

DRIFTING INVERTEBRATE COMPOSITION, DENSITIES, AND BIOMASS FROM FALL THROUGH WINTER IN THREE WYOMING TAIL WATERS

Jason L. Hebdon, Wyoming Cooperative Fish and Wildlife Research Unit, USGS, Department of
Zoology and Physiology, University of Wyoming, Laramie, WY 82071-3166
Wayne A. Hubert, Wyoming Cooperative Fish and Wildlife Research Unit, USGS, Department of
Zoology and Physiology, University of Wyoming, Laramie, WY 82071-3166

ABSTRACT

We studied three regulated rivers downstream from reservoirs (tailwaters) in Wyoming from October 1997 through February 1998 to assess the temporal variation in composition, density, and biomass of drifting invertebrates. Macroinvertebrates were numerically dominated by Diptera (primarily Chironomidae) and Ephemeroptera in the North Platte and Big Horn rivers with Trichoptera, Oligochaeta, and Arachnida (Hydracarina) also common. In the Shoshone River, the predominant macroinvertebrate taxon was Oligochaeta followed by Diptera and Ephemeroptera. Densities of drifting macroinvertebrates were lowest in November and highest in January in the North Platte and Big Horn rivers. However, densities of drifting macroinvertebrates were lowest in October and highest in November in the Shoshone River. The composition of drifting invertebrates changed from exclusively macroinvertebrates in October and November to predominantly zooplankton in December through February in all three rivers. However, drifting macroinvertebrates were relatively abundant throughout the winter in all three tailwaters compared to other river systems.

Key words: aquatic invertebrates, drifting, macroinvertebrates, river regulation, tailwaters, winter

INTRODUCTION

Dams have been constructed on many rivers to store water and regulate downstream flows thereby altering the physical conditions of the downstream river, particularly within reaches immediately downstream from reservoirs (tailwater). A notable change is the release of cool, nutrient rich water from the hypolimnion during summer (Allan 1995). As a consequence of the altered thermal regime, endemic fishes and invertebrates can be extirpated. Managers have frequently introduced trout into tailwaters to create highly valued, coldwater sport fisheries (Pfitzer 1967). In such systems, drifting macroinvertebrates are a primary food of trout (Filbert and Hawkins 1995, Simpkins and Hubert 2000, Hebdon and Hubert 2001).

Invertebrates in lotic systems are transported downstream in the water column in substantial numbers (Allan 1995). Their downstream transport has been related to a variety of biotic and abiotic factors including catastrophic events, i.e., floods, anchor ice or high water temperatures, and behavior, i.e., diel activity, avoidance of predators, or accidental dislodging. However, most research on drifting invertebrates has been conducted on unregulated streams with natural flow regimes. Few studies have been conducted on drifting invertebrates in tailwaters supporting trout, and temporal trends in drifting invertebrates and their potential effects on trout fisheries in tailwaters are poorly understood (Armitage 1977). Perry and Perry (1986) and Poff and Ward (1991) assessed the effects of short-

term variation in discharge on the magnitude of drifting invertebrates during different seasons in Montana and Colorado tailwaters. Seasonal variation in density of drifting invertebrates has been described in a Utah tailwater (Filbert and Hawkins 1995). In the only previous study of fall through winter trends known to us, Simpkins and Hubert (2000) found that densities of drifting macroinvertebrates in a Wyoming tailwater declined by almost 90 percent from September to December, but by February they recovered and surpassed September levels. How widespread such temporal patterns may be among tailwaters supporting trout in the western United States is unknown. Because long sections of tailwaters remain free of surface ice, trout continue to feed during winter (Filbert and Hawkins 1995, Simpkins and Hubert 2000, Hebdon and Hubert 2001). Understanding the dynamics of drifting invertebrates during winter could be important to managing these fisheries.

Our goal was to determine the dynamics of drifting invertebrates from fall through winter in Wyoming tailwaters. We assessed temporal variation in composition, density, and biomass of drifting macroinvertebrates and zooplankton from October through February in three selected tailwaters in Wyoming to determine if temporal trends were similar among them.

STUDY SITES

We selected for study three of the five tailwaters in Wyoming that support economically important trout fisheries: (1) the North Platte River downstream from Gray Reef Dam, (2) the Bighorn River downstream from Boysen Dam, and (3) the Shoshone River downstream from Buffalo Bill Dam. The North Platte River downstream from Kortess Dam was omitted because there is only a short segment of river (~2 km) between the dam and Pathfinder Reservoir. The Green River downstream from Fontenelle Dam was not studied because it is difficult to access during winter.

One study site was on the North Platte River, 15 km downstream from Gray Reef Dam. Mean October discharge (1904-1998) has been 18 m³/s and it generally remains constant or declines slightly during winter. This site has a mean wetted width of about 60 m during fall and winter. The tailwater supports naturalized populations of rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*), and receives annual stocking of rainbow trout.

The second study site was on the Bighorn River, 22 km downstream from Boysen Dam. Mean October discharge (1951-1998) has been 34 m³/s and often fluctuates between 30 and 34 m³/s during winter. The river is 50 m wide at this site during winter flows. The river has a naturalized population of brown trout and rainbow trout are stocked annually to maintain the fishery although a small amount of natural recruitment by rainbow trout has been observed over a short portion of the tailwater (Wiley 1995).

A third study site was on the Shoshone River, 13 km downstream from Buffalo Bill Dam. Mean discharge during October (1943-1998) has been 19 m³/s and it generally declines to 14-15 m³/s during winter. The wetted width at this site is about 30 m at winter flows. This tailwater supports populations of naturalized brown trout, stocked cutthroat trout (*Oncorhynchus clarki*), and rainbow trout that escape from Buffalo Bill Reservoir. This site was unique in that warm springs approximately 8 km upstream from the study site added concentrations of hydrogen sulfide lethal to salmonids and many invertebrate taxa and warmed the water 4-5 °C. Hydrogen sulfide dissipated so it was no longer detectable 3-4 km upstream from the study site (Dare et al. 2001), but water temperatures warmer than ambient persisted at the study site (Hebdon 1999).

METHODS

Water temperatures were recorded at 30-minute intervals from October 1997 through February 1998 using two

thermographs (Optic Stowaways, Onset Computer Corporation, Pocasset, Massachusetts) approximately 2 km upstream and downstream of each study site. Thermographs were placed in water at least 0.5 m deep with velocities greater than 15 cm/s. Daily estimates of discharge were obtained from gages between the upstream reservoirs and the study reaches (Water Resources Data System, Department of Civil and Architectural Engineering, University of Wyoming, Laramie).

We sampled during the day, 3-4 hours after sunrise. Diel variation in the density of drifting macroinvertebrates is common with greater densities during the night (Allan 1995), but whether such temporal trends occur during fall and winter in tailwaters is not known. Since our purpose was to assess temporal variation from fall through winter, we limited our sampling to a short duration during the day to reduce variability at individual sites and enhance the statistical power of comparisons among monthly sampling periods.

Field sampling occurred monthly, October 1997 through February 1998, at a single site in all three tailwaters. Twenty samples of drifting invertebrates were collected each month from each tailwater. Sampling occurred diagonally across a 50-m reach at points where the water was 0.6-0.9 m deep with velocities of 30-60 cm/s. A 363-micron-mesh net (45 x 30 x 90 cm) was placed midway between the surface and the bottom. Sampling began at the downstream boundary of the reach and progressed across and upstream to avoid collecting invertebrates dislodged by observers. Sample duration (3-5 minutes) was adjusted so that approximately 15 m³ of water was filtered for each sample.

Samples were separated into macroinvertebrate and zooplankton components by sieving through a 2-mm mesh screen. All macroinvertebrates retained by the sieve were identified to family and enumerated. Because of high densities of zooplankton in many samples, the apparatus described by Wrona et al. (1982) was used to subsample. The

zooplankton portion was placed into a 1-L graduated Imhof settling cone fitted with an aquarium airstone sealed in the bottom and connected to a compressed air supply. The total volume of the sample was increased to 1-L by adding water. The sample was mixed for 2-5 minutes by bubbling air and three subsamples were removed in known volumes of 10, 25 or 50 ml depending on the density of zooplankton in the cone. Zooplankton in subsamples were identified as Cladocera or Copepoda and enumerated. The mean and standard error (SE) of the number of zooplankton per subsample were calculated with adjustment to the SE to account for the finite population: corrected $SE = SE * (1-f)^{0.5}$ where f = number of subsamples/total number of subsamples possible. If the coefficient of variation (CV) was less than 20 percent, no additional subsamples were obtained. If the CV exceeded 20 percent, additional subsamples were drawn until the CV was reduced to less than 20 percent. The proportions of each taxon in the subsamples were multiplied by the estimate to give an estimate of the number of individuals in each taxon.

Estimates of the biomass of macroinvertebrates and zooplankton were made by multiplying the estimated number of individuals in a taxon by the mean weight of individuals in the taxon after drying. Individuals of each taxon from each river were pooled within each month and dried for 24 hr at 60 °C to estimate mean biomass/individual for each taxon.

Sample distributions of densities and biomass were consistently skewed so a Kruskal-Wallis test was used to determine if differences in density and biomass of drifting invertebrates occurred among months. Analysis was conducted using Minitab 12.21 (Minitab, Inc.) and Sigmapstat 1.0 for Windows (Jandel Scientific). Significance was determined at $\alpha = 0.05$ for all tests.

RESULTS

Water temperatures during the study were colder in the North Platte and Bighorn rivers than in the Shoshone River. Mean daily water temperature between 1 October 1997 and 28 February 1998 (151 days) was 0.0-3.9 °C with a mean <4 °C recorded 89 days in the North Platte River, 0.1-14.6 °C with a mean <4 °C recorded 86 days in the Bighorn River, and 3.8-12.6 °C with a mean <4 °C on only 2 days in the Shoshone River.

Discharge patterns varied among the three tailwaters during the study. A planned flushing flow resulted in a 50 m³/s discharge in the North Platte River between 6 and 10 October 1997 (prior to our first sampling), but during sampling the discharge was 16-17 m³/s. Discharge in the Bighorn River was 65 m³/s during most of October, but it was reduced to winter levels from 24 to 28 October 1997. For the study period, excluding October, flows were 26-34 m³/s in the Bighorn River. Flows on the Shoshone River were reduced to winter levels from 7 to 10 October 1997, and during the study period they were 13-15 m³/s.

The major taxonomic groups of drifting macroinvertebrates among samples from all three rivers were Diptera, Ephemeroptera, Oligochaeta, Trichoptera, Arachnida (Hydracarina). Diptera were composed primarily of Chironomidae and Simuliidae, but Stratiomyidae were also observed. Ephemeroptera were primarily Baetidae, Ephemerellidae, and Trichorythidae.

Trichoptera were Hydropsychidae, Limniphillidae, Hydroptillidae, and Helicopschidae with Hydropschidae being most common. Other macroinvertebrate taxa collected sporadically included Coleoptera, Hemiptera, Hymenoptera, Odonata, and Plecoptera. When zooplankton were collected, Cladocera and Copepoda were present in relatively equal proportions.

Taxonomic composition of the invertebrates was similar among samples from the North Platte and Bighorn rivers, but differed from the Shoshone River due to the high abundance of Oligochaeta and low

abundance of zooplankton in the Shoshone River (Table 1). Diptera and Ephemeroptera comprised 70-92 percent of the macroinvertebrates in samples from the North Platte and Bighorn rivers over the 5 months. Whereas, Diptera and Ephemeroptera comprised 33-78 percent and Oligochaeta comprised 17-61 percent of the macroinvertebrates in the Shoshone River. Zooplankton was absent from all samples taken in October and November, but occurred in high densities in December through February in all three rivers. In December through February, zooplankton comprised 96-99 percent of the invertebrates in samples from the North Platte and Bighorn rivers, but made up a somewhat lower percentage (60-87%) of the invertebrates in samples from the Shoshone River.

Significant differences in densities of drifting macroinvertebrates occurred from October to February among most taxa that were assessed in all three rivers (Table 1). The sampling months with minimum and maximum densities of various taxa of macroinvertebrates and zooplankton differed among the three rivers with no consistent temporal trends among tailwaters. However, Diptera and Ephemeroptera tended to increase in densities through the fall and to be most abundant in January and February.

The biomass of drifting invertebrates also varied significantly from October to February among most taxa that were assessed in all three rivers (Table 2). Biomass of drifting macroinvertebrates was dominated by Diptera and Ephemeroptera in all three rivers. Together, these two taxa comprised 66-95 percent of the biomass of macroinvertebrates in samples from the three rivers over the 5 months. However, Oligochaeta comprised up to 25 percent of the biomass of macroinvertebrates in the Shoshone River. Zooplankton comprised 53-99 percent of the biomass of drifting invertebrates in the North Platte and Bighorn rivers, but only 3-10 percent in the Shoshone River from December to February.

Table 1. Mean densities (number/100 m³) of drifting invertebrates in monthly samples during the fall and winter of 1997-1998 from three regulated rivers in Wyoming. Standard deviations in parentheses. *P*-values are for Kruskal-Wallis tests assessing differences among months.

	Month					
Taxa	October	November	December	January	February	P
North Platte						
Diptera	146 (71)	75 (55)	78 (33)	462 (247)	265 (141)	<0.001
Ephemeroptera	197 (91)	53 (47)	118 (51)	346 (353)	204 (91)	<0.001
Trichoptera	16 (19)	4 (9)	32 (29)	156 (117)	21 (24)	<0.001
Oligochaeta	29 (21)	8 (13)	14 (20)	29 (43)	8 (17)	0.109
Arachnida	5 (7)	2 (5)	4 (8)	34 (54)	15 (21)	0.012
Other	5 (15)	2 (2)	<1 (4)	25 (<1)	18 (7)	0.003
macroinvertebrates						
Zooplankton	0	0	6,470 (1,388)	127,043 (24,264)	77,458 (36,251)	<0.001
Big Horn						
Diptera	252 (175)	20 (25)	13 (16)	119 (232)	144 (172)	<0.001
Ephemeroptera	468 (242)	43 (45)	142 (74)	474 (439)	288 (141)	<0.001
Trichoptera	8 (17)	7 (9)	11 (15)	70 (239)	8 (19)	0.121
Oligochaeta	44 (7)	8 (14)	20 (22)	84 (237)	25 (51)	0.046
Arachnida	7 (11)	3 (6)	3 (6)	59 (241)	5 (18)	0.486
Other	14 (45)	1 (4)	0	41 (52)	0	<0.001
macroinvertebrates						
Zooplankton	0	0	121,479 (43,151)	43,427 (13,784)	21,913 (5,428)	<0.001
Shoshone						
Diptera	33 (24)	363 (150)	259 (289)	323 (414)	422 (270)	<0.001
Ephemeroptera	53 (44)	137 (69)	193 (189)	225 (173)	248 (149)	<0.001
Trichoptera	14 (18)	7 (15)	32 (47)	29 (38)	7 (14)	<0.001
Oligochaeta	159 (188)	737 (409)	253 (182)	121 (125)	389 (224)	<0.001
Arachnida	0	0	1 (4)	<1 (2)	4 (14)	0.544
Other	0	0	0	0	0	
macroinvertebrates						
Zooplankton	0	0	5,042 (2,666)	1,069 (434)	3,798 (1,228)	<0.001

DISCUSSION

Our results and those of previous studies indicated that Diptera and Ephemeroptera tend to be the primary taxa of drifting macroinvertebrates from fall through winter in tailwaters of the western United States. This was the case in the Bighorn and North Platte rivers and it has also been observed in tailwaters in Wyoming, Montana, Colorado, and Utah (Kroger 1974, Perry and Perry 1986, Poff and Ward 1991, Filbert and Hawkins 1995). However, the predominant macroinvertebrate taxa in samples from the Shoshone River was Oligochaeta, followed by Diptera and Ephemeroptera. This unique

situation may have resulted from the input of toxic levels of hydrogen sulfide 8 km upstream from the study site. Dare et al. 2001 found that hydrogen sulfide concentrations lethal to salmonids extended downstream to with 3-4 km of our sampling site. The relatively high abundance of Oligochaeta and Diptera may have occurred because our sampling site was within the zone of recovery associated with impacts from a point source of hydrogen sulfide (Hynes 1960).

Drifting macroinvertebrates were relatively abundant throughout the fall and winter in all three Wyoming tailwaters. Densities of macroinvertebrates in the three

Table 2. Mean biomass (mg/100 m³) of drifting invertebrates in monthly samples during the fall and winter of 1997-1998 from three regulated rivers in Wyoming. Standard deviations in parentheses. *P*-values are for Kruskal-Wallis tests assessing differences among months.

	Month					
Taxa	October	November	December	January	February	<i>P</i>
North Platte						
Diptera	13 (8)	10 (8)	13 (7)	82 (42)	42 (22)	<0.001
Ephemeroptera	7 (4)	3 (4)	14 (15)	58 (34)	29 (40)	<0.001
Trichoptera	1 (1)	<1 (1)	<1 (1)	19 (19)	<1 (<1)	<0.001
Oligochaeta	3 (2)	3 (5)	1 (3)	4 (6)	1 (2)	0.378
Arachnida	1 (1)	<1 (1)	<1 (<1)	3 (5)	<1 (<1)	0.014
Other	0	0	0	4 (3)	14 (14)	0.867
macroinvertebrates						
Zooplankton	0	0	31 (31)	607 (610)	369 (330)	<0.001
Big Horn						
Diptera	21 (15)	2 (3)	1 (2)	23 (37)	61 (67)	<0.001
Ephemeroptera	8 (9)	1 (1)	4 (2)	13 (12)	10 (6)	<0.001
Trichoptera	<1 (1)	<1 (<1)	<1 (<1)	1 (2)	<1 (<1)	0.255
Oligochaeta	2 (2)	<1 (1)	<1 (<1)	7 (20)	17 (35)	0.195
Arachnida	<1 (<1)	<1 (<1)	<1 (<1)	2 (7)	<1 (1)	0.486
Other	4 (17)	0	0	1 (2)	0	<0.001
macroinvertebrates						
Zooplankton	0	0	919 (327)	329 (104)	166 (41)	<0.001
Shoshone						
Diptera	4 (4)	26 (11)	20 (23)	23 (28)	45 (29)	<0.001
Ephemeroptera	4 (5)	8 (7)	6 (6)	11 (9)	19 (12)	<0.001
Trichoptera	3 (5)	2 (4)	5 (8)	3 (4)	1 (2)	0.103
Oligochaeta	1 (1)	6 (3)	3 (2)	1 (1)	4 (2)	<0.001
Arachnida	0	0	<1 (1)	<1 (1)	2 (5)	0.544
Zooplankton	0	0	14 (7)	3 (1)	10 (3)	<0.001

Wyoming tailwaters during fall and winter were similar to what has been observed among other tailwaters in the western United States. We observed that mean densities of drifting macroinvertebrates had ranges of 263-800/100 m³ in October, 189-777/100 m³ in December and 469-1073/100 m³ in February among the three Wyoming tailwaters. Mean densities of macroinvertebrates in the Green River, Utah, downstream from Flaming Gorge Reservoir were estimated to be to be 525/100 m³ in October 1987 and 271/100 m³ in February 1988 (Filbert and Hawkins 1995). Similarly, densities of drifting insects in the Colorado River, Colorado, downstream from Grandby Reservoir were observed to

be 540-630/100 m³ in November 1985 at stable flows (Poff and Ward 1991).

Densities of macroinvertebrates among tailwaters in the western United States appear high relative to other lotic systems during fall and winter. Culp et al. (1994) defined low densities of drifting invertebrates to be less than 50/100 m³ and high densities to be greater than 500/100 m³. Given these standards, the Wyoming tailwaters had moderate to high densities of macroinvertebrates drifting in the daytime during fall and winter. Macroinvertebrate densities during winter in Wyoming tailwaters were similar to tropical streams in Costa Rica (Pringle and Ramirez 1998) and generally exceeded large rivers in Europe

(Cellott 1989). Densities of drifting macroinvertebrates in the three Wyoming tailwaters during fall and winter appeared to be substantially greater than what has been observed in Appalachian Mountain streams (O'Hop and Wallace 1983, Cada et al. 1987) and regulated and unregulated streams in Great Britain (Armitage 1977).

Similar monthly samples of drifting macroinvertebrates were collected from October 1995 through February 1996 in the same reach of the Bighorn River that we studied (Simpkins and Hubert 2000). Densities of drifting insects in our study were similar to those in 1995-1996 during October, December, and January, but substantially lower in November and February. Water temperatures were similar during both fall through winter periods, with the exception that water temperatures cooled more rapidly in October 1995 than in October 1997 (Hebdon 1999, Simpkins and Hubert 2000).

Zooplankton originating from upstream reservoirs dominated the drifting invertebrates during winter (December-February) in the three Wyoming tailwaters, but the extent to which drifting zooplankton occur in other tailwaters of the western United States during winter is unknown. Simpkins and Hubert (2000) first described the winter pattern of high densities of drifting zooplankton in the Bighorn River downstream from Boysen Reservoir. We observed similar occurrence of zooplankton in the North Platte and Shoshone rivers. In all three tailwaters, drifting zooplankton were found after the upstream reservoirs became ice covered. However, densities of zooplankton were substantially lower in the Shoshone River than in the North Platte and Bighorn rivers. We believe that this is likely due to lethal levels of hydrogen sulfide between Buffalo Bill Reservoir and the study site (Dare et al. 2001).

Our results combined with those of Hebdon and Hubert (2001) suggest that drifting macroinvertebrates are sufficiently abundant through the fall and winter in the Bighorn and North Platte rivers to provide

adequate food resources for trout. Hebdon and Hubert (2001) studied the stomach contents and body conditions of subadult trout in these two tailwaters at the same time that our study of drifting invertebrates was conducted. They found that fish fed throughout the winter and maintained greater than average body conditions. These observations indicate that starvation was not a cause of overwinter mortality of subadult trout in these two tailwaters. However, we found that the density of drifting macroinvertebrates were lower in the Shoshone River compared to the Bighorn and North Platte rivers. Also, Hebdon and Hubert (2001) observed fewer food items in stomachs and declining body conditions during the winter in the Shoshone River. It is likely that the combination of lower densities of drifting macroinvertebrates and higher metabolic rates associated with warmer water temperatures may affect overwinter survival of subadult trout in the Shoshone River. The presence of warm springs in the Shoshone River appear to make it unique among Wyoming tailwaters and the dynamics of trout in the system appear to differ from other tailwaters as a result.

ACKNOWLEDGEMENTS

We thank J. Lockwood and D. Miller for suggestions regarding methods and critical review of the manuscript, M. Hyatt, A. Hamel, C. Jameson, S. Schmidt, and A. Seales for assistance in the field and laboratory, and the Wyoming Game and Fish Department's regional fish biologists in Cody (R. Mcknight, M. Welker, and S. Yekel) and Casper (A. Conder, J. Deromedi, and P. Mavrakis) for logistic and technical support. The research was funded by the Wyoming Game and Fish Department. The Wyoming Cooperative Fish and Wildlife Research Unit is jointly supported by the University of Wyoming, Wyoming Game and Fish Department, U.S. Geological Survey, and Wildlife Management Institute.

LITERATURE CITED

- Allan, J. D. 1995. Stream ecology. Chapman and Hill, London. 388 pp.
- Armitage, P. D. 1977. Invertebrate drift in the regulated River Tees and an unregulated tributary, Maize Beck, below Dow Green dam. *Freshwater Biology* 7:167-184.
- Cada, G. F., J. M. Loar, and M. J. Sale. 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. *Transactions of the American Fisheries Society* 116:692-702.
- Cellott, B. 1989. Macroinvertebrate movements in a large European river. *Freshwater Biology* 22:45-55.
- Culp, J. M., G. J. Scrimgeour, and C. E. Beers. 1994. The effect of sample duration on the quantification of stream drift. *Freshwater Biology* 31:165-173.
- Dare, M. R., W. A. Hubert, and J. S. Meyer. 2001. The influence of stream flow on hydrogen sulfide concentrations and distributions of two trout species in a Rocky Mountain tailwater. *North American Journal of Fisheries Management* 21:545-549.
- Filbert, R. B., and C. P. Hawkins. 1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. *Transactions of the American Fisheries Society* 124:824-835.
- Hebdon, J. L. 1999. Prey availability, diet, and body composition of sub-adult trout from fall through winter in regulated rivers, Wyoming. Master's thesis. University of Wyoming, Laramie. 73 pp.
- _____, and W. A. Hubert. 2001. Body conditions and stomach contents of subadult trout during fall and winter in three Wyoming tailwaters. *North American Journal of Fisheries Management* 21:471-477.
- Hynes, H. B. N. 1960. The biology of polluted waters. Liverpool University Press, Liverpool, England. 202 pp.
- Kroger, R. L. 1974. Invertebrate drift in the Snake River, Wyoming. *Hydrobiologia* 44:369-380.
- O'Hop, J., and J. B. Wallace. 1983. Invertebrate drift, discharge, and sediment relations in a southern Appalachian headwater stream. *Hydrobiologia* 98:71-84.
- Perry, S. A., and W. B. Perry. 1986. Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA. *Hydrobiologia* 134:171-182.
- Pfitzer, D. W. 1967. Evaluation of tailwater fishery resources resulting from high dams. Pp. 477-488 in *Reservoir Fishery Resources Symposium*. American Fisheries Society, Washington, DC.
- Poff, N. L., and J. V. Ward. 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1926-1936.
- Pringle, C. M., and A. Ramirez. 1998. Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. *Freshwater Biology* 39:359-373.
- Simpkins, D. G., and W. A. Hubert. 2000. Drifting invertebrates, stomach contents and body conditions of juvenile rainbow trout from fall through winter in a Wyoming tailwater. *Transactions of the American Fisheries Society* 129:1176-1184.
- Wiley, D. E. 1995. Development and evaluation of flushing flow recommendations for the Big Horn River. Master's thesis. University of Wyoming, Laramie, WY. 110 pp.
- Wrona, F. J., J. M. Culp, and R. W. Davies. 1982. Macroinvertebrate subsampling: a simplified apparatus and approach. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1051-1054.

Received 21 May 2001

Accepted 21 November 2001