline from nearly 30 species to 1 common species, *Baetis tricaudatus* (Vinson 2001). Though on occasion, two other somewhat rare species were also observed, *Emphemerella inermis* and *Paraleptophlebia palipes* (Vinson 2001).

Subsequent follow-up studies have demonstrated that the river is continuously changing since Vinson's original sampling of invertebrate diversity. Up until very recently, mayfly diversity and abundance seemed to be decreasing, marked by important macroinvertebrate faunal shifts over a 40 year timeframe. (See Figure 6) Overall, however, Vinson has found a higher diversity in aquatic invertebrate life including mayflies, progressing downstream. In some cases he describes that one may even be able to find "rare and unique taxa that exemplify an unregulated Colorado River Basin," further downstream. (2006)

Although certainly a major influence on the mass extinction of mayflies from this reach of the Green River, Flaming Gorge Dam was probably only one of many historically significant reasons. In addition to the alteration of downstream habitat by Flaming Gorge Dam, other contributing factors, are believed to have also led to the demise of Green River mayfly diversity. These factors include, increased competition from amphipods and New Zealand Mudsnails, increased predation by non-native trout, and other anthropogenic water management issues not related to the dam operation, such as the poisoning of the river in the mid 1960's by Utah Fish and Game.  Their effects are explored below, along with those associated directly with the dam.

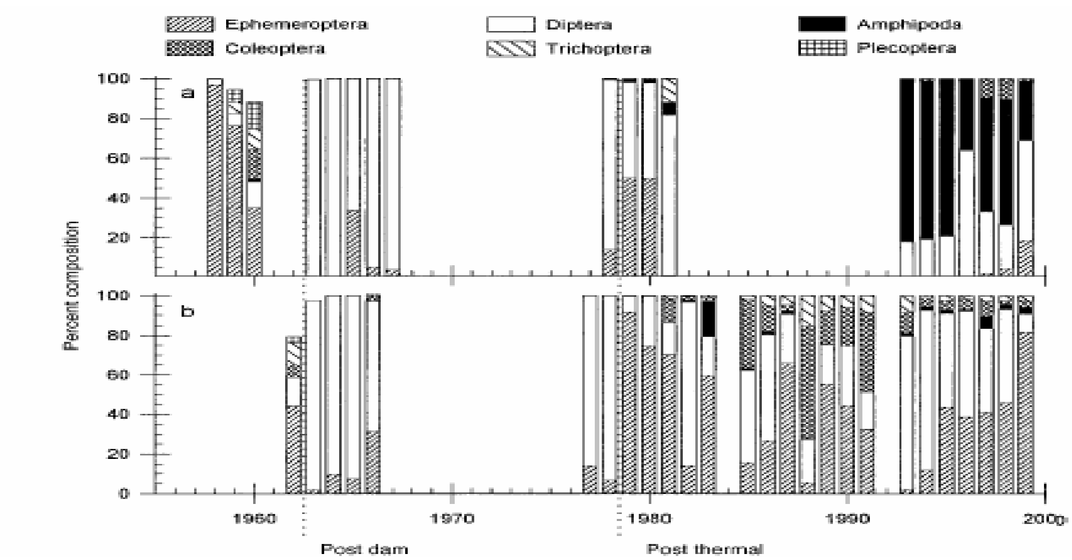


**Figure 6**. Large Scale Faunal Shifts in the Invertebrate Community of the Green River for the past 40 years (from Vinson 2001)

**Direct Dam Consequences**

With its inception, Flaming Gorge Dam immediately reduced coarse particulate organic material to the upper reach of the river. This likely had a deleterious effect on the functional feeding groups of mayflies, which rely heavily on shredding and collecting leaf litter and larger bits of organic material. This phenomenon is well documented for the Colorado River system where, a shift in the base of the food web associated with autumn inputs of leaves and detritus to spring algae blooms may account for a reduction of heptangeniid mayflies, stoneflies, and shredders in a regulated site (Rader 1988). In addition, the covering of the substrate by aquatic macro-algae drastically changed the base of the food web for this upper river section.

Secondarily, the operation of the dam decreased temperature variability of the water downstream (Vinson 2001). By limiting the proper environmental cues such as diurnal temperature rhythms, mayfly emergence and reproduction would likely have been significantly hindered. Sweeny (1978) found, that a reduction in water temperatures had a direct correlation in lowering the fecundity of the mayfly *Isonychia bicolor*. A reduction in the average water temperature below the dam may also have delayed egg development, and slowed the growth of larvae by reducing their metabolic rates.

Lastly, by reducing the input of fine sediment to the area immediately downstream, the dam would almost certainly limit the available habitat utilized by many of the specialized burrowing and sprawling type mayflies, which were once found in abundance. As a result, these mayflies, which relied on the large sandy depositional zones, can no longer be found in this particular stretch of the river, though they appear elsewhere in the system. (Figure 7)

| | | | | |
|---|---|---|---|---|
| ***Families Represented in Both Reaches*** | | | | |
| Baetidae | Universal | Swimmer, clinger | Collectors + gatherers | Both |
| Tricorythidae | Lotic- Depositional | Clinger & sprawler | Collectors + gatherers | Both |
| ***Families Found only Downstream of Red Creek After Dam Implementation*** | | | | |
| Ameletidae | Lotic- Erosional/Depositional | Swimmers, clingers | Scrapers, collectors, gatherers | DRC |
| Emphemerellidae | Lotic- Erosional/Depositional | Clinger | Collector, shredder, gatherer | DRC |
| Heptageniidae | Lotic- Erosional | Clinger | Scrapers, collectors, gatherers | DRC |
| Polymitarcyidae | Lotic- Erosional/Depositional | Burrower | Collector, gatherer, filterer | DRC |
| ***Families No longer Found*** | | | | |
| Ametropodidae | Lotic- Depositional in large river with gravel/sand | Burrower | Collector + filterer | NLF |
| Caenidae | Lotic- Depositional | Sprawler | Collects and gathers detritus | NLF |
| Isonychiidae | Lotic- Erosional | Swimmer + Clinger | Collector, filterers | NLF |
| Oligoneuriidae | Lotic- Depositional in large rivers | Burrower | Collector, filterer of filamentous algae from current | NLF |
| Pseudironidae | Lotic- Depositional in large rivers with sand | Sprawler | Predator (uses vortices to search for prey) | NLF |
| Siphlonuridae | Lotic- Depositional | Swimmer & climber | Collector, gatherer, predator | NLF |

**Figure 7**. Historic Green River Mayfly diversity according to their functional feeding groups and known locations, as reproduced from Vinson with the aid of Merrit and Cummins. NLF= No longer found in the river below Flaming Gorge Dam and below Red Creek. DRC= found downstream of Red Creek. Both= found in both sections downstream of the dam, and downstream of Red Creek.

# OTHER FACTORS WHICH MAY INFLUENCE MAYFLY DISTRIBUTION AND DIVERSITY

### Rotenone Treatment of the Green River

After dam completion, rotenone was applied to the Green River system. According to a study by Binns (1967), it had a devastating effect on all aquatic life throughout the river. Not much however is described with specific reference to mayflies.

### *H. Azteca G. Lacustris* Competition

Following dam closure major shifts in the relative abundance of the major taxon groups were reported (Vinson 2001). During the years 1963-1967, dipterans (flies) accounted for roughly 90% of the taxon composition, while mayflies, primarily *Baetis tricaudatus* accounted for the other 10% (Vinson 2001). Afterwards however, the dipterans lost ground to *Gammarus lacustris*, an amphipod, which migrated from cold springs downstream, but then eventually was overshadowed by another amphipod *Hyalella azteca* during the 1990s (Vinson 2001). (See Figure 9) Now so abundant as to comprise approximately 61% of the total individuals present below the dam, *H. azteca* appears to compete with mayflies for habitat and food. (See Figure 8) It is also believed to prey on the eggs of mayflies.

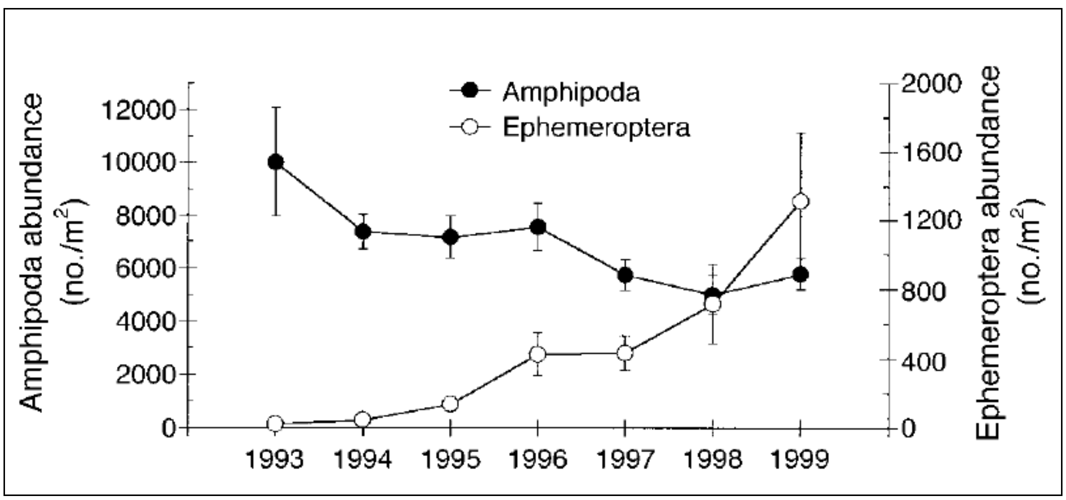


**Figure 8**. Amphipod Abundance During the 1990s (from Vinson 2001)


**Figure 9**. Amphipod Hyallela azteca. www.h-nds.de

### Introduction of Non-Native Trout to the Green River System

Once the conditions became suitable, anglers and the Utah Department of Fish and Game began to stock and manage the Green River below the dam as a blue ribbon trout fishery. These trout competed with other native fish, such as the humpback chub, for food. Their direct effect on the diversity of mayflies within Green River is unknown, though trout are know to be voracious predators on mayfly larvae and adults. In some cases trout may induce behavioral patterns in mayflies that may eventually limit their abundance. Forrester (1994) found trout "caused increased drift in some baetis mayflies," which might explain why mayflies are found in greater abundance downstream from the dam. Additionally, the presence of trout may force mayflies under the substrate, which would reduce their appearance in certain sampling methods. Overall, it is difficult to quantify how limiting trout are on the mayflies of the Green River, since many times both trout and mayflies coexist. In some cases trout can be seen as a significant impediment to mayfly growth and production, though many studies show trout may not be as limiting as once believed. Whatever the case may be, the Green River supports an extremely high density of trout (nearly 22,000 fish per square mile) in the region below the dam. Mayfly diversity and abundance is increased downstream of Red Creek, where trout are less abundant. This fact suggest that the increased presence of trout may have affected mayfly ecology below the dam.

### The Introduction of New Zealand Mudsnail

NZMS or New Zealand Mudsnails are Hydrobiid snails native to New Zealand. (Vinson 2004) They are believed to have been accidentally introduced into the Green River below

Flaming Gorge Dam by unknowing fishermen, who had snails attached to gear. After their discovery in 2001, they spread rapidly throughout this stretch of the Green River, as they can reproduce asexually up to 6 times per year. (Vinson 2004) According to Vinson, abundance was correlated highest in stretches of the river with slow water velocity and abundant aquatic vegetation. Where they are most numerous, they can reach densities of up to 100,000 per square meter, and significantly reduce the algal biomass of a river system. As a result, they affect mayflies in this region by direct competition for resources, along with the rest of the native fauna. (Vinson 2004)

## CONCLUSION

Many factors have contributed to the decline in mayfly and other aquatic invertebrate diversity directly below the dam. Due to the abiotic changes brought forth through dam operation, the stocking of trout, recent invasions of NZMS and arthropods, and rotenone poisoning of the river in the mid 1960's, the Green River has seen a dramatic reduction in aquatic invertebrate diversity downstream of Flaming Gorge Dam. In particular mayfly, diversity and abundance has been reduced immediately below the dam.

On the other hand, mayfly diversity and abundance increased downstream. While these complex interactions are not easy to understand, it appears reasonable based on the Serial Discontinuity Concept, to suggest that, in the case of the Green River, the ecological integrity of the river improves downstream. Using mayflies as an ecological indicator, they appear in relatively low diversity below the dam, and reappear downstream in much larger diversity as tributaries bring changes to the aquatic environment. Thus, the SDC appears to be valid theory to link the abiotic river functioning and riverine integrity with the aquatic invertebrate community of the Green River.

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