Anthropogenic alteration of invertebrate assemblages of the Green River downstream of Flaming Gorge Dam

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ABSTRACT

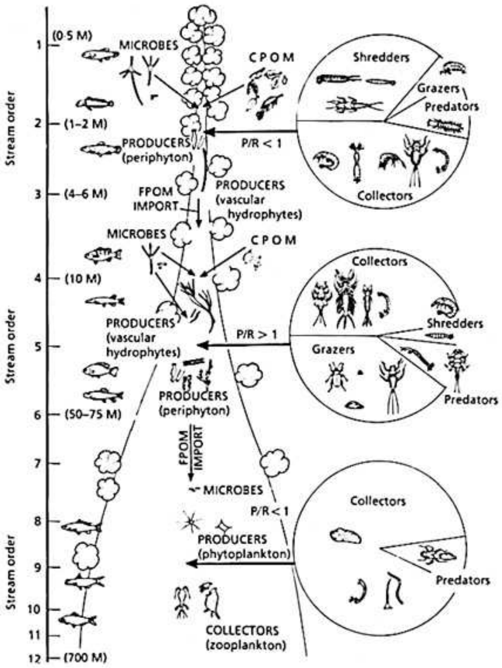
The ecological patterns and processes occurring in many rivers and streams have been drastically altered by human activities. Along with the changing hydrologic regimes and altered geomorphology caused by dam building and water diversions, the introduction of toxins and non-indigenous species can significantly alter patterns of diversity and abundance of macroinvertebrate assemblages. I begin this paper by reviewing general theory on the ecology of rivers. I then address the ways in which alteration of flow and establishment of invasive species can change aquatic invertebrate assemblages in general. I then focus more specifically on the Green River, particularly the effects of rotenone poisoning and the closure of Flaming Gorge Dam on aquatic invertebrate communities in reaches of the Green River downstream of the dam. Finally, I discuss the recent establishment of the invasive New Zealand mud snail immediately downstream of the dam and possible implications for the entire aquatic food web.

INTRODUCTION

Humans have drastically altered rivers and their watersheds through changes in land use, water storage and diversion, pollution, and introduction of non-native animals and plants. While humans have been building dams for thousands of years to manage rivers and water supply, the largest dams have been built in the last century as technical expertise has grown. In the United States, only 42 high-quality, undammed rivers longer than 200 km remained as of 1990 (Poff and Hart 2002). Our ability to build dams has outpaced our knowledge about the effects of these dams on rivers and aquatic ecosystems. In recent decades however, studies of regulated rivers have produced countless empirical observations and several theoretical frameworks. General observations include a decrease in native aquatic and riparian biodiversity downstream of dams (Allan 1995) and an increase in the establishment of non-native species in regulated rivers where natural disturbance regimes are altered (Moyle and Light 1996, Marchetti and Moyle 2001, Bernardo et al. 2003). In this paper, I will focus on the impacts of rotenone poisioning, dam building and the subsequent establishment of non-native species on aquatic invertebrate communities, with particular attention to the reaches of the Green River downstream of Flaming Gorge Dam.

River Ecology

Aquatic invertebrates, which represent a vital link in the food web between primary producers and fish, are also intrinsically valuable and serve as good indicators of the state of aquatic ecosystems (Power et al. 1997). The river continuum concept (RCC) (Vannote et al. 1980) was an early attempt to describe patterns found in energy sources and benthic invertebrate functional feeding groups from the headwaters to mainstems of rivers (see fig. 1). In essence the RCC describes a change from allochthonous (out of stream) resources such as terrestrial tree litter in the headwaters, to autochthonous (in stream) production of resources downstream as benthic algae and then phytoplankton become dominant, along with fine particulate matter from upstream. The RCC predicts that shredding and collecting insects will dominate the biomass of benthic invertebrates in low order streams, with a shift to grazing and collecting taxa downstream where benthic algae is present, and finally to collectors that can gather fine particulate matter and suspended phytoplankton in wide, deep high order streams.



Although this model initially described continuous, longitudinal changes in the aquatic community, later work amended this theory to include the importance of lateral connectivity with floodplains (Junk et al. 1989), the quality of food resources (Thorp and Delong 1994), and tributary inputs (Benda et al. 2004).

Figure 1. The River Continuum Concept
http://ww2.sjc.edu/faculty_pages/cmorgan/WildandScenic/Lessons/LU_5/Continuum.jpg

With time and continued research, increasing levels of complexity and realism have been incorporated into our understanding of patterns in river ecosystems. Given that over 75,000 dams over two meters exist in the United States (Collier et al. 1996), few, if any, rivers actually represent a longitudinal continuum of physical and ecological processes and patterns. Dams trap sediments and upstream food resources along with water, altering the carbon sources available to downstream invertebrate communities (as well as altering countless other parameters). A useful conceptual model for describing these altered rivers is the serial discontinuity concept (SDC).

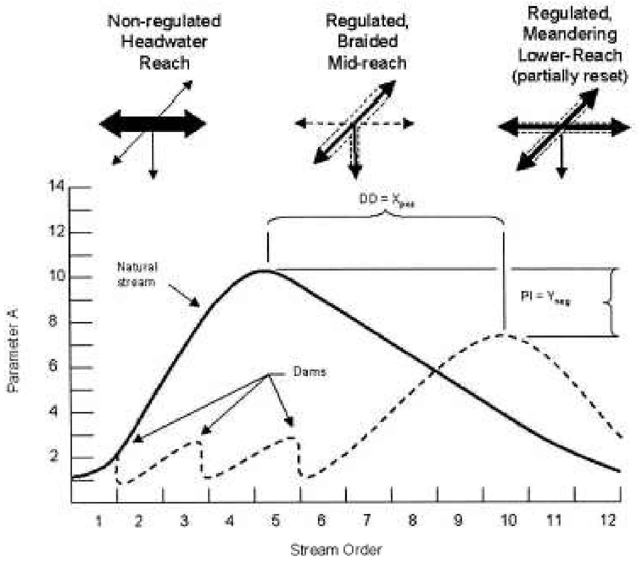


Figure 2. The Serial Discontinuity Concept (Stanford and Ward 2001)

The serial discontinuity concept predicts that dams effectively 're-set' rivers and that their effects on rivers diminish with distance downstream from these discontinuities and with input from tributaries (Ward and Stanford 1983, Stanford and Ward 2001) (see figure 2).

Empirical work has shown that benthic invertebrate taxa respond to disturbance in different ways, with implications for the entire food web. While the physical parameters and the regional species pool differ between rivers and limit the generality of empirical findings, it may be possible to make some conditional generalizations. Working in the Eel River of Northern California, Wootton et al. observed that during drought years, when natural flooding was absent, there was a large increase in the density of the large caddisfly *Dicosmoecus gilvipes* (Wootton et al. 1996). *Dicosmoecus* larvae build protective cases that reduce predation by fish but also make them more susceptible to being washed downstream by high flows. More streamlined but predation-sensitive taxa such as mayfly and midge larvae were prevalent during years with regular flooding events. This study showed that when disturbance (flooding) is reduced, energy flow to predatory fish (steelhead trout) is reduced because energy is diverted and stored in predation-resistant herbivores (*Dicosmoecus*) (Wootton et al. 1996). In general, altered flow regimes and flood control may favor non-native invertebrates with implications for food webs and nutrient cycling (Power et al. 1997). In the Green River below Flaming Gorge Dam, it is possible that the establishment of the New Zealand mud snail, a non-native, potentially predation-resistant herbivore, was facilitated by the reduction of disturbance, along with the introduction of a trout fishery that developed after the closure of the dam.

Dams cause changes in flow regime, water temperature, clarity, and the available food resources (algae, macrophytes, or particulate matter). The extent to which these changes persist downstream depend on many factors including size, type, and location of dam as well as tributary inputs downstream (Stanford and Ward 2001, Poff and Hart 2002). One study that looked at the effect of dam removal on benthic invertebrate assemblages in a Wisconsin stream found that these effects varied between sites (Pollard and Reed 2004). The assemblage at the site farthest downstream of the dam did not change, while the taxonomic composition of the community immediately below the dam changed greatly, although the diversity and functional feeding group remained similar (Pollard and Reed 2004). In general however, in tailwater reaches where water clarity is increased and there is reduced variability of flow, there is an increase in periphyton (algae growing on substrate) and macrophytes (Allan 1995). Changes in temperature of the water, which have implications for timing of invertebrate development, may also alter the benthic invertebrate assemblages. While each river segment differs, dams clearly alter abiotic and biotic parameters that influence the composition of invertebrate assemblages.

GREEN RIVER INVERTEBRATE ASSEMBLAGE

The Flaming Gorge Dam in northeastern Utah was completed in 1962, creating a 1.5 million-ha^3 reservoir to provide flood control and generate electric power (Vinson 2001). Prior to the closure of Flaming Gorge Dam, a high diversity of aquatic invertebrates, especially Ephemeroptera (>30 species) were documented in these segments of the Green River. The closure of Flaming Gorge Dam reduced the scouring late spring floods that had characterized the natural flow regime. Lower flow and increased clarity due to diminished sediment transport resulted in increased growth of bryophytes and green algae (see figure 6) (Vinson 2001). Changes in primary producers, in addition to altered hydrology and the stocking of non-native salmonids doubtless contributed to changes in the invertebrate assemblage in the tailwater sections of the Green River.

Sampling and data collection on the macroinvertebrate assemblage in the Green River began in 1947, before the completion of the dam, and has continued to the present day. Mark Vinson of Utah State University used this data, coupled with over 100 years of hydrological data, to address the long-term patterns of invertebrate assemblages downstream of Flaming Gorge Dam (Vinson 2001). This incredible data set and analysis chronicle the changes in invertebrate taxa with the closing of the dam (1962) and the partial thermal restoration (1978) implemented to increase summer water temperatures for fish. Sampling locations were all below the dam and included sites downstream and upstream of an unregulated tributary (Red Creek) (see figure 3).

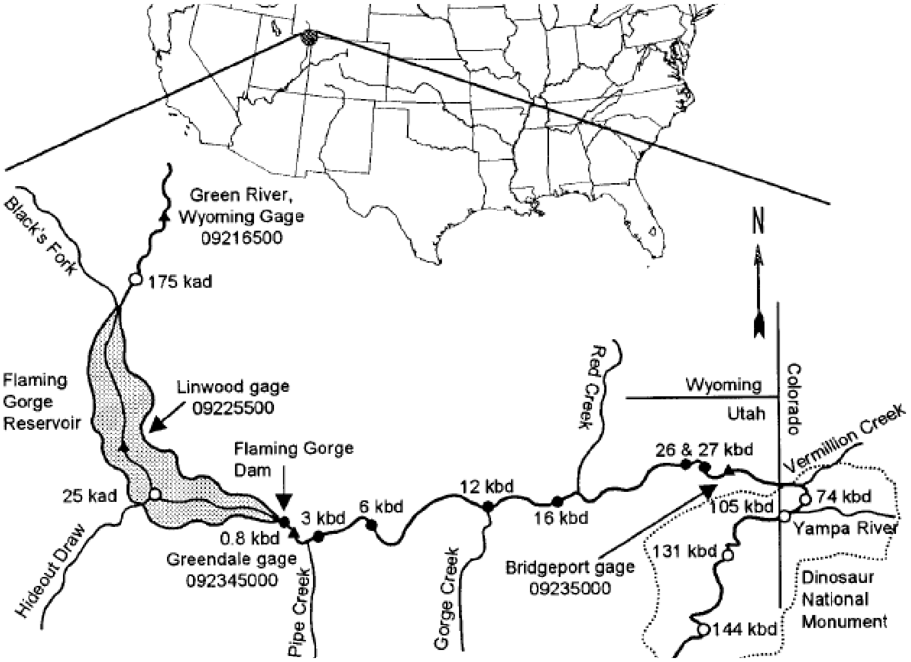


Figure 3. Map of the Green River downstream of Flaming Gorge Dam showing macroinvertebrate sampling sites (From Vinson, 2001).

The major findings of this work indicate that upstream of the intermittent tributary there was a decrease in macroinvertebrate diversity (>70 to <30 genera) and an increase in mean macroinvertebrate density. In addition taxon diversity after dam closure was found to be twice as high downstream of the tributary (Vinson 2001). This increase in diversity with increasing distance from the dam and with the input of a tributary supports predictions of the SDC. After the partial thermal restoration the abundance of amphipods increased greatly in the tailwater sections of the river, from insignificant up to >80% of the invertebrate assemblage, after the partial thermal restoration. Downstream of Red Creek, the assemblage is dominated by Ephemeroptera (mayfly) and Diptera (true fly) larvae (Vinson 2001). The partial thermal restoration, which increased mean summer water temperatures from 6°C to 12°C, did not significantly increase taxon diversity upstream of Red Creek (see figure 4) (Vinson 2001). Vinson proposes that three main factors are responsible for this lack of response: (1) competitive dominance of newly abundant amphipods over insects, (2) low rates of colonization, and (3) low reproductive success among insect taxa due to lower water temperatures.

As of 1999, the macroinvertebrate assemblage in the reaches of the Green River immediately below Flaming Gorge Dam were dominated by the amphipods *Gammarus lacustris* and *Hyallela azteca*, the mayfly *Baetis tricaudatus*, and fly larvae of the families *Chironomidae* and *Simuliidae* (see figure 5). Amphipods, which can produce multiple clutches of eggs per year when water temperatures are above 12°C, have a reproductive advantage over univoltine insects (one generation per year), which can result in faster population growth (Strong 1972). Interestingly, an increase in amphipod abundance is seen post-thermal restoration, which resulted in a mean summer water temperature of 12°C (Vinson 2001). Amphipods are grazers and deposit

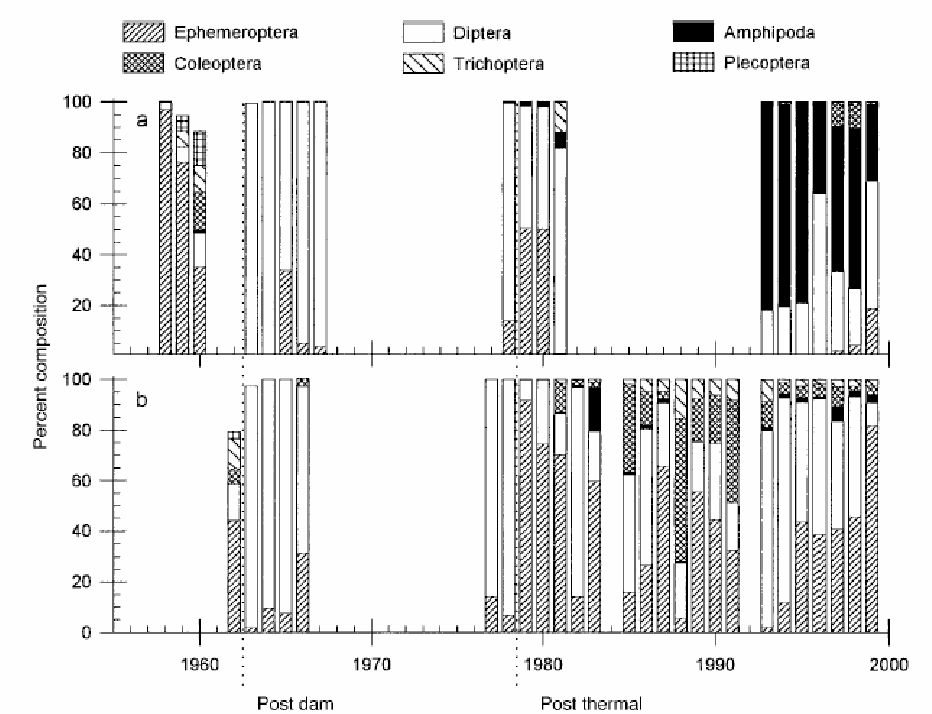
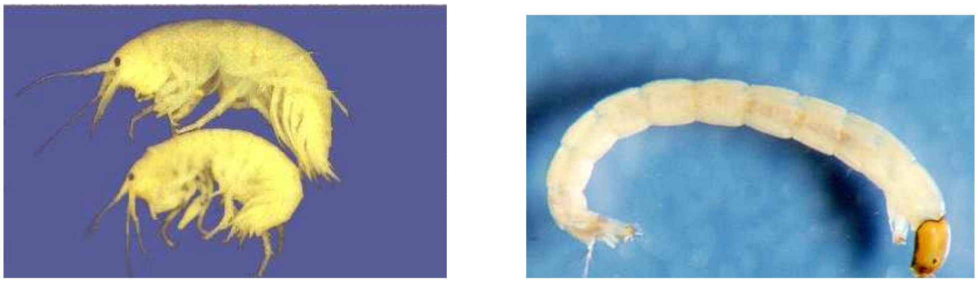


Figure 4. Mean relative contribution of invertebrate taxa (From Vinson 2001.)

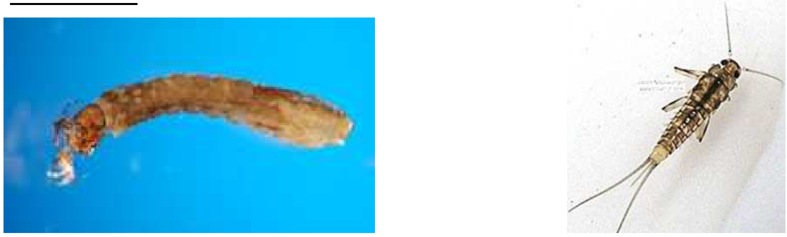
The top graph shows the relative mean annual contributions of major invertebrate taxa in the Green River upstream of Red Creek. The bottom graph shows this data below the first major tributary, Red Creek.

feeders that use algal mats and macrophytes for cover, both of which have increased with the construction of the dam and subsequent flow stabilization and increases in water clarity. Meanwhile, the summer water temperatures are still colder than pre-dam conditions, altering the number of degree days (mean temperature of days over 0°C) per year. This decrease in degree days likely impacts insect development below the dam. Colonization, which occurs both through downstream drift of animals as well as longer-distance dispersal of flying adults, has also likely been altered by the construction of the dam, which rises 149 m above the original river channel, effectively preventing much colonization from upstream (Vinson et al. 2006).



Amphipods *Gammarus lacustris* (upper) and *Hyallela azteca (lower)* http://www.usu.edu/buglab/monitor/highlake.htm

Chironomid (Midge) larva http://www.wwa-fs.bayern.de/datenufakten/Biologie/Bilder/chironomidae.jpg



Simuliidae (Blackfly) larva www.waterbugkey.vcsu.edu/image_uploads/simulidae

Baetis tricaudatus (Mayfly) naiad www.troutnut.com/.../mayflies/baetis/index3.php

Figure 5. Common invertebrates in the Green River downstream of Flaming Gorge Dam

Amblystegium- A bryophyte
home.clara.net/adhale/bryos/aripari.htm

Chara- A multicellular macro-algae
http://bib18.ulb.ac.be/cgi-bin/viewer.exe?CISOROOT=/Botanique_I&CISOPTR=257&CISOMODE=grid

Cladophora - A branching, filamentous green algae
http://www.unige.ch/sciences/biologie/biani/msg/teaching/photos%20liste/Cladophora%20rupestris.JPG

Figure 6. Primary producers that have become common downstream of Flaming Gorge Dam

ROTENONE POISONING

In 1962, prior to the closure of Fontenelle and Flaming Gorge dams, the Wyoming and Utah Game and Fish departments chose to use rotenone to aid the establishment of game fisheries in these new reservoirs. In September of 1962, over 700 kilometers of the Green River and its tributaries were treated with rotenone, a fish and invertebrate poison (Binns 1967). The goal of this treatment was to remove "coarse fish fauna", including flannelmouth suckers (*Catostomus latipinnis*), Rocky Mountain white fish (*Prosopium williamsoni*), bonytail chub (*Gila robusta*), carp (*Cyprinus sp.*) and the Colorado pikeminnow *(Ptychocheilus lucius)*. Many of these fish are now on the endangered species list. In addition to killing fish, the rotenone had the effect of killing invertebrates in the river. The target concentration was 5 parts per million (ppm) of 5% rotenone for the Green River upstream of the unfinished Flaming Gorge Dam. Unfortunately, due to lower than expected flows, the concentration reached nearly 10 ppm at some sites (Binns 1967). In addition to reaching higher concentrations, the rotenone extended farther downstream than planned due to insufficient supply of the neutralizing agent, potassium permanganate, which was added from a bridge 50 kilometers below the unfinished Flaming

Gorge Dam. Fish and invertebrates were killed in Dinosaur National Monument, more than 80 kilometers downstream of Flaming Gorge.

The Wyoming Game and Fish commission had the foresight to sample fish and invertebrate populations at multiple sites along the Green River before and after the poisoning. Although the monitoring program began only two months before the treatment and lasted only two years, the results of this study do suggest a strong impact of the rotenone poisoning on the invertebrate assemblage of the Green River. Most of this data was taken from sites upstream of Flaming Gorge Dam, but may estimate pre-dam fauna fairly well. There is a high level of variability in the data, both in time and over the sites due in part to natural variability. Drift and benthic samples were taken weekly to monthly as well as abundance (number per square foot) and composition (relative proportion of common invertebrate taxa) were measured. One of the observed trends was a decrease in mayfly (Ephemeroptera) abundance and an increase in midge (Chironomidae (formerly Tendipedidae)) abundance.

The abundances of three taxonomic groups, Ephemeroptera, Trichoptera and Chironomidae, were found to increase with time after rotenone poisoning (see figure 7). The abundance of each group increased more quickly upstream, perhaps reflecting colonization from upstream sources. The patterns reflected in these studies show a strong effect of the rotenone and recovery of biomass, if not diversity, but this is confounded with the effects of dam closure soon after the treatment. In the conclusion of Binns' 1967 report he writes, "from an ecological standpoint, the introduction of rotenone into the complex ecosystem of the river was catastrophic. The complete destruction of some species and the reduction of others, at all trophic levels, undoubtedly influenced the entire ecosystem" (Binns 1967).

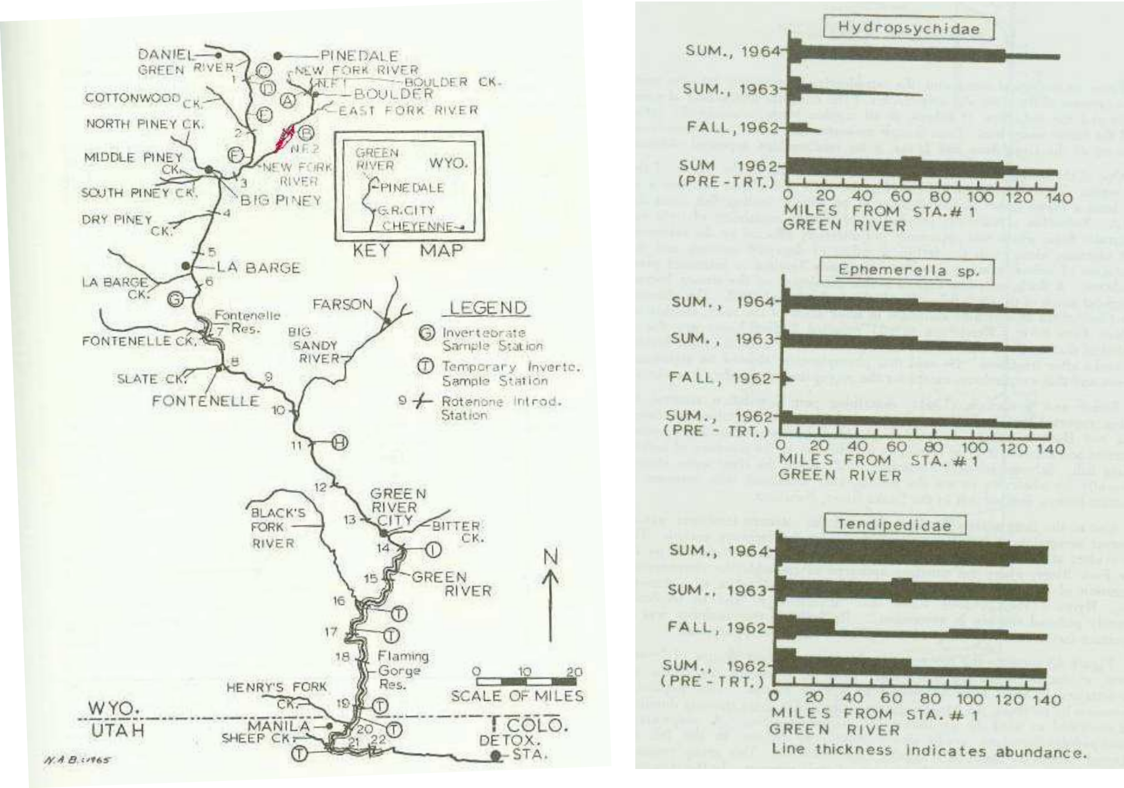


Figure 7. Map of rotenone input and sampling stations (left) and changes in the abundance of common invertebrate families across time and distance. (From Binns 1967)

EFFECTS OF INVASIVE INVERTEBRATES

Changes in the physical and biotic characteristics of the Green River below Flaming Gorge Dam have not only altered the distribution and abundance of native invertebrates, but may also have altered the susceptibility of the aquatic ecosystem to non-indigenous species. Alteration of flow regimes has been cited by several authors as an important abiotic parameter that may contribute to colonization of freshwater systems by invasive species (Moyle and Light 1996, Marchetti and Moyle 2001). In recent years research on the impacts of nonindigenous species has shown that new species can have effects at multiple scales, from direct competition for resources to alteration of nutrient cycling regimes (Parker et al. 1999). However, only a fraction of introduced species become invasive and have large impacts in their new environment. Determining the mechanisms and conditions responsible for these successful invasions is important in understanding and predicting the impact of nonindigenous species (Parker et al. 1999, Kolar and Lodge 2001).

There are several examples of invasive freshwater invertebrates that have profoundly altered aquatic communities through the impacts of their high densities on food webs (Arnott and Vanni 1996, Feyrer et al. 2003). The overbite clam (*Potamocorbula amurensis*) in the San Francisco Estuary and the zebra mussel (*Dreissena polymorpha*) in the Great Lakes have both altered food-web structure by filtering large volumes of phytoplankton and incorporating it into benthic, rather than pelagie, food webs. In the case of the zebra mussel, water clarity has increased drastically with many implications for aquatic food webs, nutrient cycling, and the assemblage of producers (i.e., cyanobacteria vs. diatoms) (Arnott and Vanni 1996). There are fewer examples of invasive invertebrate species altering river ecosystems, but species that attain high densities in these systems may have significant impacts on the community and ecosystem properties.

The New Zealand mud snail

The New Zealand mud snail, *Potamopyrgus antipodarum*, is an invasive species capable of reaching very high densities, with 300,000 to 750,000 individuals per square meter reported in some heavily colonized streams (Kerans et al. 2005). The New Zealand mud snail is a tiny prosobranch snail (5 mm) with an operculum that covers the opening to its shell and prevents desiccation. In recent years the New Zealand mud snail has spread throughout the western United States, including stretches of the Green River downstream of Flaming Gorge Dam as well as many other sites in Utah (Vinson 2004). The first documentation of this invasive snail in Utah was recorded near Swallow Canyon on the Green River downstream of the dam in September 2001(Vinson 2004). While the abundance of the mudsnail has fluctuated their range is expanding in the Green River (see figure 8) and their occurrence in trout diets is increasing (Vinson et al. 2006).

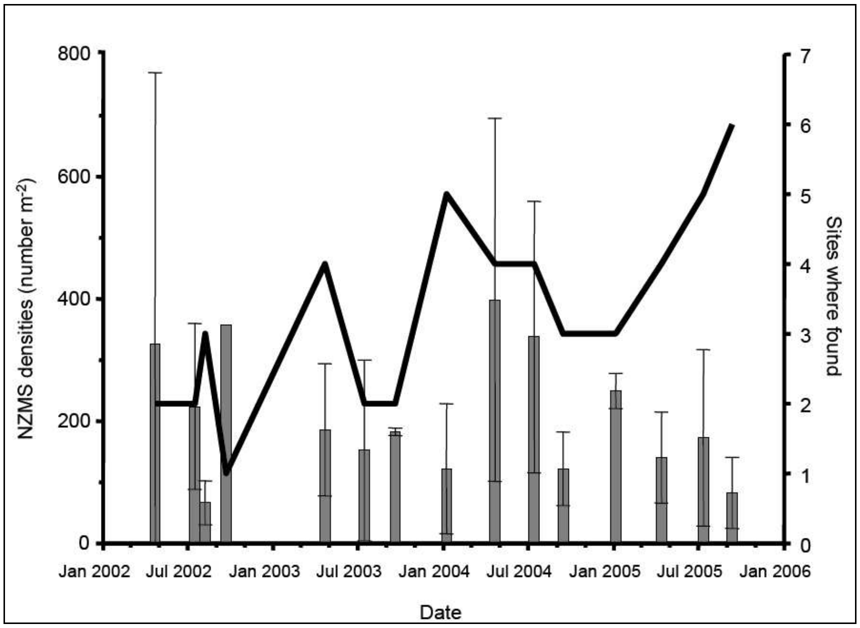


Figure 8. New Zealand mud snails in the Green River below Flaming Gorge Dam (From Vinson 2006)

The New Zealand mud snail exists in a diploid, sexually reproducing form in its home range, as well as in a triploid, parthenogenetically reproducing form that is predominant in its expanded range, including the Western U.S (Dybdahl and Kane 2005). This means that one individual can start a new population, genetically identical to itself. The densities of mud snails in New Zealand are much lower than those reported in their expanded range. This is likely due to absence of the trematode parasites in the genus *Microphallus*, which use the snail as an intermediate host in New Zealand (Levri 1999, Dybdahl and Krist 2004). In the Green River, New Zealand mud snail densities are highest (~100,000 per m^2) in habitats with aquatic vegetation and lower water velocities (see figure 9) (Vinson 2004) .

Figure 9. Sago pondweed, a preferred habitat of New Zealand mud snails in the Green River (top). NZMS are found at very high densities downstream of Flaming Gorge Dam (bottom). (Photos from (Vinson 2004) and Gustafson (NZMS close-up))

The impact of New Zealand mud snails on native benthic invertebrate communities is unclear. Short-term colonization studies in Australian streams with mud snails at low densities found a positive relationship between densities of native benthic invertebrates and the mud snail (Schreiber et al. 2002). More recently, work in heavily colonized rivers of the Greater Yellowstone Ecosystem found a negative correlation between New Zealand mud snails and native benthic invertebrate abundance (Kerans et al. 2005). The temporal and spatial scale of the Yellowstone study was much larger and included plots with much higher mudsnail densities than found in the Australian streams. These contradictory results strongly suggest that the impact of New Zealand mud snails is dependent on multiple factors such as snail density and scale of study. New Zealand mud snails is tolerant of a wide range of abiotic conditions (Alonso and Camargo 2003, Dybdahl and Kane 2005) and are less preferred and less nutritious prey for trout than other benthic invertebrates (McCarter 1986, Sagar and Glova 1995, Bruce and Moffitt 2005, Vinson 2005b). This snail has become established in diverse habitats and its spread is likely to continue due to movement of vectors (fish, anglers and boaters) between streams.

New Zealand mud snails have been as far downstream as Limestone Campground in the Lodore Canyon section of the Green River (Vinson, personal communication). This site is downstream of many tributaries, notably Red and Vermillion Creeks, but still upstream of the confluence with the Yampa River. The Yampa River is a large, unregulated tributary that doubles the discharge of the Green River and adds a considerable sediment load. The flow and temperature regulations mandated by the 1992 Biological Opinion written for endangered fish species in the Green River are specified for the portion of the river downstream of this confluence (Muth et al. 2000). According to the SDC, the distance from Flaming Gorge Dam (104 km) and the influence of the unregulated Yampa should result in a recovery of the Green River to a more natural state below the confluence. It may be the case that New Zealand mudsnails will be inhibited from spreading below the confluence due to more variable and higher magnitude flows. Aquatic macrophytes are less abundant downstream as well, reducing the availability of this preferred habitat, although mud snail do colonize cobble and silt substrates as well. However, multiple introductions via downstream drift of growing upstream populations and transport by boaters may result in continued spread of this invasive snail. It seems likely that low flow reaches, such as Browns Park, may be provide suitable habitat in times of high discharge. New Zealand mud snails have established themselves quite well in the rivers of Yellowstone National Park, in rivers with fairly natural flow regimes that are less variable than that of the Yampa (Kerans et al. 2005).

FOOD WEB IMPLICATIONS

The impact of an invasive species can be conceptualized as the product of it range, abundance and effect, where those species that have a wide range, achieve high densities and have strong effects on the community would be described as having a large impact (Parker et al. 1999). But how does one measure the effect of an invasive species? Typically, studies look at the effect of a species on a select number of other species or ecosystem properties. For example, studies have examined the effect of New Zealand mud snails on the growth rate of other snail species (Cope and Winterbourn 2004) and measured the growth rate of trout fed diets of amphipods versus mud snails (Vinson 2005a). Vinson found that trout fed mud snails lost an average of 0.2% of their body mass per day while those fed amphipods gained 1% of their body mass per day over a three month period (Vinson 2005a). Field data corroborates this pattern, trout with mud snails in their diet show a slight decrease in the condition compared to trout without mud snails in their diet (Vinson et al. 2006).

Studies that incorporate multiple trophic levels and consider indirect as well as direct effects are less common (Simon and Townsend 2003). Examples include the work of Williams which showed that the presence of non-native brown trout in New Zealand streams increase the nighttime drift of New Zealand mud snails as well as some caddisfly species (Williams 2000). Multiple studies have shown that introduced salmonids (such as those found in the Green River) can increase algal biomass indirectly, through altering both the abundance and the behavior of invertebrate grazers (Simon and Townsend 2003). Fewer studies have addressed these more complex interactions between invasive and native species in highly disturbed aquatic systems such as the Green River where the Flaming Gorge Dam represents a major discontinuity in physical and ecological processes.

CONCLUSIONS

Changes in the hydrologic regime and fluvial geomorphology of the Green River downstream of Flaming Gorge Dam have altered the native invertebrate assemblage. In addition to these abiotic changes, rotenone poisoning and the introduction of non-indigenous species at all trophic levels have likely altered community and food web structure. The successful stocking of trout below the dam, the spread of the bank and bar stabilizing *Tamarix ramosissima,* and the recent invasion of the New Zealand mud snail are all likely related to abiotic changes in the river. Conversely, the altered community structure of the Green River may also impact nutrient cycling, water quality, and channel form. The complexity of these interactions is beyond our current understanding but conceptual models such as the serial discontinuity concept may be helpful in developing testable hypotheses. Comparative studies of abiotic parameters, species distributions and food webs in reaches at varying distances upstream and downstream of major discontinuities may lend insight into the effects of dams on aquatic ecosystems. This research is essential if we are to understand and potentially ameliorate the impacts that our century of dam building has had on these natural systems.

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