Contemporary and historic comparisons of aquatic macroinvertebrates in the regulated Green River and unregulated Yampa River within Dinosaur National Monument

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Executive Summary

Similar to other large, hypolimnetic dams, Flaming Gorge Dam (FGD) has dramatically altered the hydrologic, sediment and thermal regimes of the Green River. Extensive studies of aquatic macroinvertebrate response and recovery patterns have occurred within 50 km of the dam, while quantification of downstream recovery trajectories have not been extended into Dinosaur National Monument (DINONM) where the Yampa River, a large relatively unregulated tributary, joins the Green River. Given the growing number of water development proposals on the Yampa and Green Rivers, understanding the remediating effects of the Yampa River is imperative. The National Park Service in cooperation with the BLM/USU National Aquatic Monitoring Center has intensively sampled the mainstem of the Green and Yampa Rivers throughout DINONM for over nine years. Although individual reports have resulted from such efforts, no comprehensive synthesis of this work has been conducted. Therefore, we paired short-term monitoring of a recently established network of 21 sentinel sites with exhaustive contemporary and historical macroinvertebrate inventories to quantify the extent of species extirpations and alterations to assemblage composition imposed by the management of FGD.

Our results largely support the downstream recovery trajectories of macroinvertebrate assemblages outlined by the serial discontinuity concept. We observed considerable recovery of macroinvertebrate species richness in Lodore Canyon, 70 km downstream of FGD; however, both historical and contemporary analyses suggest the persistence of significant compositional differences until the confluence with the larger Yampa River. After the confluence with the Yampa River we failed to detect significant differences in macroinvertebrate richness or assemblage composition on the Green River relative to both the Yampa and historic conditions, highlighting the significant remediating effects of the Yampa River. In contrast to other tailwaters, invasive invertebrates, although present, were not found at densities likely to have significant effects on the structure or function of the lotic ecosystem. Rather, of greater management concern is the increased hydrogeomorphic stability and water clarity created by FGD, which appears to have created an alternative steady state where invertebrate composition significantly differs from both the Yampa and historic conditions. Further research is needed to understand the effects of compositional differences on food web structure and function and the subsequent ecological stability of the system to inform FGD release patterns and management of aquatic invasives and endangered fishes of the Upper Colorado River Basin.

Introduction

The construction and management of over 2,000 large dams (> 15 m high) throughout the western United States represents an unparalleled threat to lotic ecosystems (USACE, 2009). Worldwide, river regulation has been shown to homogenize hydrologic regimes, alter sediment, thermal and nutrient dynamics and to reduce biodiversity and favor the establishment of nonindigenous species (Ligon et al., 1995; Collier et al., 1996; Vinson, 2001; Poff et al., 2007). Consequently, it is not surprising that human alterations to the natural flow regime are one of the leading detriments to freshwater biodiversity (Ward and Stanford, 1983; Richter et al., 2003).

Large, hypolimnetic dams are thought to create discontinuities in the river continua where chemical, physical and biological parameters exhibit predictable downstream response and recovery trajectories (Sensu the serial discontinuity concept [SDC], Ward and Stanford, 1983; Stanford and Ward, 2001). When applied in conjunction with the network dynamics hypothesis (NDH) (Benda et al., 2004), the SDC predicts downstream recovery rates to be greatest where the ratio of reservoir storage capacity to mean annual flow is small and multiple large tributaries enter in short succession downstream. Despite these predictions, empirical tests of the SDC have been largely constrained to relatively small rivers in montane or otherwise mesic regions (Rader and Ward, 1988; Stanford and Ward, 1989; Volez and Ward, 1989; Palmer and O'Keeffe, 1990; Harding, 1992; Camargo and Voelz, 1998; Casas et al., 2000; but see Stanford et al., 1988; Munn and Brusven, 1991; Stevens et al., 1997; Vinson, 2001), where small reservoir volumes and high drainage densities maximize opportunities for downstream recovery. In contrast, opportunities for large, higher-order rivers to reset with distance downstream might be constrained by the dearth of unregulated tributary inputs, their geographic isolation from viable source colonists and/or the intensification of anthropogenic impacts (O'Keefe et al., 1990; Palmer and O'Keefe, 1990; Camargo, 1992; Vinson, 2001). The paucity of empirical tests of the SDC in large, arid-land rivers compromises the management of these systems.

The heavily regulated Green River and the relatively free-flowing Yampa River in Dinosaur National Monument (DINONM) represent a unique opportunity to test biotic predictions of the SDC in a large, arid-land river. In his seminal comparison of historic and contemporary macroinvertebrate assemblages of the Green River, Vinson (2001) quantified macroinvertebrate response and recovery trajectories immediately below Flaming Gorge Dam (FGD). Vinson estimated that FGD has extirpated more than 30 taxa, with moderate recovery of macroinvertebrate assemblages occurring within 30 km of the dam. The National Park Service (NPS) has subsequently implemented a macroinvertebrate monitoring program from which Vinson's (2001) analyses can be extended downstream an additional 120 km to assess the impacts of FGD on the Green River within DINONM and the remediating effects of the relatively unregulated Yampa River and several smaller tributaries. The combination of intensive upstream macroinvertebrate surveys with historic and contemporary surveys in DINONM allows for unprecedented spatiotemporal analyses of the response and recovery of a large arid-land river to regulation.

Understanding the role of the largely unregulated Yampa River in restoring the Green River is of increasing importance given pending water development proposals and the dearth of unregulated systems within the Upper Colorado River Basin. Working towards this goal, we asked: 1. How does macroinvertebrate assemblage composition of the regulated Green River compare to that of the largely unregulated Yampa River; 2. How do contemporary macroinvertebrate assemblages of the Green and Yampa Rivers compare to the historical, regional species pool; 3. What remediating effects does the Yampa River have on the Green River; 4. Are macroinvertebrate communities of the Green and Yampa Rivers within DINO changing through time; and 5. What is the current distribution of aquatic invasive invertebrates within DINONM and how are populations changing through time? We chose to focus on macroinvertebrates because they disproportionately contribute to aquatic biodiversity and play critical roles in river ecosystems by serving as important conduits of energy between basal resources and higher trophic levels (Cummins, 1979; Nakano and Murakami, 2001; Baxter et al., 2005). In addition, they represent the greatest source of long-term biological data for the mainstem Green and Yampa Rivers within DINONM.

Methods

Study Area

Our study focused principally on the Green and Yampa Rivers within the boundaries of DINONM (Fig. 1). DINONM is located in northern Utah and Colorado and delineates the northern edge of the Colorado Plateau, a large region of uplifted sedimentary rocks forming part of the Uinta Mountains. The Yampa and Green Rivers geographically define DINONM, with the monument boundaries creating a corridor upstream and downstream of the confluence of the two rivers. Both the Yampa and Green Rivers originate in alpine environments of the Park and Wind River Ranges, respectively, and largely flow through sagebrush steppe before entering DINONM. Within the monument, both systems are examples of large, canyon bound rivers where local lithologies of varying resistance determine local channel form. Grams and Schmidt (1999) identified two geomorphically distinct channel forms in a detailed geomorphic evaluation of the Green River throughout DINONM. River segments dominated by relatively resistant river-level lithologies and tributary debris fans were generally straight, high gradient, canyon reaches with low width:depth ratios, coarse bank and bed material and a dominance of rapids. In contrast, areas of lower bedrock resistance and an absence of debris fans were characterized by meandering reaches with lower slopes, greater width:depth ratios and fine grained bank and bed materials. Although the canyon bound morphology largely dominates both the Green and Yampa Rivers within DINONM, the aforementioned channel types alternate with distance downstream according to the composition of local lithologies.

The Yampa River within DINONM consists of the last 76.5 km of its 402 km course before joining the Green River at Echo Park (Fig. 1). The Yampa River is one of the last large, relatively unregulated major tributaries of the Upper Colorado River Basin. The hydrograph is dominated by a spring snowmelt hydrologic regime with a mean annual peak flow of 171 m^3sec^{-1} and baseflow dominating from August – March (Fig. 2). In contrast to the Yampa, the hydrologic regime of the Green River is altered by two major dams, Fontenelle and FGD. FGD is located approximately 75 km upstream of DINONM and imparts the largest effect on the hydrology of the Green River, with an annual storage capacity of 4.67×10^9 cubic meters relative to a mean annual flow of 52 m^3 sec^{-1}. The primary function of FGD is water impoundment for hydroelectric power generation and to support downstream irrigated agriculture. Water management actions have reduced the mean annual peak flow by more than 50% causing significant alterations to hydrologic, thermal and sediment regimes, in addition to the flora and fauna of the Green River (Andrews, 1986; Merritt and Cooper, 2000; Vinson, 2001; Grams and Schmidt, 2002).

Study design

To understand how the management of FGD impacts macroinvertebrate assemblages within DINONM, as well as the potential remediating effects of the Yampa River and other tributaries, we stratified the Green and Yampa Rivers into three segments for study: the Green River from Gates of Lodore to the confluence with the Yampa in Echo Park (Lodore); the Yampa River from Deerlodge Park to the confluence with the Green (Yampa); and the Green River below the confluence with the Yampa to Split Mountain boat ramp (Confluence) (Fig. 1). Within each study segment, we located sites at two to eight km intervals to capture longitudinal variability in macroinvertebrate assemblages as related to valley confinement and the subsequent channel types identified by Grams and Schmidt (1999). Specifically, we located seven sites within Lodore, nine sites along the course of the Yampa and five sites below the confluence with the Yampa for long-term monitoring (Fig. 1; Appendix 1), hereafter referred to as ‘sentinel sites’. The Lodore and Yampa study segments are largely dominated by higher gradient, confined valley segments, while the Confluence segment has a greater proportion of wider alluvial valleys and a more sinuous planform (Grams and Schmidt, 1999).

From 2001 to 2011 we conducted both qualitative and quantitative benthic macroinvertebrate sampling on the Green and Yampa Rivers throughout DINONM; however, the 21 sentinel sites were only consistently sampled in July or August from 2009 – 2011. The objective of quantitative sampling was to standardize sampling efforts at individual sites and among river segments for quantification of macroinvertebrate densities and assemblage composition. We collected quantitative samples from riffle or fast water habitats using a 500 micron Surber net (0.09 m^2) at eight randomly located locations along the river’s margins and composited samples for a total sample area of 0.74 m^2. Quantitative samples were collected at the 21 sentinel sites in late August or early September of 2009, 2010 and 2011. Additional quantitative samples were collected at six of the 21 sentinel sites in 2001 and used for long-term temporal comparisons. We supplemented quantitative samples with qualitative collections to develop comprehensive species lists and to document the establishment and spread of invasive invertebrates. Specifically, we intermittently sampled four to eight additional reaches per segment from 2001 – 2011, with the objective of sampling all major habitat types (e.g., riffles, pools, back waters, macrophyte beds). Qualitative samples were collected using a kicknet (457 x 229 mm) with a 500 micron mesh net and by hand picking invertebrates from woody debris, emergent vegetation and large boulders. Collections from all habitats were composited to form a single sample per reach. In addition, we targeted Decapoda (crayfish) by deploying three baited minnow traps for twelve hours at two to four sites per segment in each of 2010 and 2011. Decapoda were targeted because of the recent establishment of *Orconectes rusticus* in the upstream reaches of the Yampa River (Martinez, 2011). Since 2001, we collected a total of 52, 61 and 44 qualitative samples in Lodore, Yampa and Confluence study segments, respectively, between May and September (Appendix 1).

Both qualitative and quantitative samples were processed using a 600 count subsampling procedure paired with a “big/rare” search to remove taxa potentially missed during the initial sorting process (Cuffney et al., 1993; Vinson and Hawkins, 1996). When possible, we identified macroinvertebrates to genus, with the exception that Chironomidae midges were identified to subfamily and all non-insect taxa were identified to either order or family; identifications were performed by the same three taxonomists over the duration of the study. Prior to analysis, we standardized the taxonomic resolution among all samples by assigning identified macroinvertebrates to unambiguous operational taxonomic units (OTUs)(Yuan et al., 2008), with 25% of individuals agglomerated to species, 57% to genus, 12% to family and 6% to other taxonomic levels. Individuals identified to a coarser taxonomic resolution that precluded placement into unambiguous OTUs were excluded from all analyses. Macroinvertebrate counts for quantitative samples were subsequently standardized to a fixed-count of 300 randomly selected individuals per sample for richness-based metric computation to minimize bias associated with disparate counts among samples (Gotelli and Colwell, 2001). Computed metrics included macroinvertebrate density, taxonomic richness, richness of the orders Ephemeroptera, Plecoptera and Trichoptera (EPT) and the relative abundance of the numerically dominant family. These metrics represent different components of macroinvertebrate assemblages (e.g., community structure, tolerance) and were selected based on their hypothesized sensitivity to anthropogenic impacts (Lenat and Crawford, 1994; Allan, 2004).

Historic macroinvertebrate surveys

To quantify the pre-dam regional species pool of the Green and Yampa Rivers in the vicinity of DINONM, we utilized extensive ecological inventories of the flora and fauna conducted prior to dam closure. Surveys included multi-year sampling of a single site located approximately 25 km upstream of FGD from 1947 to 1960 (not shown on Fig. 1), with a specific emphasis on Ephemeroptera (Edmunds and Musser, 1960), Plecoptera (Sessions and Gaufin, 1960) and Odonata (Musser, 1960) (Data described in more detail by Vinson, 2001). Additional data was obtained for two sites located approximately two and 25 km downstream of FGD, two sites in Lodore, two sites in Yampa and three sites in the Confluence study segment (Woodbury, 1963)(Fig. 1 and Appendix 1). In all instances, pre-dam macroinvertebrate inventories were conducted using qualitative sampling techniques where sampling area and/or time were not standardized; therefore, data was treated as presence/absence only. Data from all historic surveys, Green and Yampa Rivers, were composited into a single taxa list, reconciled with contemporary taxonomic nomenclature and standardized to operational taxonomic units to ensure concordance with contemporary collections.

Hydrologic regimes

Mean daily discharge data were obtained from U.S. Geological Survey (USGS) stream gages located approximately 75 km upstream from DINONM on the Green River (Green River at Greendale: 09234500), 75 km upstream from DINONM on the Yampa River (Yampa River at Maybell: 09251000) and 80 km downstream of the confluence on the Green River (Green River at Jensen: 09261000) for the water years 1951 – 2011.

Data Analyses

Alterations to the hydrologic regime of the Green River at the Greendale and Jensen gages were quantified using the Indicators of Hydrologic Alteration (IHA) approach (Richter et al., 1996, 1998). Of the 33 hydrologic parameters used in the IHA to characterize intra- and inter-annual hydrologic variability, we selected twelve thought to be most appropriate for hydroelectric dams in snowpack hydrologic regimes (Table 1)(Olden and Poff, 2003). Selected parameters were relatively uncorrelated and chosen to represent all the components of the natural flow regime (e.g., timing, duration, magnitude and frequency of high and low flow events)(Poff et al., 1997). For each gage we compared pre-dam conditions (water years: 1951 – 1962) with the decade immediately following dam closure (water years 1963 – 1974) and with contemporary dam management (water years: 2000 – 2011). Median values for the selected parameters were compared between the pre- and post-dam time periods, with the magnitude of change assessed via the "Range of Variability Approach" (RVA)(Richter et al., 1998). Specifically, we established the pre-dam natural range of hydrologic variability, within the 25th and 75th percentiles, for each parameter based on the decade prior to dam closure and then assessed whether post-dam conditions for a particular parameter fell within that range during any given year. The degree to which RVA targets were achieved was quantified as: ((Observed – Expected)/Expected)*100; where 'observed' is the count of years for which the hydrologic parameter was within the targeted range and 'expected' is the count of years for which the value is expected to fall within the RVA range. Negative values indicate that observed conditions fell within the RVA target range less than expected, whereas positive values occur when conditions were within the RVA target more than expected under natural conditions.

Invertebrate data were initially summarized using non-metric multi-dimensional scaling (NMS) to identify spatial and temporal gradients among the 21 sentinel sites sampled from 2009 – 2011. NMS is an indirect gradient analysis technique that uses rank community dissimilarities to iteratively search for the optimal arrangement of sample objects in as few as dimensions as possible (McCune and Grace, 2002). NMS was run with Sørensen's distance measure in PC-ORD version 6.0 (McCune and Mefford, 2011) using log transformed ($\log_{10}[x+1]$) macroinvertebrate densities. We assessed dimensionality by evaluating the relationship of final stress versus the number of dimensions; in addition, a Monte Carlo test with 250 runs of the randomized data quantified the probability of obtaining the observed stress by chance alone.

We tested for differences in assemblage composition among rivers segments and sample years using a multiple response permutation procedure (MRPP)(Mielke and Berry, 2001), where samples collected among years or within a river segment were considered replicates, respectively. MRPP is a nonparametric permutation procedure that tests for differences among two or more groups. A *p*-value assesses the probability of observed group differences under the null hypothesis, while an *A*-statistic (range: 0 – 1) quantifies the effect size and within group homogeneity (McCune and Grace, 2002). The nature of compositional differences among segments and years was quantified using indicator species analysis (ISA)(Dufrêne and Legendre, 1997). ISA contrasts the performance of individual species among two or more groups by comparing proportional abundances and proportional frequencies of occurrence among groups and combining the two proportions to generate an indicator value. Indicator values range from zero to 100 (always present and exclusive to a particular group). Statistical significance of individual indicator values is determined by a Monte Carlo test with 1000 runs of the randomized data to quantify the probability of obtaining the observed indicator value by chance alone. MRPP and ISA were run for the 2009 – 2011 sentinel samples and for three sites within the Lodore and Confluence study segments sampled in both 2001 and 2010 (Appendix 1). More specifically, MRPP was run using log ($\log_{10}[x+1]$) transformed macroinvertebrate densities and Sørensen's distance. Near decadal comparisons of macroinvertebrate assemblages were constrained to these six sites because they were the only ones sampled across identical time periods using similar, quantitative methodologies spanning a time period exceeding five years. Prior to 2009, sampling on the Yampa was constrained to the spring and preliminary analyses suggest significant differences in assemblage composition between spring and summer samples (Miller unpublished data). We chose to use the 2010 versus the 2011 samples for long-term comparisons because of a 2011 flood event. Lastly, quantitative analyses were complemented by comparing composited species lists from all qualitative samples per segment (2001 – 2011) to identify additional taxa unique to particular study segments or sampling years.

In addition to comparing macroinvertebrate assemblages, we compared the computed macroinvertebrate metrics among segments and sampling years. Specifically, we used a repeated measures analysis of variance (ANOVA) to test for differences among segments, years and the segment*year interaction for the 2009 – 2011 sentinel samples only. For long-term temporal comparisons (2001 – 2010) a simple ANOVA was used to test for differences between years blocked by river segment. Significant differences were followed up with Tukey's post hoc test for multiple comparisons with alpha levels set at 0.05. Macroinvertebrate density was log transformed to alleviate departures from normality.

Comparisons of contemporary macroinvertebrate assemblages (2001 – 2011) with historic surveys (pre-1963) were performed for four study segments: Lodore, Confluence, Yampa and a 50 km river segment located immediately below FGD, which consisted of four sites above Red Creek and three sites below Red Creek sampled quarterly from 2000 to 2011, hereafter referred to as above and below Red Creek (Fig. 1). Red Creek, Lodore and the Confluence study segments represent a downstream longitudinal gradient facilitating the quantification of recovery rates in relation to tributary inputs, principally the additions of Red Creek, Vermillion Creek and the Yampa River (Fig. 1). In contrast, comparisons of contemporary Yampa River samples with the historic species pool were used to characterize background rates of species loss through time under 'natural' conditions. Species loss per segment, relative to the pre-dam, historic Green and Yampa River species pool was subsequently computed; with concordant loses from the Yampa River excluded from each respective river segment. All comparisons were based on composite taxa lists (presence/absence) of all qualitative and quantitative samples collected per river segment and time period (pre-1963 and 2001 – 2011).

Results

Hydrologic alterations

Following closure of FGD, annual hydrologic variability of the Green River was greatly reduced due to increased base flows and reductions in the magnitude, duration and frequency of high flow events (Table 1 and Figs. 2&3). In contrast, the hydrologic regime of the Yampa River remained unchanged across the same time period (data not shown except for Fig. 2). In almost all instances, post-dam annual hydrologic conditions significantly deviated from the target range of pre-dam natural variability, with annual observations falling within the RVA less than expected. Below the confluence with the Yampa River, hydrologic alterations to the Green River were muted (Table 1 and Fig. 3). Increased baseflows and reductions in high flow events still reduced annual variability, but the magnitude, timing and duration of alterations was not as great as observed for the Greendale gage. Over the last decade, the natural timing of high and low flow events has been partially restored and the frequency of short-term high discharge pulsing events has been reduced (Table 1 and Fig. 4), but significant departures from pre-dam conditions persist.

Macroinvertebrate assemblages

We analyzed macroinvertebrate data from 305 qualitative and quantitative samples collected between 2001 and 2011. Among all samples, we found 266 taxa that were reduced to 153 operational taxonomic units. Among the quantitative samples, assemblage composition was dominated by Ephemeroptera (42 unique taxa), Diptera (26), Trichoptera (24), Coleoptera (19) and Plecoptera (12). Densities ranged from a low of 27 to a high of 5970 individuals/m^2, with a median of 774 individuals/m^2. Ephemeroptera was also the numerically dominant order comprising over 58% of individual samples on average.

Contemporary differences in macroinvertebrate assemblages among river segments

NMS ordination revealed two significant gradients that retained 85% of the variation in macroinvertebrate assemblages sampled among the sentinel sites from 2009 to 2011 (Fig. 5). The NMS solution had a stress below 15 corresponding to a stable solution with little risk of false interpretation (McCune and Grace, 2002). We rigidly rotated the ordination solution to maximize gradients along axis one, which effectively separated sample reaches by river segment and accounted for 70% of macroinvertebrate variability (Fig. 5). MRPP confirmed the distinctness of these groupings; we observed significant differences in macroinvertebrate assemblage composition among river segments ($A = 0.15$; $p < 0.001$), with Lodore significantly differing from both the Yampa and Confluence segments ($A = 0.17$; $p < 0.001$ and $A = 0.14$; $p < 0.001$, respectively), but the confluence not differing from the Yampa ($A = 0.04$; $p < 0.001$). Despite statistical significance for this latter comparison, the ecological significance was relatively weak as indicated by a low *A*-statistic.

Differences among river segments were driven by gradients in both the relative abundance and composition of macroinvertebrate assemblages. Among the computed metrics, EPT richness was significantly higher for both the Yampa and Confluence river segments ($F_{2, 18} = 21.2$, $p = < 0.001$), while the relative abundance of the dominant family also differed among segments; however, responses were not consistent among years as indicated by the significant year*segment interaction ($F_{2, 18} = 6.2$, $p = 0.009$) (Fig. 6). In contrast, macroinvertebrate richness ($F_{2, 18} = 1.6$, $p = 0.236$) and density ($F_{2, 18} = 2.8$, $p = 0.099$) did not differ among segments. Differences among segments were driven by a relatively large number of significant indicator taxa per segment, with 17 taxa having significant indicator values (i.e., high frequency of occurrence and relative abundance) for Lodore and six of them occurring exclusively in that segment (Table 2); Hemiptera and Gastropoda were uniquely represented in the Lodore segment. Five indicator taxa were exclusive to the Yampa segment, with a total of 12 taxa having significant indicator values, 85% of Yampa's indicator taxa belonged to the orders Ephemeroptera, Plecoptera and Trichoptera. In contrast, only eight taxa, particularly taxa from the orders Coleoptera, Diptera and Ephemeroptera, were significant indicators of the Confluence segment and no taxa were exclusive based on the quantitative sampling of sentinel sites. Analysis of all qualitative samples identified additional taxa unique to each segment, with 22, 14, and 11 additional taxa being unique to the Lodore, Yampa and Confluence river segments, respectively (Table 2).

Lastly, despite observed differences among segments, within segment variability for any given year was quite high with greater than 55% dissimilarity on average (data not shown). For example, in 2009, average within segment dissimilarity was 60, 55 and 53% for the Lodore, Yampa and Confluence study segments, respectively. While the observed variability appeared random for the Yampa and Confluence (i.e., no consistent, directional downstream change), macroinvertebrate assemblages within Lodore changed predictably with distance downstream (e.g., Fig. 5).

Temporal patterns of macroinvertebrate assemblages within the Green River, DINONM

The 2009 – 2011 sentinel reaches separated out by sampling year along axis two (Fig. 5), which accounted for 15% of the variation in macroinvertebrate assemblages. However, there was a high degree of overlap in assemblage composition among years with differences most pronounced for 2010 versus 2011, the flood year, for both the Confluence and Yampa study segments, while differences among years were more muted for Lodore (Fig. 7). Similarly, in 2011 we observed the lowest richness values among years, with richness ($F_{1, 18} = 7.3$, $p = 0.015$) and EPT ($F_{1, 18} = 5.5$, $p = 0.031$) richness significantly differing from the 2010 sampling year only. Macroinvertebrate density did not differ among years ($F_{1, 18} = 1.3$, $p = 0.301$), while the relative abundance of the dominant family was greater in 2011 ($F_{2, 18} = 6.2$, $p = 0.009$), but only for the Lodore and Confluence segments (Fig. 6). Taxa missing from 2011, that were present in greater than 20% of the 2009 and 2010 samples included Blephariceridae and *Chelifera* (Diptera), *Leucrocuta* and *Choroterpes* (Ephemeroptera), an aquatic Lepidopteran and *Helicopsyche* (Trichoptera); all of these taxa had significant indicator values.

Over a longer time span, we observed no significant differences in macroinvertebrate assemblages between samples collected in 2001 and 2010 on the Lodore and Confluence segments of the Green River ($A = 0.06$, $p = 0.05$). Only two taxa were significant indicators of the 2001 samples (Lepidoptera and Nemata) and three taxa (*Mayatrichia*, *Fallceon* and *Dubiraphia*) of the 2010 samples. We observed no significant difference in macroinvertebrate metrics between the 2001 and 2012 sample years blocked by river segment (all p-values < 0.11)(data not shown).

Comparisons of contemporary macroinvertebrate assemblages to the historic, regional species pool

Differences between contemporary macroinvertebrate assemblages and the historic, pre-dam regional species pool of DINONM varied as a function of river segment, with the Yampa segment having the lowest number of extirpated taxa (9) (Table 3). After removing concordant species losses from other segments (i.e., background rates of species loss), the number of extirpated taxa peaked below Red Creek (20) and then decreased with distance downstream from FGD, with a low of only seven extirpated taxa in the Confluence river segment below the Yampa River. Among all river segments, taxa from the order Ephemeroptera comprised over 56% of extirpated taxa.

Status and trend of invasive invertebrates within DINONM

The only two invasive invertebrates consistently collected in the Green and Yampa Rivers throughout DINONM were *Potamopyrgus antipodarum* (New Zealand mudsnail) and *Orconectes virilis* (Northern or Virile crayfish) (Table 4). *Orconectes virilis* was more consistently found throughout all three river segments, especially in the 2010 and 2011 samples when baited minnow traps were deployed. In contrast, *Potamopyrgus antipodarum* was only been sporadically collected in the Lodore and Confluence study segments. For the single quantitative sample containing *Potamopyrgus antipodarum*, density was less than three individuals/m^2.

Discussion

In this study we sought to quantify the impacts of FGD on macroinvertebrate assemblages within DINONM, as well as the potentially remediating effects of the largely unregulated Yampa River. We paired short-term monitoring of a recently established network of sentinel sites with exhaustive contemporary and historical macroinvertebrate inventories to quantify the extent of species extirpations and alterations to assemblage composition. Our results largely support the downstream recovery trajectories of macroinvertebrate assemblages outlined by the serial discontinuity concept (Ward and Stanford, 1983) and highlight the importance of maintaining unregulated tributaries, both small (Red and Vermillion Creeks) and large (Yampa River), to sustain the structure and function of the intensively regulated Green River. In contrast, short-term responses to a decadal flood event did not suggest significant remediating effects for macroinvertebrate assemblages within DINONM, as we observed only nominal short-term changes in assemblage composition.

Contemporary differences in macroinvertebrate assemblages among river segments and comparisons to the historic, regional species pool

The serial discontinuity concept predicts that the rate of downstream recovery from dams will vary as a function of the size and location of the dam within a watershed and the location and size of tributary inputs (Ward and Stanford, 1983; Stanford and Ward, 2001). Given the infrequency and size of tributary inputs and the geographic isolation of the Green River, we would expect only minor recovery above the confluence with the Yampa River and overall recovery may be constrained by larger scale factors (e.g., degraded special pool, geographic isolation of source populations, dispersal constraints). Our results largely supported these predictions, with little to no recovery observed below Red Creek, a small tributary (363 km^2) relative to the Green River (50,116 km^2). Rather, both historical and contemporary analyses suggest the persistence of significant compositional differences until the confluence with the larger Yampa River (19,839 km^2). For example, species loss in comparison to pre-dam conditions peaked in the segment below Red Creek and exhibited the greatest declines in the Lodore and Confluence study segments, where we conservatively estimated species loss at nine and seven taxa, respectively (Table 3). Our estimates represent less than half the number of taxa previously reported as missing from DINONM (Vinson et al., 2002); however, we believe our estimates are more accurate because of the collection of over 180 qualitative and quantitative samples at 33 unique stations over an eleven year time period. This is in comparison to the 13 samples initially collected at eight unique stations in a single year by Vinson et al., (2002).

For the taxa missing from contemporary Green River samples (2001 – 2011) within DINONM, but present in the pre-dam regional species pool (Table 3), we offer the following explanations. *Atherix*, *Ameotropus*, *Claassenia*, *Perlesta* and Siphlonuridae have likely been extirpated from the Green River as they have not been found in more than 180 samples collected over an eleven year period; a sampling effort far more exhaustive than that conducted prior to dam closure. Of these, *Atherix*, *Ameotropus*, *Claassenia* and Siphlonuridae maintain viable populations in the Yampa, but at very low densities. Taxa likely to be locally extirpated from Lodore, but present in the Confluence segment include *Hexatoma*, *Brachycercus* and *Ephemera*. In contrast, additional taxa absent from either Lodore or the Confluence segments (*Caenis*, *Calibaetis*, *Hexagenia*, *Leptophlebia*, *Isogenoides*, *Gerris*, Vellidae) were likely missed from our collections, as they are commonly collected up and/or downstream of the river segment in which they were noted as absent. Collectively, the taxa thought to be conclusively extirpated represent four Ephemeroptera, two Diptera and a single Plecoptera. All but *Claassenia* can be characterized as exhibiting preferences for depositional habitats where individuals are known to burrow into fine sediments and/or or cling to aquatic vegetation (Merritt and Cummins, 1996; Poff et al., 2006).

While macroinvertebrate assemblages of the Lodore study segment were not nearly as depauperate as observed immediately below FGD, contemporary comparisons between the Yampa and Lodore segments demonstrate the persistence of significant differences in assemblage composition prior to the confluence with the Yampa River. Specifically, given the paucity of quantitative historic data, we used a space for time substitution with contemporary data collected at sentinel sites on the Lodore and Yampa study segments to quantify persistent differences in assemblage composition. Historically, the Yampa and Green Rivers are thought to have been very similar in terms of hydrology (Fig. 2), geomorphology and water quality (Woodbury, 1963; Andrews, 1986; Merritt and Cooper, 2000). Similarly, we provide anecdotal evidence that macroinvertebrate assemblages were historically quite similar; all but two taxa historically found on the Yampa were also collected within Lodore and many of the taxa identified as significant indicators of the Yampa or Confluence segments were also historically present within Lodore.

Contemporary Yampa River macroinvertebrate assemblages were distinct from Lodore by having a greater richness and density of individuals from the EPT orders; 85 percent of Yampa indicator taxa were from these orders in comparison to 50% for Lodore. The dominance of EPT taxa, in particular Ephemeroptera, is similar to the pre-dam Green River composition described by Vinson (2001) and presented in Appendix 2. In contrast, Lodore had a greater richness and density of taxa from the orders Coleoptera, Hemiptera and Gastropoda, which were poorly represented in both other river segments and the historic, regional species pool. Taxa unique to Lodore generally differed in their habitat preferences, life histories and functional roles and likely reflect fundamental differences in the contemporary biophysical templates of the two systems (See additional discussion below). In contrast, the similarity in assemblage composition between the Yampa and Confluence segments suggests that the Yampa has significant remediating effects on the composition of macroinvertebrates within the Green River.

Vinson (2001) suggested that partial macroinvertebrate recovery below Red Creek could be attributed to incremental restoration of the thermal regime and fine sediment loading resulting from tributary inputs, principally Red Creek. Andrews (1986) and Grams and Schmidt (2002) identified Red and Vermillion Creeks as the most significant sediment inputs besides bank erosion prior to the confluence with the Yampa, suggesting the potential for significant geomorphic influences. However, Vinson (2001) hypothesized that depauperate assemblages persisted both above and below Red Creek because of the establishment of predatory amphipods, the paucity of viable source populations combined with limited dispersal capabilities and continued deviations in the thermal regime from pre-regulation conditions. Given the dearth of spatially explicit environmental data, we can only speculate on the transferability of several of these and other hypotheses to DINONM.

The absence of predatory amphipods from Lodore negates the applicability of this hypothesis to DINONM; however, we did observe high predatory richness within Lodore (55%) relative to the Yampa (30%) and Confluence (10%) study segments. Despite the high richness of predatory taxa, their compositional abundance was less than 15% and many of the observed predatory taxa (e.g., Diptera: *Clinocera*, *Chelifera*,Tanypodinae; Hemiptera: *Corisella*, *Gerris*, Naucoridae) are not likely to exhibit top-down control on assemblage composition because their distribution is likely limited to lentic-like microhabitats in an otherwise large, fast-flowing river. As for persistent thermal alterations, no temporally explicit data is available for this portion of the river, but the geographic distance (75 km) combined with the high width to depth ratios and high rates of incoming solar radiation likely interact to restore diel and annual variation to pre-dam conditions (O'Keeffe and Palmer, 1990; Munn and Brusven, 1991). Rather we believe altered assemblages persist in the Lodore segment because of persistent alterations to the hydrogeomorphic template.

FGD has fundamentally changed the physical template of the Green River through DINONM by increasing hydrogeomorphic stability and water clarity. Specifically, FGD has reduced the frequency and magnitude of flood events and depleted fine sediment sources causing a more stable hydrograph, channel narrowing, reductions in the frequency and magnitude in which tributary debris flows are reworked and the source and subsequent depositional patterns of fine sediment (Andrews 1986; Grams and Schmidt, 2002; Larsen et al., 2004). The benign environmental conditions promoted by hydrologic stabilization appear to be selecting for increased proportional richness of predatory taxa having longer life spans on average (40% of the taxa in Lodore exhibit life cycles lasting more than one month compared to less than 6% in the Yampa [e.g., *Gerris*, *Corisella*, *Gomphus*, *Agabus*, *Dubiraphia*) within Lodore. Predator richness and efficiency has been shown to increase under more benign or altered hydrologic regimes (Power et al., 1988; Peckarsky et al., 1990; Miller et al., 2010) and overall food chain length is predicted to decrease with increasing disturbance (Power et al., 1996). Lastly, increases in the proportion of low velocity, depositional habitats have been linked to elevated vascular plant richness and density in the formerly active channel, which likely changed the type and quantity of microhabitats available on the Green River (Merritt and Cooper, 2002; Vinson et. al.,, 2012). The composition of Lodore's indicator taxa disproportionately prefer lentic or lotic-depositional habitats (61% compared to 25% in Yampa). Collectively, differences in functional feeding groups, life span and microhabitat preferences of taxa characteristic of Lodore are consistent with more stable hydrogeomorphic conditions.

The establishment of submerged aquatic vegetation (e.g., *Chara*, *Cladophora*, *Amblystegium riparium*) was further facilitated by reductions in suspended sediment concentrations, which greatly increased water clarity (Vinson et. al.,, 2012). Pre-dam turbidity estimates are not available, but Andrews (1986) estimated that suspended sediment concentrations decreased from 3,266 x 10^6 kg year^{-1} to near zero following dam closure. Furthermore, in a contemporary comparison of water clarity between the Green and Yampa Rivers, Vinson et. al., (2012) found turbidity ranged from 0.3 to 310 NTUs on the Yampa, while concentrations rarely exceeded two NTUs on the present day Green River. These observations are consistent with those of the SDC, which predicts changes in the trophic basis for production where larger rivers are 'reset' to act more like lower order systems supported by autochthonous energy sources (Ward and Stanford, 1983; Stevens et al., 1997; Stanford and Ward, 2001). In their test of the SDC in the Colorado River below Glen Canyon Dam, Stevens et al., (1997) found that macroinvertebrate assemblage composition was mediated by dam-induced turbidity reductions, which changed the trophic basis supporting secondary production by altering both the standing stock and composition of primary producers. Similarly, Vinson et. al., (2012) attributed the greater richness and abundance of submerged aquatic vegetation in Lodore compared to the Yampa to increased water clarity and greater bed stability.

Temporal patterns of macroinvertebrate assemblages within the Green River, DINONM

Macroinvertebrate assemblages within DINONM appeared relatively stable over both short and long-term timescales. We failed to detect significant changes in macroinvertebrate assemblage composition between 2001 to 2010 suggesting no systematic, directional change through time, although considerable interannual variability in response to climatic conditions may exist (Scarsbrook, 2002; Collier, 2008). Over a shorter time frame, the 2011 flood event significantly altered macroinvertebrate assemblage composition by reducing overall taxa richness, while other metrics exhibited no differences. The observed responses were surprising, especially for macroinvertebrate density, given the fairly consistent declines observed in past studies for both natural and controlled flood events (Robinson et al., 2003; Vinson et al., 2006; Cross et al., 2011). We are uncertain as to why density reductions were not more significant and will continue to evaluate macroinvertebrate response and recovery patterns to the 2011 flood event in 2012. Lastly, we were surprised that Lodore's response to the flood was muted as compared to the Yampa and Confluence segments (Fig. 7) given the homogenization of the Green's hydrologic regime and the subsequent novelty of this hydrologic event to the macroinvertebrate assemblages within Lodore (Poff, 1992; Lytle and Poff, 2004); since dam closure, this was only the eighth flood event greater than power plant capacity (130 $m^3 sec^{-1}$). Overall, compositional differences among segments imposed by the current and historical management of FGD appeared greater than those imposed by the flood event.

Status and trend of invasive invertebrates within DINONM

Despite the highly altered environmental conditions imposed by FGD on the Green River through DINONM, the establishment and spread of invasive aquatic invertebrates does not appear to be a pervasive problem. The Northern Cray fish is distributed throughout the Green and Yampa Rivers within DINONM, while the New Zealand mudsnail appears limited to the Green River. In all instances, densities were extremely low and do not appear to be increasing through time suggesting that these species are not likely to exhibit inordinately large effects on native species and ecosystem function; however, more accurate estimates of crayfish densities are needed.

Conclusions

The results of our study highlight the importance of both small and large tributaries in remediating the Green River throughout DINONM. Conservation of the natural hydrologic, thermal and sediment regimes of tributary inputs should therefore be paramount in all management plans. Despite the significant remediating effects of the Yampa and other tributaries, persistent hydrogeomorphic and water quality alterations within Lodore maintain macroinvertebrate assemblages in an alternative steady state. Further research is needed to understand the effects of compositional differences on food web structure and function and the subsequent ecological stability of the system. For example, Cross et al., (2011) found that rainbow trout production was strongly tied to discharge mediated changes in the type and quality of secondary production, particularly declines in the nonnative invertebrates *Potamopyrgus antipodarum* and *Gammarus lacustris* on the Colorado River below Glen Canyon Dam. Given ongoing efforts to restore native biodiversity within the Green River, including the management of several listed fishes, understanding the susceptibility of the system to invasion and the nature of food web interactions is critical to informing adaptive management decisions.

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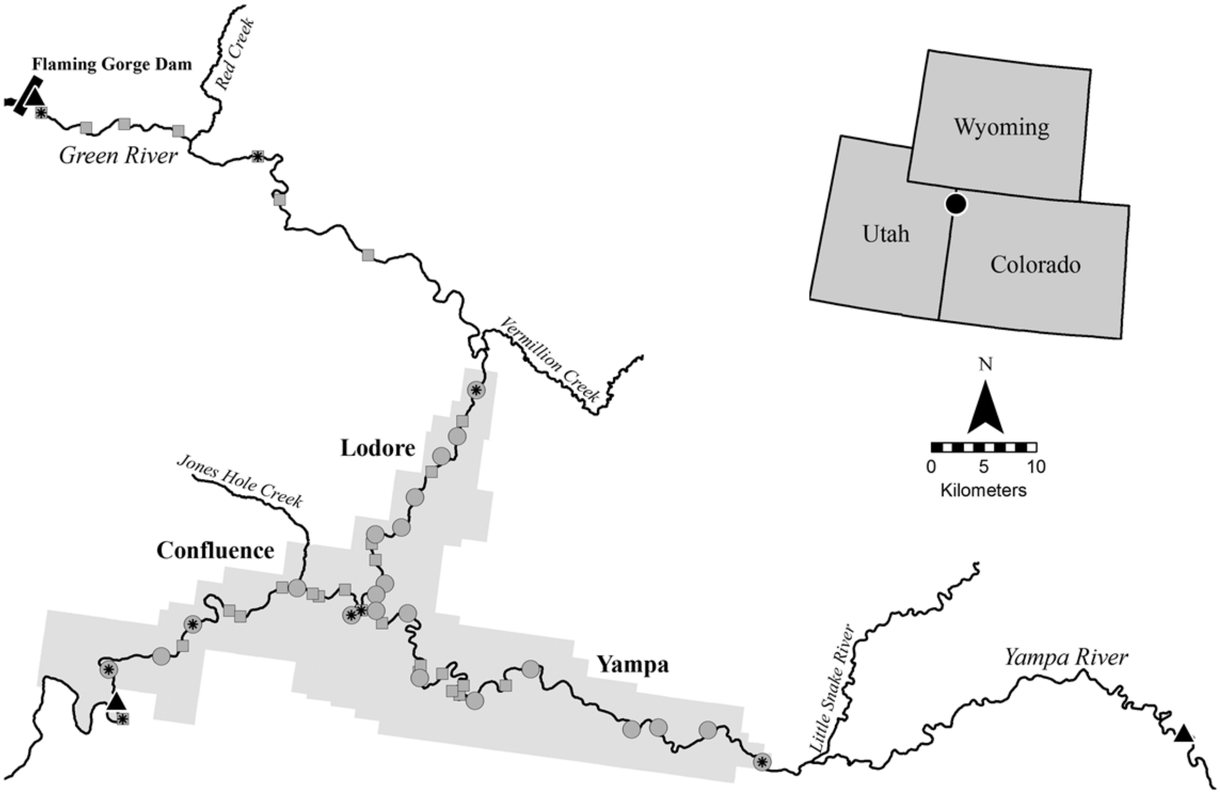

Figure 1. Map of study area illustrating the location of Dinosaur National Monument within Utah and Colorado (inset) and the boundaries of the monument along the Green and Yampa Rivers (grey shading). Also shown are the locations of Flaming Gorge Dam, USGS streamflow gages (triangles), study segments (Lodore, Yampa and Confluence), and sample sites. Samples sites are coded by sentinel (circles), non-sentinel (squares) and historical (asterix).

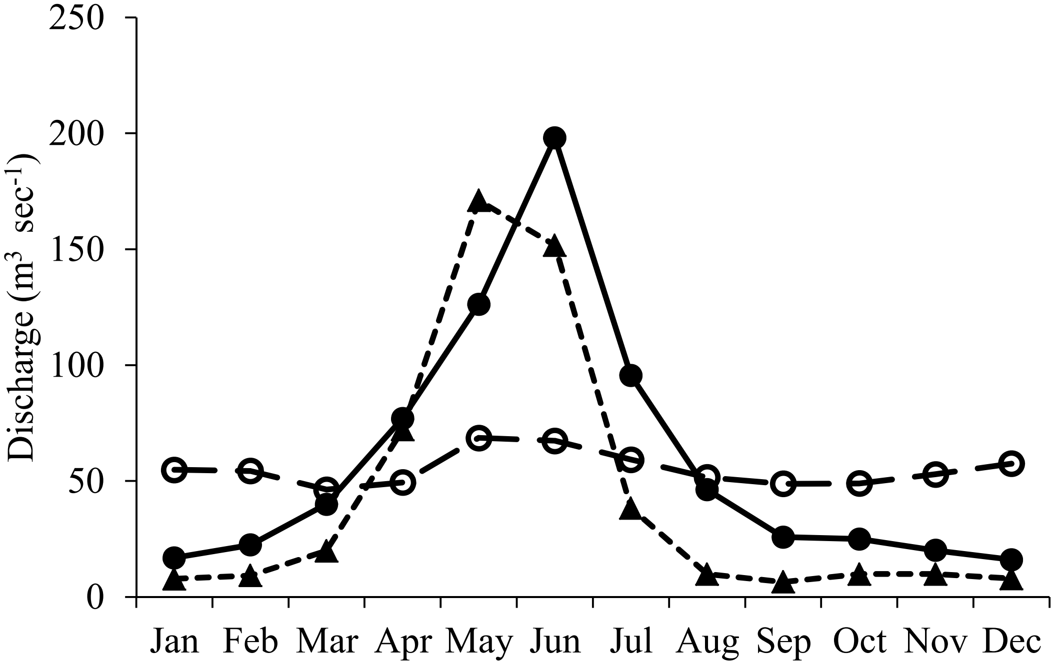

Figure 2. Average monthly discharge compared between the Green River at Greendale, pre- (1951 – 1962; filled circles) and post-dam (1963 – 2011; hollow circles), and the Yampa River at Maybell (1951 – 2011; solid triangles).

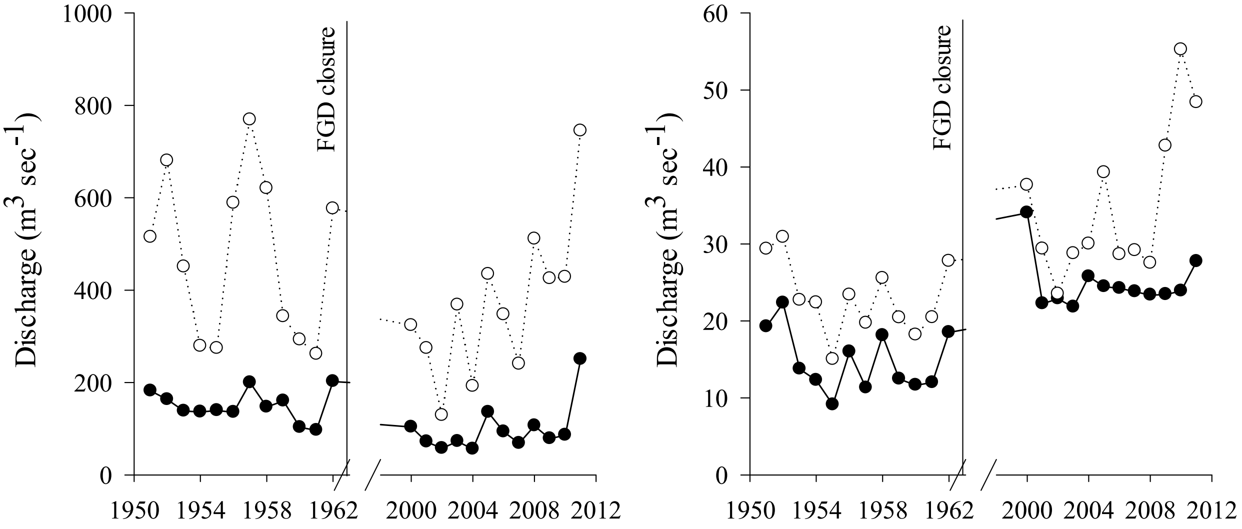

Figure 3. Annual 30-day maximum (left) and minimum (right) discharge values compared between pre-dam (1951 – 1962) and post-dam (2000 – 2011) hydrographs for the Green River at Greendale (solid circles) and at Jensen (hollow circles).

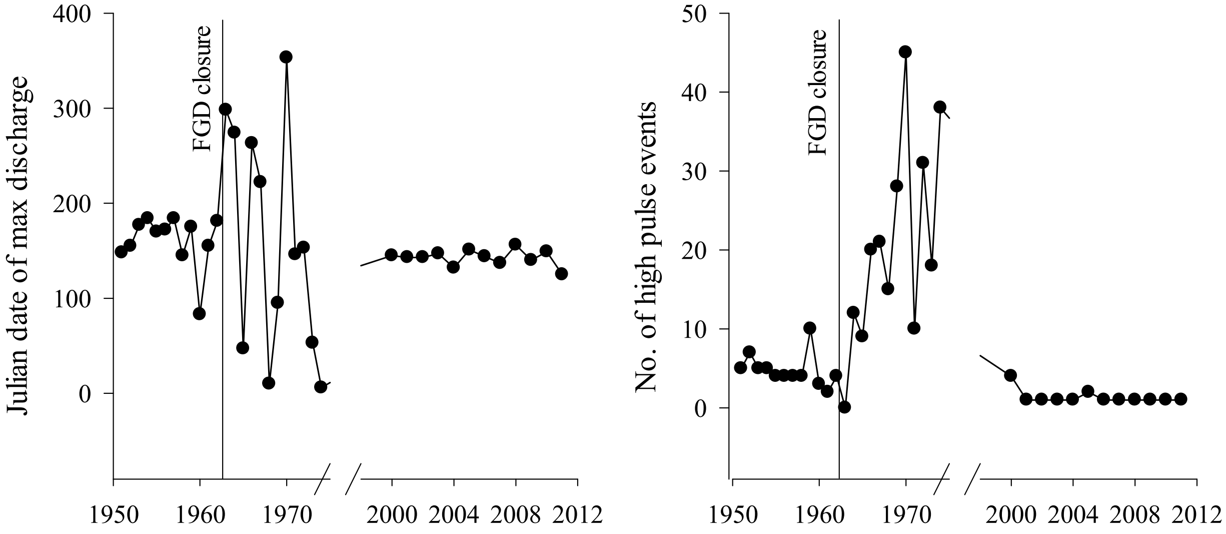

Figure 4. Julian date of the maximum annual discharge (left) and the number of high flow pulse events per year (right) compared among pre-dam (1951 – 1962), the decade following dam closure (1963 – 1974) and contemporary conditions (2000 – 2011).

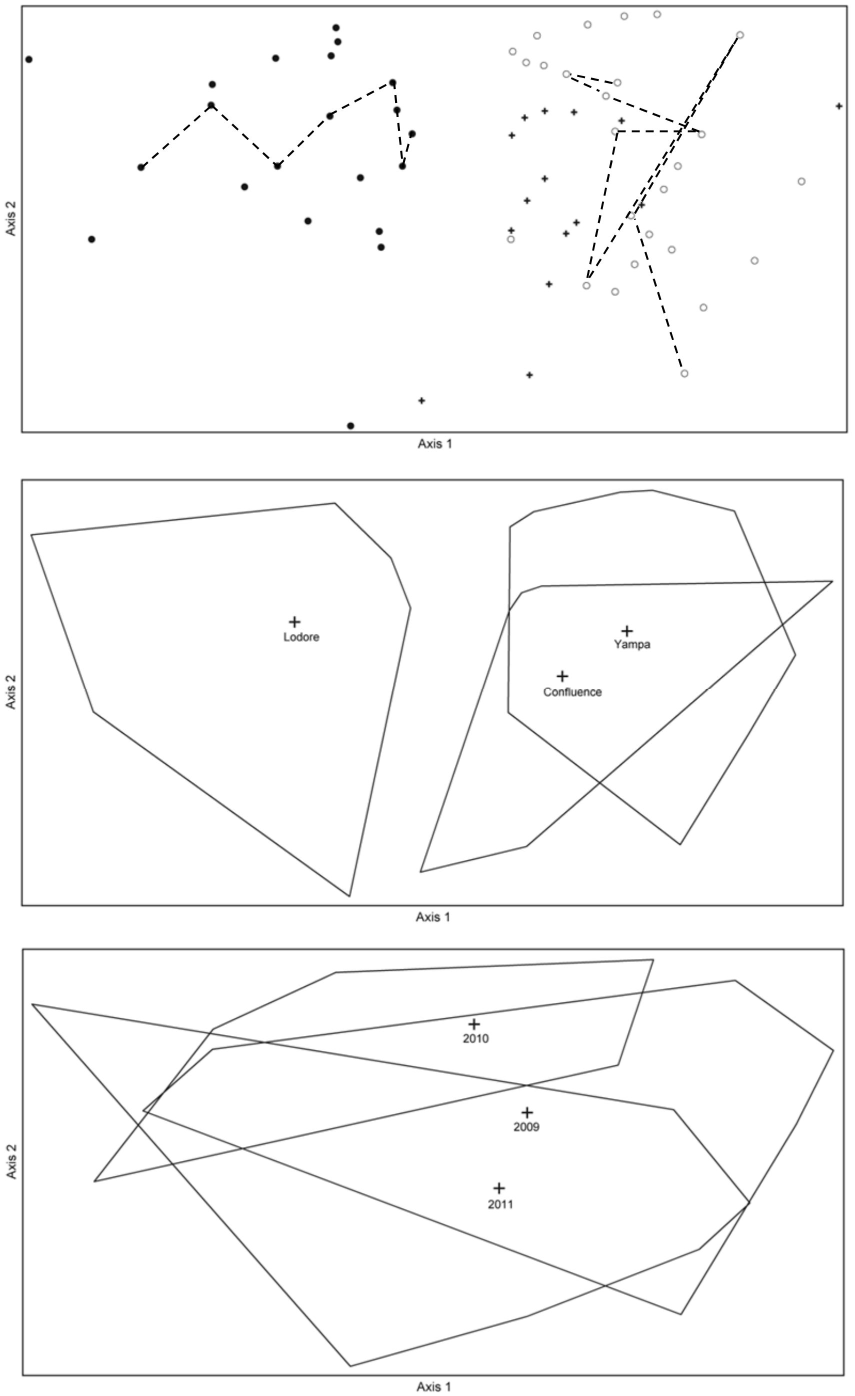

Figure 5. Non-metric multidimensional scaling (NMS) ordination of macroinvertebrate assemblages sampled at 21 sentinel sites from 2009 – 2011on the Green and Yampa Rivers within DINONM. The top panel plots individual samples grouped by river segment for Lodore (solid circles), Yampa (hollow circles) and Confluence (plus signs). Included in the top panel are dashed lines connecting successive downstream samples for both the Lodore and Yampa segments in 2009 to characterize the nature of within segment longitudinal gradients for a single year; upstream is on the left and right side of the ordination, respectively. The middle and bottom panel plots the convex hull area for samples grouped by river segment and year, respectively, with centroid labels shown.

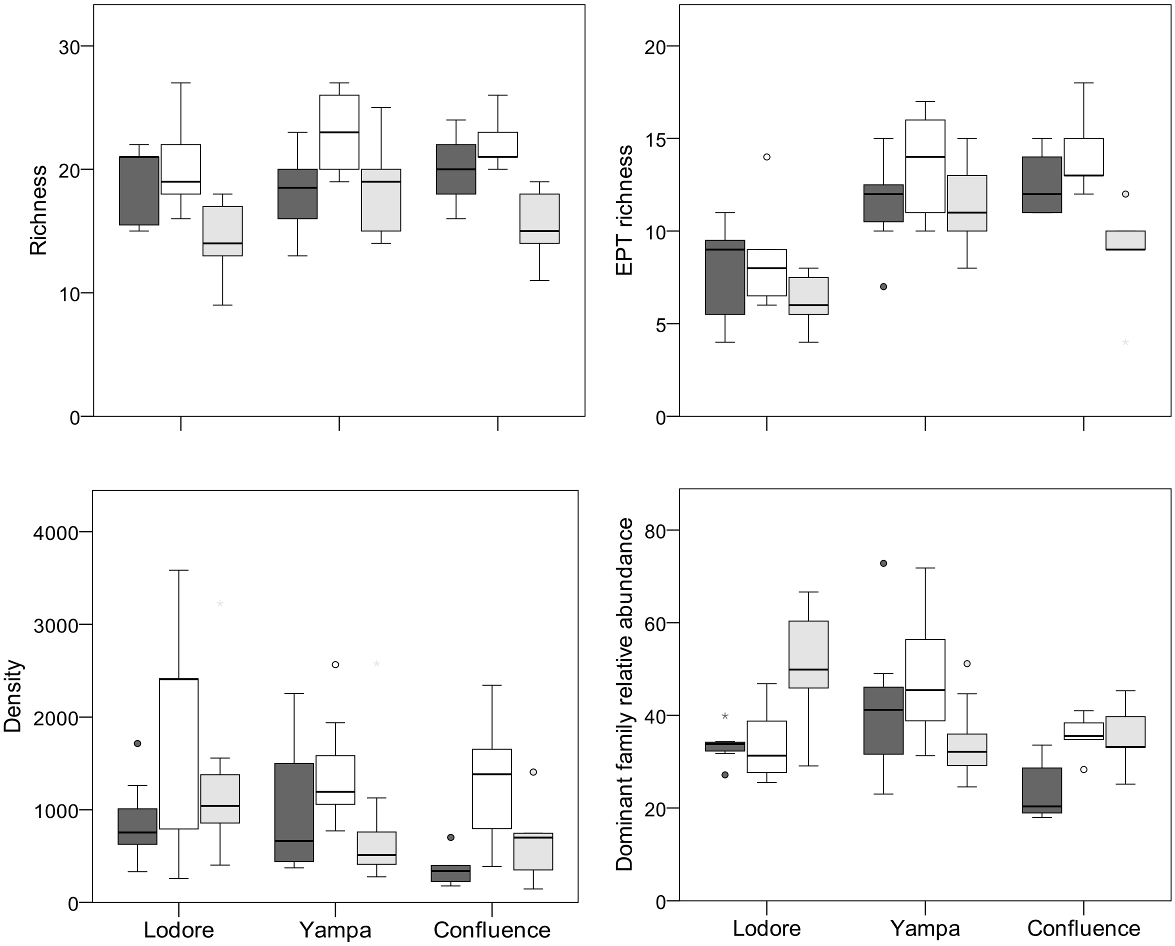

Figure 6. Macroinvertebrate richness, EPT richness, density and relative abundance of the dominant family compared among years (2009: dark grey; 2010: hollow; 2011: light grey) grouped by river segment.

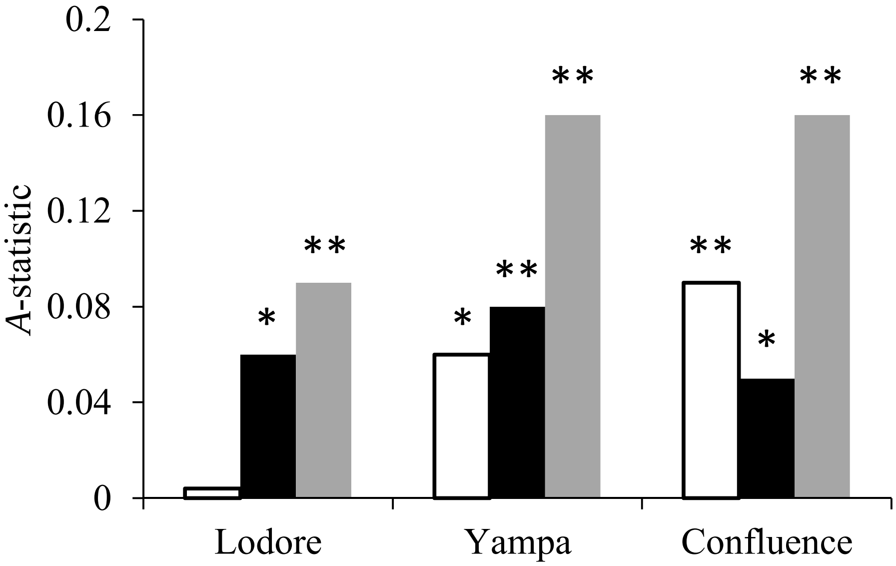

Figure 7. Results of MRPP (*A*-statistics) testing for differences among sample years (1999 – 2010: hollow; 1999 – 2011: black; 2010 – 2011: grey), blocked by study segment. Note that *A*-statistics range from 0 to 1, with values above 0.15 indicating moderately high differences among groups for ecological data (McCune and Grace, 2002). Statistical significance indicated by a single (alpha < 0.05 and > 0.01) or double (alpha < 0.01) asterix.

Table 1. Indicators of hydrologic alteration used to compare pre- and post-dam median hydrologic conditions on the Green River at the Greendale and Jensen gages. Post-dam conditions were assessed for the decade immediately following dam closure (1963-1974) and for contemporary conditions (2000-2011). The degree of hydrologic deviation per parameter was assessed using the Range of Variability Approach (RVA).

	Greendale						Jensen					
	Decade following dam closure			Contemporary conditions			Decade following dam closure			Contemporary conditions		
	Pre	Post	RVA	Pre	Post	RVA	Pre	Post	RVA	Pre	Post	RVA
Annual CV	1.0	0.6	NA	1.0	0.8	NA	1.3	0.8	NA	1.3	1.2	NA
7-day min	10.9	20.1	-0.8	10.9	23.7	-1.0	17.2	40.5	-1.0	17.2	28.4	-1.0
30-day min	13.1	26.9	-0.8	13.1	23.8	-1.0	22.5	47.8	-1.0	22.5	29.7	-0.8
7-day max	209.9	107.3	-1.0	209.9	128.3	-1.0	645.4	426.9	1.0	645.4	482.5	0.8
30-day max	143.1	94.4	-1.0	143.1	82.1	-1.0	482.4	352.1	1.5	482.4	357.4	0.8
Baseflow index	0.2	0.3	-1.0	0.2	0.6	-1.0	0.2	0.3	-1.0	0.2	0.4	-1.0
Date of min	181.5	304.0	-0.4	181.5	205.0	0.2	340.0	308.5	-0.8	340.0	250.5	-0.8
Date of max	171.0	74.0	-1.0	171.0	143.5	-0.8	153.0	144.5	-0.3	153.0	146.5	-0.3
Low pulse count	6.0	2.0	-1.0	6.0	0.0	-1.0	4.5	0.0	-0.8	4.5	2.5	-0.4
Low pulse duration	6.25	1.64	-0.5	6.25	2	-1.0	8.75	2	-1.0	8.75	6.5	-0.3
High pulse count	4.0	19.0	-1.0	4.0	1.0	-0.9	2.0	4.0	-0.5	2.0	4.0	-0.5
High pulse duration	14.75	1.034	-1	14.75	16.25	1.5	44.5	3.25	-0.5	44.5	39	-0.25

Table 2. Taxa identified by indicator species analysis as being significant indicators and having exclusive occurrence within a study segment (1), significant indicator values (2) and taxa identified from qualitative species lists as being unique to a particular study segment (3).

Order / other	Lodore	Yampa	Confluence
Coleoptera	*Dubiraphia*[2]		*Berosus*[3]
	Optioservus[2]		*Heterlimnius corpulentus*[3]
	Agabus[3]		*Hydraena*[3]
	Dineutus[3]		*Tropisternus*[3]
	Stictotarsus[3]		
Diptera	*Chelifera/Metachela/Neoplasta*[1]	*Atherix*[1]	Blephariceridae[2]
	Chironominae[2]	*Aedes*[3]	*Antocha*[3]
	Tanypodinae[2]	*Atherix pachypus*[3]	*Molophilus*[3]
	Ceratopogon[3]	*Caloparyphus*[3]	
	Clinocera[3]	*Euparyphus*[3]	
	Limonia[3]	*Psychoda*[3]	
	Tabanus[3]		
Ephemeroptera	*Centroptilum*[2]	*Leucrocuta*[1]	*Asioplax*[2]
	Pseudocloeon[2]	*Ameletus*[2]	*Ephemerella*[2]
	Drunella doddsii[3]	*Camelobatidius*[2]	*Ephoron*[2]
	Drunella grandis[3]	*Rhithrogena*[2]	*Heptagenia*[2]
	Hexagenia limbata[3]	*Acerpenna pygmaea*[3]	*Traverella*[2]
	Lachlania saskatchewanensis[3]	*Ametropus albrighti*[3]	*Apobaetis etowah*[3]
		Procloeon[3]	
		Siphlonurus[3]	
Gastropoda	*Lymnaea*[1]		*Fluminicola coloradoensis*[3]
	Physa[1]		
	Gyraulus[3]		
Hemiptera	Corixidae[2]		
	Naucoridae[2]		
	Corisella[3]		
	Gerris[3]		
	Hesperocorixa[3]		
	Trichocorixa[3]		
Odonata	*Enallagma annexum* group[3]	*Corydalus*[2]	
	Gomphus[3]	*Aeshna eremita*[3]	
Plecoptera	*Isoperla*[1]	*Acroneuria*[1]	*Malenka*[3]
	Sweltsa[3]	*Claassenia*[1]	
		Isogenoides[2]	
		Claassenia sabulosa[3]	

Table 2. Taxa identified by indicator species analysis as being significant indicators and having exclusive occurrence within a study segment (1), significant indicator values (2) and taxa identified from qualitative species lists as being unique to a particular study segment (3).

Order / other	Lodore	Yampa	Confluence
		Diura knowltoni[3]	
		Skwala americana[3]	
Trichoptera	*Helicopsyche*[1]	*Neotrichia*[1]	*Mayatrichia*[2]
	Rhyacophila coloradoensis group[1]	*Cheumatopsyche*[2]	*Limnophila*[3]
	Hydroptila[2]	*Culoptila/Protoptila*[2]	
	Oligophlebodes[3]	*Leucotrichia*[3]	
	Onocosmoecus unicolor[3]		
Other	*Hyalella*[2]		Acari[2]
	Oligochaeta[2]		*Gammarus lacustris*[3]
	Hygrobates[3]		

Table 3. Taxa missing from contemporary samples (2001 – 2010) in comparison to the historic, regional species pool of DINONM grouped by river segment ('X' indicates absence). Shown at the bottom are raw totals and corrected totals of extirpated species per segment.

		Study Segment				
Order	Genus / family	Yampa	Above Red Creek	Below Red Creek	Lodore	Confluence
Amphipoda	*Gammarus*	X			X	
Coleoptera	*Gyrinus*	X	X			
Diptera	*Atherix*		X	X	X	X
	Hexatoma		X	X	X	
Ephemeroptera	*Acentrella*		X	X		
	Ametropus		X	X	X	X
	Brachycercus	X	X	X	X	
	Caenis		X		X	
	Callibaetis					X
	Camelobaetidius		X	X		
	Epeorus	X			X	X
	Ephemera			X	X	
	Ephoron			X		
	Hexagenia	X				X
	Isonychia	X		X		
	Leptophlebia			X	X	
	Oligoneuridae		X	X		
	Pseudiron		X	X		
	Rhithrogena			X		
	Siphlonuridae		X	X	X	X
	Traverella		X	X		
Hemiptera	*Aquarius*		X			
	Gerris		X			X
	Notonectidae	X	X			
	Veliidae		X	X		X
Megaloptera	*Corydalus*		X	X		
Odonata	*Argia*		X	X		
Plecoptera	Chloroperlidae	X	X	X		X
	Claassenia			X	X	X
	Isogenoides			X	X	
	Perlesta	X	X	X	X	X
Trichoptera	*Nectopsyche*			X		
Total no. of extirpated taxa[1]		9	20	23	13	11
Corrected no. of extirpated taxa		NA	15	20	9	7

[1] Reported numbers of extirpated taxa differ from those of Vinson 2001 because of standardizations of macroinvertebrate identifications to operation taxonomic units in our analyses.

Table 4. Frequency of occurrence for the invasives *Potamopyrgus antipodarum* (New Zealand mudsnail) and *Orconectes* (crayfish) by study segment and year. Frequency of occurrence is computed as the ratio of the total number of observed sites where a particular invasive was found to the total number of sites sampled.

		Year										
Study Segment	Taxa	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010[3]	2011[3]
Lodore	*Orconectes*[1]	0	0	0	NA[2]	0	0	0	NA	0	13	11
	Potamopyrgus antipodarum	0	0	0	NA	0	25	0	NA	0	0	0
Yampa	*Orconectes*[1]	0	12	0	0	0	0	11	0	0	11	14
	Potamopyrgus antipodarum	0	0	0	0	0	0	0	0	0	0	0
Confluence	*Orconectes*[1]	0	14	20	0	0	0	0	NA	0	0	14
	Potamopyrgus antipodarum	0	0	0	0	0	0	0	NA	0	14	0

[1] 64% of collected *Orconectes* were positively identified as *Orconectes virilis* (Northern or Virile crayfish)

[2] NA reported when no samples were collected from a particular study segment within a given year

[3] Sampling effort for Orconectes was greater in 2010 and 2011 among all river segments

Appendix 1. Historic and contemporary macroinvertebrate sample sites grouped by study segment. Also indicated are whether a site is considered a sentinel monitoring site and the total number of qualitative and quantitative samples collected per site by time period.

Study segment	Location description	River Mile	Sentinel	Historical (1958-1962)	Contemporary (2001-2008)		Sentinel (2009-2011)	
					Quantitative	Qualitative	Quantitative	Qualitative
Yampa	Confluence with Green River	0	N	1	9	8	0	0
	Mouth of Sand Canyon	1	Y	0	0	0	3	1
	Box Elder Campground	2	N	0	1	3	0	0
	Warm Springs Rapid	4	Y	0	2	3	3	0
	Laddie Park	11	Y	0	4	6	3	0
	Burro Park	12.5	N	0	0	0	0	1
	Cleopatra's Couch	16	N	0	0	2	0	3
	Mather's Hole	18	N	0	3	4	0	0
	Upstream from Mathers Hole	19	N	0	1	3	0	0
	Harding Hole	20	Y	0	4	6	3	0
	Upstream from Big Joe Rapid	24	N	0	3	5	0	0
	Below 5 Springs	26	Y	0	0	0	3	1
	Near Haystack Rock	34	Y	0	1	1	3	0
	Ponderosa Campground	37	Y	0	2	4	2	1
	Anderson Hole	41.7	Y	0	5	6	3	0
	Deerlodge Campground	46	Y	1	2	3	3	0
Lodore	Above confluence of Yampa River	226	Y	0	3	3	3	0
	Above Limestone Campground	227.8	Y	0	2	3	2	1
	Wild Mountain Campground	229.5	N	0	2	2	0	0
	Rippling Brook Campsite	230.5	N	0	2	1	0	0
	Below Hells Half Mile	231	Y	0	0	0	3	0
	Upstream from Triplett Falls	233	Y	0	7	12	3	0
	Pot Creek Campsite II	235.5	Y	0	1	2	3	0
	Upstream from Disaster Falls	237	N	0	1	3	0	0
	Buster Basin Debris Flow	238	Y	0	2	1	3	0
	Upstream from Winnie's Rapid	240.6	Y	0	7	14	3	0
	Gate of Lodore	242	N	0	2	2	0	0
	Lodore Ranger Station	243.5	Y	1	5	8	3	0
Confluence	Jensen USGS gage site	197	N	1	0	0	0	0

Appendix 1. Historic and contemporary macroinvertebrate sample sites grouped by study segment. Also indicated are whether a site is considered a sentinel monitoring site and the total number of qualitative and quantitative samples collected per site by time period.

Study segment	Location description	River Mile	Sentinel	Historical (1958-1962)	Contemporary (2001-2008)		Sentinel (2009-2011)	
					Quantitative	Qualitative	Quantitative	Qualitative
	Split Mountain boatramp	200	Y	2	3	2	3	0
	School Boy	204	Y	0	0	0	3	0
	Moonshine Rapid	206	N	0	0	1	0	0
	Rainbow Park	207.8	Y	1	1	3	3	0
	Big Island	213.5	N	0	4	6	3	0
	Cove Camp	215	N	0	1	1	0	0
	Compromise Camp	217	N	0	1	3	0	0
	Jones Hole	218.6	N	0	2	3	3	0
	Above Jones Hole	219	Y	0	0	0	3	0
	Stateline Campground	220	N	0	1	2	0	0
	Kabloohee debris fan	219.5	N	0	3	2	0	0
	Echo Park Dam Site	222.4	N	0	0	3	0	0
	Echo Park	224.3	Y	1	4	5	3	0
Below Red Creek	Swinging Bridge	259.8	N	0	34	2	11	0
	Swallow Rapid	265	N	0	34	3	12	0
	Taylor Flats Bridge	273.6	N	1	34	2	12	0
Above Red Creek	Grasshopper Island	280.8	N	0	34	2	12	0
	Upstream from Little Hole	283.3	N	0	34	3	33	0
	Secret Riffle	286.5	N	0	34	1	12	0
	Tail Race (immediately below FGD)	290	N	5	34	0	31	0

Appendix 2. Unique macroinvertebrate taxa found on the Green and Yampa Rivers grouped by study segment, 2001 – 2011; taxonomy not standardized to operational taxonomic units, but rather to the lowest taxonomic resolution per genus.

Order / Group	Scientific Name	Confluence	Lodore	Yampa
Amphipoda	*Gammarus*	■		
	Hyalella	■	■	■
Coleoptera	*Agabus*		▒	
	Berosus	▒		
	Chaetarthria			▒
	Cleptelmis	■	■	
	Dineutus		■	
	Dubiraphia vittata	■	■	■
	Gyrinus	▒	■	▒
	Helichus	▒	■	■
	Heterlimnius corpulentus	■		
	Hydraena	▒		
	Laccophilus maculosus	▒	▒	▒
	Microcylloepus pusillus	■	■	■
	Optioservus	■	■	■
	Ordobrevia nubifera		■	■
	Paracymus	▒	▒	
	Stenelmis	■	■	■
	Stictotarsus		▒	
	Tropisternus	▒		
	Zaitzevia parvulus	■	■	■
Decapoda	*Orconectes virilis*	■	▒	▒
Diptera	*Antocha*	■		
	Atherix pachypus			■
	Caloparyphus			■
	Euparyphus			▒
	Ceratopogon		■	
	Culicoides		■	■
	Dasyhelea	■	■	
	Probezzia	■	■	■
	Chelifera	■	■	■
	Neoplasta	■	■	
	Chironominae	■	■	■
	Clinocera		■	
	Aedes			▒
	Hemerodromia	■	■	■
	Hexatoma	■		■
	Limnophila	■		
	Limonia		■	
	Molophilus	■		
	Nemotelus	■	■	■
	Orthocladiinae	■	■	■

Appendix 2. Unique macroinvertebrate taxa found on the Green and Yampa Rivers grouped by study segment, 2001 – 2011; taxonomy not standardized to operational taxonomic units, but rather to the lowest taxonomic resolution per genus.

Order / Group	Scientific Name	Confluence	Lodore	Yampa
	Pericoma	■		■
	Psychoda			■
	Simulium	■	■	■
	Tabanus		░	
	Tanypodinae	■	■	■
	Tipula	■	■	■
Ephemeroptera	*Acentrella*	■	■	■
	Acerpenna pygmaea			■
	Ameletus	■	■	■
	Ametropus albrighti			░
	Apobaetis etowah	■		
	Asioplax edmundsi	■	■	■
	Baetis tricaudatus	■	■	■
	Brachycercus	■		
	Caenis amica	░		■
	Callibaetis		■	░
	Camelobaetidius similis	■	■	■
	Camelobaetidius warreni	■	■	■
	Centroptilum	■	■	■
	Choroterpes albiannulata/inoranta	■	■	■
	Cinygmula	■	░	
	Diphetor hageni		■	■
	Drunella doddsii		■	
	Drunella grandis		░	
	Ephemera simulans	■		■
	Ephemerella inermis/dorothea	■	■	■
	Ephemerella aurivillii			░
	Ephoron album	■	■	■
	Fallceon quilleri	■	■	■
	Heptagenia elegantula	■	■	■
	Hexagenia limbata		░	
	Isonychia campestris	■	■	
	Leptophlebia	░		■
	Leucrocuta petersi	■		■
	Maccaffertium terminatum		■	■
	Neochoroterpes	■		■
	Homoeoneuria alleni	■	░	░
	Lachlania saskatchewanensis		░	
	Paracloeodes	■		■
	Paraleptophlebia	■		■
	Procloeon			■

Appendix 2. Unique macroinvertebrate taxa found on the Green and Yampa Rivers grouped by study segment, 2001 – 2011; taxonomy not standardized to operational taxonomic units, but rather to the lowest taxonomic resolution per genus.

Order / Group	Scientific Name	Confluence	Lodore	Yampa
	Pseudiron centralis	▨	▨	■
	Pseudocloeon propinquum	■	■	■
	Rhithrogena	■	■	■
	Serratella	■	■	
	Siphlonurus			▨
	Traverella albertana	■	■	■
	Tricorythodes minutus	■	■	■
Gastropoda	*Ferrissia rivularis*	■		▨
	Fluminicola coloradoensis	■		
	Gyraulus		■	
	Lymnaea	■	■	■
	Oreohelix strigosa		▨	
	Physa	■	■	■
	Potamopyrgus antipodarum	■	▨	
Hemiptera	*Aquarius*	▨	▨	▨
	Sigara	■	■	■
	Trichocorixa		■	
	Corisella		▨	
	Hesperocorixa		▨	
	Gerris		■	
	Metrobates	▨		
	Ambrysus	■	■	■
	Notonecta	▨	▨	
	Rhagovelia		■	■
Lepidoptera	*Petrophila*	■	■	■
Megaloptera	*Corydalus cornutus*	■	■	■
Odonata	*Aeshna eremita*			▨
	Argia emma		■	■
	Argia moesta	■		
	Argia plana		▨	
	Hetaerina americana		■	■
	Hetaerina vulnerata		▨	
	Ophiogomphus severus	■	■	■
	Stylurus intricatus	▨	■	▨
	Gomphus		▨	
	Enallagma annexum group		▨	
Plecoptera	*Acroneuria abnormis*	■	■	■
	Capniidae		▨	■
	Sweltsa		■	
	Claassenia sabulosa			■
	Diura knowltoni			■
	Hesperoperla pacifica	■	■	▨

Appendix 2. Unique macroinvertebrate taxa found on the Green and Yampa Rivers grouped by study segment, 2001 – 2011; taxonomy not standardized to operational taxonomic units, but rather to the lowest taxonomic resolution per genus.

Order / Group	Scientific Name	Confluence	Lodore	Yampa
	Isogenoides elongatus	■		
	Isogenoides zionensis			■
	Isoperla	■	■	■
	Malenka	■		
	Skwala americana			■
	Zapada	■	■	
Rhynchobdellida	*Helobdella stagnalis*		■	▒
Trichoptera	*Agapetus*		▒	
	Brachycentrus americanus			■
	Brachycentrus occidentalis	■	■	■
	Cheumatopsyche	■	■	■
	Culoptila	■	■	■
	Helicopsyche borealis	■	■	■
	Hydropsyche	■	■	■
	Hydroptila	■	■	■
	Lepidostoma	■		■
	Leucotrichia			■
	Limnephilus	■	▒	
	Mayatrichia	■	■	■
	Micrasema	■	■	
	Nectopsyche	■	■	▒
	Neotrichia	■	■	■
	Oecetis	■	■	■
	Oligophlebodes		■	
	Onocosmoecus unicolor		▒	
	Polycentropus	■	■	■
	Rhyacophila betteni group		▒	
	Rhyacophila brunnea/vemna group	■	■	
	Rhyacophila coloradensis group		■	
	Rhyacophila grandis group	■		
	Smicridea	■	■	■
Trombidiformes	*Hygrobates*		■	
	Lebertia	■	■	■
	Sperchon	■	■	■
	Torrenticola	■		■
Veneroida	*Pisidium*		■	■
	Sphaerium simile	▒		▒
Other	*Oligochaeta*	■	■	■
	Turbellaria	■	■	