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NOTES

MACROINVERTEBRATE DRIFT IN THE TAILWATER OF A REGULATED RIVER BELOW GLEN CANYON DAM, ARIZONA

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Many benthic organisms exhibit downstream drift, and abundance varies among taxa and with flow, season, and diel period (Brittain and Eikeland, 1988). Macroinvertebrates in the drift provide a trophic link between benthic flora and fishes (Angradi, 1994; Shannon et al., 1994; Stevens et al., 1997) and are an important food resource for rainbow trout (*Oncorhynchus mykiss*—Elliott, 1973; Scullion and Sinton, 1983; Bres, 1986; Cada et al., 1987). Thus, understanding the dynamics of invertebrate drift is relevant to the ecology and management of rainbow trout (Jenkins et al., 1970; Elliott, 1973; Slaney and Northcote, 1974; Cada et al., 1987; Filbert and Hawkins, 1995). We examined drift exported from the 26 km clear-water section of the Colorado River immediately below Glen Canyon Dam. Specifically, we determined seasonal densities and composition, and flow-dependent (daily hydrograph) densities and composition. This tailwater supports a recreational trout fishery.

Glen Canyon Dam impounds the Colorado River near the Utah–Arizona border and forms Lake Powell, a 653 km² warm-meromictic reservoir (Stanford and Ward, 1991). Hypolimnetic releases from Lake Powell result in clear and cold water in the 26 km tailwater between the dam (river kilometer = RK -26) and Lee's Ferry (RK = 0—Stanford and Ward, 1991; Stevens et al., 1997). During much of the period following closure of Glen Canyon Dam in 1963, minimum and maximum releases were 28 m³s⁻¹ and 895 m³s⁻¹, and ramping rate was unrestricted. Since implementation of more stable flow regimes in late 1991, releases from the dam have been restricted to between 142 m³s⁻¹ and 566 m³s⁻¹, and ramping rates (per hour) are limited to 71 m³s⁻¹ upramp and 43 m³s⁻¹ downramp (United States Department of Interior, 1995). Daily range of discharge

from the reservoir during this study generally was about 150–425 m³s⁻¹.

We collected drift samples monthly between May 1993 and July 1994 about 250 m above Lee's Ferry over 24 h periods coincident with low, ascending, peak, and descending flows of the hydrograph ($n = 1$ per month at each flow stage). Means and ranges (in parentheses) for flows during sampling were: low = 263 m³s⁻¹ (184–313 m³s⁻¹); ascending = 384 m³s⁻¹ (277–532 m³s⁻¹); peak = 406 m³s⁻¹ (304–544 m³s⁻¹); descending = 294 m³s⁻¹ (180–400 m³s⁻¹). We collected samples at: low—0700–0850 h; ascending—1030–1300 h; peak—1600–1930 h; descending—0130–0540 h.

We sampled drift using a metered (flow meter attached centrally in net mouth) net (0.5 m diameter, 1 mm mesh) while traversing a transect perpendicular to direction of river flow at minimal boat speed. Samples were depth-integrated by slowly raising and lowering the weighted net (6.8 kg “fish” on a 1 m drop chain attached to towline 0.6 m in front of the net). Sampling duration was generally 15 min, and a mean volume of 87.08 m³ (± 1.74 SE) of water passed through the towed nets. We used the metered tow net, rather than high speed sampling devices with smaller apertures (Scullion and Sinton, 1983; Angradi and Kubly, 1994), because of clogging of Miller tubes by coarse particulate organic matter during preliminary efforts. Clogging of the metered tow net was not measurable during 15 min of sampling.

Macroinvertebrates in samples were sorted (*Gammarus lacustris*; chironomid adults, larvae or pupae; gastropods; other macroinvertebrates) and enumerated. Sexual maturity of *Gammarus* (adults ≥ 7 mm [males = 7–22 mm, females = 7–14 mm]; juveniles < 7 mm) was determined by measuring to the nearest millimeter from the front of the head to base of the telson (Hynes, 1955; Hynes and Harper,

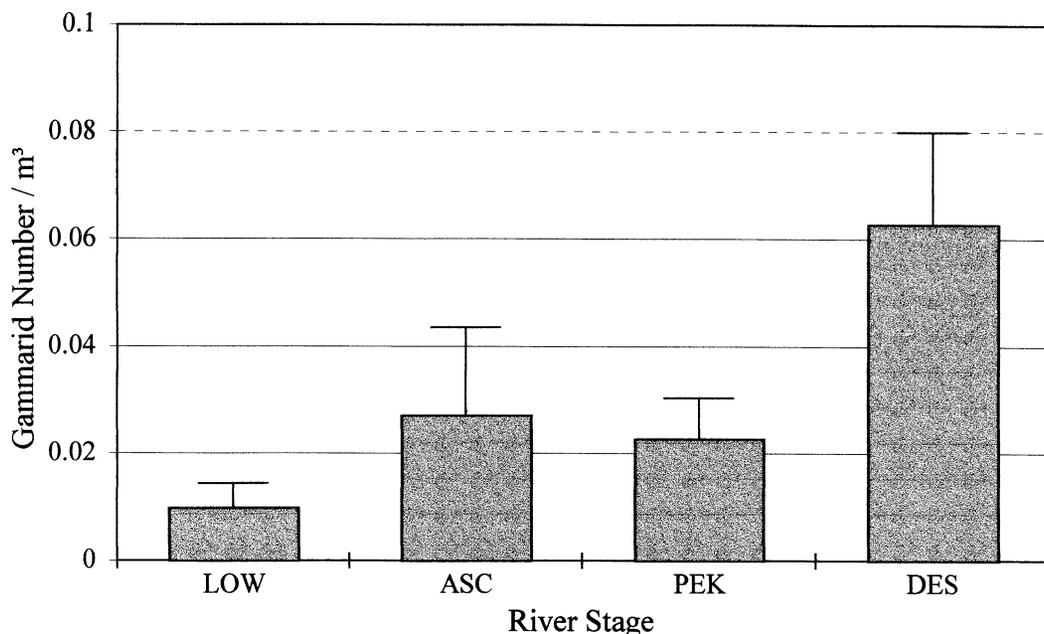


FIG. 1—Mean ($\pm SE$) stage-related densities (number/m³) of *Gammarus lacustris* in the drift at Lee's Ferry, May 1993–July 1994. LOW = low flow; ASC = ascending flow; PEK = peak flow; DES = descending flow.

1972). Densities (number/m³) of macroinvertebrates were analyzed using Kruskal-Wallis ANOVA.

Chironomids and *Gammarus* were the predominant macroinvertebrates in the drift, and mean density of chironomids exceeded that of the amphipod, which is consistent with previous findings by Shannon et al. (1996). Mean density of *Gammarus* (adults and juveniles combined) for all months and stages combined was 0.031/m³ ($\pm 0.007 SE$). Mean densities of chironomid larvae, pupae, and adults, respectively, were 0.018/m³ ($\pm 0.006 SE$), 0.024/m³ ($\pm 0.006 SE$) and 0.078/m³ ($\pm 0.030 SE$). Mean density of gastropods was 0.002/m³ ($\pm 0.001 SE$). Other macroinvertebrates were found infrequently and are not reported. Compared to other flow stages, there was a significant ($P < 0.01$) increase in *Gammarus* densities during the descending phase of the hydrograph (Fig. 1). Densities of adult or juvenile amphipods and of chironomids and gastropods did not differ significantly ($P > 0.05$) among flow stages.

Drift densities (total/24 h sampling period) of adult and juvenile *Gammarus* were maximal in summer and in winter (Fig. 2). Densities of adult and juvenile amphipods were compara-

ble in most months, but juvenile densities during seasonal peaks in June and December increased to as much as about 3–5 times greater than those of adults (Fig. 2). Most chironomid larvae (April–May = 58%) and pupae (March–May = 51%) were collected during the spring. Ninety one percent of adult chironomids were collected in January–February and in May. No seasonal change in drift densities was apparent for gastropods.

Greater drift densities of chironomid larvae and pupae during spring and the absence of apparent diel variation in the drift at Lee's Ferry reflect general patterns for chironomids (Armitage, 1977; Scullion and Sinton, 1983; Brittain and Eikeland, 1988; Poff and Ward, 1991; Mackay, 1992; Sagar and Glova, 1992). In comparison, others (Leibfried and Blinn, 1987; Blinn et al., 1994; Shannon et al., 1996) reported that drift densities and biomass of chironomid larvae at and below Lee's Ferry were greatest during summer and lower during winter and early spring. We found no significant differences in chironomid drift densities among flow stages, and Shannon et al. (1996) reported that daily fluctuations in releases from Glen Canyon Dam had no significant in-

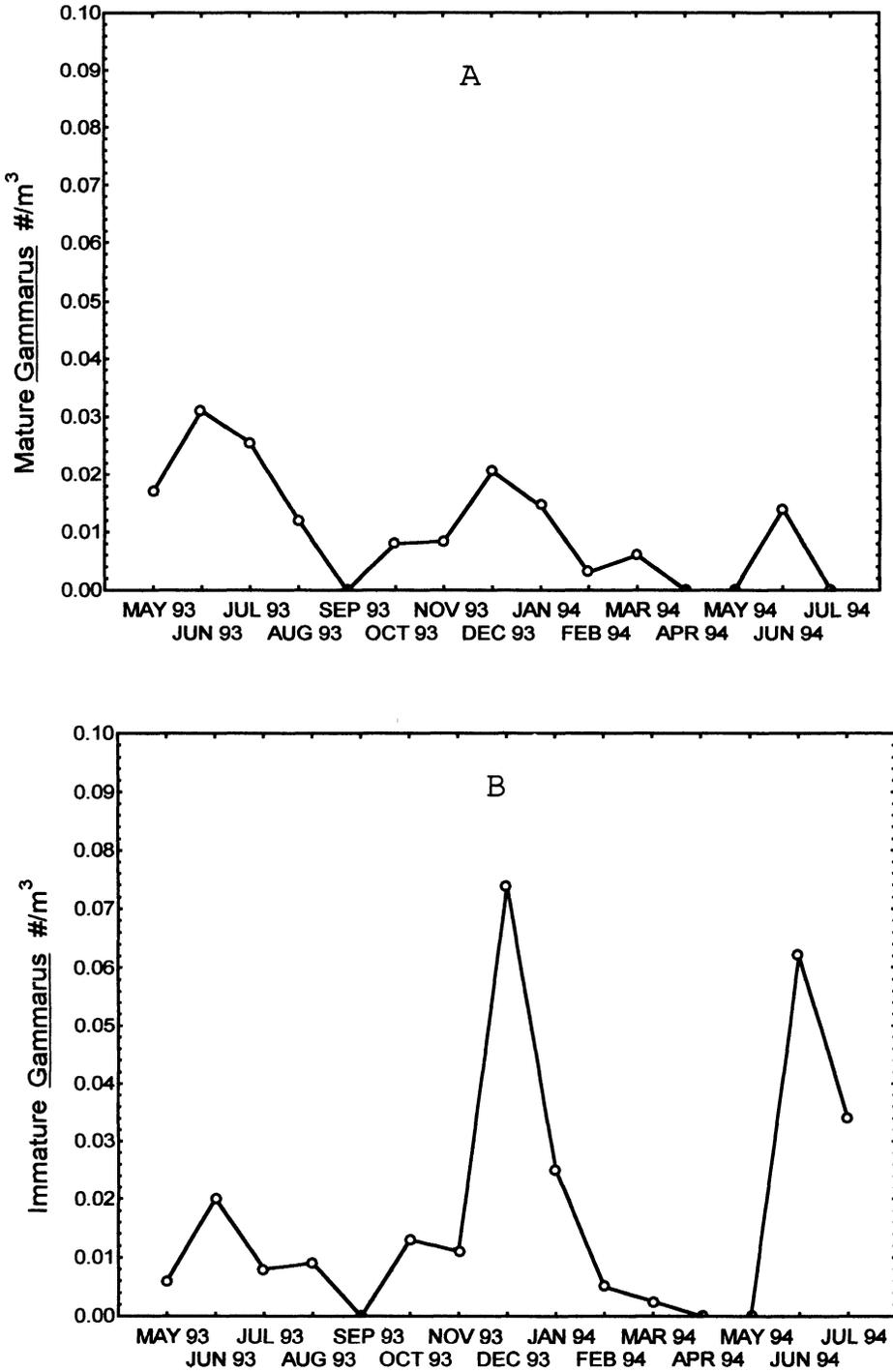


FIG. 2—Densities (number/m³ during 24 h sampling period) of sexually mature A) and immature B) *Gammarus lacustris* in the drift at Lee's Ferry, May 1993–July 1994.

fluence on mass and composition of the drift. However, greater abundance of chironomids may correspond with increasing or decreasing flows in other regulated rivers (Minshall and Winger, 1968; Scullion and Sinton, 1983; Perry and Perry, 1986). Brittain and Eikeland (1988) observed that drift of chironomids tends to correspond with current/discharge regimes. Peak flows during sampling in this study were only 60% to 70% above low stage. Thus, lower magnitude of flow fluctuations, as compared with other results (Minshall and Winger, 1968; Scullion and Sinton, 1983; Perry and Perry, 1986), might explain lack of changes in flow-related chironomid drift in this study.

Flow regime, discharge, and distance from the dam influence drift of macroinvertebrates in the Colorado River (Shannon et al., 1996; Stevens et al., 1998; Sublette et al., 1998). Prior to inception of a more stable flow regime in 1991, drift of *Gammarus* increased during the ascending limb of the daily hydrograph (Leibfried and Blinn, 1987). However, discharge and amphipod drift mass were negatively correlated through Grand Canyon in later studies (Blinn et al., 1994; Shannon et al., 1996). During this study, drift densities of *Gammarus* at Lee's Ferry also were greatest during the descending limb of the hydrograph.

Greater densities of *Gammarus* during the descending flow stage possibly reflect diel behavioral drift (Waters, 1961, 1965; Müller, 1974), because we collected samples during that flow stage only at night. Leibfried and Blinn (1987) also frequently observed higher drift densities of the amphipod downriver from Lee's Ferry during darkness. Moreover, stranding at night during the falling limb of the hydrograph in the absence of behavioral drift might be expected to result in increased macroinvertebrate densities during the rising flow stage (Scullion and Sinton, 1983; Cushman, 1985; Perry and Perry, 1986; Blinn et al., 1995).

Cladophora glomerata is the predominant filamentous green alga in the Glen Canyon Dam tailwater (Blinn et al., 1994). Exposure of phyto-benthos in the de-watered zone as discharge from the dam fluctuates daily may dry and weaken holdfast systems of the alga, causing filaments to detach and enter stream drift during the rising limb of the hydrograph (Usher and Blinn, 1990). *Cladophora* is a structural host for *Gammarus* and chironomids below

Glen Canyon Dam (Shannon et al., 1994; Stevens et al., 1997), and diatom epiphytes on the alga provide a food resource for these invertebrates (Blinn et al., 1992; Stevens et al., 1997). The alga and amphipods in the drift may not correspond closely (Blinn et al., 1994; Shannon et al., 1996), further suggesting that *Gammarus* drift is not passive. However, Blinn et al. (1994), based on results obtained with fixed nearshore surface nets, suggested that behavioral drift of macroinvertebrates may not occur below Glen Canyon Dam.

Prior to inception of the more stable regime in 1991, drift densities of the amphipod at Lee's Ferry were highest in early summer and late fall, and were lowest in late spring (Leibfried and Blinn, 1987). In contrast, drift of *Gammarus* biomass after 1991 did not exhibit seasonal variation at Lee's Ferry or downstream (Blinn et al., 1994; Shannon et al., 1996). We observed the greatest drift densities of *Gammarus* in early summer and winter, possibly reflecting differences in sampling method.

During early summer and winter, drift of juvenile amphipods in the Glen Canyon Dam tailwater tended to be greater than that of adults. Drift of gammarids may be size-selective in association with diel changes (Allan and Malmqvist, 1989) and current velocity or substratum composition (Pearson and Jones, 1987). Iversen and Jessen (1977) reported that size-selective drift of *G. pulex* was sporadic. Greater drift of adult male *Gammarus* during periods of mate-seeking (Müller, 1974; Brittain and Eikeland, 1988) and seasonal onset of amphipod reproductive activity (Hynes, 1955; Hynes and Harper, 1972; de March, 1982) possibly contributed to higher drift of amphipods in the Glen Canyon Dam tailwater during winter than at other times. Increased drift of *Gammarus* during summer may have corresponded with mortality of adults following breeding (Hynes, 1955) and seasonal production of young (Hynes, 1955; Hynes and Harper, 1972; de March, 1982).

The depth-integrated sampling procedure that we employed may be applicable in larger riverine systems for quantification of macroinvertebrate drift in channel cross-sections (Perry and Perry, 1986; Brittain and Eikeland, 1988). Our results indicate that chironomids and *Gammarus* in the drift potentially provide

an important, seasonally variable, and discharge-related food resource for rainbow trout (Bres, 1986; Angradi, 1994) in the Glen Canyon Dam tailwater. Chironomids were more abundant than *Gammarus* in the drift, and adult chironomids were more abundant than larvae or pupae. We suggest that season and dam operations together influence macroinvertebrate drift dynamics and likely the diet and feeding behavior of trout in the tailwater (Jenkins et al., 1970; Elliott, 1973; Bisson, 1978; Benke et al., 1986; Cada et al., 1987; Poff and Ward, 1991). Although higher and lower trophic levels are closely linked below Glen Canyon Dam (Angradi, 1994), relationships between rainbow trout and the aquatic food base as functions of dam operations are poorly understood.

Resumen—Se colectaron muestras a varias profundidades para determinar los cambios temporales y los efectos de operación de la presa sobre la composición y abundancia de macroinvertebrados a la deriva en la columna de agua, a la salida de la Presa Glen Canyon, en el Río Colorado, Arizona. *Gammarus lacustris* y quironómidos fueron los macroinvertebrados más predominantes a la deriva y la abundancia media de quironómidos excedió a la de los anfípodos. La abundancia de *Gammarus* alcanzó su pico durante la parte descendiente de la curva hidrográfica diaria. En el curso del año, los adultos y juveniles de *Gammarus* exhibieron patrones temporales más o menos iguales y alcanzaron su abundancia máxima durante el verano y el invierno. La abundancia de quironómidos no varió en función de la descarga de la presa. La mayoría de las larvas y pupas de quironómidos fue colectada durante la primavera, mientras que la mayoría de los adultos fue colectada durante la primavera e invierno. De esta manera, sugerimos que los cambios temporales y la manera de operar la presa, de manera conjunta influyen la dinámica de los macroinvertebrados a la deriva en la columna de agua.

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