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Driftwood: an alternative habitat for macroinvertebrates in a large desert river

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Abstract

Driftwood was an important substratum for macroinvertebrates in the Colorado River, a desert river in southwestern U.S.A. with high suspended sediments and limited cobble substrata. Higher light availability and reduced abrasion on driftwood substrata resulted in a significantly higher ash-free dry mass (AFDM) of biofilm when compared to cobbles. Overall mean mass of biofilm on driftwood was 3.76 g m^{-2} AFDM (SE $\pm$0.19) compared to 2.45 g m^{-2} AFDM ($\pm$0.15) on cobbles. Total macroinvertebrate AFDM was not significantly different between cobble and driftwood substrata. However, there were differences in the Ephemeroptera assemblage on the two substrata which were attributed to the type of food resources available in each habitat. Driftwood was dominated by the scraper/collector *Heptagenia elegantula* (Eaton), while the filterer/collector, *Traverella albertana* (McDunnough) dominated cobbles. Twenty taxa were found on driftwood substrata. This habitat expands the types of niches available to macroinvertebrates in lotic systems with high suspended sediments. We calculated that 4.4 m^2 of driftwood substratum passed our sample station each minute during a 12-h sampling period on the rising limb of the hydrograph. River impoundments limit the supply and transport of driftwood, which may have negative implications on macroinvertebrate communities in desert rivers with high suspended sediment. Studies in turbid desert rivers that do not sample driftwood may underestimate both the total standing mass/energy of the system and taxon richness.

Introduction

Previous studies have shown stable coarse woody debris to be an important habitat for macroinvertebrates in streams that have both fine and coarse substrata (Benke et al., 1984; Smocke et al., 1989; Borchardt, 1993; Phillips & Kilambi, 1994). In streams with fine, unstable substrata, submerged wood provides stable attachment points and refugia (Benke et al., 1984; Borchardt, 1993; Hax & Galloday, 1998). Also, fallen trees alter the geomorphology of streams creating habitat for many taxa (Dudley & Anderson, 1982; Triska, 1984; Harmon et al., 1986). Free-floating wood has been overlooked as a potential substratum for macroinvertebrates in these discussions.

Submerged wood provides a food source for xylophages (Dudley & Anderson, 1982; Phillips & Kilambi, 1994) and a substratum for the production of biofilm (Golladay & Sinsabaugh, 1991; Tank & Winterbourn, 1995). The importance of this biofilm may vary with the stream system. Jones et al. (1997) found that allochthonous materials had limited importance in the lotic food web of Sycamore Creek, AZ (a low order desert stream). In contrast, these materials play an integral role in the food web of some larger order desert streams (Haden, 1997). In large desert streams, autochthonous production is limited by low light availability and allochthonous material may be more available because of larger drainage basins. River regulation and land use changes which limit the amount and transport of woody debris in these rivers may have serious impacts on populations of invertebrates that rely on this substratum and food source.

We examined the potential of driftwood as an alternative habitat for macroinvertebrates in a southwestern desert river where large wood snags are not common. We propose that driftwood expands the types of available niches in turbid southwestern rivers allowing for a more diverse assemblage of macroinvertebrates. In our study area, floating woody debris provides a habitat with decreased potential for scour, higher light availability and potentially higher standing mass of biofilm than cobble or fine substrata. Furthermore, due to limited cobble substrata, epilithic food is low and the macroinvertebrate community is dominated by filterer/collector taxa (Haden, 1997). Driftwood provides substratum and food that creates better conditions for grazing macroinvertebrates than are found on cobbles or fine substrata. In addition, driftwood provides a refugium for drifting organisms during extended periods of high discharge when submerged substrata are subject to scour and movement.

Study area

This study examined portions of two midorder streams, the Green and Colorado Rivers within the Colorado Plateau geologic province (Figure 1). The area sampled is within Canyonlands National Park (CNP) in southern Utah, at the end of the longest unregulated reach that remains on the Colorado or Green Rivers (Ward et al., 1986). Although major dams upstream of CNP regulate flows on both rivers, their effects are lessened by distance ($\sim$650 km) from the dam (Ward & Stanford, 1983). The Colorado Plateau is very dry and although it represents over 37% of the drainage area it provides only 15% of the total runoff for the basin (Andrews, 1991).

Hard, stable substrata are rare in the Green and Colorado Rivers above the confluence in CNP (Haden, 1997). These two rivers are characterized by low gradient (0.57 m/km) and alluvial channels with beds of sand and silt (Valdez, 1990). Cobble bars are found only at the mouths of side canyons where sporadic flooding supplies coarser material. The channel margins alternate as alluvial flood plains or shear cliff walls. Riparian vegetation consists mainly of tamarisk (*Tamarix pentandra* Pall.) and willows (*Salix* spp.) which grow in dense stands in the alluvial flood plains. Large riparian trees are represented by the occasional older cottonwood (*Populus* spp.) or hackberry (*Celtis reticulata* Torr.). Most of the water is supplied by the mountainous headwaters (Andrews, 1991); as a result, most runoff for the year occurs during spring snowmelt. Spring runoff can be prolonged with flows above baseflow extending from April through the beginning of July in most years. Peak annual discharge for water years 1994 through 1997 measured at U. S. Geological Survey gauges at Cisco, UT and Green River, UT (Figure 1) ranged from 500 to 1500 $m^3 s^{-1}$ for both rivers, while baseflow was approximately 85 $m^3 s^{-1}$. Although low water prevails for most of the year, summer convective storms produce stochastic floods from ephemeral drainages which increased both the flow, sediment concentration and allochthonous inputs to the river (Sellers & Hill, 1974; Andrews, 1991). The exposed sedimentary rock and sparse vegetation of the plateau region provides large quantities of sediment to the river. Consequently, the river is turbid for all but short periods of the year when flows are low and stable (Woodbury, 1959; Andrews, 1991). Gauging stations downstream of the study area in the Grand Canyon recorded a mean annual sediment load of 85.9 million tons before construction of GCD (Andrews, 1991).

Cobble substratum is only available at the mouths of side canyons where flooding in ephemeral channels has deposited enough material to increase the gradient of the river. In the 54 km reach of our study area on the Green River above the confluence with the Colorado River there were only three cobble bars greater than 30 m in length. The rest of the channel was composed of sand or silt. We visually estimated the maximum total area of these cobble bars to be $\sim$20 000 m^2. The Colorado River above the confluence is similar to the Green River in this respect. As a comparison, we calculated that on the rising limb of the hydrograph the river carried a surface area of driftwood equal to the estimated area of the cobble bars within the 54 km study reach on the Green River in 3.2 days.

Methods

Macroinvertebrate samples were collected during July 1995, October 1995, March 1996, July 1996 and October 1996 as part of a larger study on the ecology of the benthic community in CNP. Macroinvertebrates were collected from randomly selected pieces of driftwood and cobbles from three reaches; the Green River above the confluence, the Colorado River above the confluence, and Cataract Canyon below the confluence (Figure 1). At least 10 samples were collected from each substratum in each reach on each collecting trip. All driftwood was floating on the surface of the water, either in eddies or the channel, and all cobbles were collected from depths $\leq$ 0.5 m. Invertebrates were collected from within 20 cm^2 templates randomly placed

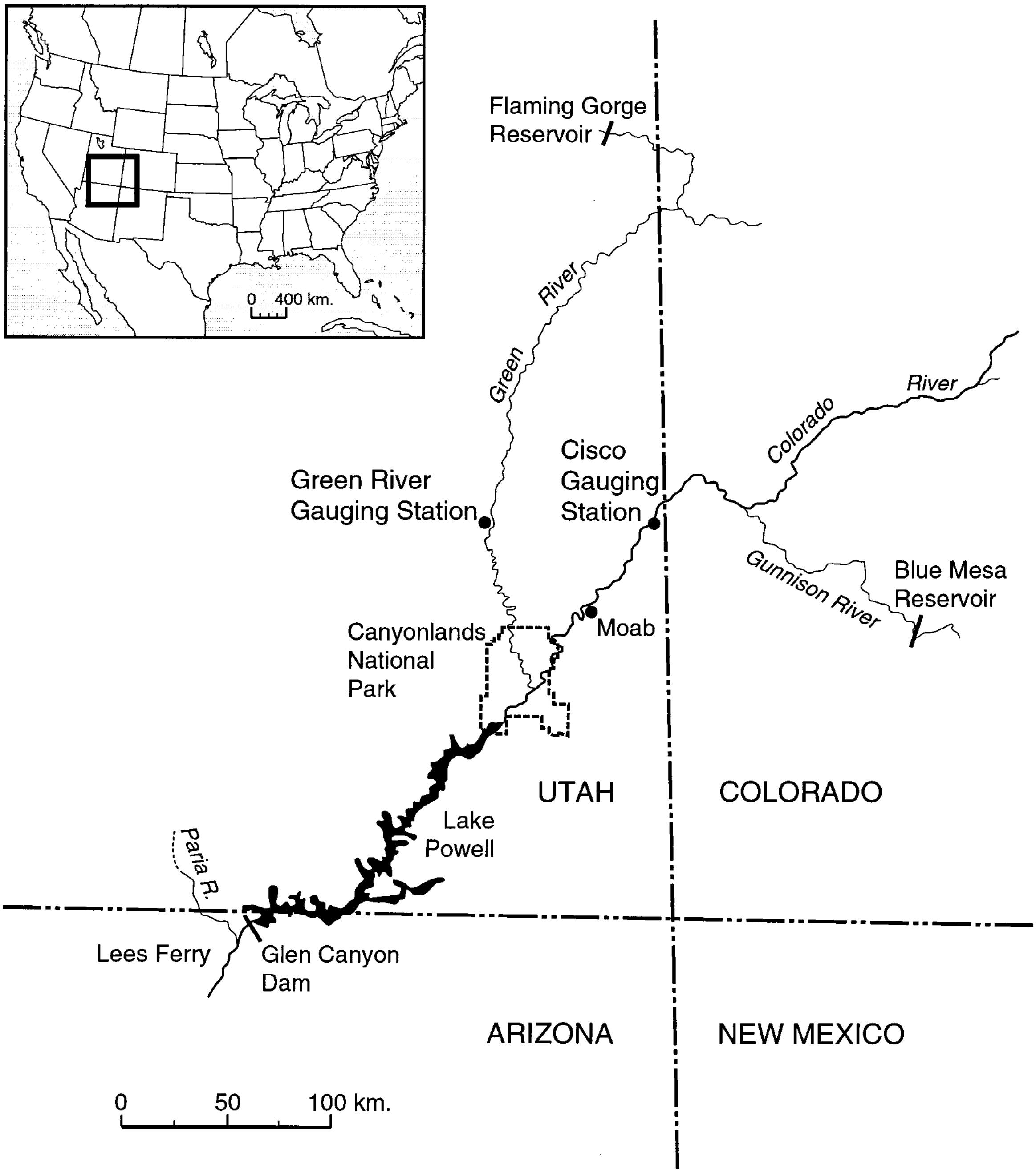

Figure 1. Study area in Canyonlands National Park (CNP). All collections were taken from the Green and Colorado Rivers within CNP boundaries.

on cobbles or from a measured area of driftwood. The collection area of driftwood was estimated from the surface area of a cylinder with a circumference equal to the average of maximum and minimum circumferences of the area sampled. Additional samples of subsurface dwelling invertebrates were taken for taxonomic purposes by allowing driftwood to dry suspended over a collecting pan. Macroinvertebrates were placed in 70% ETOH for identification and enumerated in the laboratory. Biofilm samples were taken from the same section of cobble or driftwood as the macroinvertebrate sample. Biofilm was collected by brushing a 20 cm^2 area for 30 sec with a soft bristled toothbrush. Collected material was rinsed into a Whirl Pak™ with distilled water and filtered onto Whatman™ GF/C glass filters.

The amount of driftwood substratum available for colonization was estimated visually in May 1996. During the rising limb of the annual hydrograph on the Green River, observers on shore counted the number of driftwood pieces larger than 12 cm length × 21 cm circumference (the size of an average soda can) during a 3 min period for 12 periods. During this same time, 30 pieces of driftwood were randomly collected from the channel and their surface areas estimated as above. Estimates of the area of driftwood substratum available during this period were made by multiplying the average number of pieces per min by their average size.

In order to characterize conditions for photosynthesis, Secchi depths were taken at each cobble collection site. Light attenuation coefficients were estimated by measuring scalar irradiance (μE m^2 s^{-1}) with a LiCor™ scalar irradiation sensor for at least four different depths in each river. Sediment concentrations were estimated by taking 950 ml integrated water samples from the top 50 cm of the water column. Each sample was filtered onto Whatman 934/AH glass filters, dried and weighed.

In the laboratory, macroinvertebrates were sorted into three categories (chironomids, simuliids and other macroinvertebrates). Individual macroinvertebrates were counted and identified to genus. Total ash-free dry mass (AFDM) of each category was estimated by drying samples for 96 h at 60 °C, weighing and ashing at 500 °C for 1 h. Estimates of biofilm AFDM were made by drying, weighing and ashing the glass filters containing samples. Weights for all samples were measured to the nearest 0.00001 g.

Comparisons of macroinvertebrate and biofilm AFDM on driftwood and cobble substrata were made using Mann-Whitney U and Kruskall–Wallis tests in Systat ver. 5.2 (SYSTAT INC. 1992).

Results

Light penetration of the water column in the Colorado and Green Rivers was limited during all sampling periods. Secchi depths averaged 0.11 m (SE ± 0.01) for the periods sampled and only increased to 0.4 m for brief periods of the year in response to steady low flows. Light attenuation coefficients showed that compensation depths ($<$ 20 μE m^2 s^{-1}) ranged between 1.06 m and 0.12 m for the sampling periods. Light in the first 0.05 m of the water column (the average depth of the wetted area of driftwood) ranged from 400 to 700 μE m^2 s^{-1}. The probable source for this high attenuation of light was high suspended sediment. We estimated sediment load in the top 0.5 m of the water column to be between 0.09 and 2.54 g L^{-1}depending on flow and local runoff conditions. Total suspended sediment concentrations were probably much higher considering that our sampling did not include bed load concentrations.

An average of 15.5 pieces of driftwood min^{-1} (± 0.96, n = 12 counts) was entrained in the thalweg during the rising limb of the hydrograph on the Green River during May 1997. The average surface area of each piece was 0.283 m^2 (± 0.105). We calculated that 4.4 m^2 min^{-1} of driftwood substratum passed our sample station during this 12 h sampling period. However, this is an underestimate since it reflects only the size of the main trunk of the driftwood. During this sample period discharge increased from ~384 to 510 m^3 s^{-1}.

Ash-free dry mass of biofilm was significantly (Mann-Whitney U = 15 809, $p < 0.001$, n = 298) higher on driftwood (3.76 g m^{-2} AFDM, ± 0.19) than cobbles (2.45 g m^{-2} AFDM, ± 0.15), and was consistently higher throughout the periods sampled.

Seasonal patterns of biofilm AFDM were similar for both substrata. Biofilm AFDM estimates from October 1995, March 1996, July 1996 and October 1996 varied significantly (Kruskall–Wallis = 10.10, p = 0.02, n = 147 for driftwood and Kruskall–Wallis = 24.48, $p < 0.001$, n = 151 for cobbles). Biofilm AFDM on both substrata declined during the March and July samples when compared to the two October sampling periods. Seasonal variation in biofilm AFDM ranged from 4.78 g m^{-2} ±0.44 to 3.28 g m^{-2} ±0.32 on driftwood and from 2.69 g m^{-2} ±0.31 to 1.49 g m^{-2} ±0.12 on cobbles.

Macroinvertebrate AFDM on driftwood substrata was not significantly different from that on cobbles (Mann-Whitney U = 235, p = 0.17, n = 250). Overall mean standing mass of combined macroinvertebrate categories on cobbles was 479.8 mg m^{-2} AFDM (±107.1) compared to 333.8 mg m^{-2} AFDM (±182.1) on driftwood.

Nearly all taxa found on driftwood in CNP were also found on cobbles; however, there were significant

Table 1. Macroinvertebrate feeding guilds and densities on driftwood and cobble subtrata from the Colorado River and Green River in Canyonlands National Park, UT. Mean densities (#m^{-2}, ± SE) are given for each taxon during three different sampling periods in 1996)

		March		**July**		**October**	
	Feeding	Cobble	Driftwood	Cobble	Driftwood	Cobble	Driftwood
Odonata							4.3 (3.2)
Argia sp.	P				3.2 (1.9)		
Ephemeroptera							
Heptagenia elegantata	S			16.7 (16.7)	33.3 (13.7)	16.7 (16.7)	10.2 (0.6)
Rithrogena hageni	S		0.14 (0.1)				
Tricorthodes minutus	C				45.4 (36.8)		
Ephoron album	F				0.1 (0.1)		
Traverella albertan	F			566.6 (252.3)	31.3 (19.7)		
Baetis sp.	S		1.1 (0.6)		6.8 (6.1)		
Lachlania sp.	F				8.9 (6.2)		
Megaloptera							
Corydalus sp.	P			16.6 (16.6)	6.1 (6.1)		
Plecoptera							
Isogenoides sp.	P				0.4 (0.4)		
Isoperla sp.	P		1.6 (0.9)				
Doroneuria sp.					1.2 (0.9)		
Taenionema sp.			3.1 (1.1)				
Trichoptera							
Smicridea sp.	F		0.6 (0.6)			33.3 (33.3)	2.7 (2.0)
Ceratopsyche sp.	F			216.7 (78.4)	31.9 (21.2)		
Cheumatopsyche sp.	F		0.6 (0.6)				0.6 (0.6)
Nectopsyche sp.	P			33.3 (33.3)	2.7 (1.7)		
Coleoptera							
Microcylloepuss sp.	S				0.3 (0.3)		
Diptera							
Chironomidae	C,F	733.3 (291.4)	116.1 (84.9)	300.0 (165.4)	105.7 (32.2)	116.7 (66.4)	
Simuliidae	F	650.0 (258.4)	20.3 (9.4)	3100.0 (849.1)	1743.8 (1210.6)	3350.0 (1931.8)	359.1 (283.7)

Feeding guilds are represented by: predator (P), collector/gatherer (C), filterer/collector (F) and scraper/collector (S).

compositional differences between the two substrata associated with feeding behavior. Of the 51 taxa of aquatic invertebrates collected from cobble and soft substrata over a 4-year sampling program in CNP (Haden, 1997), 20 were found on driftwood (Table 1). In many samples, both predatory and primary consumer invertebrates were present on the same piece of driftwood suggesting trophic interactions occurred on these small, floating islands. The only known xylophage found in our samples was the chironomid larvae *Polypedilum* sp. (Anderson et al., 1984; Anderson, 1989) which burrowed below the surface of the wood and could only be found by allowing driftwood to dry. Simuliid larvae were generally only found on driftwood that was snagged along the shoreline in flowing current. Small larval instars of chironomids were also found on driftwood substrata.

Predatory taxa on driftwood substrata were the same as those on cobbles. They included the stoneflies *Isogenoides* sp. and *Isoperla* sp., as well as the damselfly *Argia* sp., the caddisfly *Nectopsyche* sp. and the dobsonfly *Corydalus* sp.

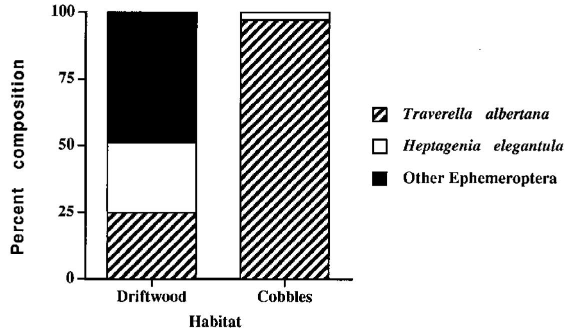

Figure 2. Percent numerical composition of mayfly (Ephemeroptera) taxa on cobbles and driftwood during July 1996 in CNP, Utah. n = 30 samples for each substrate.

Differences in assemblage composition on driftwood and cobbles were best shown by the Ephemeroptera which was the numerically dominant group during July 1996. *Traverella albertana* (McDunnough) was the numerically dominant taxon in benthic collections over this time period and was the dominant taxon on cobble collections (Figure 2). *Heptagenia elegantula* (Eaton) was found in the cobble; however, it was only numerically dominant on driftwood. The number of different mayfly taxa was higher in driftwood samples than cobble samples. Cobbles either had *T. albertana* or *H. elegantula*, whereas driftwood supported six mayfly taxa, including *Trichorthodes minutus* Traver, *Baetis* spp., *Rithrogena hageni* Eaton and *Isonychia* sp., all of which are scraper/collectors (Merritt & Cummins, 1996). Other taxa of mayflies found on driftwood included *Lachlania* sp., *Ephoron* sp. and *T. albertana* (Table 1.).

Discussion

Our study showed that driftwood is an important substratum in the Green and Colorado Rivers in CNP. By providing a hard substratum with a higher mass of biofilm, it provides a habitat for grazing invertebrates that may otherwise be rare in this system. The constantly high sediment loads of southwestern rivers hinder the development of an autotrophic benthic food base (Shaver et al., 1997; Blinn et al., 1998). Growth of periphyton is reduced by low light levels and scouring in southwestern streams (Fisher et al., 1982; Duncan & Blinn, 1989). Consequently, the food base for organisms that depend on this type of energy source is limited.

Our study demonstrated higher biofilm mass on driftwood than cobbles. Light levels on driftwood substrata were high since it is always near the water surface, and photosynthesis by periphytic algae was, therefore, always possible. Likewise, abrasion was reduced since driftwood moves with the flow of the water, reducing scouring at the substratum level. The tumbling and spinning motion of drifting wood allows nutrient exchange for periphytic growth. Additionally, Bowen et al. (1998) speculated that algae may be able to utilize nutrients leached from woody debris to enhance growth.

The brushing technique we used to collect biofilm probably removed some of the soft wood material from the surface of the driftwood; however, microscopic inspection of the collected material showed that diatoms made up most of the driftwood biofilm mass. It is also likely that this biofilm contained fungal and bacterial matter which could also be utilized as food by macroinvertebrates (Merritt & Cummins, 1996).

Woody debris that is not free floating does not provide equivalent habitat to driftwood. Abrasion and accumulation of inorganic sediments have been shown to limit microbial activity in biofilms on fixed wood surfaces (Galloday & Sinsabaugh, 1991; Tank et al., 1993), and sunken wood may also have less biofilm due to the abrasive action of suspended sediment and low light. Furthermore, shifting soft substratum buries organic matter in depositional zones making it unavailable for colonization by surface-dwelling macroinvertebrates.

The feeding strategies of the dominant organisms on both types of substrata reflected the kind of food available in each habitat. *T.albertana* is a filterer/collector which has large brushes of hairs on its mandibles to remove particles from the current (Ward & Kondratieff, 1992; Merritt & Cummins, 1996). In contrast, *H. elegantula* is a scraper/collector which feeds on attached benthos (Ward & Kondratieff, 1992; Merritt & Cummins, 1996). Cobble substrata are dominated by the filterer/collector *T. albertana*. Scraper/collectors are the dominant taxa on driftwood where biofilm is more abundant. Densities of *T. albertana* are lower on driftwood since filtering efficiency may be reduced in the low velocity habitat of driftwood. The differences in mayfly assemblages on driftwood and cobbles provide further evidence that driftwood provides an alternative food source in this lotic ecosystem.

Our collections indicated that driftwood served a major function in maintaining a diverse macroinvertebrate assemblage at our study site. During July 1996, cobbles sampled contained only 2 taxa of mayflies, whereas driftwood supported 6 taxa. Three of these taxa were scraper/collectors that could utilize biofilm from driftwood. Lotic systems that have limited autochthonous production due to high suspended sediment are dependent mainly on allochthonous sources of energy. Without alternative habitats that offer different food sources, the macroinvertebrate assemblage would be limited to those that feed on allochthonous materials. This limitation was compounded in our study area since organic matter that accumulated in depositional zones was soon buried by settling sediment. Without driftwood, the only organic material available to macroinvertebrates would be drifting fine particulate matter, accessible only to filter feeding organisms.

Driftwood also provided habitat for secondary consumers including predatory odonates, trichopterans and plecopterans. The utilization of driftwood and its standing mass of secondary consumers indicates that a portion of the energy flow takes place on a mobile substratum in these river systems. Comparisons of macroinvertebrate standing mass on cobbles and driftwood indicate that a large proportion of the total energy in the system could be found on driftwood. Studies of southwestern desert rivers that do not sample driftwood substrata may underestimate both the total standing mass/energy of the system and taxon richness.

We concede that driftwood is an ephemeral substratum in these systems. However, in a 24-h period during high flow, driftwood contributed nearly 33% of the total area of hard substrata in a 50 km reach in our study area. The greatest abundance of driftwood in the river occurred during flood periods when cobbles were most disturbed by high velocities and sediment movement. Increased invertebrate drift also coincides with increased amount of woody debris in the river, as cobble substrata were scoured by sediment (Borchardt, 1993). Driftwood may provide macroinvertebrates with refugia from such disturbances which can last for at least 2 months (May and June) in most years. Survival of invertebrates that drift long distances between cobble bars may be enhanced since the drifting substrate may provide refugia from fish predators. The availability of driftwood during this period helps to maintain macroinvertebrate production.

We do not know what role driftwood plays in the dispersal of aquatic organisms. The residence time for driftwood within a specific reach of river is unknown and may contribute to the strategies used by macroinvertebrates on this substratum. However, Galloday & Hax (1995) recovered 45% of driftwood pieces within 500 m of the release point after an experimental flood in a Texas stream. Undoubtedly, many macroinvertebrates on driftwood are transported down river, but it seems unlikely that many organisms could carry out their entire life cycles on driftwood since it may be dry for at least part of the year. Nevertheless, we were able to find small amounts of driftwood in the rivers throughout the year and numerous exuviae were found on driftwood surfaces.

Our observations showed that driftwood was seasonally abundant in the Green and Colorado Rivers in CNP. More driftwood was entrained in the channel during periods of high flow in spring and early summer, or during stochastic flow events from local ephemeral tributaries during summer convective storms. During periods of steady low flows driftwood was found along shorelines or floating in eddies, but a large portion had been deposited along shorelines or floated out of the system into Lake Powell (Figure 1).

The dynamics of driftwood in southwestern desert streams are likely to be more vulnerable to impacts from land use changes and river regulation (Minckley & Rinne, 1985). River regulation decreases the amount of driftwood entrained in a river as well as the distance that driftwood travels through the system. Impoundments block the downstream transport of coarse particulate matter (Ward & Stanford, 1983; Ward & Stanford, 1995) and flood control diminishes the interaction of the river with flood plain vegetation (Bayley, 1995). Rivers in desert biomes are characterized by sparsely vegetated drainages and the affects of regulation may further limit the amount of driftwood entrained in the system. Further study should be directed at the function of woody debris in southwestern desert rivers and the effect that management practices have on the macroinvertebrate community that utilizes this habitat.

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