Organic drift in a regulated desert river

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Abstract: Coarse particulate organic mass varied seasonally and changed from autochthonous to allochthonous organic matter along a 386-km section of the Colorado River below Glen Canyon Dam, Arizona. Dam operations influenced drift components selectively throughout the hydrograph; however, ramping rate had no effect on drift mass. Eddies and pools collected ~50% of the main-stem drift with only detritus retained long enough to settle in pools. Coarse particulate organic drift mass was negatively correlated with stream gradient in the Colorado River. *Cladophora* drift packets were pulverized by rapids, which subsequently increased fine particulate organic matter at downriver sites. Tributary type (spring stream or large desert watershed river) significantly altered the mass and composition of tributary drift; however, tributaries contributed <0.1% of the total organic matter to main-stem drift. Terrestrial insects represented <0.001% of the total invertebrate mass in main-stem drift. As a result of hydraulics and suspended sediment, organic drift mass throughout the river corridor is reach specific. Longitudinal change in drift composition corresponds with a shift in fish species.

Résumé : Les masses de particules organiques grossières présentaient des variations saisonnières et leur composition passait des matières organiques autochtones à allochtones le long d'un tronçon de 386 km du fleuve Colorado, en aval du barrage de Glen Canyon (Arizona). Les opérations du barrage modifiaient sélectivement les constituants des matières dérivantes dans tout le bassin hydrographique mais toutefois, le débit de décharge n'avait aucun effet sur les masses dérivantes. Les bassins à tourbillons recueillaient environ 50% des matières dérivantes du courant principal, ainsi que les détritus qui pouvaient être retenus assez longtemps pour s'y déposer. Les masses dérivantes de particules organiques grossières présentaient une corrélation négative avec la pente du Colorado. Les masses dérivantes de *Cladophora* étaient pulvérisées par les rapides, ce qui augmentait par la suite la teneur en matières organiques fines à des emplacements en aval. Le type de tributaire, soit des ruisseaux de printemps par rapport à des grands cours d'eau à bassin versant désertique, avait une influence significative sur la masse et la composition des matières dérivantes des tributaires. Toutefois, ceux-ci fournissaient moins de 0,1% des matières organiques totales des matières dérivantes du courant principal. Les insectes terrestres représentaient moins de 0,001% de la masse totale d'invertébrés de ce courant. Dans tout le cours d'eau, à cause des caractéristiques hydrauliques et des sédiments en suspension, la masse organique dérivante dépendait de chacun des tronçon. Les changements longitudinaux de la composition de la masse dérivante correspondaient à une variation de la répartition des espèces de poissons.
[Traduit par la Rédaction]

Introduction

Stream drift has received considerable attention over the past several decades (reviewed by Brittain and Eikeland 1988); however, relatively few studies have focused on drift in regulated rivers, especially those in arid biomes. Discharge variability in a regulated river can increase the amount of drifting material through scouring during high flows (Brooker and Hemsworth 1978; Blinn and Cole 1991; Lieberman and Burke 1993), and by behavioural responses during low flows (Minshall and Winger 1968; Perry and Perry 1986; Blinn et al. 1995).

Over 60% of the algal standing stock (primarily *Cladophora glomerata*) and invertebrate biomass in the Colorado River corridor through Glen and Grand canyons (386 km) is produced in the upper 26 km clear-water section between Glen Canyon Dam (GCD) and the Paria River (Blinn et al. 1994, Fig. 1). High loads of suspended sediments delivered by the Paria (river kilometre (RKM) 1) and Little Colorado rivers (RKM 98.7) increase patchiness and decrease the standing crop of *Cladophora glomerata* and associated assemblages downriver (Hardwick et al. 1992; Blinn et al. 1994).

Although *Cladophora glomerata* is adapted to lotic environments (Usher and Blinn 1990; Dodds and Gudder 1992), filaments frequently detach from cobble in the tail waters of GCD and drift downstream, especially with variable flows associated with hydroelectric power production (Angradi and Kubly 1993, 1994; Angradi 1994; Blinn et al. 1995). Because of the interruption of normal allochthonous riverine drift caused by Lake Powell and the limited aquatic primary production below the Paria River, it has been proposed that stream drift, and especially *Cladophora glomerata* with associated assemblages, provides coarse particulate organic matter (CPOM) to downstream biota in the Colorado River. Understanding the factors that control CPOM drift in this large desert river is valuable from a trophic standpoint in regard to the distribution of native and exotic fish. GCD tail waters support an exotic trout fishery, while tributary mouths downriver are the preferred habitats for native fish and exotic trout (Minckley 1991).

We examined several related aspects of organic drift in the Colorado River. Specifically, we (*i*) determined the quantity and composition of stream drift in the Colorado River along a 386-km corridor below GCD, (*ii*) estimated the contribution of stream drift from tributaries to the Colorado River corridor, (*iii*) compared the quantity and composition of stream drift

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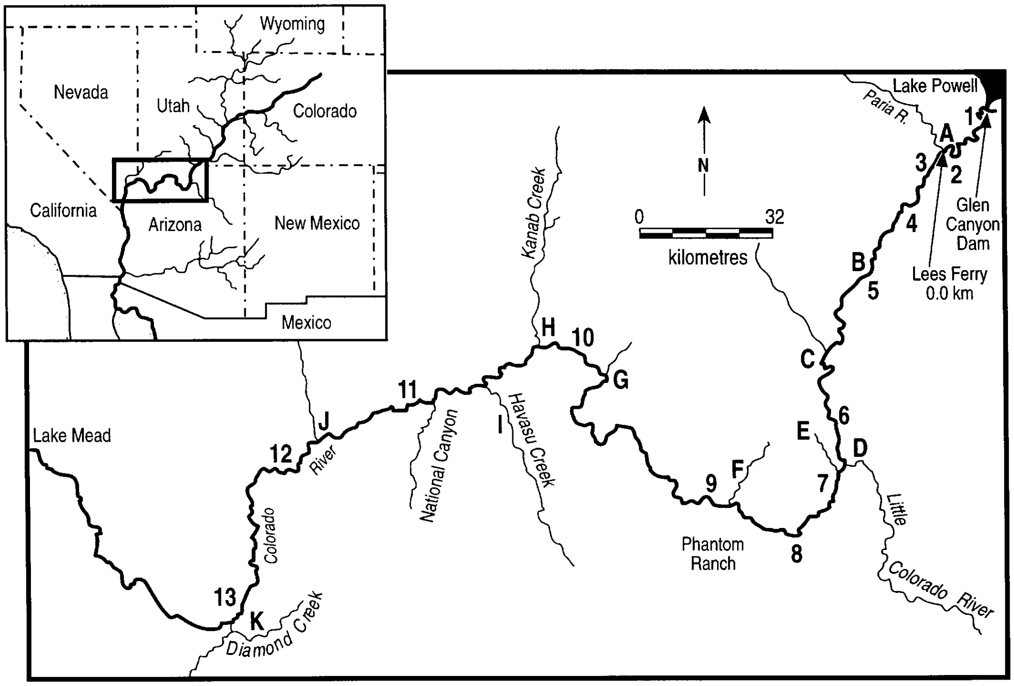
Fig. 1. Map of drift collection stations in the Colorado river (1–13) and major tributaries (A–K) through Grand Canyon National Park, Arizona. Glen Canyon Dam is located 25.3 km upriver from Lees Ferry, Arizona, which is designated as 0.0 km.



MAINSTEM

Site	Kilometre	Name
1	-24	Glen Canyon
2	0	Lees Ferry
3	3	2 Mile Wash
4	31	House Rock
5	67	40 Mile
6	88	54 Mile
7	104	Morning Star Mine
8	116	Tanner
9	150	Horn Creek
10	228	Ponchos Kitchen
11	272	Tuckup
12	339	Granite Park
13	358	224.5 Camp

TRIBUTARY

Site	Kilometre	Name
A	1	Paria River
B	51	Vasey's Paradise
C	83	Nankoweap Creek
D	98	Little Colorado River
E	104	Lava Chuar
F	141	Bright Angel Creek
G	214	Tapeats Creek
H	231	Kanab Creek
I	250	Havasu Creek
J	327	Spring Canyon
K	362	Diamond Creek

during variable and steady flows, (*iv*) determined the effects of river hydraulics (rapids) on the mass, invertebrate composition, and food energy of *Cladophora glomerata* drift packets throughout the Colorado River corridor, and (*v*) examined organic-matter retention processes associated with channel morphology.

Materials and methods

Study area

We investigated the quantity and composition of stream drift below GCD in the Colorado River through Grand Canyon National Park between Lees Ferry and Diamond Creek (386 km distance; Fig. 1). Lees Ferry, located 25.3 km below GCD, is designated 0.0 RKM.

Glen Canyon Dam releases hypolimnial water from Lake Powell and has a maximum power plant discharge of 934 $m^3 \cdot s^{-1}$ (Stanford and Ward 1991). Flows below GCD have a peak discharge of 566 $m^3 \cdot s^{-1}$ and a minimum of 141 $m^3 \cdot s^{-1}$ with a maximum up-ramp of 71 $m^3 \cdot s^{-1}$ and a maximum down-ramp of 42 $m^3 \cdot s^{-1}$. Maximum ranges of daily fluctuations vary from 170 to 226 $m^3 \cdot s^{-1}$ on the basis of projected monthly water allotments.

The aquatic communities throughout the canyon are shaped by discharge regulation, channel morphology, and biome effects via tributary inputs of suspended sediments (Blinn et al. 1994). Waters above the Paria River (1.0 RKM) support high standing crops of *Cladophora glomerata* and an invertebrate assemblage of *Gammarus lacustris*, chironomid larvae, oligochaetes, and gastropods (Blinn et al. 1995). The consistently clear, cold tail waters (8–10°C) below GCD are dramatically altered at the Paria River confluence, where about 3 million tons of suspended sediments enter the Colorado River annually (Andrews 1991). The Colorado River within Grand Canyon is a run-pool-drop river with a shallow gradient of 1.5 $m \cdot km^{-1}$. Pools and rapids are formed by channel constrictions created by tributary debris flows. Summer air temperatures exceed 35°C, whereas winter air temperatures drop below 0°C at night.

Drift collections

Nearshore surface drift samples (0–0.5 m deep) were collected in September 1993 and January, March, and June 1994 at 13 downriver sites (Fig. 1). Collections were made with a circular tow net (48 cm diameter opening, 0.5-mm mesh) held in place behind a moored pontoon raft or secured to the river bank. Collections were taken in triplicate at approximately 06:00 and 18:00 at each site to establish the effects of discharge on drift. September samples were preserved with alcohol, formalin, and acetic acid (AFA) whereas all other collections were processed live within 48 h and sorted into seven categories: *Gammarus lacustris*, chironomid larvae, simuliid larvae, miscellaneous invertebrates, *Cladophora glomerata*, miscellaneous algae and macrophytes, and detritus. Miscellaneous invertebrates included lumbriculids, tubificids, physids, trichopterans, terrestrial insects, and unidentifiable animals. Detritus was composed of both autochthonous (algal, bryophyte, and macrophyte fragments) and allochthonous (tributary upland and riparian vegetation; twigs, leaves, seeds, bark) flotsam. Invertebrates were enumerated, oven dried at 60°C, weighed, ashed (500°C, 1 h), and reweighed.

Current velocity was measured for volumetric calculations ($g \cdot m^{-3} \cdot s^{-1}$) using a Marsh–McBirney electronic flow meter. River discharge was determined from United States Geological Survey gauge data (Jeanne Korn, Glen Canyon Environmental Studies, Flagstaff, Arizona, personal communication). The duration of all drift collections ($n = 276$) was 4 ± 0.16 min (mean ± SE) with an average of 24.4 ± 1.4 m^3 of water sampled through nets. The standard sampling error was within ±10% of the mean total drifting mass (0.054 ± 0.005 $g \cdot m^{-3} \cdot s^{-1}$, Culp et al. 1994); therefore, collections were consistent and representative of the study site.

To understand organic retention processes within the Colorado River we collected drift in March 1995 from main-stem channel and eddy–pool habitats as well as benthos from eddies–pools and compared mass estimates within each of the three habitats. Our assumptions are that residence time of drift mass is positively correlated to benthic mass in eddies and pools and drift is neutrally buoyant, therefore following current patterns (Edmund Andrews, United States Geological Survey, Lakewood, Colorado, personal communication). Collections were made at sites 2–6, 10–12, and 13 along the Colorado River corridor; sites 1 and 7–9 were excluded because they lacked eddy–pool habitats (Fig. 1). Channel drift ($n = 3$; 0.5-mm net mesh) was collected from behind an 8-m pontoon motorboat held steady in midchannel. Eddy–pool drift was collected perpendicular to the channel on three transects set 30 m apart. The drift net was pulled ~56 m into shore from the channel–eddy interface along each transect three times and volumetric determinations were made. This sampling design accounted for drift patchiness owing to variable surface currents. Eddy–pool habitats were further separated into two geomorphic categories for comparison; true eddies or backwaters that had recirculating flow below rapids (sites 2–6 and 12 in Fig. 1) and pools above rapids with unidirectional flow (sites 10, 11, 13). Four benthic collections were made with either a Petite Ponar or Peterson dredge along the same three transects used for eddy–pool drift collections ($n = 12$). Current velocity was measured at a depth of 50 cm for each dredge drop while the boat was held steady, in an effort to define the flow patterns within the habitat. The average velocity per transect was used in volumetric calculations for the eddy–pool drift samples. Collections were analyzed for size fractions in the laboratory after dry mass estimates were obtained. Benthic samples were sieved through a 0.6-mm screen. Materials from each habitat (channel drift, eddy–pool drift, and benthos) were combined and dry sieved into <1, 1–9, and ≥10 mm size fractions at each site. Each sample was then shaken for 30 s, which allowed the separation of size fractions without particulate degradation.

The contribution of organic drift to the Colorado River from 11 tributaries was measured between Lees Ferry and Diamond Creek in January, March, and June 1994 (Fig. 1). A rectangular drift net (0.14 m^2; 0.363-mm mesh) was positioned in each tributary for at least 10 min ($n = 3$), 200 m upstream from the confluence. Volumetric data were collected in the same manner as for main-stem collections. Discharge was estimated for all tributaries except the Little Colorado River (RKM 98.6), for which United States Geological Survey data were available.

We compared drift mass from tributaries within two distinct drainage types: (*i*) large basins originating outside of Grand Canyon National Park (>500 km^2; mean discharge 1.67 $m^3 \cdot s^{-1}$), including the Paria River, Little Colorado River, Kanab Creek, Havasu Creek, and Diamond Creek (Fig. 1), and (*ii*) small basins, primarily spring fed, originating within Grand Canyon National Park (<260 km^2; mean discharge 0.43 $m^3 \cdot s^{-1}$), including Vasey's Paradise, Nankoweap Creek, Lava Chuar, Bright Angel Creek, Tapeats Creek, and Spring Canyon.

Cladophora glomerata drift packets

Twelve to 20 packets of drifting *Cladophora glomerata* were randomly collected in January, March, June, and September 1992 with a hand dip net (0.5-mm mesh) from the surface down to 1 m at Lees Ferry (RKM 0.0), below the confluence of the Paria River (RKM 1.0), Nankoweap Creek (RKM 83.2), Tanner Creek (RKM 108.8), and Diamond Creek (RKM 361.6). Twenty samples were also collected above and below Badger Creek rapid (RKM 12.8) to ascertain the effect of a single large rapid on the integrity of *Cladophora glomerata* packets. Samples were sorted in the field into 10 categories: *Cladophora glomerata*, detritus, miscellaneous algae and macrophytes, *Gammarus lacustris*, chironomid larvae, simuliid larvae, tubificids, lumbriculids, gastropods, and miscellaneous invertebrates. Tubificid densities were estimated by regression ($r^2 = 0.89$) from mass measurements of intact specimens. Total energy was calculated for *Cladophora glomerata* drift packets at various sites from energy equivalents determined by Blinn et al. (1995).

Epiphyton slides were prepared using ashed material from *Cladophora glomerata* packets placed in vials and diluted into a homogeneous solution with distilled water. An aliquot of 0.5 mL was drawn from each sample, placed onto a cover slip, heated until dry, and mounted onto slides with Hyrax®. A minimum of 200 diatoms at 1000× magnification was counted and identified to species for each sample and converted to number of diatoms per milligram ash-free dry mass (AFDM) of *Cladophora glomerata*.

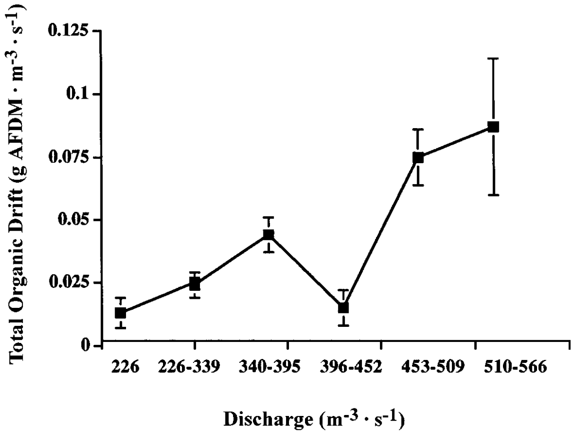
Steady versus fluctuating flows

We examined the influence of steady versus repeated fluctuating flows on stream drift at Lees Ferry by collecting drift with a circular net (48 cm diameter opening, 1-mm mesh). The net was held at the surface by a float and deployed from a navigational buoy so each set would be in the same position in the channel. Collections were made at 6-h intervals starting at 06:00 for 5 days. Discharges from GCD were held steady (226 $m^3 \cdot s^{-1}$) for the first 3 days (29–31 May 1993) followed by 2 days of fluctuating flows (discharges from 141 to 283 $m^3 \cdot s^{-1}$). Water velocity was measured with a Marsh–McBirney electronic flow meter before and after each collection period.

Statistical analyses

Multivariate analyses of variance (MANOVA) were used to analyze categorical predictor variables (mass estimates) and multiple response variables (physical parameters–treatment) for drift collections. Drift packets above and below a rapid were compared with a Student's *t* test. Multiple regression analyses were used to predict the percentage of channel drift retained by eddies and pools and the mass that eventually settled to the benthos. All calculations were performed with SYSTAT computer software on natural log ($1n(x + 1)$) transformed data (version 5.1, Wilkinson 1989).

Fig. 2. Comparison of nearshore stream drift collections (g AFDM·m^{-3}·s^{-1}) and discharge (m^{-3}·s^{-1}) in the Colorado River corridor through Glen and Grand canyons, Arizona. Errors bars represent ± 1 SE.



Results

Downriver drift

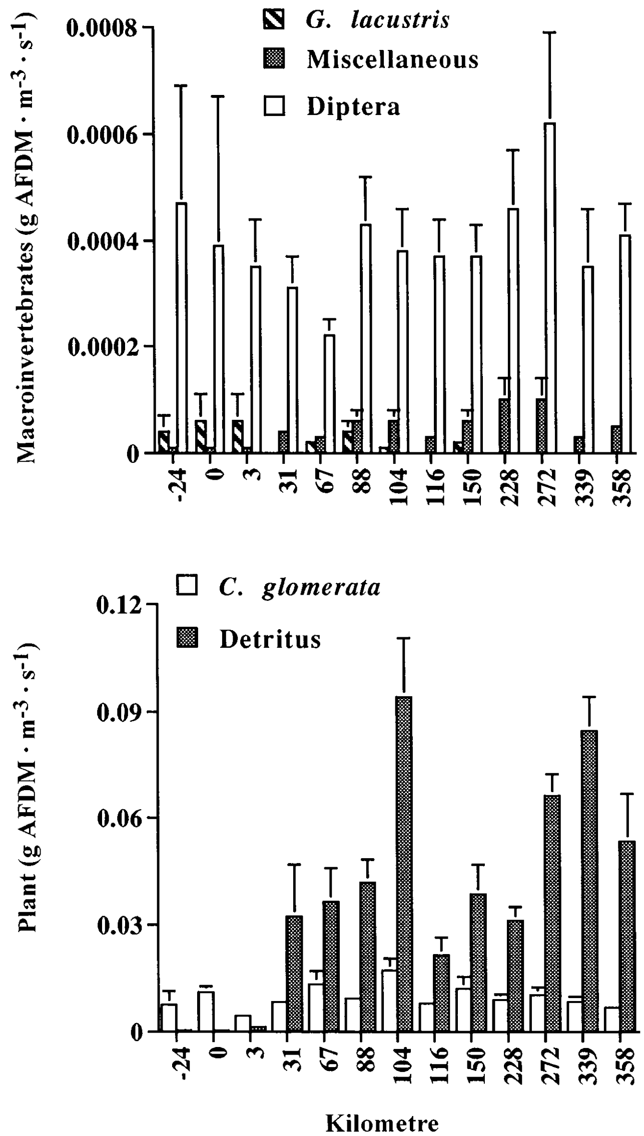
There was a significant positive correlation ($p < 0.001$) between drift mass and both discharge and distance from GCD. Discharge (226 to 566 m^3·s^{-1}) affected drift components selectively, with a significant positive relationship noted between detritus and discharge ($p < 0.001$), and a significant negative relationship ($p < 0.001$) noted between *Gammarus lacustris*, *Cladophora glomerata*, chironomids, simuliids, tubificids, and gastropods. The relationship between drift and discharge, however, was complicated by a dramatic drop in drift mass between 340 and 452 m^3·s^{-1} and an increase in drift mass at discharges from 266–340 to 340–395 and >452 m^3·s^{-1} (Fig. 2).

Daily fluctuations in the hydrograph from electric power production had no significant ($p = 0.25$) influence on overall mass or composition of drift ($p > 0.05$) for all sites. Ramping rates ≤71 m^3·s^{-1}·h^{-1} lacked adequate energy to consistently carry drift on the rising arm of the hydrograph.

Drift composition changed with distance from GCD. There was a significant increase in detrital drift through Grand Canyon ($p < 0.01$), whereas the mass of *Gammarus lacustris* and miscellaneous algae and macrophytes showed no significant differences between sites ($p = 0.99$ and 0.09, respectively) but decreased with distance downriver (Fig. 3). The mass of drifting aquatic diptera and miscellaneous invertebrates varied significantly between sites ($p < 0.001$) and increased with distance, while *Cladophora glomerata* drift peaked at RKM 104 (Fig. 3). Chironomid larvae made up 72% of the dipteran drift through Marble Canyon (RKM 0–99), while simuliid larvae comprised 81% of the dipteran drift below RKM 99. Terrestrial insects comprised <0.001% of the total number of animals in all drift samples.

All drift categories, except *Gammarus lacustris* and miscellaneous algae and macrophytes ($p = 0.82$ and 0.28, respectively), varied seasonally. The highest total organic drift mass (0.08 g·m^{-3}·s^{-1} AFDM) was recorded in September 1993 and consisted primarily of detritus. *Cladophora glomerata* drift reached a seasonal maximum of 0.015 g·m^{-3}·s^{-1} AFDM in June. Invertebrate drift mass increased from 2.3 ± 0.03 g·m^{-3}·s^{1} in

Fig. 3. Average mass (g AFDM·m^{-3}·s^{-1}) of plant and macroinvertebrate drift at collection sites in the Colorado river between Lees Ferry (RKM 0) and Diamond Creek (RKM 362) during September 1993 and January, March, and June 1994. Only trace amounts of miscellaneous algae, bryophytes, and macrophytes were collected (<0.001 g·m^{-3}·s^{-1}). Names of sites corresponding to RKM are given in Fig. 1. Errors bars represent ± 1 SE.



March to 5.9 ± 0.8 g·m^{-3}·s^{-1} in June, owing primarily to a 55% increase in dipterans and a 66% increase in miscellaneous invertebrates.

Organic drift was retained by eddies and pools but the residence time was apparently brief as <50% of the retained drift mass became saturated and settled to the bottom. Detrital mass was the only category to show a significant positive relationship between channel drift and mass in both eddies and pools and benthic collections (Table 1). A significant positive relationship was found between drifting *Cladophora glomerata* and dipteran drift mass between eddy–pool and channel drift samples ($p < 0.05$). No significant relationship was found be-

Table 1. Eddy–pool retention.

Source	Variable	Coefficient	Probability	Standard error of estimate
Channel drift × eddy–pool drift[a]	*Cladophora glomerata*	–99.3	<0.001	0.38
	Detritus	–1.7	0.003	
	Aquatic dipterans	–654.7	0.04	
	Constant	1.9		
Benthic × eddy–pool drift[b]	Detritus	0.004	0.03	0.47
	Constant	2.4		
Channel drift × benthic[c]	Detritus	0.009	0.02	0.93
	Constant	4.2		

Note: Eddy–pool retention was measured by sampling three adjacent habitats (channel drift, eddy–pool drift, and eddy–pool benthos) and using multiple regression analyses to predict significant correlations between habitats. Detritus was the only drift component from the channel that was entrained in eddies and pools and accumulated in the benthos. *Cladophora glomerata* and aquatic diptera channel drift were briefly entrained in the eddies and pools but did not accumulate in the benthos. Only significant biotic categories are listed ($p < 0.05$).

[a]ANOVA: $F_{[4,56]} = 12.5$, $p < 0.001$, multiple $R^2 = 0.47$.

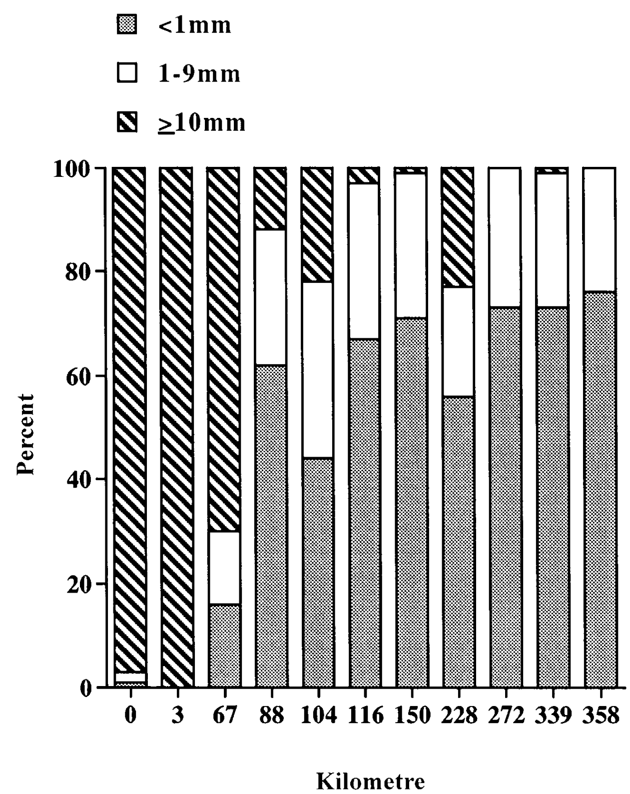
[b]ANOVA: $F_{[6,54]} = 2.4$, $p < 0.04$, multiple $R^2 = 0.21$.

[c]ANOVA: $F_{[6,59]} = 2.8$, $p < 0.02$, multiple $R^2 = 0.22$.

tween eddy–pool drift and benthic samples for *Cladophora glomerata* or diptera, suggesting that these biotic components are not readily deposited in pools (Table 1). Detritus ($1.0\ g \cdot m^{-3} \cdot s^{-1}$) was dominant in channel drift and made up 0.5 $g \cdot m^{-3} \cdot s^{-1}$ in eddy–pool drift. Detritus was the only category that showed a significant relationship between eddy–pool types ($p = 0.01$) with an average of 50% more detritus moving through both channel and eddy–pool collections in pools above rapids than in the backwaters below rapids, indicating little retention of organic matter.

Size fractions of CPOM did not differ significantly between channel drift, eddy–pool drift, and benthos at each site. However, significant longitudinal changes in size fractions of organic matter were noted, with <1 and 1–9 mm size fractions increasing and ≥10 mm size fractions decreasing with distance downriver ($p < 0.01$; Fig. 4). Fractions ≥10 mm were composed primarily of *Cladophora glomerata* packets, with occasional fragments of *Equisetum* spp. and the aquatic moss *Fontinalis* sp. The 1–9 mm size fraction was made up of nearly equal proportions of detritus and *Cladophora glomerata* filaments, while fractions <1 mm were exclusively pulverized detrital material.

Fig. 4. Percent size fraction of channel drift in the Colorado River through Grand Canyon during March 1995. Names of sites corresponding to RKM are given in Fig. 1.

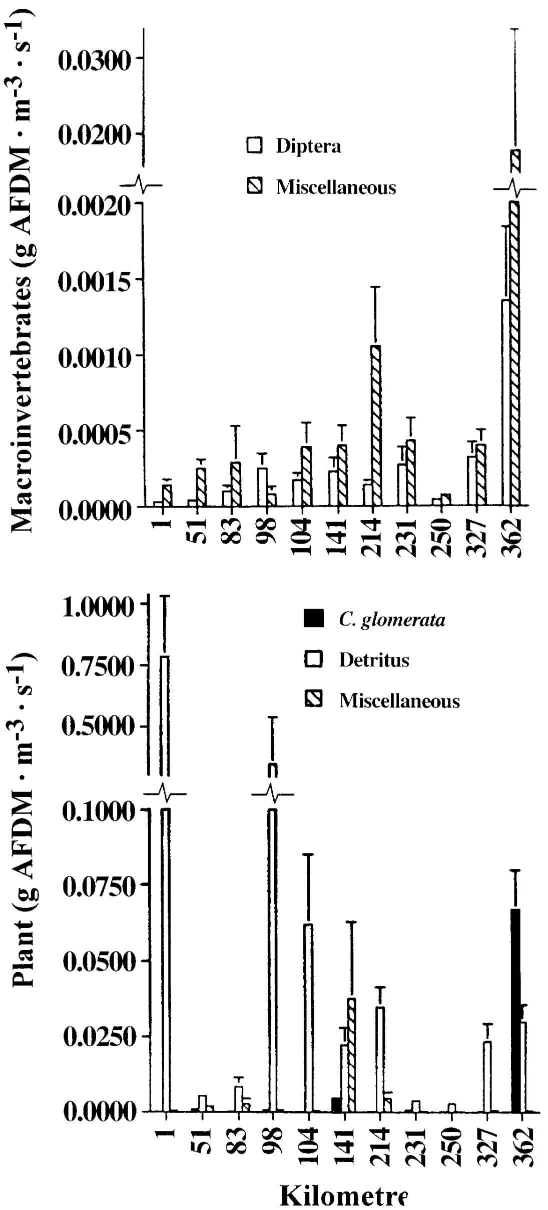


Tributary drift

Tributaries contributed little organic drift to the Colorado River. Mean organic drift (AFDM) from tributaries was $0.13 \pm 0.04\ g \cdot m^{-3} \cdot s^{-1}$, compared with $0.5 \pm 0.004\ g \cdot m^{-3} \cdot s^{-1}$ in the main stem of the Colorado River. On the basis of mean discharges for tributaries ($1.1\ m^{-3} \cdot s^{-1}$) and the main stem ($374\ m^{-3} \cdot s^{-1}$), we estimated that <0.1% ($\sim 0.14\ g \cdot m^{-3} \cdot s^{-1}$) of organic drift in the Colorado River (total drift = $167\ g \cdot m^{-3} \cdot s^{-1}$) is contributed by tributaries. We calculated that tributaries released an average of 2.8 animals$\cdot m^{-3} \cdot s^{-1}$ (3 animals at $1.1\ m^{-3} \cdot s^{-1}$), while the mainstem transported 3.2 animals$\cdot m^{-3} \cdot s^{-1}$ (1200 animals at $374\ m^{-3} \cdot s^{1}$). Drift varied significantly among tributaries ($p < 0.001$; Fig. 5); however, no significant seasonal patterns were detected within tributaries under base-flow conditions during January, March, and June ($p = 0.4$). The Paria River, Little Colorado River, and Diamond Creek contributed the highest average stream drift to the Colorado River, 0.78, 0.35, and 0.12 $g \cdot m^{-3} \cdot s^{-1}$, respectively. Drift from the Paria and Little Colorado rivers was primarily detritus, while *Cladophora glomerata* was the dominant drift component at Diamond Creek.

Aquatic dipterans, *Cladophora glomerata*, and detritus varied significantly by tributary ($p < 0.01$), while other biotic categories did not vary significantly between tributaries ($p > 0.06$; Fig. 1). Diamond Creek released the most aquatic dipteran larvae ($0.001\ g \cdot m^{-3} \cdot s^{-1}$; 0.05 simuliids$\cdot m^{-3} \cdot s^{-1}$ and 7 chironomids$\cdot m^{-3} \cdot s^{-1}$), compared with $0.02\ g \cdot m^{-3} \cdot s^{-1}$ (4.8 animals$\cdot m^{-3} \cdot s^{-1}$) for other invertebrates. Plecoptera, Trichoptera, Ephemeroptera, Odonata, gastropods, lumbriculids, and terrestrial insects were the dominant invertebrate groups in

Fig. 5. Average mass (g AFDM$\cdot$m$^{-3}\cdot$s^{-1}) of plant and macroinvertebrate stream drift at selected tributaries in the Colorado River between Lees Ferry and Diamond Creek (RKM 362). Values represent means for samples collected during January, March, and June 1994. Names of sites corresponding to RKM are given in Fig. 1. Errors bars represent ± 1 SE.



tributary drift (0.002 g$\cdot$m$^{-3}\cdot$s^{-1}; 1.2 animals$\cdot$m$^{-3}\cdot$s^{-1}), but contributed little to the overall drift mass in the main stem (0.0007 g$\cdot$m$^{-3}\cdot$s^{-1}; 0.38 animals$\cdot$m$^{-3}\cdot$s^{-1}).

Large drainages that extend outside Grand Canyon National Park released 90% more organic matter than small spring-fed tributaries that originate within the canyon ($p = 0.002$). *Cladophora glomerata* and detrital drift were significantly greater in larger drainages than that for spring-fed tributaries ($p < 0.01$). Large drainages contributed an average of 0.01 g$\cdot$m$^3\cdot$s^{-1} *Cladophora glomerata* and 0.204 g$\cdot$m$^3\cdot$s^{-1} detrital drift to the Colorado River, while small spring-fed drainages released an average of 0.0008 g$\cdot$m$^3\cdot$s^{-1} of *Cladophora glomerata* and 0.019 g$\cdot$m$^3\cdot$s^{-1} of detritus. Diamond Creek is primarily responsible for the high AFDM of *Cladophora glomerata* drift from the large drainage tributaries (Fig. 5).

Cladophora glomerata drift packets

The mass of *Cladophora glomerata* in drift packets decreased downriver ($p < 0.01$) and varied among seasons ($p < 0.05$) in the Colorado River through Grand Canyon. AFDM of *Cladophora glomerata* in drift packets was highest at Lees Ferry (0.16 ± 0.06 g), but dropped 4-fold below the confluence of the Paria River and 10-fold (0.01 ± 0.01 g AFDM) below RKM 85. The mass of *Cladophora glomerata* drift packets was highest in September (0.6 ± 0.2 g AFDM) and lowest in March (0.01 ± 0.002 g).

There was a significant ($p = 0.015$) reduction in the mass of *Cladophora glomerata* drift packets above (0.046 ± 0.01 g) and below (0.012 ± 0.004 g) Badger Creek rapid (RKM 12.8). No invertebrates were found in the Badger Creek rapid collections; they were apparently lost while passing through the smaller upstream Paria River rapid. Badger Creek is the first major rapid below Lees Ferry and has a 2.0-m vertical drop (Kieffer 1985).

Epiphytic diatom densities on *Cladophora glomerata* drift packets changed significantly with distance from GCD ($p <$ 0.01, Fig. 6). Epiphyton density was highest at Lees Ferry (450×10^3 cells/mg AFDM *Cladophora glomerata*) and decreased by 40% below the Paria confluence (RKM 3.2) and by 64% at Tanner (RKM 109). The proportion of upright and prostrate diatom taxa remained consistent with distance downstream, although the composition changed (Fig. 6). The more prostrate taxa included *Cocconeis pediculus*, *Gomphonema* spp., and *Achnanthes* spp., while upright taxa included *Rhoicosphenia curvata*, *Diatoma tenue*, and *Diatoma vulgare*. The greatest difference in composition by site was between Lees Ferry and Marble Canyon (Two Mile – Tanner Washes) where *D. vulgare* was replaced by *D. tenue* and *Cocconeis pediculus* (Fig. 6).

The mass of chironomid larvae associated with *Cladophora glomerata* drift packets differed spatially ($p < 0.01$) and seasonally ($p = 0.015$). Maximum standing mass of chironomid larvae occurred in packets at Lees Ferry (x = 0.000 14 g AFDM), but decreased 10-fold at RKM 5 (0.000 02 g AFDM). Other invertebrates were absent from drift packets by RKM 5. Average chironomid larvae mass in *Cladophora glomerata* drift was highest during the summer (x = 0.006 02 ± 0.002 g) and much lower during other seasons: fall, 0.0009 ± 0.000 01 g; winter, 0.000 12 ± 0.000 06 g; and spring, 0.000 10 ± 0.000 04 g.

Energy contained in drift packets of *Cladophora glomerata* was negatively correlated with distance from GCD. Drift packets in the Lees Ferry tail waters contained an estimated seasonal average of 5700 J$\cdot$mg DW^{-1}, while the Marble Canyon reach (RKM 0.0–99) carried 1800 J$\cdot$mg DW^{-1} and drift packets in the Grand Canyon (RKM 99–360) contained only 2 J$\cdot$mg DW^{-1}.

Organic drift in steady versus fluctuating flows

Comparisons between 3 days of steady (227 m$^3\cdot$s^{-1}) and 2 days of fluctuating flows (141–283 m$^3\cdot$s^{-1}) at Lees Ferry showed a significant difference between treatments for algal and invertebrate mass and density ($p < 0.001$, Table 2). There was an overall significant increase in algal and invertebrate drift mass and density ($p < 0.001$; Table 2) during fluctuating flows. Univariate analysis showed that macrophytes, *Cladophora glomerata*, detritus, tubificids, and gastropods had a significant positive correlation with discharge ($p < 0.001$).

Drift mass of primary producers was dominated by *Cladophora glomerata* (98.5%) in both steady and fluctuating flows (Table 2), and the aquatic macrophyte *Potamogeton* sp., the red algae *Rhodochorton* sp. and *Batrachospermum* sp., and the macroalga *Chara* sp. made up the remaining 1.5%. Drift of total living plant material at Lees Ferry was estimated at ~428 $g \cdot s^{-1}$ AFDM assuming a mean annual discharge of 283 $m^3 \cdot s^{-1}$.

Cladophora glomerata and macrophyte AFDM changed significantly on a diurnal basis ($p = 0.01$ and 0.04, respectively). Mean AFDM of drifting plants from 06:00 and 12:00 was 1.3 ± 0.3 $g \cdot m^{-3} \cdot s^{-1}$, while drifting mass from 18:00 and 24:00 was 1.0 ± 0.2 $g \cdot m^{-3} \cdot s^{-1}$. Neither invertebrate AFDM nor abundance changed diurnally through the collection period.

Mean drifting mass and abundance of invertebrates were 0.015 ± 0.008 $g \cdot m^3 \cdot s^{-1}$ and 49.5 ± 9.0 $animals \cdot m^{-3} \cdot s^{-1}$ during fluctuating flows (Table 2). We calculated a total mass of 4.5 $g \cdot s^{-1}$ for invertebrate drift at a discharge of 283 $m^3 \cdot s^{-1}$. Chironomid and *Gammarus lacustris* made up 62 and 33%, respectively, of the drifting invertebrate mass.

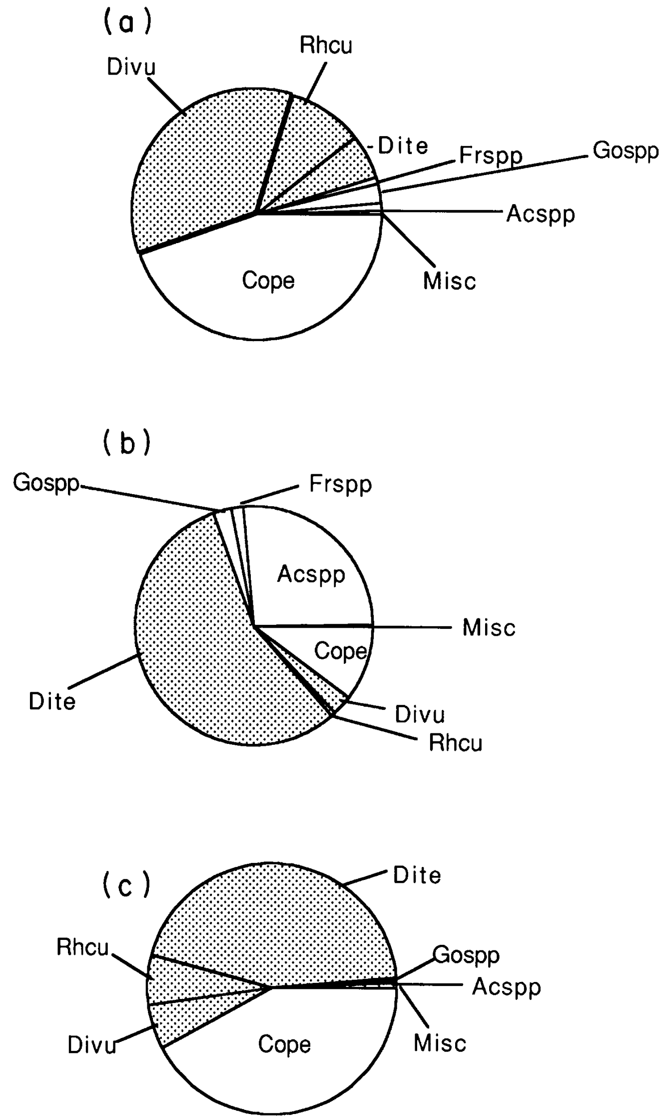
Discussion

The high benthic standing mass in the tail waters immediately below GCD contributes a negligible amount of CPOM (>1 mm) to downstream aquatic communities in the Colorado River corridor through Grand Canyon. Although operations of GCD dislodge large packets of *Cladophora glomerata* and associated invertebrates from cobbles through variable discharge and intervals of desiccation (Angradi and Kubly 1993; Blinn et al. 1995), rapids along the river corridor, in which water velocity can increase more than 10-fold, quickly pulverize packets and limit transport of CPOM to downstream communities.

There was a dramatic reduction in energy in *Cladophora* drift packets downstream. *Cladophora* mass yielded an average of 5700 J/drift packet at Lees Ferry, but the energy was reduced by 22% below the confluence of the Paria River, just 1.0 km downstream. There was an additional 26% reduction in the energy in drift packets below Badger Creek rapid (RKM 12.8). Invertebrates in *Cladophora glomerata* packets displayed an even greater distance-related reduction in AFDM and energy than algal components through the first two rapids. Invertebrate mass in *Cladophora glomerata* drift packets averaged 0.015 g AFDM (~1550 J) at Lees Ferry, but was reduced by >80% below the Paria River and by 99% below Badger Creek rapid (RKM 12.8). This suggests that autochthonous CPOM energy is negatively correlated with stream gradient in the river corridor through Grand Canyon National Park.

In contrast, Power (1990) reported high densities of insect larvae in floating mats of *Cladophora glomerata* in the unregulated pool-riffle reach of the Eel River, California. These comparisons indicate that drifting CPOM can provide important links in the trophic ecology for small rivers, but large lotic ecosystems with hydraulic turbulence greatly reduce downstream transport of CPOM.

Fig. 6. Density and composition of epiphytic diatoms on *Cladophora glomerata* drift packets at (*a*) Lees Ferry (RKM 0; 450 000 cells/mg AFDM), (*b*) Two-Mile Wash (RKM 3; 274 000 cells/mg AFDM), and (*c*) Tanner Wash (RKM 116; 750 000 cells/mg AFDM) in the Colorado River, Arizona. Stippled sections represent upright diatom taxa, whereas clear sections represent more prostrate taxa. Divu, *Diatoma vulgare*; Cope, *Cocconeis pediculus*; Rhcu, *Rhoicosphenia curvata*; Dite, *Diatoma tenue*; Gospp, *Gomphonema* spp.; Frspp, *Fragilaria* spp.; Ascpp, *Achnanthes* spp.; Misc, miscellaneous diatom taxa.



Our data indicate that tributary and terrestrial insects comprise a small portion of the stream drift in the river corridor through Grand Canyon National Park, yet Minckley (1991) reported that terrestrial insects are commonly found in stomachs of the endemic humpback chub (*Gila cypha*). Perhaps terrestrial invertebrate drift is highly punctuated during and immediately after rainstorms and is therefore a rare but locally

Table 2. Comparison of ash-free dry mass and density in the drift during steady and fluctuating flows in the Colorado River at Lees Ferry, Arizona.

Drift category	Steady flows (227 $m^3 \cdot s^{-1}$)		Fluctuating flows (158–354 $m^3 \cdot s^{-1}$)	
	Mass ($g \cdot m^3 \cdot s^{-1}$)	Density ($animals \cdot m^{-3} \cdot s^{-1}$)	Mass ($g \cdot m^{-3} \cdot s^{-1}$)	Density ($animals \cdot m^{-3} \cdot s^{-1}$)
Cladophora glomerata	0.583 14		2.282 72	
Other algae	0.010 84		0.033 574	
Detritus	0.024 91		0.032 94	
Chironomids	0.004 49	31.7	0.008 89	58.0
Gammarus lacustris	0.001 49	1.7	0.006 38	4.8
Simuliids	0.000 12	0.1	0.0	0.0
Lumbriculids	0.0	0.0	0.000 48	0.1
Tubificids	0.000 09	2.4	0.000 39	6.6
Gastropods	0.000 17	0.08	0.000 16	0.01
Miscellaneous macroinvertebrates	0.000 48	0.2	0.000 47	0.7

Note: Multivariate analyses revealed a significant overall difference between steady and fluctuating flows (Wilks' lambda; $F_{[3,85]} = 44.1$, $p < 0.0001$).

important resource for the fisheries in the Colorado River through Grand Canyon. The narrow band of riparian vegetation along the shores of the Colorado River in the arid Southwest provides limited habitat for terrestrial insects (Stevens 1989). In the regulated Caney Fork River, Tennessee, Layzer et al. (1989) indicated that terrestrial insects made up a significant amount of stream drift mass (9.2%) in June when river fluctuations were highest, but contributed little during the remaining months of the year. In contrast, Armitage (1977) reported that terrestrial insects contributed ~10% of the annual drift mass in the mesic watershed of the River Tees, Great Britain.

The positive correlation between the composition of drift packets and the benthic community within each corresponding reach throughout the Colorado River suggests that composition and quantity of autochthonous drift are reach specific and not cumulative throughout the study site. Both tail-water benthic communities and drift between GCD and the Paria River confluence have high standing crops of *Cladophora glomerata* and associated *Gammarus lacustris* and chironomid larvae (e.g., *Cricotopus annulator*), whereas downriver drift is primarily simuliids and *Cladophora glomerata* filaments, which is similar to the benthos. Shannon et al. (1994) reported that the reduction in *Cladophora glomerata* mass and change in invertebrate composition in downstream reaches resulted from elevated suspended sediments from tributaries draining arid landscapes. Thorp and Delong (1994) found similar patterns of reach-based CPOM production from shallow benthic hard substratum and riparian zones in clear rivers.

Suspended sediments dislodged from the channel bottom during fluctuations in discharge coupled with tributary input may be important factors contributing to invertebrate drift in the Colorado River. Doeg and Milledge (1991) increased the level of suspended sediments in experimental channels in the Acheron River, Australia, to mimic natural flood events. They reported a 7-fold increase in the number of drifting invertebrates after 45 min of sediment additions compared with the numbers in control channels. Doeg and Milledge (1991) also reported that the composition of drifting taxa was also variable, with amphipods and some species of Chironomidae very susceptible to suspended sediment loads. This corroborates the reduction in drifting *Gammarus lacustris* below the Little Colorado River and the relatively high numerical level of dipteran drift dominated by simuliids. Other investigators have also suggested that sediment saltation during high-discharge events increases invertebrate drift (Rosenberg and Weins 1978; Culp et al. 1985).

Downriver shifts in fishes can also be linked to the increase in suspended sediments and resulting changes in drift and benthic composition. Rainbow trout (*Oncorhynchus mykiss*) have been introduced into the clear tail waters of GCD, but decrease in number through Marble Canyon and are restricted to tributary mouths below the Little Colorado River confluence (Carothers and Brown 1991). Trout are replaced in downriver sections by bottom-feeding carp (*Cyprinus carpio*), channel catfish (*Ictalurus punctatus*), and several native fish species: humpback chub (*Gila cypha*), flannelmouth sucker (*Catostomus latipinnis*), and bluehead sucker (*Catostomus discobolus*). Minckley (1991) stated that while these endemic fish are opportunistic feeders they are primarily detritivores. Food may be a limiting factor for fish in western Grand Canyon, and may explain their concentrated numbers near tributary mouths (Minckley 1991). Dam operations that deliver low flows with little fluctuation may improve benthic and drift biomass for upper trophic levels, as was recorded in the spring of 1993 (Blinn et al. 1994).

Detritus, which represents a large portion of the total downriver drift mass, was the only component to show a positive correlation with discharge. The low flows and erratic ramping rates of the past decade below GCD may have resulted in detritus being the only component directly affected, perhaps owing to buoyancy. The nonlinear relationship of total drift and discharge (Fig. 2) may be a function of eddies and pools emptying during discharges above 450 $m^{-3} \cdot s^{-1}$ and below 400 $m^{-3} \cdot s^{-1}$, and filling between 400 and 450 $m^{-3} \cdot s^{-1}$. Our data also indicate a threshold of about 480 $m^{-3} \cdot s^{-1}$ beyond which total drift mass dramatically increases. As the stage increases from low to moderate and high flow months, the varial zone is swept of duff accumulated from riparian vegetation. A threshold of ~480 $m^{-3} \cdot s^{-1}$ probably begins to entrain pool-stored drift. Leibfried and Blinn (1986) reported a similar pattern at Lees Ferry.

Entrapment and decomposition of drifting material in the eddy-dominated Colorado River through Grand Canyon National Park occurs in recirculation zones (eddies) and pools. The Colorado River through the Grand Canyon has an average width/mean depth ratio of 12.1 at 680 $m^3 \cdot s^{-1}$ and an average channel width of 67 m (United States Department of Interior 1994). Therefore, the size of the channel and the magnitude of annual discharges (283 $m^3 \cdot s^{-1}$) are great enough to eliminate debris dams that play an important role in resource processing in many lower order lotic ecosystems (Bilby and Ward 1991).

Comparisons between mainstem channel and eddy–pool drift and benthic samples within eddies and pools revealed limited retention capabilities of eddies and pools in this geomorphically constrained river. Although organic matter flows through eddies and pools, water velocity is reduced by 60% on average and therefore may retain organic material for brief periods. This momentary retention pattern may explain the high catch rates of fish in eddies and pools compared with that in the channel (Rich Valdez, BioWest Inc., Logan, Utah, personal communication).

Detritus breaks apart and (or) is transported through the Grand Canyon. The Little Colorado River (RKM 99), the single largest tributary in the study, flooded several times during the winter of 1993. At that time large rafts of organic flotsam, largely composed of sticks and logs, covered the surface of 500-m^2 eddies. Benthic sampling during the subsequent year recovered minor percentages of the flotsam.

Fluorescent dye dispersion studies between GCD and Diamond Creek by Graf (1995) support our conclusion that organic matter is transported swiftly through the Grand Canyon, with little retention in pools or eddies throughout the river corridor. Graf (1995) showed that discharge variability did not significantly affect water velocity in the Colorado River. These data corroborate the insignificant change in drift mass with ramping state.

Our study shows how a constricted, large-volume desert river with fluvial tributary effects can act as a conduit for organic matter produced in the upper tail waters. Drift mass shifts from autochthonous to allochthonous material owing to tributary input of suspended sediments that limits autochthonous production. Debris flows at tributary mouths create large rapids that pulverize algal drift (CPOM), resulting in reach-based drift patterns. Arid land tributaries contribute <0.1% of the total organic matter to main-stem drift.

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