

MINIREVIEW

ALGAL ECOLOGY IN TAILWATER STREAM COMMUNITIES: THE COLORADO RIVER BELOW GLEN CANYON DAM, ARIZONA¹

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Abbreviations: CPOM, Coarse particulate organic matter; DO, dissolved oxygen; FPOM, fine particulate organic matter; GCD, Glen Canyon Dam; PQ, photosynthetic quotient; Rkm, river kilometer

Water discharges from hydropower dams exert major influences on the standing crop and structure of downstream algal communities. Dams typically reset physicochemical conditions in downstream tailwaters to those of lower order streams, which results in critical changes throughout the food web (Ward and Stanford 1979, Lillehammer and Saltveit 1984, Blinn and Cole 1991, Stevens et al. 1997). Those physicochemical and hydrologic changes that have the greatest influence on tailwater algal communities include: (1) diel and seasonal constancy of water temperatures, (2) modifications in nutrient regimes, (3) removal of sediment and clarification of water, (4) formation of stable armored substrates, (5) unnatural fluctuations in water levels that subject biota to diel drying and wetting, and (6) reductions in seasonal flow variability and alterations in the timing or occurrence of extreme flows. The greatest changes in biotic communities result from alterations in timing or occurrence of discharge patterns that have produced community interactions over evolutionary time and result in the invasion of exotic species (Resh et al. 1988). Channel geomorphology, discharge volume, and relative tributary size influence the recovery from these altered conditions over distance downstream from the dam (Ward and Stanford 1983, Stevens et al. 1997).

This minireview focuses on the influences that regulated discharges have placed on the algal community below Glen Canyon Dam (GCD), Arizona, compares these alterations to findings below other hydropower dams, and addresses how algae can be used in environmental management below dams. Lowe (1979) and Biggs (1987) provided earlier reviews on the ecology of algae in regulated rivers. We also experimentally measured: (1) primary productivity of the phytobenthos in submerged and varial zones (that shoreline region in the tailwaters of dams that enlarges and contracts in response to dam

operations) below GCD (Stanford and Hauer 1992) and (2) changes in allochthonous and autochthonous energy below GCD during the test flood of March 1996 using stable isotopes.

STUDY AREA

The Colorado River flows through the arid American Southwest and its flow is regulated by more than 40 large man-made structures (Hirsch et al. 1990). One of the largest structures is GCD, which was completed in 1963 and lies 24.6 km upstream from Lees Ferry, Arizona (Fig. 1). Cool (~10° C), nutrient-rich, clear water is released from the upper hypolimnion of the Lake Powell reservoir into the river below the dam (Blinn and Cole 1991, Stanford and Ward 1991). From that point, the river flows 472 km through Glen, Marble, and Grand Canyons in northern Arizona to Lake Mead (Fig. 1). Because of narrow canyons and high walls, water temperatures average ~10° C throughout much of the river corridor, nearly 11° C lower than average summer temperatures prior to the construction of the dam (Stevens et al. 1997). Also, water clarity decreases over distance from GCD as tributaries such as the Paria and Little Colorado Rivers contribute seasonally varying suspended sediment loads (Andrews 1991, Stevens et al. 1997). This creates a cold stenothermic (9.5° ± 1° C SE), clear-water segment between GCD and the Paria River (~25 km) and a seasonally turbid segment, with a greater temperature range (11° to 16° C) between the Paria River and Lake Mead. Although mean daily flows (340 m³·s⁻¹) below GCD did not change greatly, impoundment had a major influence on flood frequency and magnitude of flows in the Colorado River (Stanford and Ward 1991). The selected flow regime determined from the Environmental Impact Statement process included minimum flows of 227 m³·s⁻¹ from 0700 to 1900 and 142 m³·s⁻¹ at night with a maximum flow of 708 m³·s⁻¹ (USBR 1995).

RESPONSE OF ALGAL COMMUNITIES TO REGULATED DISCHARGES

The conditions of thermal constancy, high water clarity, stable substratum, higher than normal winter temperatures, and elevated nutrient regimes in tailwaters provide an environment highly suitable for the prolific growth of filamentous green algae, especially *Cladophora glomerata* (L.) Kütz. (Ward 1976, Lowe 1979, Dufford et al. 1987, Blinn and Cole 1991). Biomass estimates for *C. glomerata* in the clear tailwater section between GCD and the Paria River are typically ≥15 (± 0.9, SE) g ash-free dry mass·m² (Usher and Blinn 1990, Shannon et al. 1994, Stevens et al. 1997). Other common chlorophytes below dams, depending upon water temperature, flow regimes, and nutrient loads, include *Microspora* and *Ulothrix*, as well as the chrysophyte *Hydrurus*, the cyanobacterium *Tolythrix*, and assorted rhodophytes (Ward 1976, Skulberg 1984, Dufford et al. 1987).

Although modified physicochemical features below dams provide adequate conditions for certain

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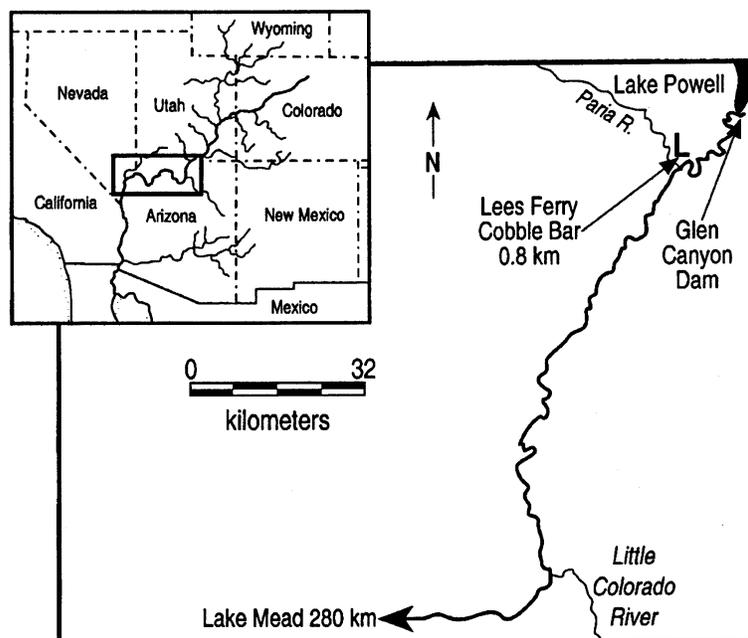


FIG. 1. Map of the regulated Colorado River between Glen Canyon Dam and Lake Mead in Glen and Grand Canyon National Parks, Arizona. Note river kilometers start at 0.0 at Lees Ferry.

phytobenthos, the features may modify reproductive strategies of these algae. For example, recruitment by *C. glomerata* below GCD appears to occur primarily by fragmentation and/or expansion of the holdfast, while zoosporogenesis is absent in the cold stenothermic river water (Shaver et al. 1997). Laboratory studies have shown that zoospore production in *C. glomerata* occurs at temperatures $\geq 16^\circ\text{C}$ (Hoffmann and Graham 1984). This implies that potential losses of *C. glomerata* biomass during wet-dry cycles in tailwaters are even more critical because recruitment by fragmentation is slower than by zoospore production. We have observed zoosporogenesis in splash zones at the waterline along the canyon walls of the Colorado River where temperatures exceed 16°C (Benenati, unpubl.).

Cladophora is considered to be a keystone species below GCD in that it provides a substrate for the attachment of a primary food resource (epiphytes), a refugium from predation and current, and a site of reproduction for stream invertebrates (Blinn and Cole 1991, Shannon et al. 1994). The attributes that make *Cladophora* a relatively successful colonizer in tailwater communities include a streamlined thallus with thick cell walls and a durable rhizoidal holdfast, all designed to withstand high flows, and highly branched collapsing filaments that trap water and reduce desiccation of interior filaments during exposure. The outer portion of *Cladophora* tufts retain water within the inner thallus for at least 12 h and protect interior filaments from desiccation and ultraviolet light (Usher and Blinn 1990). Typically during drawdown periods, surface filaments are

bleached white while the interior filaments remain moist and green. In fact, Usher and Blinn (1990) and Angradi and Kubly (1993) found that *C. glomerata* lost $\sim 40\%$ of its chlorophyll *a* in a 10–12 h exposure to natural light. The epiphytic diatom and cyanobacteria assemblages on *Cladophora* may provide some protection from desiccation by retaining water in their mucilages during emersion (Usher and Blinn 1990). Dodds (1991a) also reported that epiphytes may reduce photoinhibition of *Cladophora* during emersion. These interactions between epiphytes and *Cladophora* host are likely beneficial during exposure to the atmosphere.

The epiphytic assemblage also is shaped by physicochemical and hydraulic conditions of regulated discharges. Typically, cold-water stenotherms and rheobionts such as *Diatoma vulgare* Bory, *Rhoicosphenia curvata* (Kütz.) Grun and *Diatomella*, are common epiphytes in tailwaters with hypolimnial releases (Lowe 1979, Dufford et al. 1987, Blinn and Cole 1991). The high abundance of these more readily available upright and stalked diatom taxa may in fact increase the numbers of grazers, which in turn influences the overall foodweb. Invertebrate diversity, especially aquatic insects, is typically reduced in tailwaters (Ward and Stanford 1979, Valentin et al. 1995). Over 80% of the invertebrate mass below GCD is composed of *Gammarus lacustris*, chironomid larvae, oligochaetes, and gastropods, many of which graze on epiphytes and filter fine particulate matter (Shannon et al. 1994, Blinn et al. 1995, Stevens et al. 1997). The grazing invertebrates “prune” epiphyton, leaving the *Cladophora* host intact. Larger insect shred-

ders and predators are frequently absent below dams due to changes in food type (Valentin et al. 1995). Shannon et al. (1994) demonstrated close interactions, via chemical cues, between *G. lacustris*, diatom epiphytes, and *C. glomerata* below GCD. Finally, exotic trout in the tailwaters of GCD consume *Cladophora* with associated epiphytes but only digest epiphytes and pass the host alga through their digestive tracts in a viable condition (Leibfried 1988).

Fluctuations in discharge from dams also can selectively modify the physiognomy of tailwater epiphyton. Hardwick et al. (1992) reported that the upright, horizontally positioned epiphytic diatoms (*D. vulgare*, *R. curvata*) in the permanently wetted zone were replaced with smaller, more closely adhering forms (*Achnanthes* spp., *Cocconeis pediculus* Ehr.) in the varial zone. This change in community physiognomy is consequential in energy transfer because larger upright diatoms are more easily grazed than smaller, closely adhering forms (Colletti et al. 1987, Steinman et al. 1987). Peterson (1987) also reported changes in diatom composition in the tailwaters of Lake Mead, Nevada, with assemblages in the more rigorous environment of high discharges being more resilient to desiccation than assemblages that developed in sheltered habitats.

Although *Cladophora* has several adaptations to help tolerate the diel submergence and emersion cycles in varial zones, large quantities of this alga still are removed and exported downstream during dam operations (Blinn et al. 1995, Shannon et al. 1996). Studies below GCD have shown that over 50% of the *C. glomerata* mass is lost from established algal communities in varial zones after several weeks of repeated 12-h exposures during both summer (day or night exposures) and subzero winter conditions (Usher and Blinn 1990, Angradi and Kubly 1993, Blinn et al. 1995). These tufts are exported downstream as coarse particulate organic matter (CPOM) and quickly pulverized to fine particulate organic matter (FPOM) as they pass through rapids (Shannon et al. 1996). Although the fate and importance of FPOM in the Colorado River corridor is not fully understood, Stevens et al. (1997) have estimated that over 70% of the total algal biomass in the 472-km river corridor is produced in the upper 26 km clear water reach when the lower section is turbid (Fig. 1).

The losses in phytobenthos reduce localized primary productivity and potential energy in regulated rivers. We measured net productivity of the phytobenthos under different dam operations below GCD. These treatments included the continuously submerged channel (<142 m³·s⁻¹ stage) and upper and lower varial zones (142 to 280 m³·s⁻¹ stage) of the Colorado River at Lees Ferry (Fig. 1). The varial zones had been inundated for 45 days prior to the study; the lower varial was totally submerged and the upper varial was exposed for 12 h each night. Clear plastic circular chambers (23.5 cm diameter, 18.5 cm height) sealed with a lid and an airtight circular

plunger were used in these measurements. An airtight port for an oxygen probe (YSI model 55, Yellow Springs, Ohio) was located in each chamber. Three cobbles with phytobenthos (~25 cm in circumference) from either the upper or lower varial or submerged zone were placed in each chamber, and the plunger was lowered to the top of cobbles to eliminate gas exchange with the atmosphere. Electric submersible pumps circulated water within each chamber at a flow rate of 0.5 L·s⁻¹. Chambers were placed at a depth of 15 cm to maintain ambient river temperature. Irradiance (μmol photons·m⁻²·s⁻¹) was measured at a depth of 15 cm every 5 min with a Li-Cor photometer (Model 185-B). Temperature and dissolved oxygen (DO) were recorded every 5 min until ~2 mg·L⁻¹ DO were produced in each chamber. Incubations were made between 1000 and 1400. Respiration was measured in chambers submerged in 80 L of river water in a 164-L cooler covered with a reflective blanket. After all measurements, the macroalgae were removed from each cobble and sorted into the two principal phytobenthic components, *Cladophora glomerata* or *Oscillatoria* spp., with the aid of a dissecting microscope. The algae were oven-dried at 60° C to a constant weight, and ash-free dry mass was estimated after 1 h combustion at 500° C. Reach-wide calculations for primary productivity followed those outlined in Greenberg et al. (1992). Reach-wide estimates for phytobenthos mass were obtained from Hess substrate collections (n = 6 per treatment). Both gross and net productivity were measured as g O₂·m⁻²·h⁻¹ and converted to carbon (g C·m⁻²·h⁻¹) by multiplying each by 1.46 (Cole 1994). This assumes a photosynthetic quotient (PQ) of 1.2.

Our measurements indicated that net carbon productivity in varial zones was at least an order of magnitude lower than those in continuously submerged zones of the regulated Colorado River (Table 1). *Cladophora glomerata* made up nearly 100% of the biomass on submerged cobbles and ≤55% on cobbles in the varial zone, with most of the balance comprised of *Oscillatoria* (Table 1). Clearly, productivity and structure of the phytobenthic community differ under different dam operations. Hence, the type of dam operation will influence the system's food base.

Also, in a 5-day *in situ* experiment, Blinn et al. (1995) estimated that over 5900 MJ of energy as epiphyton mass would be removed from the varial zone at the Lees Ferry reach at regulated discharges between 142 and 227 m³·s⁻¹, and only 1000 MJ of energy would be lost at discharges in varial zones between 425 and 793 m³·s⁻¹. Calculations from map and image processing indicated that about 11.2 ha of the wetted perimeter at Lees Ferry is in the varial zone between discharges of 142 and 227 m³·s⁻¹ and only 1.9 ha for discharges between 425 and 793 m³·s⁻¹ (Blinn et al. 1995). This points to the importance of channel morphometry when estimating potential losses in ecosystem energy in tailwaters. The

TABLE 1. Net primary productivity estimates and composition of phytoplankton biomass for the upper and lower varial zones ($142\text{--}280\text{ m}^3\text{ s}^{-1}$ stage) and continuously submerged channel ($<142\text{ m}^3\text{ s}^{-1}$ stage) in the Colorado River at Lees Ferry, Arizona, below Glen Canyon Dam during June 1994. Varial zones were inundated for 45 d; lower varial zone was continuously submerged and upper varial zone was subjected to a 12-h exposure each night. $n = 3$ for all treatments, except the continuously submerged channel treatment, where $n = 6$. Light energy ranged from $1800\text{--}2300\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during incubations.

Treatment	Net C Productivity ($\text{g C}\cdot\text{m}^{-2}\cdot\text{h}^{-1} \pm \text{SE}$)	Phytoplankton composition <i>Cladophora/Oscillatoria</i> ($\text{g AFDM}\cdot\text{m}^{-2} \pm \text{SE}$)
Continuously submerged channel	0.89 ± 0.01	$15.8 (\pm 2.1):0.001 (\pm 0.002)$
Submerged lower varial zone	0.02 ± 0.01	$1.3 (\pm 0.8):1.1 (\pm 0.4)$
Desiccated upper varial zone	0.002 ± 0.001	$0.03 (\pm 0.002):12.0 (\pm 4.6)$

above estimates were based on the assumption that epiphytic mass was uniformly distributed across the river channel and of a similar age and physiological state for the macroalgae. However, Hardwick et al. (1992) noted an inverse relationship between epiphyton density and water depth. Therefore, even minor cycles in river discharge may cause major losses in biomass energy depending on stream morphology and stage level of discharge. This pattern intensifies with distance downstream in the Colorado River or in rivers that periodically run turbid, because zones of maximum benthic plant mass move up the shoreline as water clarity decreases (Hardwick et al. 1992, Stevens et al. 1997). Water clarity also dictates the recruitment rate by phytoplankton following major drawdown events. Shaver et al. (1997) reported ≥ 9 months were required for *C. glomerata* to reach control values in turbid water, whereas recent studies in the Colorado River showed a recruitment period of ≤ 3 months in clear water (Shannon, Pers. observ.). Because the phytoplankton serves as critical habitat for stream invertebrates in the Colorado River (Blinn and Cole 1991, Blinn et al. 1995, Stevens et al. 1997), the diel fluctuations in discharge not only result in major losses to localized ecosystem energy, but also critical habitat for upper trophic levels.

The interactions between cycles of submersion and emersion in varial zones and the periodic entry of suspended sediments play a major role in structuring algal communities in regulated desert rivers. Between GCD and the Paria River, water is relatively free of sediment, whereas below the Paria River the water periodically carries heavy loads of sediment (Andrews 1991); both sections have varial zones that undergo emersion on a diel basis. Shaver et al. (1997) and this study (Table 1) found that *C. glomerata* grows best in continuously submerged, clear-water, stable habitats, whereas the cyanobacterium *Oscillatoria* forms dense mat-like matrices of trichomes and sand in varial zones, especially in the presence of high concentrations of suspended sediments. *Oscillatoria* filaments avoid desiccation in the varial zone by migrating into the sediment during emersion (Shaver et al. 1997). The relative importance of this shift in phytoplankton along the river corridor relates to the fact that *C. glomerata* supports a considerably greater mass of epiphytic diatoms, and hence invertebrate energy, than the *Oscillatoria*

assemblage (Shaver et al. 1997). Also, the compact mat-like matrix of *Oscillatoria* provides minimal habitat for animals.

SOURCES OF ECOSYSTEM ENERGY IN REGULATED RIVERS

Impoundments typically interrupt the export of coarse allochthonous organic matter along rivers by allowing particulate material to settle out. These conditions produce optimum clear-water habitats for filamentous algae to become the dominant food resource in tailwater ecosystems (Blinn and Cole 1991, Angradi 1993). However, any major discharge from the dam would likely change the food source back to allochthonous organic matter. We tested this hypothesis with stable isotope analysis on stream drift at various sites along the Colorado River corridor below GCD 4 days prior to and on days 1 and 4 during the 7-day test flood ($1274\text{ m}^3\text{ s}^{-1}$) of March 1996 and 4 days after the test flood. Stable isotopes allow one to follow organic carbon and nitrogen from primary food sources through the food web. These primary food sources have different $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ ratios, which can be detected in upper trophic levels and therefore provide information on the principal food in the diets of consumers (Hershey and Peterson 1996). For a review of stable isotope use in ecological research see Lajtha and Michener (1994).

In order to examine the origin of food resources below GCD, plankton samples ($>1\text{ g}$ dry weight) were collected in Lake Powell with a $63\ \mu\text{m}$ mesh net to obtain reference signals for ^{13}C and ^{15}N . Triplicate drift samples also were collected below the confluences of the Paria River (3.1 River kilometer, Rkm), the Little Colorado River (98.7 Rkm), and National Canyon (278 Rkm) prior to, during, and after the flood (Fig. 1). All samples were air-dried, ground to $<0.5\text{ mm}$ with a Whirl-L-BugTM, and analyzed for ^{13}C and ^{15}N on a mass spectrophotometer. Samples were run with Dumas combustion except for post test flood collections at Rkm 278, where depleted ^{15}N required cryofocus extraction (Fry et al. 1996). Results were compared with ^{13}C and ^{15}N ratios for phytoplankton, macroinvertebrates, and riparian and upland vegetation previously reported by Angradi (1994) from the Colorado River system.

The strongest $\delta^{13}\text{C}/\delta^{15}\text{N}$ signals in the upper tailwaters (3.1 Rkm) prior to and after the test flood were for lake plankton and phytoplankton (autoch-

TABLE 2. Dual isotope ($\delta^{13}\text{C}/\delta^{15}\text{N}$ [0/00]) analyses for drifting organic material at selected stations along the Colorado River through the Grand Canyon prior to, during, and after the 7-d test flood hydrograph ($1274 \text{ m}^3 \text{ s}^{-1}$) during March 1996. POM = particulate organic matter from Lake Powell; Phytobenthos = *Cladophora glomerata* and associated filamentous green algae; Riparian = tamarisk and cottonwood; Upland = floodplain litter from tributaries. Range of isotope ratios for organic sources after Angradi (1994): Lentic POM (-23.8 to $-28.5 \delta^{13}\text{C}/6.8$ to $9.6 \delta^{15}\text{N}$); Phytobenthos (-21.2 to $-33.5 \delta^{13}\text{C}/4.6$ to $9.5 \delta^{15}\text{N}$); Riparian vegetation (-24.9 to $-29.0 \delta^{13}\text{C}/5.0$ to $7.4 \delta^{15}\text{N}$); Upland (-23.8 to $-29.0 \delta^{13}\text{C}/-0.1$ to $5.0 \delta^{15}\text{N}$).

Site (Rkm)	Discharge ($\text{m}^3 \text{ s}^{-1}$)				
	227 Prior to	1274 Hydrostatic wave	1274 Day 1	1274 Day 5	227 After
3	-25.3/9.0 (lentic POM, phytobenthos) ^a	-26.5/6.8 (riparian)	-25.6/7.3 (riparian)	-27.1/6.2 (riparian)	-28.5/9.9 (lentic POM, phytobenthos) ^a
98	-25.2/2.9 (upland)	-25.3/3.9 (upland)	-24.9/2.0 (riparian, upland) ^a	-24.8/1.3 (upland)	-27.1/7.4 (riparian)
278	-15.8/6.0 (unknown)	-23.3/1.4 (upland)	-24.5/1.4 (upland)	-19.3/1.7 (unknown)	-24.1/2.0 (riparian, upland) ^a

^a Overlapping carbon and nitrogen signals were confirmed through visual analysis of drift during each collection.

thonous), compared to riparian and upland vegetation (allochthonous) at downstream sites (≥ 98.7 Rkm, Table 2). During the test flood, $\delta^{13}\text{C}/\delta^{15}\text{N}$ ratios indicated that riparian and upland vegetation was the dominant food resource throughout the river corridor (Table 2). Our data suggest that under constrained hydrographs below dams, autochthonous algal matter is the primary food source in the upper tailwaters below GCD, whereas allochthonous energy from riparian and upland communities become more important during flood events. These flood events provide critical outside energy for the trophic food web. These modifications in the source of organic matter may have consequential effects on the structure of upper trophic levels. Composition of previous drift collections as well as drift examined during the flood concur with findings from stable isotope analysis (Shannon et al. 1996).

INFLOW AND RESERVOIR INFLUENCE ON PHYTOBENTHOS

In addition to the potential release of vital plant nutrients from the hypolimnion of reservoirs, other dissolved chemicals released from turbine outlets may display negative features. Reduced chemical conditions that occur in the lower anoxic regions of reservoirs during the summer may periodically result in the release of harmful compounds. For example, Hannan and Young (1974) reported elevated concentrations of H_2S in the tailwaters of a regulated stream in Texas. Also, hypolimnetic discharges from reservoirs located in arid regions of the American Southwest, where runoff and evaporation rates are high, periodically carry elevated levels of dissolved salts if water is released from below chemoclines. Under select climatic and hydrologic conditions, conductivity of discharges from GCD vary by more than 50% over relatively short time periods (S. Hueftle, pers. commun.). The potential importance of reduced compounds and periodic fluctuations in

ionic concentrations (osmotic potential) on tailwater algal assemblages needs further study.

Occasionally the economics of dam operations deem it necessary to increase discharges because of energy demands and/or higher than normal precipitation in upper watersheds. The high runoff in the upper Colorado River basin during the past few years has dictated high and steady releases from GCD. Prior to May 1995, daily discharge from GCD ranged between 142 and 425 $\text{m}^3 \text{ s}^{-1}$, but with higher snowpacks in the Colorado Rockies these discharges have averaged $>450 \text{ m}^3 \text{ s}^{-1}$ over the past few years, with minimal daily or monthly fluctuations. The constant high inflows have reduced the ionic concentration of water released from GCD (≥ 1000 to $<500 \mu\text{S}$; S. Hueftle, pers. commun.) and may have altered the phytobenthic community. Under the high flows, especially in the winter, *C. glomerata* has been largely replaced by an algal assemblage of filamentous green algae (*Zygnematales*, *Ulotrichales*), cyanobacteria, diatoms, and rhodophytes, all of which produce great quantities of mucilage (Benenati et al. 1997). The occurrence of mucilage-producing assemblages in high constant flows also has been reported by Biggs and Hickey (1994) and Peterson (1996). Dodds (1991a) also reported that epiphyte mucilage, and mucilage in general, lowers drag on the phytobenthos during high flows by decreasing the effective surface area.

Benenati et al. (1997) found a strong positive correlation between reduced nutrients, especially nitrogen, and the mucilage-producing phytobenthic community below GCD. They also reported a strong positive relationship between *C. glomerata* and nutrients prior to the high constant flows. Many studies have documented the association of *C. glomerata* with high nutrient inputs. In fact it is cited as a reason for its occurrence below hypolimnetic releases from reservoirs (Robinson and Hawkes 1986, Dodds 1991b). The increased abundance ($\geq 30\%$) of mucilaginous

cyanobacteria, such as *Tolypothrix*, during the high constant flows below GCD suggests that nitrogen is being fixed by these organisms in the anaerobic mucilage matrices of the new phytobenthic community. This infers that dilutions in nutrients due to higher snowpacks in upper watersheds may modify tailwater algal assemblages. Regardless of whether the production of mucilage functions in reducing hydraulic stress or is a response to nutrient limitations or a combination of both, the functional significance of this change in phytobenthos is a potential loss in food resource. The new mucilaginous phytobenthic assemblage below GCD supports nearly 50% fewer epiphytic diatoms than the non-mucilage-producing *C. glomerata* (Benenati, unpubl.). In addition, the tightly compact mucilaginous matrices of the new phytobenthos assemblage make unicellular forms less available to grazers than loosely attached epiphyton on *Cladophora*. Since many of the invertebrates graze on epiphytic diatoms in the tailwaters of GCD, periodic modifications in the phytobenthic community may intermittently influence the trophic structure of the Colorado River system. This is especially critical because these tailwaters support several endemic fishes (Minckley 1991). In addition to modifications in nutrient concentration and food base energy, elevated discharges increase shearing stress on the phytobenthic community. There have been a number of studies on the selective effect of hydraulic stress on algal communities at elevated velocities (Duncan and Blinn 1989, Biggs and Hickey 1994, Biggs and Stokseth 1996, Peterson 1996).

Surface release reservoirs or selective withdrawal systems can potentially discharge water with constant, elevated temperatures to downstream sites. Just like cold stenothermic conditions produced by hypolimnetic releases, warm stenothermic waters can produce dramatic changes in downstream algal communities. There currently is a proposal to modify the water release program at GCD in order to improve the habitat for the humpback chub (*Gila cypha* Miller), a species endemic to the Colorado River (USNPS 1977). The plan proposes to release warm subsurface water (18–21° C) from Lake Powell into the Colorado River. In a study with circulation chambers, Blinn et al. (1989) reported a significant change in the composition and physiognomy of the diatom epiphyte community on *Cladophora* at Lees Ferry between 12° and 18° C, with no significant change between 18° and 21° C. At the two higher temperatures, smaller and more closely attached taxa such as *C. pediculus* and *Achnanthes* spp. replaced *D. vulgare* and *R. curvata* in treatments at 12° C. Changes in community physiognomy of this nature may have major ramifications on the grazer community in the Colorado River, as previously discussed (Colletti et al. 1987, Steinman et al. 1987).

SUMMARY AND MANAGEMENT CONSIDERATIONS

Hydropower dams modify downstream physicochemical and hydrologic conditions, which may

change the primary food resource from allochthonous to autochthonous carbon (Table 2). The autochthonous energy in upper tailwaters typically includes filamentous chlorophyte algae with associated epiphyton as opposed to coarse particulate carbon (trees, twigs, etc) in unregulated rivers. These shifts in food resource modify the trophic structure of tailwater food webs with a tendency toward invertebrate grazers as opposed to shredders, collectors, and detritivores. Therefore, management issues that alter the ecology of food webs will result in major consequences in the trophic structure of regulated rivers (Table 2). Regulated rivers, like the Colorado River, that harbor endemic species are of even more concern. Oftentimes the economics of energy production and irrigation demands are not compatible with optimum conditions for biota in downstream tailwaters.

Algae provide an excellent biotic index for the management of hydropower dams because they have a relatively quick response time to existing environmental conditions and provide the dominant primary food resource below dams. Therefore, the quantity and quality of the algal resource is critical in the management of tailwater ecosystems. Changes in algal physiognomy and biomass can be monitored along gradients of water releases from dams. Initially, epiphytic assemblages are reduced to adnate forms, and ultimately, under higher discharges ($\geq 935 \text{ m}^3 \cdot \text{s}^{-1}$), overall biomass of both epiphyton and host are eliminated or greatly reduced. Water clarity is critical in the recovery of phytobenthic communities; therefore, the management of dam operations, particularly in arid biomes, should be coordinated with seasonal climatic conditions. Furthermore, the diel variation in water discharges greatly modifies the structure of phytobenthic communities. Certain algae, such as *Oscillatoria* spp., are especially well adapted to tolerate varial zone habitats below dams; however, these taxa may provide minimal support to upper trophic levels, both in habitat and food. Therefore, since algal communities provide the dominant food resource below dams, it is critical to restrict the extent of the varial zone and maintain as large of a wetted perimeter as electric energy demands permit.

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Andrews, E. D. 1991. Sediment transport in the Colorado River basin. In Committee on Glen Canyon Environmental Studies [Eds.] *Colorado River Ecology and Dam Management*. National Academy Press, Washington, D.C., pp. 54–74.

Angradi, T. R. 1993. Stable carbon and nitrogen isotope analysis of seston in a regulated Rocky Mountain river, USA. *Regul. Rivers* 8:251–70.

— 1994. Trophic linkages in the lower Colorado River: multiple stable isotope evidence. *J. North Am. Benthol. Soc.* 13:479–95.

- Angradi, T. R. & Kubly, D. M. 1993. Effects of atmospheric exposure on chlorophyll *a*, biomass and productivity of the epilithon of a tailwater river. *Regul. Rivers* 8:345-58.
- Benenati, P., Shannon, J. P., Blinn, D. W. & Wilson, K. P. 1997. Temporal changes of phytobenthos in the tailwaters of Glen Canyon Dam in the Colorado River, Arizona. *Bull. North Am. Benthol. Soc.* 14:61.
- Biggs, B. J. F. 1987. Periphyton. In Henriques, P. R. [Ed.] *Aquatic Biology and Hydroelectric Power Development in New Zealand*. Oxford University Press, New York, pp. 192-205.
- Biggs, B. J. F. & Hickey, C. W. 1994. Periphyton responses to a hydraulic gradient in a regulated river in New Zealand. *Freshwat. Biol.* 32:49-59.
- Biggs, B. J. F. & Stokseth, S. 1996. Hydraulic habitat suitability for periphyton in rivers. *Regul. Rivers* 12:251-61.
- Blinn, D. W. & Cole, G. A. 1991. Algal and invertebrate biota in the Colorado River: comparison of pre- and post-dam conditions. In Committee on Glen Canyon Environmental Studies [Eds.] *Colorado River Ecology and Dam Management*. National Academy Press, Washington, D.C., pp. 85-104.
- Blinn, D. W., Shannon, J. P., Stevens, L. E. & Carter, J. P. 1995. Consequences of fluctuating discharge for lotic communities. *J. North Am. Benthol. Soc.* 14:233-48.
- Blinn, D. W., Truitt, R. & Pickart, A. 1989. Response of epiphytic diatom communities from the tailwaters of Glen Canyon Dam, Arizona, to elevated water temperature. *Regul. Rivers* 4:91-5.
- Cole, G. A. 1994. *Textbook of Limnology*, 4th ed. Waveland Press, Prospect Heights, Illinois.
- Colletti, P., Blinn, D. W., Pickart, A. & Wagner, V. T. 1987. Influence of different densities of the mayfly grazer *Heptagenia criddlei* on lotic diatom communities. *J. North Am. Benthol. Soc.* 6:270-80.
- Dodds, W. K. 1991a. Community interactions between the filamentous alga *Cladophora glomerata* (L.) Kuetzing, its epiphytes, and epiphyte grazers. *Oecologia* 85:572-80.
- 1991b. Factors associated with dominance of the filamentous green alga *Cladophora glomerata*. *Water Res.* 11:1325-32.
- Dufford, R. G., Zimmermann, H. J., Cline, L. D. & Ward, J. V. 1987. Response of epilithic algae to regulation of Rocky Mountain streams. In Craig, J. F. & Kemper, J. B. [Eds.] *Regulated Streams: Advances in Ecology*. Plenum Press, New York, pp. 383-90.
- Duncan, S. W. & Blinn, D. W. 1989. Importance of physical variables on the seasonal dynamics of epilithic algae in a highly shaded canyon stream. *J. Phycol.* 25:455-61.
- Fry, B. R., Garritt, R., Thorpe, K., Neil, C., Michener, R., Merish, F. & Brand, W. 1996. Cryoflow: cryofocusing nanomole amounts of CO₂, N₂, and SO₂ from an elemental analyzer for stable isotope analysis. *Rapid Commun. Mass Spectrom.* 10:953-8.
- Greenberg, A. E., Clesceri, L. S. & Eaton, A. D. [Eds.] 1992. *Standard Methods for the Examination of Water and Wastewater*, 18th ed. American Public Health Association, Washington, D.C., 1527 pp.
- Hannan, H. & Young, W. J. 1974. The influence of a deep-storage reservoir on the physicochemical limnology of a central Texas river. *Hydrobiologia* 44:177-207.
- Hardwick, G. G., Blinn, D. W. & Usher, H. D. 1992. Epiphytic diatoms on *Cladophora glomerata* in the Colorado River, Arizona: longitudinal and vertical distribution in a regulated river. *Southwest. Nat.* 37:148-56.
- Hershey, A. E. & Peterson, B. J. 1996. Stream food webs. In Hauer, F. R. & Lamberti, G. A. [Eds.] *Methods in Stream Ecology*. Academic Press, San Diego, pp. 551-30.
- Hirsch, R. M., Walker, J. F., Day, J. C. & Kollio, R. 1990. The influence of man on hydrologic systems. In Wolman, M. G. & Riggs, H. C. [Eds.] *Surface Water Hydrology*. Geologic Society of America, Boulder, Colorado, pp. 329-59.
- Hoffmann, J. P. & Graham, L. E. 1984. Effects of selected physicochemical factors on growth and zoosporegenesis of *Cladophora glomerata* (Chlorophyta). *J. Phycol.* 20:1-7.
- Lajtha, K. & Michener, R. H. [Eds.] 1994. *Stable Isotopes in Ecology and Environmental Science*. Blackwell Scientific Publications, London, England, 316 pp.
- Leibfried, W. C. 1988. The utilization of *Cladophora glomerata* and epiphytic diatoms as a food resource by rainbow trout in the Colorado River below Glen Canyon Dam, Arizona. M.S. thesis, Northern Arizona University, Flagstaff, AZ, 41 pp.
- Lillehammer, A. & Saltveit, S. J. [Eds.] 1984. *Regulated Rivers*. University of Oslo Press, Oslo, Norway, 540 pp.
- Lowe, R. L. 1979. Phytobenthos ecology and regulated streams. In Ward, J. V. & Stanford, J. A. [Eds.] *The Ecology of Regulated Streams*. Plenum Press, New York, pp. 25-34.
- Minckley, W. L. 1991. Native fishes of the Grand Canyon region: an obituary? In Committee on Glen Canyon Environmental Studies [Eds.] *Colorado River Ecology and Dam Management*. National Academy Press, Washington, D.C., pp. 124-77.
- Peterson, C. G. 1987. Influences of flow regime on development and desiccation response of lotic diatom communities. *Ecology* 68:946-54.
- 1996. Responses of benthic algal communities to natural physical disturbance. In Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. [Eds.] *Algal Ecology: Freshwater Benthic Ecology*. Academic Press, San Diego, pp. 375-402.
- Resh, V. H., Brown, A. V., Covich, A. P., Gurtz, M. E., Li, H. W., Minshall, G. W., Reice, S. R., Sheldon, A. L., Wallace, J. B. & Wissmar, R. C. 1988. The role of disturbance in stream ecology. *J. North Am. Benthol. Soc.* 7:433-55.
- Robinson, P. K. & Hawkes, H. A. 1986. Studies on the growth of *Cladophora glomerata* in laboratory continuous-flow culture. *Br. Phycol. J.* 21:437-44.
- Shannon, J. P., Blinn, D. W., Benenati, P. L. & Wilson, K. P. 1996. Organic drift in a regulated desert river. *Can. J. Fish. Aquat. Sci.* 53:1360-9.
- Shannon, J. P., Blinn, D. W. & Stevens, L. E. 1994. Trophic interactions and benthic animal community structure in the Colorado River, Arizona, U.S.A. *Freshwat. Biol.* 31:213-20.
- Shaver, M. L., Shannon, J. P., Wilson, K. P., Benenati, P. L. & Blinn, D. W. 1997. Effects of suspended sediment and desiccation on the benthic tailwater community in the Colorado River, USA. *Hydrobiologia* 357:63-72.
- Skulberg, O. M. 1984. Effect of stream regulation on algal vegetation. In Lillehammer, A. & Saltveit, S. J. [Eds.] *Regulated Rivers*. University of Oslo Press, Oslo, Norway, pp. 107-24.
- Stanford, J. A. & Hauer, F. R. 1992. Mitigating the impacts of stream and lake regulation in the Flathead River Catchment, Montana, USA: an ecosystem perspective. *Aquat. Conserv.* 2:35-63.
- Stanford, J. A. & Ward, J. V. 1991. Limnology of Lake Powell and the chemistry of the Colorado River. In Committee on Glen Canyon Environmental Studies [Eds.] *Colorado River Ecology and Dam Management*. National Academy Press, Washington, D.C., pp. 75-123.
- Steinman, A. D., McIntire, C. D., Gregory, S. V., Lamberti, A. & Ashkenas, L. R. 1987. Effects of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. *J. North Am. Benthol. Soc.* 6:175-88.
- Stevens, L. E., Shannon, J. P. & Blinn, D. W. 1997. Colorado River benthic ecology in Grand Canyon, Arizona, USA: dam, tributary and geomorphological influences. *Regul. Rivers* 13:129-49.
- [USBR] U.S. Bureau of Reclamation. 1995. *Operation of Glen Canyon Dam. Environmental Impact Statement*. Salt Lake City, Utah.
- [USNPS] U.S. National Park Service. 1977. *Grand Canyon National Park, Arizona*. National Resource Management Plan and Environmental Assessment. Grand Canyon National Park, Grand Canyon, Arizona.
- Usher, H. D. & Blinn, D. W. 1990. Influence of various exposure periods on the biomass and chlorophyll *a* of *Cladophora glomerata* (Chlorophyta). *J. Phycol.* 244-49.
- Valentin, S., Wasson, J. G. & Philippe, M. 1995. Effects of hydro-power peaking on epilithon and invertebrate community trophic structure. *Regul. Rivers* 10:105-19.
- Ward, J. V. 1976. Comparative limnology of differentially regulated sections of a Colorado mountain river. *Arch. Hydrobiol.* 78: 319-42.
- Ward, J. V. & Stanford, J. A. [Eds.] 1979. *The Ecology of Regulated Streams*. Plenum Press, New York, 398 pp.
- 1983. The serial discontinuity concept of lotic ecosystems. In Fontaine, T. D. & Bartell, S. M. [Eds.] *Dynamics of Lotic Ecosystems*. Ann Arbor Science, Ann Arbor, Michigan, pp. 29-42.