Salmonid Abundance and Distribution in the middle Green River

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ABSTRACT

Salmonid abundance and distribution in the Green River between Flaming Gorge Dam the Split Mountain Boat Ramp (middle Green River, Figure 1) are governed by recruitment, habitat requirements and interspecific competition, played out on the framework of the Green river hydrology and geomorphology. Although salmonids historically did not inhabit the middle Green River after the end of the last glaciation, construction of the Flaming Gorge Dam in 1962 drastically reduced water temperature and silt in the middle Green River, creating habitat that meets salmonid needs for cool, clear water. The tail water and downstream section of the Green support four types of salmonids: brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), Snake River cutthroat trout (*Oncorhynchus clarki bouvieri*), and mountain whitefish (*Prosopium williamsoni*).

While the brown trout and the whitefish are self- sustaining populations, the rainbow and cutthroat trout are maintained through a large stocking effort (Schneidervin 2006, personal communication). Salmonid abundance patterns result from both food availability and the influx of new trout every year through natural reproduction and stocking.

With the exception of *P. williamsoni*, the salmonids are closely related and have very similar habitat requirements. On a broad scale, temperature and food

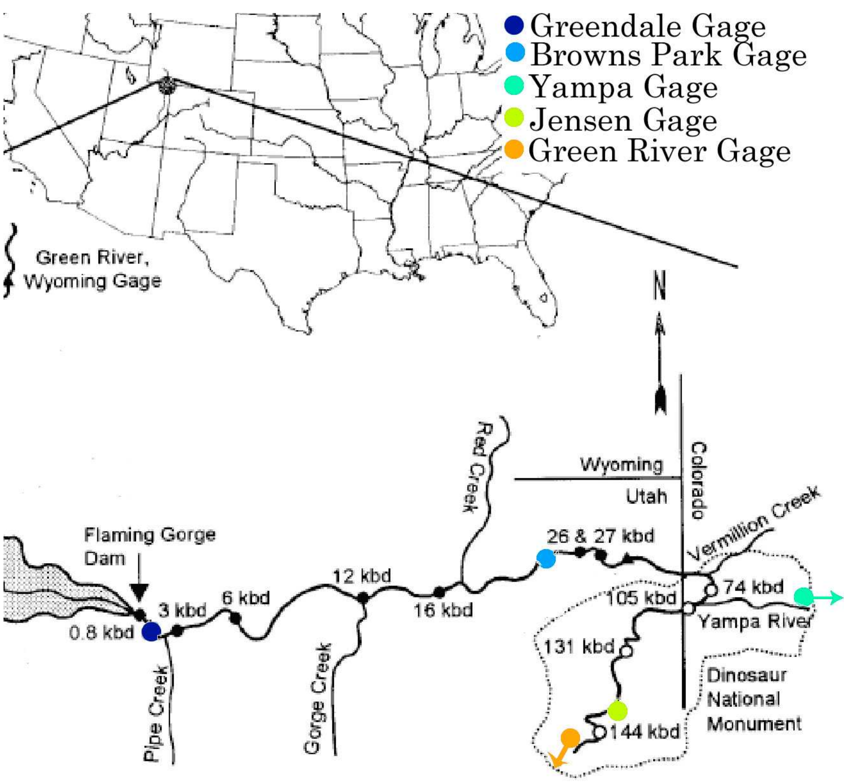

Figure 1. Middle Green River. From Figure 1, Vinson 2001.

limit the distribution of all salmonids in the middle Green River. On the microhabitat scale, competition between species determines where individuals from a given species are found. The serial discontinuity concept, which provides a paradigm for understanding the impacts of a dam and their pattern of amelioration (Stanford and Ward 2001), informs consideration of the abundance and distribution of these fishes. For example, as water temperatures downstream from the Flaming Gorge dam return to more natural, warmer temperatures, habitat suitability for salmonids tapers off, until the water temperature finally exceeds their tolerance levels. Overlaying salmonid habitat requirements and competitive interactions on the river model generated by the serial discontinuity concept generates testable hypotheses concerning salmonid abundance and distribution in the middle Green River.

EVOLUTION AND COEXISTENCE

The distribution of the salmonids below Flaming Gorge Dam depends on their habitat requirements. The evolution and biogeography of the four salmonids present in the middle Green River provides context to their interactions and habitat requirements. The family Salmonidae originated in North America roughly 100 million years ago (MYA) as the result of a genome duplication event, and the subfamily Coregoninae (whitefishes) branched off by the Eocene, roughly 50 MYA (Behnke 1992). The relationships between the three remaining genera of salmonids in North America are less clear, although the most recent molecular analysis suggests that *Salmo* (Atlantic salmon and brown trout) branched off first (time unknown, estimated 15-30 MYA), followed by another branching event that led to *Oncorhynchus* (Pacific salmon, rainbow trout, and cutthroat trout) and *Salvelinus* (Char) (Crespi and Fulton 2004) (time unknown, estimated 15-30 MYA). After *Salmo* split from the rest of the salmonids, the seagoing Atlantic salmon spread the genus into Europe, where the brown trout originated. The brown trout returned to North America via stocking in 1883 and entered the Green River in 1965. With the exception of the Bull trout, all native trout in western North America come from the genus *Oncorhynchus*, and Behnke (1992) suggests that all western North American trout arose from a common ancestor as little as two million years ago. The rainbow trout was historically limited primarily to the Pacific coastal region, with a few populations of red band trout found up to several hundred miles inland. Widespread stocking, begun in the 1870s, added rainbow trout to all 50 states and myriad other countries (Behnke 1992). The coldwater streams of the interior

American West were originally only populated by cutthroat trout subspecies, although anthropogenic intervention has removed the native cutthroat from much of their historical range. In the middle Green River, rainbow trout were stocked immediately after closure of the dam in 1963, and the cutthroat were added in 1967 (Schneidervin 2005).

Box 1. Niches
A species' fundamental niche consists of all habitat conditions that allows that species to survive (Hutchinson 1957), generally based on physiological tolerance. A species' habitat use *en situ* is always more restricted. The set of habitat characteristics that actually define a species' occurrence in the wild is termed the realized niche. The realized niche is determined both by a species fundamental niche and by its interactions with other species. Among these four fish, the interactions are negative (i.e. shrink the realized niche) and are dominated by competition and predation.

The salmonid family exhibits a high degree of niche conservatism (Behnke 1992), meaning that as new species originate, they tended to occupy similar fundamental niches (Box 1).This may have resulted from the evolution of many salmonids in isolation from other salmonid competitors; for example, *Salmo* species evolved without significant interactions with other salmonids, and new *Oncorhynchus* species are generally believed to have arisen in isolation in patchy cold-water habitats. Due to isolation, this pattern of evolution does not drive species to shift their habitat requirements to avoid competition with their congeners, leading to a lack of niche diversification among many salmonids (Gatz et al. 1987). Thus the species assemblage below the Flaming Gorge Dam combines three trout species that have similar requirements, none of which has evolved to co-exist with the others. Nonetheless, the middle Green River provides the habitat and conditions necessary to sustain trout in high abundance, and the presence of three different species actually increases the total salmonid abundance. As Behnke (1992) notes:

> Coexistence tends to force a change in strategy from generalist to specialist in regard to habitat selection and feeding preference. […] The better efficiency allows two coexisting trout species to maintain more biomass in a habitat than one species by itself. The higher biomass results when species segregate into habitats where they are more efficient, i.e. have a comparative advantage over the other fish. The

Box 2. Microhabitat
A microhabitat is the specific location where an individual organism is found. These are small habitat patches – the eddy behind a rock, a clump or grass, etc. The size of a microhabitat depends on the size of the species in question, but for salmonids can range from a 100 cm^2 to several square meters.

overall abundance of salmonids in the middle Green River should depend on the annual influx of fish to the river and on the river's carrying capacity, a function of its productivity. The abundance of individual species within the salmonid assemblage should be determined by competitive interactions – effectively the size of the species realized niche. Distribution of the family Salmonidae in the Green River should be determined by their collective fundamental niche, while the distribution of individual species, on both a broad and microhabitat scale (Box 2), should be determined by interspecific competition.

SALMONID ABUNDANCE

Persistence of trout and whitefish populations requires both adequate physical habitat for all life stages and sufficient food to allow for survival and reproduction. The abundance of salmonids in the middle Green River depends on water temperatures, food availability, and adequate microhabitats, which influence recruitment success and survival of adult fish. Recruitment, through stocking and spawning, determines the number of young trout entering the river every year.

Recruitment Mechanisms

For wild rainbow and cutthroat trout, spawning occurs in the spring, when warming water temperatures and lengthening days trigger the spawning impulse (Behnke 2002). In wild brown trout and whitefish, shortening days and cooling temperatures trigger spawning. Female trout initiate spawning by beginning to dig a redd, a depression in the gravel substrate, free from silt, that ranges in size from 100 cm^2 to several square meters (for very large brown trout), depending on the size of the fish (Bjornn 1991). Optimal water velocity around the redds is estimated at 40 to 70 cm/s (Raleigh et al. 1986), and gravel diameters in redd sites range from 5 to 15 cm, again varying by the female's size (Bjornn 1991). The males compete for proximity to the female as she digs the redd and then swim along side her once the redd is complete. Eggs and milt (fish ejaculate) are released in unison and the fertilized eggs settle into the inter-gravel spaces. After the initial egg deposit, the female may move slightly upstream to dig another egg pocket, covering the first egg

Figure 2. Alevin and eggs. Picture from Klamath Resource Information System.

deposit with gravel. The process continues until the female has deposited all her eggs.

The incubation time for all salmonid species varies with the water temperature, such that higher temperatures, to a point, result in faster hatching (Watson 1993). The fertilized eggs hatch into alevins (Figure 2), tiny fish with yolk sacs, that stay buried in gravel as their maturation progresses and the yolk sacs are absorbed. When the yolk is gone, the young emerge as fully formed, albeit tiny, fish, termed fry, and begin feeding on their own. Incubation ends with the emergence of the fry from the gravel.

<u>Box 3. Spawning Requirements</u>

Brown trout
- Upper limit: 14-16°C (Ojanguren and Braña 2003)
- Lower limit: ~4°C (Bjornn 1991)
- Ideal: 8 - 10° C, (Ojanguren and Braña 2003)
- Dissolved oxygen: Average 8 mg/L, must be >5 mg/L (Phillips and Campbell 1961)

Mountain whitefish
- Upper limit: 9-11°C (Rajagopal 1979)
- Lower limit: probably ~2°C (McCauley 1991)
- Ideal: 6° C (Rajagopal 1979).)
- Dissolved oxygen: Average >6 mg/L, no ill effects at 3 mg/L (Chambers et al. 2000)

The literature indicates a high degree of overlap in habitat requirements for successful incubation for all of the trout in the middle Green River. As an example of the requirements, brown trout requirements are presented in Box 3. Most coldwater streams are well oxygenated throughout most of the water column (Behnke 1992), and the oxygen problems related to spawning success are primarily an issue of egg placement. Eggs and embryos do not have functioning circulatory systems, so all required oxygen must come via diffusion (Bjornn 1991). In the absence of adequate inter-gravel flows, the zone around eggs will become depleted in oxygen and the eggs will die. Trout generally build redds in areas that promote inter-gravel water flow, notably over springs, and in the transition areas between springs and pools (Raleigh et al. 1986). Siltation poses a major threat to egg and alevin survival, with total loss of all eggs

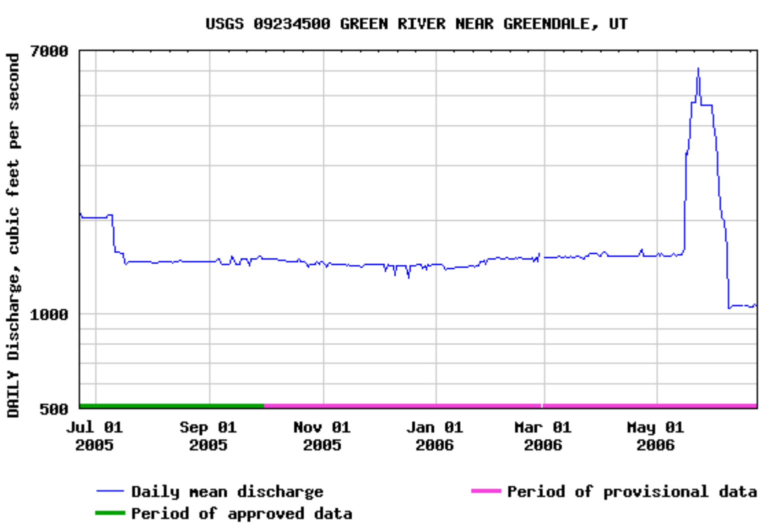

Figure 3. Based on USGS data, Greendale gauge.

reported at as little as 30% fine sediment in the redd material (Bjornn 1991). Sediment less than 0.85 mm appears to have the highest impact (McNeil and Ahnell 1964), and anything smaller than 6.4 mm can potentially smother redds (Lisle 1989).

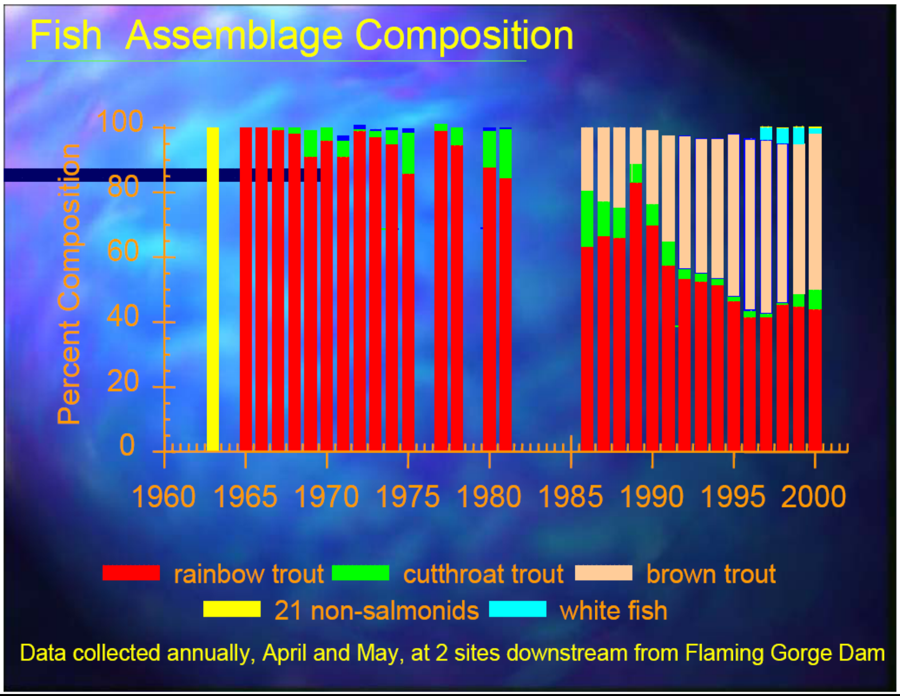

Figure 4. Originally from Schneidervin 2005.

Trout and mountain whitefish utilize different approaches to spawning. Mountain whitefish spawn in the late fall, with peak spawning activity beginning when temperatures fall below 6°C (Northcote and Ennis 1994). Whitefish are broadcast spawners, meaning they do not construct nests for their eggs, but instead broadcast the eggs over gravel substrate (McPhail and Troffe 1998). Males release milt, at the same time in order to fertilize the eggs. The incubation period begins as the fertilized eggs lodge in cervices in the gravel. Box 3 presents requirements for successful whitefish spawning. Egg maturation times are temperature dependent, and embryos hatch after accumulation of 444.4 thermal units (TUs), with one TU equal to one degree Fahrenheit above freezing for 24 hours (Rajagopal 1979). Emergence from the gravel occurs thereafter, although the time from hatching to emergence has not been established (Northcote and Ennis 1994).

Box 4. Vinson et al. (2006) documented the presence of fish in the stomachs of brown and rainbow trout. The only salmonid identified as prey was the rainbow trout, which was consumed by both brown trout and other rainbow trout. This suggests the possibility of differential rates of predation on different trout species, which may also play a role in relative abundances. No study has looked at this possibility in the Green.

Recruitment and Relative Abundance

In the middle Green River, only brown trout and mountain whitefish are able to spawn successfully enough to maintain their populations. The success of these two species indicates that adequate spawning habitat exists below Flaming Gorge Dam, and given the overlap among trout species with regard to spawning requirements, one would expect rainbow and cutthroat trout to also experience spawning success. Roger Schneidervin (2006) hypothesized that the cause lies in the recent change in hydrology below the dam. Since 1992, when the river shifted to a flow regime with a large spring flood and relatively constant flows throughout the rest of the year (Muth et al. 2000. See Figure 3 for a representative flow year), brown trout populations have increased dramatically in the tail water (Schneidervin 2005). In the last six years, brown trout have increased from 40% of the tail water species composition to 65% (Schneidervin 2005). Whitefish have also increased dramatically, more than doubling in relative abundance over the last ten years (Figure 4, Schneidervin 2005). These species spawn in habitat very similar to that required by rainbow and cutthroat trout; the major difference lies in their spawning season. Given their fall spawning season, brown trout and whitefish fry emerge from the gravel up to several months before rainbow or cutthroat fry, depending on temperature. This earlier emergence may allow brown trout and whitefish fry to develop and move to safer backwater habitat where they are able to avoid being swept downstream in the spring floods. This hypothesis comports with studies on several other rivers that show significantly higher recruitment when there are no high flows during incubation and for several weeks after emergence of the fry (Bettoli et al. 1999, Latterell et al. 1998, Nehring et al. 1993, Heggenes et al. 1988), but no formal analysis has yet taken place on the middle Green River. Another possibility relates to differences in brown trout behavior (Box 4). Regardless of the underlying mechanism, the increase in brown trout and whitefish indicates that conditions in the river are allowing successful spawning.

Box 5. Interaction of habitat and food. Behnke (1992) notes the interaction between habitat availability and food use. Improved habitat effectively makes more food available to trout, by providing better forage opportunities and by reducing trout energy expenditures in seeking food. Thus delineating streams as habitat or food limited may be a false dichotomy. There is a strong relationship between the variables.

The primary factor controlling the influx of new rainbow and cutthroat trout below the Flaming Gorge Dam is stocking, although 10% of rainbow and cutthroat trout sampled every fall are wild-born fish (Grass 2004). The number of fish stocked every year is determined by a biennial stream survey, where fish are electroshocked and their condition is assessed. If the condition of the fish is decreasing, fewer fish may be stocked to allow for faster growth and larger fish. Currently, the Utah State Division of Wildlife Resources stocks 25,000 seven inch rainbow trout every spring.

Habitat, Diet, and Abundance

Salmonids emerge from their gravel beds as fry and generally achieve sexual maturity within one to two years (Behnke 1992). Young salmonids face high mortality for their first year to two years of life from sources such as predation (Butler 1991), intraspecific territorial behavior (Mortensen 1977), and high water flows during emergence and for the first several weeks of free-swimming life (Latterell et al. 1998). Survival over the first year can be as low as 2.7% for *S. trutta* (Mill 1971), and the survival of the young for all trout is highly habitat dependent. The four salmonid species in the Flaming Gorge Dam tail water exhibit negligible differences in habitat requirements during the early period of life (Watson 1993, Behnke 1992). Newly emerged salmonids benefit from lower water flows during the emergence period (Nehring et al. 1993), and require ample backwater habitat during the first year to two years of life (Moore and Gregory 1988). Cover in the form of woody debris can also increase juvenile survivorship (Roni and Quinn 2001).

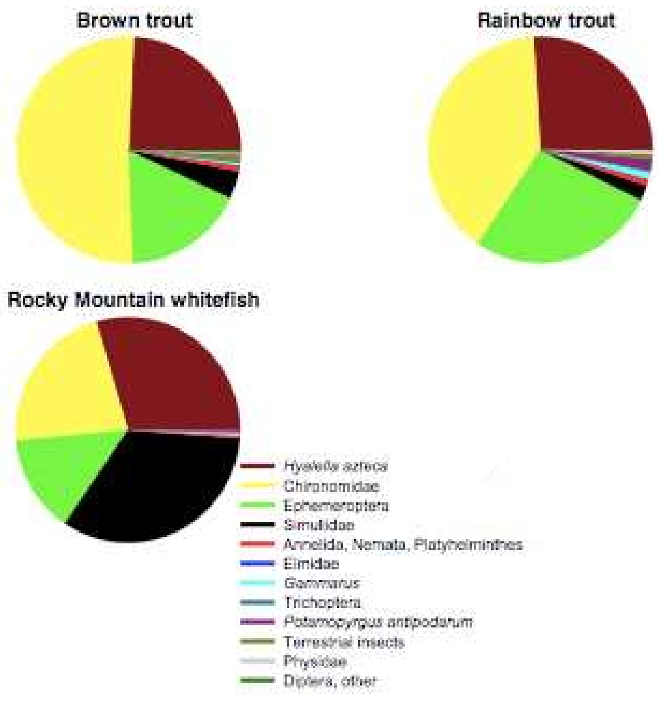

Figure 5. Trout prey selection. Figure 16 in Vinson et al. 2006.

Abundance of adult trout is controlled by recruitment, but given sufficient recruitment, a growing body of evidence suggests that abundance is ultimately limited by the food availability (Filbert and Hawkins 1995). Studies vary as to the limiting factor for trout abundance, sometimes citing microhabitat availability over food availability, but the Green River appears to be food limited (Filbert and Hawkins 1995, but see Box 5). Salmonids are generalist foragers, taking a wide array of prey items depending on availability (Behnke 2002).

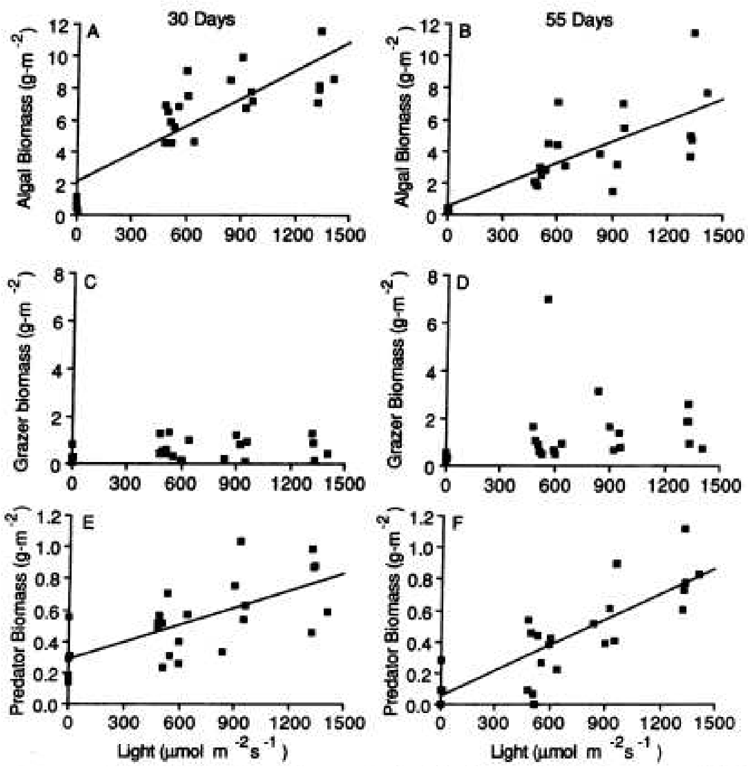

Figure 6. Influence of light on primary production, primary consumers, and predators. Originally Figure 2 from Wootton and Power 1993.

Mountain whitefish generally feed on nymph forms of caddis flies (Trichoptera), mayflies (Ephemoptera), stoneflies (Plecoptera), and true flies (Diptera) , generally feeding on or near the bottom of rivers and streams (Northcote and Ennis 1994). Trout feed on a much wider array of prey, adding terrestrial insects, crustaceans, mollusks, and other fish (Keeley and Grant 2001). Young trout tend to feed more on insects, while larger fish shift away from insects toward other fish, generally between 27 and 31 cm (Keeley and Grant 2001), with brown trout generally tending more towards piscivory than other species (Bachman 1991). Diets of Green River trout of all sizes, however, were strongly dominated by invertebrates (Figure 5, Vinson et al. 2006) (data for cutthroat diets in the Green are not available). Based on the Filbert and Hawkins study (1995) and the work by Vinson et al. on trout diets (2006), the abundance of salmonids in the middle Green River is controlled to a large degree by the abundance of macroinvertebrates.

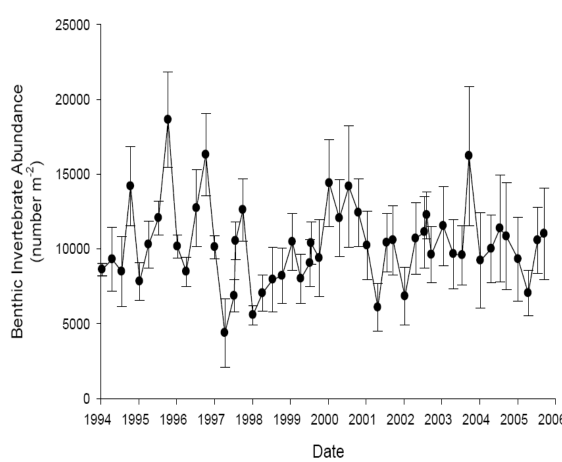

Figure 7. Aquatic invertebrate abundance, 1994 – 2005. Figure 8 from Vinson et al. 2006.

Macroinvertebrate Abundance in the Green River

The abundance of macroinvertebrates in a river ecosystem is determined both by primary productivity (i.e. photosynthesis, dependent on nutrients and energy input) and by the effects of predation (Forrester et al. 1999). The effects of predation are variable, depending on the number of trophic levels and on prey selection in a given ecosystem (Power 1990), although in the simplified Green River food web, increased fish densities should increase primary productivity by lowering primary consumer density. The addition of either energy, via light or higher temperatures (Kishi et al. 2005), or nutrients to a river system generally results in increased primary productivity (Forrester et al. 1999) ultimately resulting in higher predator (trout, in this case) densities (Figure 6). This is particularly evident on the middle Green River. Installation of Flaming Gorge Dam resulted in drastic decrease in sediment and a concomitant increase in available light, thus greatly increasing productivity. Vinson (2001) documented an increase in macroinvertebrate abundance from 1,000 organisms/m^2 to 10,000 organisms/ m^2, creating significant new forage opportunities for trout (Figure 7). For comparison, the most productive Wyoming trout streams have just over 5,000 organisms/m^2. This high level of prey availability supports an enormous salmonid population. At the population's peak in 1987 – 1989, the river supported 20,000 to 22,000 salmonids per mile. This number has since been reduced, primarily though reduced stocking to produce larger, healthier fish, and current estimates range from 8,000 to 14,000 fish per mile. Finally, the importance of macroinvertebrate abundance is further supported by changes in fish condition over the last several years. The abundance of macroinvertebrates has been decreasing, perhaps as a result of invasion by the New Zealand Mud Snail, and this reduction has been paralleled by a drop in fish condition, measured by a Kilograms to length ratio (KTL) (Figure 8, Schneidervin 2005). This strongly suggests a deterministic role for food availability in the abundance of salmonids. The reduction in

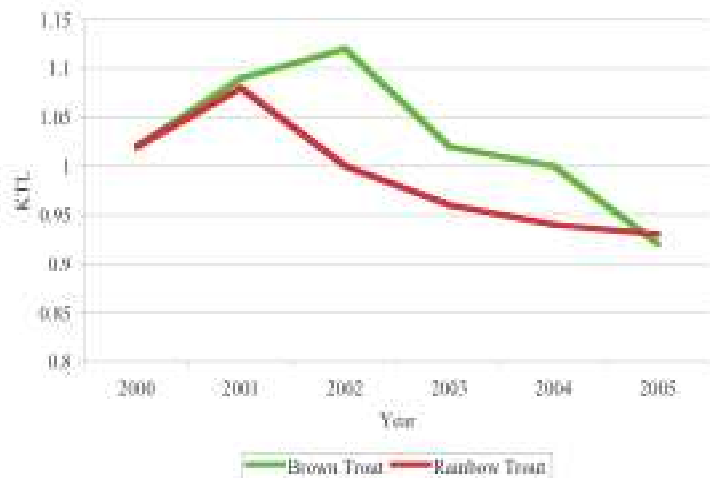

Figure 8. Kilogram to length ratio for brown and rainbow trout. From Schneidervin 2005.

macroinvertebrates may also explain the increase in the relative abundance in brown trout, given their ability to escape the limit of macroinvertebrate abundance through their predilection for piscivory.

Box 6. Temperature Requirements

Brown Trout		
	Optimum	16.4°C (Armour 1994)
		13.2°C (fed on insects (Elliott et al. 1995))
	Maximum:	29.8°C (Armour 1994)
		23.0°C (Cherry et al. 1977)
Rainbow Trout		
	Optimum	13.1°C (Bear et al. 2005)
		17.0°C (Hokanson et al. 1977)
	Maximum	21°C to 26.0°C (McCauley 1991)
		24.2°C (Bear et al. 2005)
Cutthroat Trout (westslope subspecies)		
	Optimum	13.6°C (Bear et al. 2005)
	Maximum	22.8°C (Bell 1998)
		27.0°C (Bonneville subspp. Schrank et al. 2003)
Mountain Whitefish		
	Optimum	9-12°C (Ihnat and Bulkley 1984) (for juveniles, adults likely lower)
	Maximum	23.1°C (Eaton and Scheller 1996)

SALMONID DISTRIBUTION

Abundance and distribution exhibit both positive and negative interactions. Just as a low abundance severely limits the extent of a species' range and tends to concentrate it in the best available habitat, high abundance can expand the range of a species by forcing some individuals into marginal habitat (i.e. source/sink dynamics). These four salmonids share enough niche space that they too should create significant interspecific competitive pressure. The value to the less competitive individuals of the good habitat is lowered by the presence of the competitors. Interactions can force individuals into marginal habitat, provided that the negative interactions in better habitat reduce the value of that habitat to the poorer competitors (Filbert and Hawkings 1995). With fish densities and recruitment maintained at a high level, as they are on the middle Green River, one may find some fish pushed into relatively marginal habitat. However, the conserved salmonid habitat requirements will still govern the distribution of salmonids as a family. Within that restricted habitat, selection of microhabitats will be governed by their interspecific interactions.

Broad Distribution of the Salmonid Family

In the context of the serial discontinuity concept, temperature and forage abundance appear the most interesting limiting habitat requirements for salmonid distribution in the middle Green River. The largest effect of the dam, from the perspective of the trout, was the creation of a

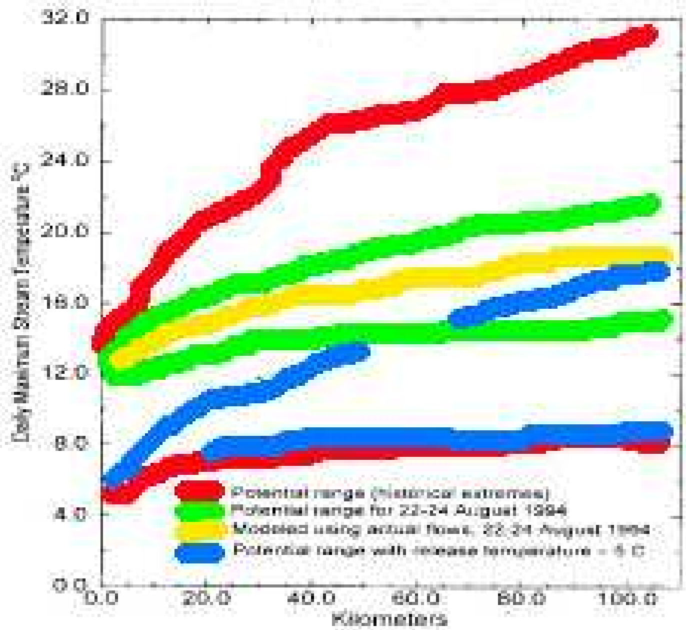

Figure 9. Modeled temperature vs distance downstream from Flaming Gorge Dam. Red outlines the historical range, green demarcates the range for 22-24 August 1994, Gold shows the modeled temperature, and blue shows the range that the water would have occupied if the water released at the dam was 4°C. Originally figure 8 in Carron and Rajaram 2001.

constant cool water source that allows their existence. The river's temperature increases with distance from the dam, and the pattern of temperature change plays a major role in the length of river salmonids habit.

Temperature, food, and growth are closely related in adult salmonids, as warmer waters allow faster growth which requires additional prey (Filbert and Hawkins 1995). Fish tend to prefer temperatures in the range of their growth optimum, where they are most efficient at converting food to biomass. While this conceptual framework would suggest well-delineated temperature preferences for each species, the actual water temperatures tolerated by salmonids paint a much more complicated picture. For example, estimates of the upper thermal limit for rainbow trout (the threshold where rainbow trout cannot survive), range from 16.9°C to 22.4°C (Huff et al. 2005) to 26°C (McCauley 1991). Upper thermal limits change depending on how the fish are acclimatized, such that trout who are gradually transitioned to warmer waters can

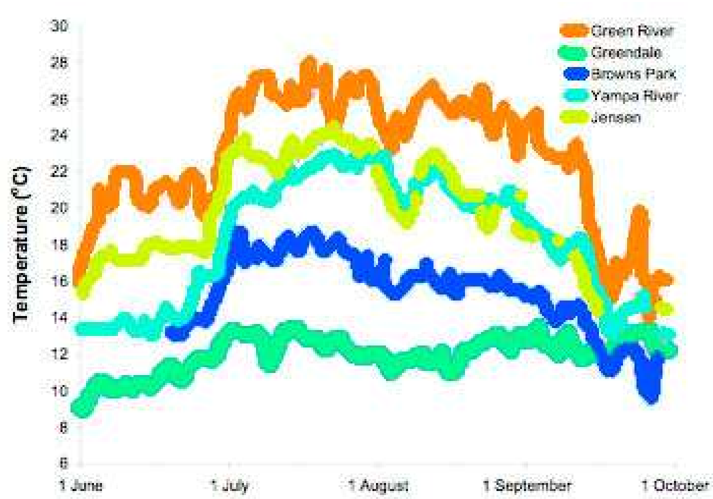

Figure 10. Water temps at five gauges on the Green River. Refer to figure 1 for locations. Originally figure 3.14 in Muth et al. 2000.

survive in water 4 to 5°C warmer than their counterparts who move directly to warm water (McCauley 1991). Thermal optima are no better defined than the upper thermal limits, but examples of both for the four salmonid species in the middle Green River (Box 6, from laboratory settings in isolation from other species), but generally temperatures consistently above 20°C present a challenge to salmonid survival.

For these four species, maximum values designate the high end of a fundamental thermal niche; the low end probably falls from 0 to 2°C, out of the range of water temperatures normally encountered in the middle Green River. Note that the temperatures above are the thermal niche of adults of these species; other life stages, embryos in particular, have a much more restricted thermal niche. Interactions can shift the growth optimum from the inherent physiological optimum (noted above) to a realized optimum that maximizes conversion of energy to biomass while also minimizing competition and predation. Through this mechanism, the influence of temperature is moderated by a species' habitat requirements for food and cover, as delineated by interactions with the other species present in the stream. Some data suggest that cutthroat trout have the lowest realized thermal niche, followed by rainbow and then brown trout (Huff et al. 2005, McCauley et al.), but these results are impossible to isolate from systemic factors such as geographic distribution and local factors such as availability of thermal refugia or the presence of other fish (Ebersol et al. 2001), and are neither robust nor predictive.

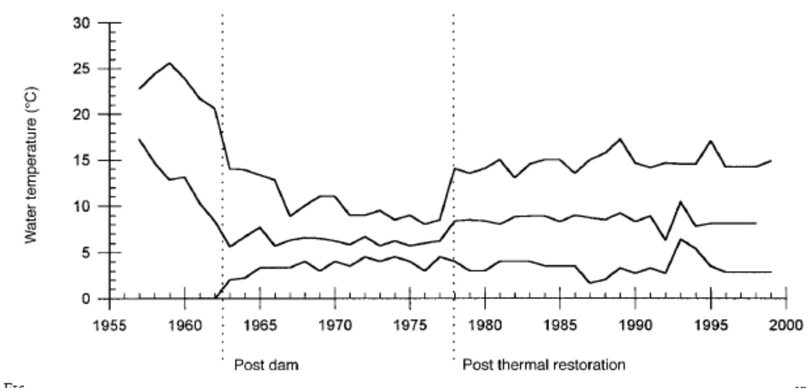

Figure 11. Maximum, minimum, and mean temp at the Greendale gauge. Figure 2 from Vinson 2001.

Temperatures in the middle Green River

Temperature regimes in the middle Green River vary by distance downstream from the Flaming Gorge Dam (modeled in Figure 9, actual temperatures in Figure 10). The temperatures in the tail water are determined by the releases from Flaming Gorge Dam, and release water temperature can be controlled by a selective withdrawal structure (Muth et al. 2000). The withdrawal structure, installed in 1978, allowed an increase in water temperatures toward the optimum for trout growth (Vinson 2001,

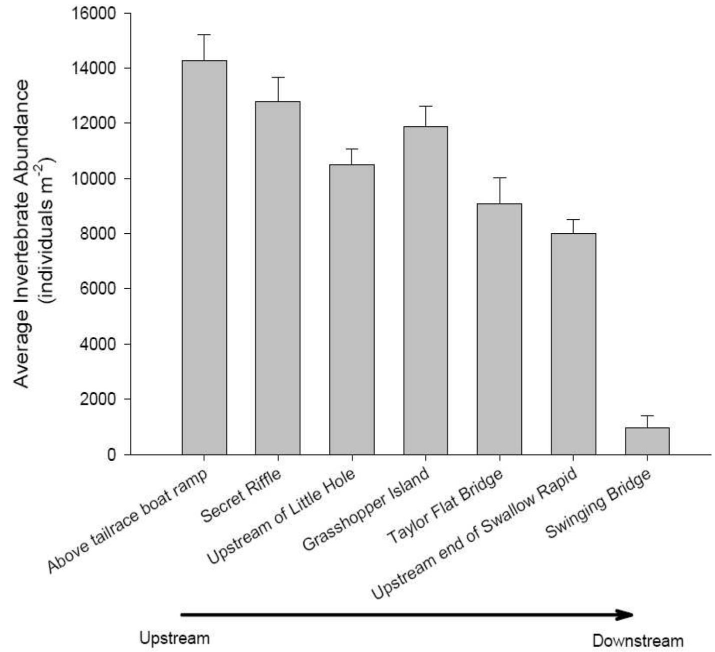

Figure 12. Insect abundance. Swinging Bridge is located in Brown's Park. Originally figure 9 from Vinson et al. 2006.

Figure 11). Temperatures at the Greendale Gage, just downstream from the dam, stay in or near the optimal growth range for trout throughout much of the summer, dropping to 4°C (warmest water available) during the winter (Filbert and Hawkins 1995) (See Map, Figure 1, with temperature stations labeled). Farther down the river, temperatures near the critical thermal maximum for salmonids in Lodore Canyon, and exceed the critical thermal maximum for several weeks in the summer at the Jensen gage, downstream from confluence with the Yampa River. Rainbow trout abundance exceeds that of brown trout in the Little Hole region, above Brown's Park, but relative or actual abundances within and downstream of Brown's Park have not been reported. Based on the thermal profiles present by Muth et al. (2000) and Carron and Rajaram (2001), one would expect salmonids to decrease in abundance around 60 km downstream from the dam, depending on atmospheric conditions and water flow. Data on insect abundance from Vinson et al. (2006) also shows a major decline in Brown's Park (Figure 12). Limited insect abundance may make the tolerable temperature range much smaller, although salmonids in very low densities may persist in the marginal habitat that reaches upwards of 22°C, perhaps using thermal refugia or lower nighttime temperatures (Ebersole et al. 2001). Lodore Canyon is the location furthest downstream where trout have been reported, and one study found that brown trout made up 25% of fish collected in the canyon (U.S. DOI 2005). Under almost any scenario, the influx of warm water from the Yampa should prohibit colonization by salmonids downstream from the confluence. The distribution of salmonids as a whole should be determined largely by the progressive increase of stream temperatures downstream of Flaming Gorge Dam and may be further restricted by reductions in insect abundance. In contrast, the microhabitat selection by individual species of salmonids is determined primarily by interspecific interactions.

Microhabitat Selection and Optimal Foraging Theory

Optimal foraging theory provides a reasonable explanation for many salmonid behaviors (e.g. Gowana and Fausch 2002, Heggenes 1993, Werner and Mittelbach 1981). Optimal foraging theory assumes that selection favors those individuals most efficient at maximizing their contribution to the following generation, which hinges in part on their ability to maximize the benefits of their food by minimizing the costs associated with feeding (Pyke et al. 1977). Costs associated with feeding include the energetic costs such as the cost of holding a position in moving water or pursuing prey and other costs such as exposure to predators. Prey choice provides a good example of the implications of optimal foraging theory; trout should tend to take prey of the size that maximizes their energy benefit. This has been born out by studies of prey size versus the average size of prey in the river, which showed that trout tended to take larger items than were the norm, which increased their energetic benefit above the cost of taking the prey (Meissner et al. 2006, Figure 13).

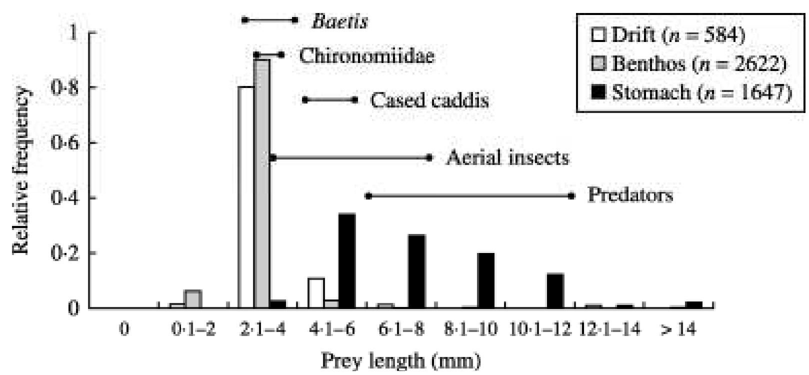

Figure 13. Prey availability vs. prey consumed by trout. Originally figure 7 in Meissner and Muotka 2006.

In the context of microhabitat selection, optimal feeding hinges on maximizing exposure to prey while minimizing energy expenditures and exposure to predators. Much of a trout's diet comes from invertebrate drift, so trout will generally face upstream into the current to spot prey items as they approach. Fish experience a tradeoff in selecting optimal water velocities, in that prey items will pass more frequently in fast water but holding in fast water entails a higher energetic cost. Salmonids generally resolve this problem by finding low velocity water, called holding areas, near higher velocity flows, termed feeding lanes (Bachman 1984). These holding areas occur behind rocks in the channel, under undercut banks, at the head or tail of pools, in eddy zones, essentially anywhere fast current meets slower current. The best holding areas also provide cover for the fish, reducing their exposure to predation as they are feeding (Borger

1995). The selection of microhabitat can be amazingly specific, as demonstrated by Bachman's findings (1984). One trout, photographed while in its holding position over the course of three years, varied its location by no more than 2 to 4 cm in any direction (Bachman 1984). Mountain whitefish tend to use habitats that are deeper and less rocky than habitat preferred by trout, and they often hold 2 to 10 cm off the bottom in lower velocity water flows (Northcote and Ennis 1994). Very little additional information about mountain whitefish microhabitat selection has been documented.

When one species of trout occurs alone in a stream, a strict hierarchy determines which individuals occupy the best holding sites (Fausch 1991). The hierarchy is determined by complex interactions ranging from posturing to nipping and fighting, with larger, healthier fish generally having a higher rank. The ranking extends through the population of fish, and if higher ranked fish are removed, the lower ranked fish will move into the better foraging position (Fausch 1991). The lowest ranked fish, called floaters, do not have set positions and move frequently, foraging wherever they can (Fausch 1991). The middle Green River, with its unusually high fish and forage levels, may support a high number of floaters in marginal habitats. As noted above, fish habitat requirements change throughout the life of the fish, such that older fish and younger fish may not be in competition. For example, younger fish generally prefer slower moving lateral habitats, while larger fish generally prefer deeper waters.(Harvey and Steward 1991). Finally, as would be predicted by optimality theory, an abundance of food increases the range of acceptable habitats and increases trout condition, particularly for floater and other less dominant trout (Rosenfeld 2005).

Microhabitat Selection, Species by Species

In rivers with multiple salmonid species, more complex interactions govern microhabitat selection. In addition to the intraspecific competition, the species compete with each other. This is particularly true of the three trout species present in the middle Green, given the overlap in their habitat preference (e.g. Gatz et al. 1987). Brown trout are generally the most dominant trout in interspecific interactions, due to their higher innate aggression and generally larger size (Baran et al. 1995, Gatz et al. 1987, Newman 1956). In a study comparing rainbow trout microhabitat use in streams with and without brown trout, habitat use by the rainbows in the stream with the brown trout shifted relative to depth, velocity, substrate, overhead vegetation, and surface turbulence, indicating that the rainbows were displaced by the brown trout (Gatz et al. 1987). In a separate study, Baran et al. (1995) found that habitat use by brown trout explains 77% of the change in rainbow trout habitat use in a stream with brown trout compared to a stream without brown trout. Brown trout habitat use has been shown not to change significantly when they occur alone versus with rainbow trout (Shirvell and Dungey 1983). Fewer studies compare the change in habitat use by cutthroat trout in sympatry with other trout species, although cutthroats in aquaria rank below rainbow trout of equal size, and are generally excluded from their preferred habitat by rainbow trout (Trotter 1991). The literature did not reveal any indication of the relative ranking of mountain whitefish.

The angling literature suggests certain preferences for different species of trout. In streams, brown trout tend to be found close to the bottom in shallower areas with slower water and more cover (Bachman 1991, Fausch 1991), rainbow trout higher in the water column in areas of faster water, often midchannel (Fausch 1991, Smith 1991), and cutthroat in colder water, generally in smaller tributaries (Smith 1991). These tendencies may be more due to competitive exclusion that to microhabitat preference, given that any of the three species will inhabit all the full range of stream habitats when occurring in isolation from the others. The habitats they occupy in sympatry are those microhabitats where they have the competitive advantage. Thus the actual range of microhabitats inhabited by each of the salmonid species in the middle Green River depends on the rank of individuals of a given species relative to each other and relative to the other species of fish. As a whole, salmonids will tend to locate in microhabitats that maximize their exposure to food items while minimizing their energy expenditures and their exposure to predation.

SUMMATION

The overall abundance of salmonids in the middle Green River is determined by stocking rainbow and cutthroat trout to achieve overall levels of salmonid abundance that do not compromise fish condition (measured by KTL). This overall number is a function of habitat and food availability. The relative abundance of each species is determined by rates of recruitment, both from stocking and natural spawning, and potentially by differential predation. Salmonid distribution on the broad scale is limited by the interaction between food and temperature. Salmonids prefer microhabitats that maximize exposure to food items while minimizing energy expenditures and their exposure to predation, and competition determines allocation of these preferred sites, both within and between species.

HYPOTHESES UNDER THE SERIAL DISCONTINUITY CONCEPT

The serial discontinuity concept (Stanford and Ward 2001) puts dams into the context of the river continuum concept (Vannote et al., 1980), which attempts to explain changes in rivers as they move from their headwaters to the their ends. In the middle Green River, the Flaming Gorge Dam creates a discontinuity, most notably by moderating the flow regime, reducing water temperatures, and eliminating sediment. According to the serial discontinuity concept, these impacts should be moderated with increasing distance downstream from the dam. Vinson (2001) presented some data that supported these predictions on the Green River, showing that conditions farther from the dam became closer to pre-dam conditions. The influx of warm, sediment-laden water from the largely unregulated Yampa also acts to move the Green closer to natural conditions (Stanford and Ward 2001). Given this pattern of amelioration, one expects to see certain patterns in the distribution and abundance of salmonids in the middle Green River. Based on salmonid habitat requirements and the geologic and hydrologic information presented above, the following four predictions could be made:

1. Directly below the dam, armoring of the substrate will prevent spawning. Below the first major tributary that provides substantial new rocky inputs to the Green, trout spawning will be at its highest. From that point, spawning will decrease with distance from the dam, because the influx of fine sediment will smother any potential redd sites.
2. Trout abundance will decrease downstream from the dam as temperatures increase and additional sediment lowers the productivity of the river.
3. Trout growth rates will increase downstream from the dam, as temperatures approach and surpass the growth optimum, until hitting a threshold where warmer temperatures and a lack of available prey becomes detrimental to growth.
4. The huge number of stocked fish will result in some individuals being driven into water that is far less than the optimum for them, including reaches of water near the confluence with the Yampa that are in the upper echelon of salmonid thermal tolerance.

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