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**A COMPARISON OF SALMONFLY DENSITY UPSTREAM AND DOWNSTREAM OF ENNIS RESERVOIR** 

### **ABSTRACT**

*Ennis Reservoir on the Madison River,, southwest Montana, has been linked with changes in macroinvertebrate and fish assemblages. We tested the hypothesis that life history, distribution, and abundance of the salmonfly* (Pteronarcys califomica *Newport) differ upstream and downstream of Ennis Reservoir. We sampled larvae, shed exuviae, and discarded wings of salmonfiies in 1994 and 1995 upstream and downstream of the reservoir. Wolman pebble counts and estimation of substrate embeddedness were made at nine exuviae collection sites to determine habitat availability. Predation rate on adult salmonfties and crayfish densities also were examined. Salmonflies downstream of Ennis Reservoir were 6-8* X *less abundant, significantly larger, and possibly required one less year as larvae to complete development compared to salmonflies upstream of the reservoir. Adult salmonfly abundance both upstream and downstream of Ennis Reservoir was* 3. 2 *to 4.* 0 X *higher in 1995 than 1994. Numbers of exuviae were correlated with substrate embeddedness suggesting that abundance was influenced by habitat availability. Predation accounted for 5 to 15 percent of adult salmonfly mortality. Crayfish were at least 6.6* X *more abundant downstream of Ennis Reservoir.* 

**Key words:** biomonitoring, competition, predation, *Pteronarcys californica,* river regulation, salmonflies, water quality

#### **INTRODUCTION**

River regulation deleteriously affects aquatic ecosystems worldwide. Impoundments can alter thermal regimes (Webb and Walling 1997), erosion and sedimentation rates (Ligon et al. 1995), hyporheic zones (Stanford 1998), riparian areas (Andersson *et al.*  2000, Friedman and Auble 1999), primary production (Benenati et al. 1998), macroinvertebrate assemblages

(Cazaubon and Giudicelli 1999), and fish assemblages (Ligon *et al.* 1995, Peaz et al. 1999). The effect of Ennis Reservoir on the Madison River ecosystem is important to fishery and recreational management and is of concern to many. Ennis Reservoir was formed on the Madison River by the construction of Montana Power Company's top release Madison Dam, near Ennis, Montana, in 1907 (Fig. 1). Ennis Reservoir has been accumulating sediment since its construction and present water depths average 2.5 to 4 m. Sediment export during spring runoff has been diminished by flow regulation. Changes in Madison River sediment accumulation and its effects on macroinvertebrate habitat availability

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**Figure 1.** *Madison River and study sites. Legend of sample locations: 1) McAtee Bridge; 2) Varney Bridge; 3) Eight-Mile Hole; 4) Burnt Tree; 5) Beartrap; 6) Split-Rock (Beartrap Canyon); 7) West-side Parking Lot; 8) Duke's Rock; 9) Norris Bridge; 10) Black's Ford; 11) Roadcut; 12) Grey Cliffs; 13) Cobblestone.* 

have not been published. Because Ennis Reservoir is relatively shallow, summer temperatures in the Madison River downstream are often greatly elevated from pre-dam conditions. Changes in the Madison River's thermal regime have been documented to affect aquatic macroinvertebrate assemblage changes, including stonefly (Plecoptera) densities (Fraley 1978), downstream of Ennis Reservoir.

Stoneflies are an important food source for trout and are important to the biological functioning of rivers and streams. However, the life cycles and ecology of many Plecoptera are poorly known (Hassage 1990). The salmonfly *(Pteronarcys californica* Newport) is the largest (40 to 60 mm in length) stonefly in western North America (Poole 1981). Salmonfly larvae (nymphs) are

detritivorous shredders (Cummins *et al.*  1973, Short and Maslen 1977) and feed on both allochthonous and autochthonous coarse particulate organic matter (CPOM) (Fuller and Stewart 1979). Because of its body size and role in reducing CPOM to fine particulate organic matter (FPOM), it is an important link in the aquatic food web (Cummins *et al.* 1973, Short and Maslin 1977).

Salmonfly larvae typically have 3 to 4 year life cycles in western rivers, depending on water temperatures (Branham and Hathaway 1975, Merrit and Cummins 1984). Larvae usually occur in patches with age-segregated distributions (Elder and Gaufin 1973, Poole 1981, Freilich 1991) and prefer large, fast, well-oxygenated rivers with unconsolidated (unembedded) cobble

and boulder substrates (Elder and Gaufin 1973). Salmonflies are currently used as indicators of water quality in state and federal monitoring programs, particularly for non-point sedimentation impacts (Barbour *et al.*  1999). Because impoundments often alter thermal regime and sediment characteristics, we predicted that life history and abundance of salmonflies would be altered downstream of Ennis Reservoir.

Body weights of larval salmonflies have been used to estimate year class strength (Branham and Hathaway 1975). Fraley (1978) reported that salmonfly adults below Ennis Reservoir were 13 percent smaller than those upstream of Ennis Reservoir. This difference was attributed to higher nymphal metabolic rate resulting from elevated water temperatures below the reservoir.

Crayfish sometimes prey on *Pteronarcys* species (Moore and Williams 1990) and also may compete with salmonflies for limited, unembedded cobble habitat where their ranges overlap. Also, predation on adult salmonflies in the Madison River riparian area has not been documented.

We conducted a survey of salmonflies in the Madison River and tested the hypothesis that life history, distribution, and abundance of salmonflies differ above and below Ennis Reservoir. We also tested the specific hypothesis that abundance of salmonflies is correlated with substrate embeddedness and we report observations of predation on adult salmonflies and possible competition with crayfish.

# **STUDY SITE**

The Madison River is a mediumsized, 5th order river (Fig. 1). The upper portion of the Madison River, upstream of Ennis Reservoir, flows mostly through Tertiary basin fill and is comprised of a heterogeneous mixture

of cobbles, gravel, sand, silt, and clay. Directly downstream of Ennis Reservoir, the Madison River cuts through Archean, high-grade metamorphic rock to form the Beartrap Canyon. Below the Beartrap Canyon, the Madison River again flows through Tertiary basin fill, similar to the upper Madison River (Alt and Hyndman 1986)

The upstream portion of the Madison River is typically of moderate gradient with well-developed riffle-run habitat and predominant cobble substrate. For about 3 km upstream of Ennis Reservoir, the river braids into numerous channels and substrate size decreases. In the Beartrap Canyon, the river flows through boulder-filled rapids, many of which were formed by rockslides within the narrow canyon. Below Beartrap Canyon, the lower portion of the Madison River reestablishes a cobble-riffle morphology, with increased inputs of fine sediments resulting from the canyon's geologic parent materials.

# **MATERIALS AND METHODS**

## **Larval Collections**

Salmonfly larvae were sampled using a standard D-net with a 1 mm mesh. Live (wet) weights were recorded from the upstream ( $n = 241$ ) and downstream ( $n = 203$ ) portions of the river with a Pesola<sup>TM</sup> spring scale  $(0.05)$ g) in May 1995. We also recorded the number of crayfish caught in our samples. We created a histogram of weight distributions of salmonflies from these samples to delineate size and year classes. It was difficult to determine the sex of very small  $( $0.5 \text{ g}$ )$  larvae in the field; therefore, half of the larval salmonflies less than 0.5 g were considered female and half were considered male. Male and female preemergent larval weights in both the upper and lower portions of the Madison River were statistically compared using Student's t-test



**Figure 2.** *Weight frequency distribution of female larval salmonflies in the upstream and downstream sites of the Madison River, 1995* (n **=** *109 larvae downstream,* n **=** *92 larvae upstream).* 

analysis (two-tailed, equal variances). Pre-emergent larvae were determined to be those from the largest weight group in our histogram analysis (Fig. 2).

### **Exuviae Collections**

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Transects, each 15 m long and 1 m wide, were sampled at 24 sites along the banks of the Madison River in June of 1994 and June and July of 1995 (Fig. 1). We sampled 15 sites downstream and nine sites upstream of Ennis Reservoir (Fig. 1). One-meter wide transects were chosen because very few salmonfly exuviae were observed further than 1 m from the water's edge. We selected transects that were free of obstructions and contained recently shed exuviae. Sites consisted of rocks or small cliffs, grassy areas, or willow areas. Sampling involved walking in the river along each transect and recording the number and sex of exuviae. Exuviae were then crushed and dropped into the river to avoid being recounted. To estimate the number of adult salmonflies produced per m<sup>2</sup> of river, we assumed that half of the last instar larvae cohorts crawled to

each side of the river. Determination of exuviae gender was facilitated by dimorphic genitalia and size. Females have distinctly pointed epiprocts whereas males have rounded epiprocts; females also tend to be larger.

#### **Wing Counts**

Wings of recently emerged salmonflies were counted at seven sites in 1994 and one site, Eight-Mile Hole, in 1995, to estimate bird predation. The total number of wings at each site was divided by four, which is the number of wings on an adult salmonfly. This estimated the number of salmonflies eaten by predators that selectively remove salmonfly wings.

## **Substrate Sampling and River Measurements**

We conducted Wolman 100-pebble count substrate sampling (Wolman 1954) during late summer at three exuviae collection sites in the upstream section and seven sites in the downstream section in 1994 and 1995. From two to four transects were made

at each site except the Norris Bridge site where only one transect was made because of the combination of high water velocity and depth.  $D_{50}$ 's (median particle size) were estimated for each transect. Particles were categorized as 'embedded' or 'not embedded' and percent embeddedness was estimated at each transect. An estimate of river width was made at each exuviae collection site using a compass and tape measure (Hauer and Lamberti 1998) because many sections of the Madison River in the Beartrap Canyon were difficult to cross, even at low water.

#### **Statistical Analyses**

We used STATISTICA for Windows (Statsoft, Inc. 1995) for all statistical analyses. Student's t-test (two-tailed, equal variances) was used to compare larval weights and exuviae abundance. Correlation coefficients (Pearson Rvalues) and P-values were used to compare substrate size and percent stream embeddedness (arc sin transformed) with number of exuviae.

### **RESULTS**

#### **Larval Weights**

Both female and male pre-emergent larvae were significantly heavier in the downstream section than in the upstream section of the river. Mean preemergent female larval weight was 1.83  $g (+ 0.20 SD, minimum = 1.35 g,$ maximum =  $2.30$  g,  $n = 83$ ) in the lower section and  $1.63$  g ( $\pm$  0.19 SD, minimum = 1.25, maximum= 2.05 g, *n* = 45) in the upper section, whereas mean male preemergent larval weight was  $0.99$  g (+ 0.11 SD,  $n = 78$ ) in the lower section and 0.83 g  $(± 0.9 SD, n = 26)$  in the upper section. Pre-emergent female salmonfly larvae in the lower section of the river were 1.85 X heavier than males. Larval sex ratio was 0.57 females: 0.43 males.

It appears that salmonfly larvae developed in two years downstream of Ennis Reservoir, but may have required an additional year upstream as judged

by the weight-frequency distributions of female larvae (Fig. 2). Two distinct peaks corresponding to separate age classes were evident for larvae from the downstream reach, but the size distribution upstream was not as clear. A minor peak at 0.9-1.0 g may have indicated a separate year class, but may alternatively have been the result of sampling error, as numbers of individuals in these size classes were low. We also would expect this peak to be distinct and equidistant between the other two peaks to be considered a separate age class, but it overlaps broadly with the one-year old size class. Therefore, it remains unclear if two or three age classes of larvae were present in the upstream section.

Most of the female larvae (77.1 %) downstream of Ennis Reservoir were  $\ge$ 1.4 g and large enough to emerge as adults and there was an absence of  $< 0.5$ g larvae. This can be seen as a right shift in the weight frequency distribution histogram (Fig 2). Upstream of Ennis Reservoir, the largest proportion (43.5 %) of female larvae were < $0.7$  g while only 27.2 percent were large enough  $(21.4 \text{ g})$  to emerge as adults (Fig 2).

### **Exuviae Abundances**

Estimated number of adult salmonflies produced per  $m<sup>2</sup>$  in the upper Madison River was  $2.58$   $(+2.21)$ SD) in 1994 and 8.25 (+ 5.83 SD) in 1995. Estimated numbers of adult salmonflies produced per  $m<sup>2</sup>$  of river in the lower Madison River were  $0.43$  (+  $0.32$  SD) in 1994 and 1.37 ( $\pm$  1.28 SD) in 1995. Numbers of exuviae decreased rapidly downstream of the Beartrap Canyon (sites  $5, 6, 7$ , and  $8$  in Fig. 1) and Norris Bridge (site 9). No exuviae were found in 1994 and 1995 at the Cobblestone Fishing Access (site 13) and only one exuviae was found at Black's Ford (site 10) in 1995, none were found in 1994. Grey Cliff Fishing Access (site 12) produced only two exuviae in 1994 and 22 exuviae in 1995. In contrast, in the

Beartrap Canyon, the mean number of mean  $D_{50}$ 's in the 96 mm s exuviae was 53.4 per transect in 1994 and 147.6 per transect in 1995. Mean numbers of exuviae in the upstream portion per transect (sites 1,2,<sup>3</sup> , and 4) were 120.9 in 1994 and 452.9 in 1995. McAtee Bridge (site 1) produced the most exuviae per transect at 620.0 in 1995.

Emergence times of adult salmonflies in the Madison River varied among sites and between years, with downstream emergence starting prior to upstream emergence. Emergence occurred 1-10 June 1994 in the lower Beartrap Canyon and 28 June to 11 July 1994 at Varney Bridge. In 1995 emergence occurred from 16-27 June in the lower Beartrap Canyon and 17-21 July at Varney Bridge. Male salmonflies typically emerged one or two days before females and male peak emergence usually occurred before female peak emergence.

#### **Predation**

Red-winged blackbirds *(Agelaius phoeniceus)* were the on<sup>l</sup> y species of bird observed that immediately removed wings of recently emerged salmonflies. Other bird species were not observed removing salmonfly wings. We did observe other bird species capturing adult salmonflies but were unable to get an estimate of predation rates. We cou<sup>n</sup> ted 118 discarded salmonf<sup>l</sup> y wings, representing 30 salmonflies during a 2 day collection period (29, 30 June, 1995) at the Eight-mile Hole study site. We collected 208 exuviae; therefore, at this study site an estimated minimum of 14.4 percent of adult salmonflies was captured by predators. Estimated predation ranged between zero and 15 percent at the other sites.

#### **Substrate composition**

Much of the substrate throughout the river, excluding the Beartrap Canyon section, was composed of cobbles, with six of nine sites having

mean  $D_{50}$ 's in the 96 mm size class. Substrate sizes were not significantly different between the upstream and downstream sections of the river. In <sup>I</sup>*rl*   $(1,2,3,$  and 4) contrast, the percent of the substrate embedded with sand and silt was significantly higher in the lower section of the river (mean = 22.4 % embedded in the downstream section; mean  $= 6.3$ % embedded in the upstream section; *P*   $= 0.00$ ). Salmonfly exuviae abundance was significantly negatively correlated with percent substrate embeddedness (arc sin transformed  $R = -0.70$ ,  $P = 0.02$ ) for 1994 and  $R = -0.63$ ,  $P = 0.04$  for 1995,  $n = 11$ ) but not significantly correlated with substrate size  $(R = 0.45)$ ,  $P = 0.17$  for 1994 and R = 0.46,  $P = 0.16$ for 1995,  $n = 11$ ).

#### **Crayfish Abundance**

Crayfish were more abundant in the lower Madison River than in the upper Madison River. We caught 6.6 times as many crayfish per salmonf<sup>l</sup> y larvae in the lower Madison River than in the upper Madison River in 1995. 200 crayfish were caug<sup>h</sup> t in the lower Madison R<sup>i</sup>ver with 203 salmonfly larvae, whereas on<sup>l</sup> y 36 crayfish were caught with 241 salmonfly larvae in the upper Madison R<sup>i</sup>ver.

#### **DISCUSSION**

If our density estimates are correct, then differences in salmonfly densities between the upper and lower Madison River are greater than we have demonstrated. If the upper Madison River salmonflies develop in 3 years, then we have sampled 1/3 of the population by using exuviae counts. Likewise, we have measured 1/2 of the population in the lower Madison River. Also, our estimates of predation probably under-represented the true mortality because we were unable to estimate the number of adult salmonflies captured by predators that did not remove the wings or that captured molting larvae.

Madison Dam (Ennis Reservoir) and Hebgen Dam (Hebgen Reservoir) on the Madison River (Fig. 1) have altered thermal regimes and patterns of discharge and run-off in downstream reaches. Elimination of 'flush flows' and the resulting changes to downstream ecosystems has been well documented in the Colorado River (Bureau of Reclamation 1995) and other river systems (Stanford and Ward 1984). The geology of the Beartrap Canyon section of the Madison River provides inputs of fine sediments to the lower Madison River. Without flood events, sedimentation is likely to increase in the lower Madison River with greater loss of salmonfly habitat.

Our observation of an accelerated 2 year life cycle in the downstream portion of the river support Fraley's (1978) findings on the effects of water temperature on macroinvertebrates in the Madison River. Effects of water temperature on periphyton, macroinvertebrate, and fish assemblages in the Madison River have been well documented (Dodds 1991, McMichael and Kaya 1991, Jourdonnais *et al.* 1992, Marcus 1980, Gillespie 1969, Brown and Kemp 1942, and Montana Fish, Wildlife, and Parks 1999). Daily water temperatures upstream and downstream of Ennis Reservoir are available from the U.S. Geological Survey and the Montana Department of Fish, Wildlife, and Parks.

Higher average water temperatures may have also allowed for the greater relative abundance of eurythermal crayfish in the lower Madison River, although sedimentation could also be important. Crayfish can compete with salmonflies for limited substrate habitat; however, crayfish were observed digging retreats under embedded cobbles in the lower Madison River. Salmonflies have never been observed digging retreats. Freilich (1991) reported that salmonflies avoid

sand bottomed pools. Therefore, we suggest that as sediment levels increase, intra and inter-specific, pre-emptive competition may also increase. This study was conducted during a dry spring (1994) and a wet spring (1995); therefore, continued exuviae counts could help illustrate the relationship between abundance and discharge.

#### **CONCLUSION**

Salmonfly abundance, distribution, and life history differs, both spatially and temporally, between the upper portion and the lower portion of the Madison River. These differences can be attributed to both human and natural causes. Salmonflies are good bioindicators of water quality, including sedimentation impacts and this study was designed to facilitate future monitoring of salmonflies.

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# **LITERATURE CITED**

- Alt, D. and D. Hyndman. 1986. Roadside Geology of Montana. Mountain Press Publishing Company, Inc. 435 pp.
- Andersson, E., Nilsson, C. and M. E. Johansson. 2000. Effects of river fragmentation on plant dispersal and riparian flora. Regulated Rivers: research and management 16: 83-89.
- Barbour, M.T, J. Gerritsen, B.D. Snyder, and J.B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, second edition. EPA841-B-99-002. U.S. Environmental Protection Agency; Office of W<sup>a</sup> ter; Washington, D.C.
- Benenati, P. L., Shannon, J.P., and D. W. Blinn. 1998. Desiccation and recolonization of phytobenthos in a regulated desert river: Colorado River at Lees Ferry, Arizona, USA. Regulated Rivers: research and management 14:519-532.
- Branham, J. M., and R. R. Hathaway. 1975. Sexual differences in the growth of *Pteronarcys californica*  Newport and *Pteronarcella badi*  Hagen (Plecoptera). Can. J. Zool. 53:501-506.
- Brown, *C.].D.* and G. C. Kemp. 1942. Gonal measurements of egg counts of brown trout *(Salmo trutta)* from the Madison River, Montana. Trans. Amer. Fish. Soc. 71:195-200.
- Bureau of Reclamation. 1995. Operation of Glen Canyon Dam: Final Environmental Impact Statement. U.S. Department of Interior. Salt Lake City, UT. 337 pp.
- Cazaubon, A. and J. Giudicelli. 1999. Impact of the residual flow on the physical characteristics and benthic community (algae, i <sup>n</sup>vertebrates) of a regulated Mediterranean river: the

Durance, France. Regulated Rivers research and management 15:4<sup>4</sup> 1-461.

- Cummins, K.W., Petersen, R.C., Howard, F.O., Wuyeheck, J.C., and V.1. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54:336-345.
- Dodds, W. K. 1991. Community interactions between filamentous alga *Cladophora glomerata* (L.) Kuetzing, its epiphytes, and epiphyte grazers. Oecologia 85:572-580.
- Elder, J. A., and R. A. Gaufin. 1973. Notes on the occurrence and distribution of *Pteronarcys californica*  Newport (Plecoptera) within streams. Great Basin Nat. 33:218-221.
- Fraley, J. J. 1978. Effects of elevated summer water temperatures below Ennis Reservoir on the macroinvertebrates of the Madison River, Montana. MS thesis. Montana State University, Bozeman, MT. 63 pp.
- Freilich, J.E. 1991. Movement patterns and ecology of *Pteronarcys* nymphs (Plecoptera): observations of marked individuals in a Rocky Mountain stream. Freshwater Bio. 25:379-394.
- Friedman, J. M. and G.T. Auble. 1999. Mortality of riparian box elder from sediment mobilization and extended inundation. Regulated Rivers: research and management 15:463-476.
- Fuller, R. L., and K. W. Stewart. 1979. Stonef<sup>l</sup> y (Plecoptera) food habits and prey preference in the Dolores River, Colorado. Am. Midland Nat. 10:170-179.
- Gillespie, D. M. 1969. Population studies of four species of mollusks in the Madison River, Yellowstone National Park. Limnol. Oceanogr. 14:101-114.

Hassage, R.L., and K.W. Stewart. 1990. Growth and voltinism of five stonefly species in a New Mexico mountain stream. SW. Nat. 35:130-134.

Hauer, F. H. and G. A. Lamberti. 1998. Methods in Stream Ecology. Academic Press. London. 674 pp.

Jourdonnais, J. H., Walsh, R. P., Pickett, F., and D. Goodman. 1992. Structure and calibration strategy for a water temperature model of the lower Madison River, Montana. Rivers 3: 153-169.

Ligon, F. K., Dietrich, W. E., and W. J. Trush. 1995. Downstream ecological effects of dams: a geomorphic perspective. Bioscience 45: 183-192.

Marcus, M. D. 1980. Periphytic community response to chronic nutrient enrichment by a reservoir discharge. Ecology 61:387-399.

McMichael, G. A. and C. M. Kaya. 1991. Relations among stream temperature, angling success for rainbow trout and brown trout, and fisherman satisfaction. N. A. J. Fish. Manag. 11:190-199.

Merrit, K., and R. Cummins. 1984. Aquatic insects of North America. 2nd edition. Dubuque, IA. 722 pp.

Moore, K. A., and D. D. Williams. 1990. Novel strategies in the complex defense repertoire of a stonefly *(Pteronarcys dorsata)* nymph. Oikos 57: 49-56.

Peaz, M., Baru, V., and M. Proke. 1999. Changes in the structure of fish assemblages in a river used for energy production. Regulated Rivers: research and management 15:169-180.

Poole, R. W. 1981. The bioenergetics of *Pteronarcys californica.* Ph. D. thesis. Idaho State University. Pocatello, ID. 122 pp.

Short, R.A. and P.E. Maslin. 1977. Processing of leaf litter by a stream detritivore: effect on nutrient availability to collectors. Ecology 58:935-938.

Stanford, J. A. 1998. Rivers in the landscape: introduction to the special issue on riparian and groundwater ecology. Freshwater Bio. 40:402-406.

Stanford, J. A. and J. V. Ward. 1984. The effects of regulation on the limnology of the Gunnison River: a North American case history. Pages 467-480 *in* A. Lillehammer and S. J. Saltveit, eds., Regulated Rivers. Universitetsforlaget, Oslo, Norway.

- Statsoft Inc. 1995. STATISTICA for Windows. 2300 East 14th Street, Tulsa, OK.
- Webb, B.W. and D. E. Walling. 1997. Complex summer water temperature behaviour below a UK regulating reservoir. Regulated Rivers: research and management 13: 463-477.

Wolman, M.G. 1954. A method of sampling coarse river-bed material. Trans. Am. Geophys. Union 35:951- 956.