# Environmental Conditions Associated with *Cladophora glomerata*, *Oscillatoria* spp and Miscellaneous Algae, Macrophytes, and Bryophytes (MAMB)

Prepared by:

Dean W. Blinn

G. Allen Haden

Joseph P. Shannon

Emma P. Benenati

Department of Biological Sciences

Northern Arizona University

Flagstaff, Arizona 86011

Draft Report Submitted To: Grand Canyon Monitoring and Research Center

Flagstaff, Arizona 86004

July 2000

GCMRC Library
DO NOT REMOVE

*Cladophora glomerata* is an ubiquitous filamentous green alga that typically grows attached to stones and other solid substrata in both lentic and lotic habitats (Blum 1956, Whitton 1970, Round 1981, Dodds and Gudder 1992, van den Hoek et al. 1995). Luxuriant growths of this alga are also frequently reported in tailwater communities below dams throughout the world (Lowe 1979, Skulburg 1984, Blinn and Cole 1991). Until recently, *Cladophora glomerata* has been especially prolific in the Colorado River below Glen Canyon Dam, AZ (GCD) where allochthonous carbon (riparian and upland vegetation) was replaced by autochthonous carbon, namely *C. glomerata* (Angradi 1994, Blinn et al. 1998, Blinn et al. 1999, Shannon et al. In Press). It should be noted that Wilson et al. (1999) reported large variations in cell morphology for *C. glomerata*, along suspended sediment gradients in the river corridor, that encompass several morphological species of *Cladophora*.

*Cladophora glomerata* has served as a keystone species in the food web in the tailwaters below GCD (Blinn and Cole 1991, Angradi 1994, Shannon et al. 1994, Blinn et al. 1995a, McKinney and Persons 1999, Blinn et al. 1999, also refer to references in Appendix 1). Previous studies on the tailwaters below GCD have repeatedly shown that *C. glomerata* is the preferred habitat for the exotic macroinvertebrate assemblage in the regulated river in comparison to other available habitats including filamentous algae and macrophytes, as well as, *Oscillatoria* spp. and detritus (Blinn and Cole 1991, Blinn et al. 1992, Angradi 1994, Shannon et al. 1994, Shaver et al. 1997, Stevens et al. 1997, Ayers and McKinney 1998, Benenati 1998, Shannon et al. 1998, Benenati et al. In Press, also refer to references in Appendix 1). The non-mucilaginous, highly branched filaments of *C. glomerata* provide a large surface area for the colonization of epiphytes as well as a habitat for invertebrate reproduction and a refugium from predators (Stevenson and Stoermer 1982, Leskinen and Hallfors 1990, Dodds and Gudder 1992, Hardwick et al. 1992). Other investigators have also noted the importance of *C. glomerata* as a prime habitat for invertebrates as well as a potential food resource in nonregulated streams (Dudley et al. 1986, Feminella et al. 1989, Holomuzki 1989, Power 1990, Dodds and Gudder 1992). The dense

filamentous tufts of *Cladophora glomerata* may also mitigate high current velocities and provide a more stable habitat for biota (Dodds 1991b, Dodds and Gudder 1992).

Due to the high occurrence of *C. glomerata* below dams, particularly below GCD, and its potential as a prime habitat for macroinvertebrates, we propose this alga be considered an indicator of stream health below GCD, and perhaps in other tailwater communities as well. For this report, stream health refers to Meyer's (1997) definition...."an ecosystem that is sustainable and resilient, maintaining its ecological structure and function over time while continuing to meet societal needs and expectations". Therefore, this document: 1) reviews the environmental conditions optimum for the growth and proliferation of *C. glomerata*, as well as the other phytobenthic assemblages, *Oscillatoria* spp. and miscellaneous algae, macrophytes and bryophytes (MAMB) in the tailwaters of GCD; and 2) synthesizes the work conducted on the phytobenthic community, particularly on *C. glomerata,* in the tailwaters below GCD. Seventy-five references are provided on the phytobenthic community in the Colorado River below GCD in Appendix I. In addition, studies on the effects of regulated rivers on the phytobenthic community in other regions are reviewed in Baxter (1977), Ward and Stanford (1979), Obeng (1981), Lillehammer and Saltveit (1984), Petts (1984), Stanford and Ward (1986), Craig and Kemper (1987), and Henriques (1987), Special Issue of Regulated Rivers (1997), Seventh International Symposium on Regulated Streams (1999).

**Reproductive Strategies of *Cladophora glomerata*:**

Unlike marine species of *Cladophora*, the freshwater taxon of *C. glomerata* apparently never produces functional gametes, but instead commonly reproduces asexually by the production of biflagellated zoospores in a variety of aquatic habitats (van den Hoek et al. 1995). *Cladophora glomerata* can also propagate by the fragmentation of filamentous tufts, by the formation of akinetes (spores), or by the regeneration of rhizoidal basal holdfasts (Mason 1965, Dodds and Gudder 1992, Graham and Wilcox 2000). Zoosporogenesis is typically the fastest mode of habitat

recolonization due to the release of numerous zoospores by each cell within the filament, each of which potentially produce a new plant (van den Hoek 1995).

Due to existing conditions in the tailwaters of GCD, zoosporogenesis has never been reported in the main channel of the Colorado River, but was observed along the splash zone through Marble Canyon during March 1997 under near-stable flows (Benenati and Shannon, personal observation). Shaver (1995) monitored *C. glomerata* below the varial zone (≥0.5 m deep) at monthly intervals in the Colorado River at Lees Ferry for one year and reported neither zoospore nor akinete formation.

Photoperiod is considered to be the primary factor in the formation of zoosporangia and the process is favored by short-day conditions (8 h light/16 h dark; Hoffman and Graham 1984). The fluctuating water levels, and perhaps the high suspended sediment loads down river, likely reduce the opportunity for *C. glomerata* to become established along a stable waterline throughout the river corridor, even under optimum photoperiods. Constant flows would likely provide better conditions for zoosporogenesis in the tailwaters below GCD and a more rapid proliferation of *C. glomerata* after a disturbance from regulated flows and/or high suspended sediment loads. The proposed study by the Glen Canyon Monitoring and Research Center (GCMRC) will provide more insight on this hypothesis (M. Yard, pers. comm.).

Akinetes are resting spores developed from vegetative cells and are characterized by increased levels of reserve storage products, increased dry matter content, and reduced metabolic activity (O'Neal and Lembi 1983). Prolonged illumination with red light has been found to increase the rate of akinete formation (Pantastico and Suayan 1973).

Due to the restricted conditions for zoosporogenesis and the infrequent observance of zoospore formation, it is hypothesized that the common method of proliferation by *C. glomerata* in the tailwaters of GCD is either by drifting fragments of *C. glomerata* becoming entrapped by stationary substrata and/or recolonization by basal holdfast cells. Dodds and Gudder (1992) have also noted that *Cladophora* tufts become detached from their original substrate, drift downriver until they become entangled around a submerged stable substrate, and continue to be

photosynthetic. However, this process only allows for the recolonization of downstream habitats. The slow recolonization by *C. glomerata* after a disturbance in the tailwaters below GCD (Angradi and Kubly 1993, Blinn et al. 1995b, Shaver et al. 1997, Benenati et al. 1998) supports the hypothesis of limited zoospore production since the latter strategy is typically a faster mode of recolonization (van den Hoek et al. 1995). The periodic high suspended sediment loads further reduce colonization rates by *C. glomerata* throughout the river corridor. Additional studies on the reproductive strategies of *C. glomerata* in the tailwaters of GCD need to be undertaken, particularly in light of the importance of this alga in the food web, to better manage the regulated Colorado River tailwater system.

**Light Requirements of** *Cladophora glomerata*:

*Cladophora glomerata* typically displays an annual bimodal curve in biomass throughout the year with high mass in the spring, low mass in mid-summer, and high biomass again in the fall (Whitton 1970, Madsen and Adams 1988). Initial growth in the spring may depend on the overwintering of basal holdfasts that are stimulated by increasing day length (Bellis and McLarty 1967, Blum 1982), which appears to be the case for *C. glomerata* below GCD.

The annual bimodal pattern of growth for *C. glomerata* may, in part, be attributed to light requirements of the alga. Graham et al. (1982) estimated from laboratory experiments that optimum rates of photosynthesis occurred between 300 and 600 $\mu$mol quanta • $m^{-2}$ • $s^{-1}$. They further reported that light saturation for the pigment system of *C. glomerata* occurred between 345 and 1125 $\mu$mol quanta • $m^{-2}$ • $s^{-1}$. Therefore, the reduced growth of *C. glomerata* in the winter and summer may be due, in part, to reduced light energy in the winter and light saturation in the summer, respectively. Yard et al. (1995) and Yard and Blinn (1998) have further documented the importance of light energy in the seasonal dynamics of *C. glomerata* below GCD.

High sediment loads delivered to the mainstem by major tributaries such as the Paria and Little Colorado rivers further reduce light penetration in the water column and greatly reduce the biomass

of *C. glomerata* (Yard et al. 1995, Shaver et al. 1997, Yard and Blinn 1998,, Wilson et al. 1999). This phenomenon is especially critical downriver within incised canyons where the "life band" of *C. glomerata* is restricted to only a few centimeters, due to restricted light penetration and the sharp slope of the shoreline (Usher and Blinn 1990, Shannon et al. 1994, Blinn et al. 1999, Wilson et al. 1999). Therefore, fluctuations in water level due to operations of GCD have major ramifications on the presence and growth of *C. glomerata* downriver under turbid water conditions. *Cladophora glomerata* is common in low mass in the "unregulated" section of the Colorado River above Lake Powell where suspended sediment loads are commonly high (Haden 1997, Haden et al. 1999). Wilson et al. (1999) reported on the ability of *C. glomerata* to modify its cell morphology to accommodate the abrasive force of suspended particles down stream in the Colorado River corridor.

**Temperature Requirements of** *Cladophora glomerata*:

*Cladophora glomerata* is found at a variety of temperatures throughout the world (Whitton 1970). Maximum growth of *C. glomerata* has been reported to range at temperatures from 13-17°C (Graham et al. 1982), with an upper limit of 24°C (Wong et al. 1978). Several authors have used temperature to described seasonal patterns of *C. glomerata* (Whitton 1970, Auer et al. 1983, Muller 1983, Robinson and Hawkes 1986), however, the role of temperature in the seasonal dynamics of this alga is not clear. For example, Wong et al. (1978) explained the summer die-off of *Cladophora* in many rivers by the inability of the alga to maintain dominance above 23.5°C. However, Brock and Hoffmann (1974) reported photosynthesis by *Cladophora* at temperatures up to 35°C, with optimum rates at 27°C. In contrast, Graham et al. (1982) showed that net photosynthesis decreased at 25°C which coincided with the summer die-off in Lake Huron.

The luxuriant growth of *C. glomerata* in the tailwaters of GCD at temperatures of 11°C suggests that several races of this taxon exist, perhaps a "tailwater race" that has adjusted to the cool hypolimnetic water released from the Lake Powell reservoir. Brock et al. (1999) reported gross primary production (GPP) rates for the phytobenthic community at Lees Ferry during 1991

that were high (33.9 g $O_2$ $m^{-2}$ $d^{-1}$) compared to other North American streams. These high photosynthetic rates suggest the *C. glomerata* "race" in the tailwaters of GCD is capable of high photosynthetic rates at relatively low temperatures (e.g. 11-13°C). Other investigators have also reported relatively high photosynthetic rates by the *C. glomerata* assemblage in the tailwaters of GCD (Angradi and Kubly 1993, Blinn et al. 1994, Blinn et al. 1999).

Due to the varied photosynthetic responses by *C. glomerata* under a variety of temperatures, it appears that temperature alone does not determine seasonal biomass of this alga. It is likely that multiple factors including light, nutrients, biotic interactions, and variable flows all contribute to the seasonal dynamics of *C. glomerata.*

**Nutrient Requirements of *Cladophora glomerata*:**

*Cladophora glomerata* is associated with moderate to high nutrient concentrations, particularly soluble reactive phosphorus (SRP), and therefore favors such environments (Herbst 1969, Whitton 1970, Pitcairn and Hawkes 1973, Lowe 1979, Lohman and Priscu 1992, Wharfe et al. 1984, Dodd and Gudder 1991), including tailwaters that receive hypolimnetic waters from reservoirs (Lowe 1979, Dufford et al. 1987, Blinn and Cole 1992, Blinn et al. 1998, Benenati et al. In Press). In fact, *Cladophora* may become a nuisance in some streams with high nutrient loads (Whitton 1970, Horner and Welch 1981, Lembi, et al. 1988, Dodds 1991 a and b). Optimum growth for *C. glomerata* has been reported at 1.5 mg/L TP with no significant increase in growth above that concentration (Pitcairn and Hawkes 1973). Pitcairn and Hawkes (1973) also reported that concentrations ≤0.5 mg/L TP were limiting and Wong and Clark (1976) observed a direct relationship between ambient TP concentration and the TP content of *Cladophora* tissue.

Dodds (1991a) reported a positive correlation between *C. glomerata* and $NH_4^+$ concentrations and Benenati et al. (In Press) attributed reductions in *C. glomerata* biomass in the tailwaters below GCD to reductions in $NO_3$-N delivered from the Lake Powell reservoir. Benenati et al. (In Press)

proposed that a strong linkage exists between the seasonal dynamics of the Lake Powell reservoir and the physicochemical conditions of the downstream tailwaters. This in turn has an influence on the phytobenthic community throughout the river corridor.

Gerloff and Fitzgerald (1976) reported the minimum cell concentration for N and P that permits maximum yield (critical cell concentration) for *C. glomerata* is 1.1% and 0.06%, respectively. Any tissue with critical concentrations below these levels is presumably nutrient limited. In contrast, other investigators have found no significant correlation between nitrogen and the growth of *Cladophora* (Wong and Clark 1976, Mantai et al. 1982, Manuel-Faler et al. 1984).

The anomaly of high growth rates and biomass for *C. glomerata* and limited ambient phosphorus concentrations in the upper tailwaters of the Colorado River is likely the result of the fast delivery rates of upstream soluble nutrients to *C. glomerata*. Concentrations of total phosphorus (TP) in the upper tailwaters are typically ≤0.01 mg/L (Benenati et al. In Press). However, the high discharges (≥285 $m^3 s^{-1}$) from GCD deliver large amounts of upstream phosphorus across cell membranes over relatively short periods of time (e.g. ≥0.285 mg/L $s^{-1}$). Furthermore, increased velocities have been shown to increase nutrient uptake rates across cell membranes in attached algae (Whitford and Schumacher 1961, 1964). Stanford and Prescott (1988) described a new species of *Cladophora* that was apparently able to survive low ambient concentrations of phosphorus.

**Desiccation of** *Cladophora glomerata:*

The variable discharges from GCD have major implications on the growth and development of *C. glomerata* and the overall trophic health of the Colorado River ecosystem. Several investigators have shown in laboratory and field experiments that even short-term exposures to the atmosphere drastically reduce the biomass of *C. glomerata* below GCD (Usher and Blinn 1991, Angradi and Kubly 1993, Blinn et al. 1995b, Shaver et al. 1997, Benenati et al. 1997, also refer to references in Appendix I). In fact, Blinn et al. (1995b) showed a 50% reduction in *C. glomerata* mass after only

2 d of repeated 12-h summer exposures; 5 d of similar exposures resulted in >70% reduction in *C. glomerata*. Also, one 12-h summer exposure resulted in ≥85% loss in macroinvertebrate mass.

Bleaching of surface filaments within the *C. glomerata* tuft is normally visible after a 1-d summer exposure. Angradi and Kubly (1993) reported that only 57% of the initial chlorophyll *a* remained after a 10-h summer exposure. Even a 3-h exposure to subzero winter air temperatures at night resulted in a ≥50% loss in chlorophyll *a* and *C. glomerata* mass which resulted in a 90% loss of invertebrate mass associated with the phytobenthic assemblage (Blinn et al. 1995b). The bleached filaments eventually detach from the algal tuft and drift downstream where they are pulverized by turbulent rapids (Haury 1981, Shannon et al. 1994).

Although *C. glomerata* biomass is greatly reduced in fluctuating tailwater systems, the alga has several attributes that make it a relatively successful colonizer in these habitats. For example, the alga has a streamlined thallus with thick cell walls and a durable basal holdfast, all designed to help withstand high flows, and highly branched collapsing filaments that trap water and reduce desiccation of interior filaments during exposure (Blinn et al. 1999). Usher and Blinn (1990) reported that *C. glomerata* tufts retain water within the inner thallus after emersion for at least 12 h and protect interior filaments from desiccation and ultraviolet light. Furthermore, the epiphytic diatom and cyanobacteria assemblages on *C. glomerata* may provide some protection from desiccation by retaining water within their mucilages during emersion (Usher and Blinn 1990). Dodds (1991a) also reported that epiphytes may reduce photoinhibition during emersion. These interactions between epiphytes and *C. glomerata* host are likely beneficial during exposure periods.

As previously mentioned, recolonization by *C. glomerata* is slow due to the mode of regeneration in the regulated Colorado River. Blinn et al. (1995b) reported that up to 4 mo may be required for *C. glomerata* to recover in clear water reaches and perhaps as much as 10 mo in turbid water reaches. Other studies in the tailwaters of GCD have reported similar recovery times (Benenati et al. 1998, Shaver et al. 1997). Benenati et al. (1998) found only 30% recovery of *C. glomerata* after 18 weeks of fluctuating flows. It has generally been found that steady flows

enhance the growth and development of *C. glomerata* below GCD (Blinn et al. 1999, Shannon et al. In Press).

Shaver et al. (1997) reported that *C. glomerata* grows poorly in habitats with variable water levels and high turbidity. Shaver et al. (1997) also reported that varial zone conditions demonstrated a stronger influence on community structure than habitats with high suspended sediments. Newcombe and MacDonald (1991) review the detrimental aspects of suspended sediments to phytobenthic communities.

From a trophic ecology standpoint, high daily discharges from GCD drastically influence ecosystem energy within a given tailwater reach. At the extreme end of variation, Blinn et al., (1995b) estimated that daily fluctuations in discharge between 793 (28,000 cfs) and 142 $m^3 s^{-1}$ (5,000 cfs) reduce overall energy of *C. glomerata*, associated epiphyton, and the macroinvertebrate assemblage in the Lees Ferry reach by nearly two-fold. Daily fluctuations in discharge from 793 to 425 (15,000 cfs) and 227 $m^3 s^{-1}$ (8000 cfs) reduce energy by approximately 10% and 30%, respectively (Blinn et al. 1995b). This reduction in ecosystem energy is amplified in downriver reaches due to restricted light penetration from high suspended sediments and the sharp slope of shorelines (refer to references in Appendix I).

**Influence of Flow Variability on** *Cladophora glomerata:*

Various studies have shown that high discharges remove periphyton, including *C. glomerata,* from natural substrata (Statzner and Higler 1986, Biggs and Close 1989, Oberlin 1995, Blinn et al. 1999, McKinney et at. 1999, Shannon et al. In Press). Peterson (1996) provides an excellent summary on the response of various alga taxa and assemblages to assorted discharge regimes. In some instances, high discharges may selectively benefit certain biota by increasing nutrient exchange within dense periphyton mats and filamentous algal tufts as well as reduce interspecific competition and predation from larger biota that are removed by hydraulic scour (Statzner and Higler 1986, Duncan and Blinn 1989, Dodds 1991b, Peterson 1996). Different algal growth forms may show

differential resistance to high discharges (Power and Stewart 1987, Steinman and McIntire 1990). For example, Power and Stewart (1987) found the filamentous chlorophyte *Rhizoclonium*, a close relative of *Cladophora* with a strong basal holdfast system, was able to tolerate high discharges better than the filamentous alga, *Spirogyra*, that has a weaker lateral holdfast system. Horner and Welch (1981) reported that filamentous algal forms appear to be susceptible to dislodgement at current velocities exceeding 50 cm $s^{-1}$. The actual threshold discharge for the removal of *C. glomerata* from substrata has not been determined. However, the 1274 $m^3$ $s^{-1}$ experimental flood removed over 90% of the phytobenthos and ≥50% of the benthic invertebrates from the Lees Ferry reach below GCD (Shannon et al. 1996, Blinn et al. 1999, Shannon et al. In Press).

*Cladophora* scoured from upstream substrates drifts downstream and is typically pulverized by the hydraulic force of rapids (Shannon et al. 1996). The invertebrate composition and density within the drifting packets of *C. glomerata* are considerably lower than that for attached *C. glomerata*.

**Biotic Interactions (Grazing):**

To date, there is no evidence that the exotic invertebrate assemblage in the tailwaters of GCD graze on *C. glomerata* to any extent (Blinn and Cole, 1991, Pinney 1991). Pinney (1991) examined the gut contents of *Gammarus lacustris* and chironomid larvae at the Lees Ferry reach and found only incidental amounts of *C. glomerata* in the diet. Instead, it appears that the microscopic diatom assemblage attached to *C. glomerata* is the primary constituent of the diet for most invertebrates in the tailwaters of GCD (Czarnecki and Blinn 1978, Blinn et al. 1989, Blinn and Cole 1991, Shannon et al. 1994, Blinn et al. 1998).

Studies in other freshwater systems have also reported that *C. glomerata* is a poor, nonpreferred food source for grazers (Gregory 1983, Patrick et al. 1983, Bronmark et al. 1991). In fact, there are reports that *C. glomerata* contain toxic fatty acids that may explain why the alga is not consumed by many freshwater invertebrate grazers (LaLonde et al. 1979).

Although *C. glomerata* does not appear to be a food resource for invertebrates in most freshwater habitats, there have been several reports of caddisflies (Feminella and Resh 1991), gastropods (Bronmark et al. 1991), aquatic Lepidoptera (Bergey 1995), and assorted freshwater invertebrates (Koslucher and Minshall 1973) that graze on *Cladophora* in some aquatic ecosystems. *Cladophora glomerata* appears to serve more as a substrate for the epiphytic microalgae assemblage rather than a direct food source in the tailwaters of GCD.

There have been several reports of trout foraging on *C. glomerata* in the Lees Ferry reach (Leibfried 1988, McKinney and Persons 1999, McKinney et al. 1999). Leibfried (1988) reported that *C. glomerata* was consumed by trout but passed through the digestive tract undamaged and free of diatom epiphytes. In other words, *C. glomerata* entered the digestive tract a brownish color, due to the golden brown epiphytic diatoms, and exited the digestive tract green and free of diatoms.

**Ecological Conditions for** *Oscillatoria* spp.

Species of the cyanobacterian, *Oscillatoria*, are common phytobenthic components under specific ecological conditions in the tailwaters below GCD. It's possible the cyanobacterian taxa change along the river corridor to adjust to changing conditions in suspended sediment, light climate, temperature, dissolved nutrients, and discharge, although this has not been documented. Unfortunately, little attention has been given to the *Oscillatoria* assemblage due to its perceived limited role in the food web in the tailwaters of GCD. Angradi (1994) suggested the *Oscillatoria* assemblages in the tailwaters below GCD was not a nitrogen-fixer, based on a multiple isotope study of the food web.

The *Oscillatoria* and *C. glomerata* assemblages in the tailwaters below GCD show distinctly different habitat preferences. In an *in situ* study with reciprocal cobble transplants in clear and turbid habitats in the Lees Ferry reach, *C. glomerata* preferred clear water with low suspended sediments and flows with minimal variation in discharge, whereas *Oscillatoria* dominated in habitats with high suspended sediments and highly variable flows (Shaver et al. 1997, Stevens et al.

1997, Benenati et al. 1998). Shaver et al. (1997) reported a >80% reduction in *C. glomerata* ash-free dry mass on cobbles translocated from clear to turbid water habitats with variable hydrographs, whereas *Oscillatoria* showed a substantial increase in the latter habitat. Benenati et al. (1998) also found that *C. glomerata* was the dominant phytobenthic species on cobbles below the baseflow in the tailwaters of GCD and *Oscillatoria* spp. was dominant on cobbles in the varial zone.

*Oscillatoria* spp., unlike *C. glomerata*, can tolerate extended periods of desiccation and the abrasive and light-limited environment of high suspended sediments (Fogg et al. 1973, Carr and Whitton 1973, Round 1981. This is due, in part, to the protective mucilaginous sheath that surrounds cyanobacterian cells and trichomes. The encompassing mucilage helps retain moisture to reduce damage from atmospheric exposure during variable flows and protects the sensitive pigment systems in cyanobacterian cells from ultraviolet light during periods of emersion in the absence of a protective water filter (Fogg et al. 1973, Carr and Whitton 1973) .

The mucilaginous matrix that surrounds the cyanobacterian cell can also assist in cell motility (van Den Hoek et al. 1995, Graham and Wilcox 2000). During emersion in the tailwaters of GCD, trichomes migrate into the surface sediments to retain moisture and reduce damage from ultraviolet light. This is evidenced by the appearance of a blue-green film of cyanobacterian filaments on the surface sediments during submergence but disappear into the moist surface sediments during exposures (Joseph Shannon, personal observations). Similar movements have been reported by Castenholz (1973) in hot spring environments. Other investigators have found *Oscillatoria* mats to survive desiccation and recover rapidly upon hydration (Round 1981, Hawes 1993, Vincent and Howard-Williams 1996).

Variable flows reduce potential energy flow in the tailwaters of GCD by displacing *C. glomerata* and producing habitat more suitable for *Oscillatoria*. Commonly the ash-free dry mass of the epiphytic assemblage associated with *C. glomerata* is considerably greater than that associated with the *Oscillatoria* assemblage. The loosely interwoven filaments of *C. glomerata* provide substantially more surface area for the attachment of epiphytes than the more compact, mat-

like matrix of *Oscillatoria*. The difference in diatom epiphytes between the two phytobenthic assemblages is reflected by the invertebrate assemblage as well, with *C. glomerata* supporting considerably more invertebrates than *Oscillatoria*. Shaver et al (1997) reported the invertebrate assemblage in the *C. glomerata* assemblage comprised nearly a two-fold higher energy level than the invertebrate assemblage in *Oscillatoria*.

**Ecological Conditions for *Miscellaneous Algae, Macrophytes and Bryophytes:***

Miscellaneous algae, macrophytes, and bryophytes (MAMB) have had a strong presence in the Colorado River below GCD since late summer of 1995. In the spring of 1995, high snowmelt delivered from tributaries into Lake Powell filled the reservoir to capacity for only the second time in its 33-year existence. This resulted in a freshened or diluted reservoir and subsequent high flow releases from GCD to facilitate lake drawdown. Within three months, >50% of the once dominant non-mucilaginous chlorophyte, *C. glomerata* (L.), was replaced with a mixed, mucilaginous phytobenthic assemblage consisting of miscellaneous algae, macrophytes and bryophytes (MAMB) in the tailwaters. *Cladophora glomerata* was documented as the dominant alga below GCD within six years of the 1963 closure (Czarnecki et al. 1976, Mullan et al. 1976, Carothers and Minckley 1981, Blinn et al. 1989) and remained dominant until August 1995 (Blinn and Cole 1991, Blinn et al. 1995, Benenati et al. 1998).

*Cladophora glomerata* is considered important to the Colorado River foodweb below GCD because of its role as a host, refugium, and provider of food to upper trophic levels throughout the river corridor (Blinn and Cole 1991, Shannon et al. 1994, Blinn et al. 1998). Other algal constituents provide lower epiphytic diatom biomass and inadequate refugia for invertebrates (Shaver et al. 1997, Benenati et al. 1998). The relative phytobenthic composition by biomass prior to June 1995 was: *Cladophora glomerata* = 91.5%, MAMB = 3.5%, and cyanobacteria = 5.0% compared to 49.6, 47.9, and 2.5%, respectively, after the initiation of high discharges (Benenati et al.

In Press). *Cladophora glomerata* and MAMB had an inverse relationship that fluctuated seasonally. *Cladophora* was found to be positively associated with increased nutrient concentrations and lower discharge during summer-fall, while MAMB was positively correlated with decreased nutrients and higher discharge during winter-spring. *Cladophora* was positively associated with invertebrate biomass and also had greater epiphyton biomass and density than MAMB. This major compositional change in phytobenthos following changes in reservoir water quality and releases has been widespread below GCD since 1995 and illustrates the need for greater understanding of lentic-lotic interactions.

## LITERATURE CITED


Angradi, T.R. 1994. Trophic linkages in the lower Colorado River: multiple isotope evidence. Journal of North American Benthological Society 13:479-495.

Angradi, T.R. and D.M. Kubly. 1993. Effects of atmospheric exposures on chlorophyll *a*, biomass, and productivity of the epilithon of a tailwater river. Regulated Rivers 8:345-358.

Auer, M.T., J.M. Graham, L.E. Graham and J.A. Kranzfelder. 1983. Factors regulating the spatial and temporal distribution of *Cladophora* and *Ulothrix* in the Laurentian Great Lakes. *In*:: Wetzel, R.G. (ed.) Periphyton of Freshwater Ecosystems. Junk, The Hague. pp 136-145.

Baxter, R.M. 1977. Environmental effects of dams and impoundments. Annual Review of Ecology 8:255-283.

Bellis, V.J. and D.A. McLarty. 1967. Ecology of *Cladophora glomerata* (L.) Kütz. in southern Ontario. Journal of Phycology. 3:57-63.

Benenati, P.L. 1998. Effects of regulation on the phytobenthic community in the Colorado River below Glen Canyon Dam. PhD. Dissertation, Northern Arizona University, Flagstaff, AZ.

Benenati, E.P., J.P. Shannon, D.W. Blinn, K.P. Wilson and S.J. Hueftle. Reservoir-river linkages: Lake Powell and the Colorado River, Arizona. Journal of the North American Benthological Society. IN PRESS.

Benenati, P.L., J. P. Shannon and D.W. Blinn. 1998. Desiccation and recolonization of phyto benthos in a regulated desert river: Colorado River at Lees Ferry, Arizona, USA. Regulated Rivers 14:519-532.

Bergey, E.A. 1995. Local effects of a sedentary grazer on stream algae. Freshwater Biology 33:401-409.

Biggs, B.J.F. and M.E. Close. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. Freshwater Biology 22:209-231.

Blinn, D.W. and G.A. Cole. 1991. Algal and invertebrate biota in the Colorado River: comparison of post and post-dam conditions. *In*: Colorado River Ecology and Dam Management. (eds) Committee on Glen Canyon Environmental Studies. National Academy Press, Washington, D.C. pp. 102-123.

Blinn, D.W., J.P. Shannon, K.P. Wilson and L.E. Stevens. 1995a. Interim flow effects from Glen Canyon Dam on the aquatic food base in the Colorado River in Grand Canyon National Park, Arizona. Cooperative Agreement CA 8024-8-0002.

Blinn, D.W., J.P. Shannon, K.P. Wilson, C. O'Brien and P.L. Benenati. 1999. Response of benthos and organic drift to a controlled flood. *In*: Webb, R., J.C. Schmidt, G.R. Marzolf, and R.A. Valdez (eds.), The Controlled Flood in Grand Canyon. Geophysical Monograph 110. pp. 259-272.

Blinn, D.W., J.P. Shannon, L.E. Stevens and J.P. Carder. 1995b. Consequences of fluctuating discharge for lotic communities. Journal of the North American Benthological Society 14:233-248.

Blinn, D.W., L.E. Stevens and J.P. Shannon. 1992. Interim flow effects of Glen Canyon Dam on the aquatic food base in the Colorado River corridor in Grand Canyon, Arizona. Report No. CA-8009-8-0002, Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, AZ.

Blinn, D.W., J.P. Shannon, P.L. Benenati and K.P. Wilson. 1998. Algal ecology in tailwater stream communities: The Colorado River below Glen Canyon Dam, Arizona. Journal of Phycology 34:734-740.

Blinn, D.W., L.E. Stevens and J.P. Shannon. 1994. Interim flow effects of Glen Canyon Dam on the aquatic food base in the Colorado River corridor in Grand Canyon, Arizona. Report No. GCES II-02. Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, AZ.

Blinn, D.W., R. Truitt and A. Pickart. 1989. Response of epiphytic diatom communities from the tailwaters of Glen Canyon Dam, Arizona, to elevated water temperature. Regulated Rivers. 4:91-96.

Blum, J.L. 1956. The ecology of river algae. Botanical Review 22:291-331.

Blum, J.L. 1982. Colonization and growth of attached algae at the Lake Michigan water line. Journal of Great Lakes Research 8:10-15.

Brock, J.T., T.V. Royer, E.B. Snyder and S.A. Thomas. 1999. Periphyton metabolism: A chamber approach. *In*: Webb, R., J.C. Schmidt, G.R. Marzolf, and R.A. Valdez (eds.), The Controlled Flood in Grand Canyon. Geophysical Monograph 110. pp. 217-223.

Brock, T.D. and J. Hoffmann. 1974. Temperature optimum of algal living in the outfall of a power plant on Lake Monona. Transactions of the Wisconsin Academy of Science, Arts, and Letters 62:195-203.

Bronmark, C, S.D. Rundle and A. Erlandsson. 1991. Interactions between freshwater snails and tadpoles: competition and facilitation. Oecologia (Berl.) 87:8-18.

Carothers, S.W. and C.O. Minckley. 1981. A survey of the fishes, aquatic invertebrates, aquatic plants of the Colorado River and selected tributaries from Lees Ferry to Separation Rapids. U.S. Bureau of Reclamation: Water and Power Research Service, Lower Colorado River Region. Boulder City, NV.

Carr, N.G. and B.A. Whitton (eds.) 1973. The Biology of Blue-Green Algae. Botanical Monographs Volume 9. University of California Press. Berkeley, CA.

Castenholz, R.W. 1993. Movements (of blue-green algae). *In*: Carr, N.G. And B.A. Whitton (eds.). University of California Press, Berkeley. pp. 320-329.

Craig, J.F. and J.B. Kemper (eds.). 1987. Regulated Streams: Advances in Ecology. Plenum Press, New York.

Czarnecki, D.B. and D.W. Blinn. 1978. Diatoms of the Colorado River in Grand Canyon National Park and vicinity: diatoms of southwestern USA. Bibliotheca Phycologia 38:1-182.

Czarnecki, D.B., D.W. Blinn and T. Tompkins. 1976. A periphytic microflora analysis of the Colorado river and major tributaries in Grand Canyon National Park and vicinity. Colorado River Research Program Publication 6:1-106.

Dodds, W.K. 1991a. Factors associated with dominance of the filamentous green alga *Cladophora glomerata*. Water Research 25:1325-1332.

Dodds, W.K. 1991b. Micro-environmental characteristics of filamentous algal communities in flowing freshwaters. Freshwater Biology 25:199-209.

Dodds, W.K. and D.A. Gudder. 1992. The ecology of *Cladophora*. Journal of Phycology 28:415-427.

Dudley, T.L., S.C. Cooper and N. Hemphill. 1986. Effects of macroalgae on stream invertebrate community. Journal of the North American Benthological Society 5:93-106.

Dufford, R.G., H.J. Zimmermann, L.D. Cline and J.V. Ward. 1987. Response of epilithic algae to regulation of Rocky Mountain streams. *In*: Craig, J.F. and J.B. Kemper (eds.). Regulated Streams: Advances in Ecology. Plenum Press, NY, pp. 383-390.

Duncan, S.W. and D.W. Blinn. 1989. Importance of physical variables on the seasonal dynamics of epilithic algae in a highly shaded canyon stream. Journal of Phycology 25:455-461.

Feminella, J.W. and V.H. Resh. 1991. Herbivorous caddisflies, macroalgae, and epilithic microalgae: dynamic interactions in a stream grazing system. Oecologia 87:247-256.

Fogg, G.E., W.D.P. Stewart, P. Fay and A.E. Walsby. 1973. The Blue-Green Algae. Academic Press, New York.

Gerloff, G.C. and G P. Fitzgerald. 1976. The nutrition of Great Lakes *Cladophora*. United States Environmental Protection Agency, EPA 60013-76-044, 111 pp.

Graham, J.M. M.T. Auer, R.P. and J.P. Hoffmann. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 4. Photosynthesis and respiration as functions of light and temperature. Journal of Great Lakes Research 8:100-111.

Graham, L.E. and L.W. Wilcox. 2000. Algae. Prentice Hall, NJ.

Gregory, S.V. 1983. Plant-herbivore interactions in stream systems. *In*:: Barnes, J.R. and G.W. Minshall (eds.). Stream Ecology. Plenum Press, NY., pp. 157-189.

Haden, G.A. 1997. Benthic ecology of the Colorado River system through the Colorado Plateau region. MSc. Thesis. Northern Arizona University, Flagstaff, AZ.

Haden, G.A., D.W. Blinn, J.P. Shannon and K.P. Wilson. 1999. Driftwood: An alternative habitat for macroinvertebrates in a large desert river. Hydrobiologia 397:179-186.

Hardwick, G.C., D.W. Blinn and H.D. Usher. 1992. Epiphytic diatoms on *Cladophora glomerata* in the Colorado river, Arizona: Longitudinal and vertical distribution in a regulated river. The Southwestern Naturalist 37:148-156.

Haury, L.R. 1981. *Cladophora* drift and plankton crustaceans in the Colorado River: Lees Ferry to Diamond Creek. Report submitted to the Museum of Northern Arizona, Flagstaff, AZ.

Hawes, I. 1993. Photosynthesis in thick cyanobacterial films: A comparison of annual and perennial antarctic mat communities. Hydrobiologia 252:203-209.

Henriques, P.R. 1987. Aquatic Biology and Hydroelectric Power Development in New Zealand. Oxford University Press, London.

Herbst, R.P. 1969. Ecological factors and the distribution of *Cladophora glomerata* in the Great Lakes. American Midland Naturalist 82:90-98.

Hoffmann, J.P. and L.E. Graham. 1984. Effects of selected physiochemical factors on growth and zoosporogensis of *Cladophora glomerata* (Chlorophyta). Journal of Phycology 20:1-7.

Holomuzki, J.R. 1989. Predation risk and macroalga use by the stream-dwelling salamander *Ambystoma texanum*. Copeia 1:22-28.

Holomuzki, J.R. and T.M. Short. 1988. Habitat use and fish avoidance behaviors by the stream-swelling isopod *Lirceus fontinalis*. Oikos 52:79-86.

Horner, R.R and E.B.Welch. 1981. Stream periphyton development in relation to current velocity and nutrients. Canadian Journal of Fisheries and Aquatic Sciences 38:449-457.

Koslucher, D.G. and G.W. Minshall. 1973. Food habits of some benthic invertebrates in a northern cold-desert stream (Deep Creek, Curlew Valley, Idaho-Utah). Transactions of the American Microscopical Society 92:441-452.

LaLonde, R.T., C.D. Morris, C.F. Wong, L.C. Gardner, D.J. Eckert, D.R. King and R.H. Zimmerman. 1979. Response of *Aedes triseriatus* larvae to fatty acids of *Cladophora.* Journal of Chemical Ecology 5:371-381.

Leibfried, W.C. 1988. Utilization of *Cladophora glomerata* and epiphytic diatoms as a food source by rainbow trout in the Colorado river below Glen Canyon Dam, Arizona. MSc. Thesis, Northern Arizona University, Flagstaff, AZ. 41 pp.

Lembi, C.A., S.W. O'Neil and D.F. Spencer. 1988. Algae as weeds: economic impact, ecology and management alternatives. *In:* Lembi, C.A. and J.R. Waaland (eds.) Algae and Human Affairs. Cambridge University Press, Cambridge, pp. 455-481.

Leskinen, E. and G. Hallfors. 1990. Dynamics of epiphytic diatoms on *Cladophora glomerata* in the Tvarminne Archipelago, Northern Baltic Sea. 11Th Diatom Symposium 425-435.

Lillehammer, A. and S.J. Salveit (eds.) 1984. Regulated Rivers. University of Oslo Press, Oslo, Norway.

Lohman, K. and J.C. Priscu 1992. Physiological indicators of nutrient deficiency in (Chlorophyta) in the Clark Fork of the Columbia River, Montana. Journal of Phycology 28:443-448.

Lowe, R.L. 1979. Phytobenthos ecology and regulated streams. *In*: Ward, J.V. And J.A. Stanford (eds.). The Ecology of Regulated Streams. Plenum Press, Corp. N.Y., pp. 25-34.

Madsen, J.D. and M.S. Adams. 1988. The seasonal biomass and productivity of the submerged macrophytes in a polluted Wisconsin stream. Freshwater Biology 20: 41-50.

Mantai, K.E., P.E. Garwood and L.E. Peglowski. 1982. Environmental factors controlling physiological changes in *Cladophora* in Lake Erie. Journal of Great Lakes Research 8:61-65.

Manuel-Faler, C.Y., G.W. Minshall, R.W. Dunn and D.A. Bruns. 1984. *In situ* nitrogen enrichment experiments in two Idaho (USA) streams. Environmental Monitoring Assessment 4:67-79.

Mason, C.P. 1965. Ecology of *Cladophora* in farm ponds. Ecology 46:421-428.

McKinney. T. and T.S. Rogers. 1999. Lotic community response in the Lees Ferry reach. *In*:: Webb, R., J. C. Schmidt, G.R. Marzolf, and R.A. Valdez (eds.), The Controlled Flood in Grand Canyon. Geophysical Monograph 110. pp. 249-258.

McKinney, T., D.W. Speas, R.S. Rogers, and W.R. Persons. 1999. Rainbow trout in the Lee's Ferry recreational fishery below Glen Canyon Dam, Arizona, following establishment of minimum flow requirements. Final Report to U.S. Bureau of Reclamation, Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

McKinney, T. and W.R. Persons. 1999. Rainbow trout and lower trophic levels in the Lee's Ferry tailwater below Glen Canyon Dam, Arizona: A review. Report to U.S. Bureau of Reclamation, Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

Meyer, J.L. 1997. Stream health: incorporating the human dimension to advance stream ecology. Journal of the North American Benthological Society. 6:439-447.

Mullan, J.W., V.J. Starostka, J.L. Stone, R.W. Riley, and W.J. Wiltzius. 1976. Factors affecting Upper Colorado River Reservoir tailwater trout fisheries. *In*: Orsborn, J.F. and C.E. Allman (eds.) Instream Flow Needs. Vol. II. American Fisheries Society, Bethesda, MD.

Muller, C. 1983. Uptake and accumulation of some nutrient elements in relationship to the biomass of an epilithic community. *In*: Wetzel, R.G. (ed.) Periphyton of Freshwater Ecosystems. Dr. W. Junk, The Hague, pp. 147-151.

Oberlin, G. 1995. Aquatic invertebrates in Montezuma Castle National Monument: Response to physicochemical parameters. MSc. Thesis, Northern Arizona University, Flagstaff, AZ.

Newcombe, C.P. and D.D. MacDonald. 1991. Effects of suspended sediment on aquatic ecosystems. North American Journal of Fish Management 11:72-82.

Obeng, L.E. 1981. Man's impact on tropical rivers, *In*: Lock, M.A. And D.D. Williams (eds.). Perspectives in Running Water Ecology. Plenum Press, New York.

O'Neal, S.W. and C.A. Lembi. 1983. Physiological changes during germination of *Pithophora oedogonica* (Chlorophyta) akinetes. Journal of Phycology 19:193-199.

Pantastico, J.B. and Z.A. Suayan. 1973. Akinete differentiation in *Cladophora* sp. Part 3: effects of aging and related factors. Philippines Agriculture 57:305-312.

Patrick, R., C.F. Rhyne, R.W. Richardson III, R.A. Larson, T.T. Bott and K. Rogenmuser. 1983. The potential for biological controls of *Cladophora glomerata*. United States Environmental Protection Agengy, EPA 600/3-83-065, 153 pp.

Peterson, C.G. 1996. Response of benthic communities to natural physical disturbance in algal ecology, *In*: R. J. Stevenson, M.L. Bothwell, and R. L. Lowe. (eds.). Algal Ecology: Freshwater Benthic Ecosystems. pp. 375-402.

Petts, G.E. 1984. Impounded Rivers: Perspectives for Ecological Management. John Wiley and Sons, New York.

Pinney, C.A. 1991. The response of *Cladophora glomerata* and associated epiphytic diatoms to regulated flow and the diet of *Gammarus lacustris*, in the tailwaters of Glen Canyon Dam. MSc. Thesis, Northern Arizona University, Flagstaff, AZ.

Pitcairn, C.E. and H.A. Hawkes. 1973. The role of phosphorus in the growth of *Cladophora*. Water Research 7:159-171.

Power, M.E. 1990. Benthic tufts vs floating mats of algae in river food webs. Oikos 58:67-79.

Power, M.E. and A.J. Stewart. 1987. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. American Midland Naturalist 117:333-345.

Robinson, P.K. and H.A. Hawkes. 1986. Studies on the growth of *Cladophora glomerata* in laboratory continuous-flow culture. British Phycological Journal 21:437-444.

Round, F.E. 1981. The Ecology of Algae. Cambridge University Press, New York.

Seventh International Symposium on Regulated Streams. 1999. Regulated Rivers 15:1-270.

Shannon, J.P., D.W. Blinn, K.P. Wilson, P.L. Benenati, G.A. Haden and K.E. Pomeroy. 1998. Monitoring the aquatic food base in the Colorado River, Arizona during fiscal years 1998 and 1999. Final Report submitted to Glen Canyon Environmental Studies, Flagstaff, AZ.

Shannon, J.P., D.W. Blinn, K.P. Wilson, P.L. Benenati and G.E. Oberlin. 1996. Interim flow and beach building spike flow effects from Glen Canyon Dam on the aquatic food base in the Colorado River in Grand Canyon National Park, Arizona. Final Report submitted to Glen Canyon Environmental Studies, Flagstaff, AZ.

Shannon, J.P., D.W. Blinn and L.E. Stevens. 1994. Trophic interactions and benthic animal community structure in the Colorado River, Arizona, USA. Freshwater Biology 31:213-220.

Shannon, J.P., D.W. Blinn, P.L. Benenati, C. O'Brien, J.Hagen and K.P. Wilson. 1997. 1997 monitoring of the aquatic food base under modified fluctuating flows in the Colorado River through Grand Canyon. Final Report submitted to Glen Canyon Environmental Studies, Flagstaff, AZ.

Shannon, J.P., D.W. Blinn, P.L. Benenati and K. P. Wilson. 1996. Organic drift in a regulated desert river. Canadian Journal of Fisheries and Aquatic Sciences 53:1360-1369.

Shannon, J.P., D.W. Blinn, E. P. Benenati, K.P. Wilson and C. O'Brien. Aquatic food base response to the 1996 spike flow below Glen Canyon Dam: Colorado River, Arizona. Ecological Applications. IN PRESS.

Shaver, M.L. 1995. Turbidity and desiccation structuring of benthic communities in the tailwaters of Glen Canyon Dam, Arizona. MSc. Thesis, Northern Arizona University, Flagstaff, AZ.

Shaver, M. L., J.P. Shannon, K.P. Wilson, P.L. Benenati and D.W. Blinn. 1997. Effects of suspended sediment and desiccation on the benthic tailwater community in the Colorado River, USA. Hydrobiologia 357:63-72.

Skulburg, O.M. 1984. Effects of stream regulation on algal vegetation. *In*: Lillehammer, A. and S.J. Saltveit (eds.). Regulated Rivers. University of Oslo Press, Oslo, Norway. pp. 107-124.

Special Issue of Regulated Rivers. 1997. The River Great Ouse. Regulated Rivers 13: 203-315.

Stanford, J.A. and G.W. Prescott. 1988. Limnological features of a remote alpine lake in Montana, including a new species of *Cladophora* (Chlorophyta). Journal of the North American Benthological Society 7:14-151.

Stanford, J.A. and J.V. Ward. 1986. The Colorado River system. *In*: Davies, B. and K.F. Walker (eds.) The Ecology of River Systems. Dr. Junk.

Statzner, B. and B. Higler. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biology 9:251-262.

Steinman, A.D. and C.D. McIntire. 1990. Recovery of lotic periphyton communities after disturbance. Environmental Management 14:589-604.

Stevens, L.E., J.P. Shannon and D.W. Blinn. 1997. Colorado River benthic ecology in Grand Canyon, Arizona, USA: Dam, tributary and geomorphological influences. Regulated Rivers 13: 129-149.

Stevenson, R.J. and E.F. Stoermer. 1982. Seasonal abundance patterns of diatoms on *Cladophora* in Lake Huron. Journal of Great Lakes Research 8:169-183.

Usher, H.D. and D.W. Blinn. 1990. Influence of various exposure periods on the biomass and chlorophyll *a* of *Cladophora glomerata* (Chlorophyta). Journal of Phycology 26:244-249.

van den Hoek, D.G. Mann, and H.M. Jahns. 1995. Algae: An introduction to phycology. Cambridge University Press, N.Y.

Valdez, R.A., and R.J. Ryel. 1995. Life history and ecology of the humpback chub *(Gila cypha)* in the Colorado River, Grand Canyon, Arizona. Final Report to Glen Canyon Environmental Studies, Flagstaff, AZ.

Vincent, W.F. and C. Howard-Williams. 1986. Antarctic stream ecosystems: Physiological ecology of a blue-green algal epilithon. Freshwater Biology 16:219-233.

Ward, J.V. and J.A. Stanford. 1979. The Ecology of Regulated Streams. Plenum Press, New York.

Wharfe, J.R., K.S. Taylor and H.A.C. Montgomery. 1984. The growth of *Cladophora glomerata* in a river receiving sewage effluent. Water Research 18:971-979.

Whitton, B.A. 1970. Biology of *Cladophora* of freshwaters. Water Research 4:457-476.

Whitford, L.A. and G.J. Schumacher. 1961. Effect of current on mineral uptake and respiration by a fresh-water alga. Limnology and Oceanography 6:423-425.

Whitford, L.A. and G.J. Schumacher. 1964. Effect of current on respiration and mineral uptake of *Spirogyra* and *Oedogonium*. Ecology 45:168-170.

Wilson, K.P., J.P. Shannon and D.W. Blinn. 1999. Effects of suspended sediment on biomass and cell morphology of *Cladophora glomerata* (Chlorophyta) in the Colorado River, Arizona. Journal of Phycology 35:35-41.

Wong, S.L. and B. Clark. 1976. Field determination of the critical nutrient concentrations for *Cladophora glomerata* in streams. Journal of the Fisheries Research Board of Canada 35:866-870.

Wong, S.L., B. Clark, M. Kirby and R.F. Kosciuw. 1978. Water temperature fluctuations and seasonal periodicity of *Cladophora* and *Potamogeton* in shallow rivers. Journal of Fisheries Research Board of Canada 35:866-870.

Yard, M.D. and D.W. Blinn. 1998. Factors influencing benthic algal standing mass in the Colorado River: Light, drift, and velocity. Cooperative Agreement 98-FC-40-0540. Annual Report to Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

Yard, M.D., G.A. Haden, and W.S. Vernieu. 1995. Photosynthetically available radiation (PAR) in the Colorado River: Glen and Grand Canyon. Glen Canyon Environmental Studies, Flagstaff, AZ.

APPENDIX 1. Literature on the Phytobenthic Community in the Colorado River below Glen Canyon Dam, Arizona. Asterisk (*) indicates technical report.

---


Angradi, T.R. 1994. Trophic linkages in the lower Colorado river: multiple isotope evidence. Journal of North American Benthological Society 13:479-495.

Angradi, T.R. and D.M. Kubly. 1993. Effects of atmospheric exposures on chlorophyll *a*, biomass, and productivity of the epilithon of a tailwater river. Regulated Rivers 8:345-358.

Angradi, T.R. and D.M. Kubly. 1994. Concentration and transport of particulate organic matter below Glen Canyon Dam on the Colorado River, Arizona. Journal of the Arizona-Nevada Academy of Science 28:12-22.

*Ayers, A.D. and T. McKinney. 1996a. Ecosystem processes and lower trophic levels. Glen Canyon Environmental Studies Interim Monitoring Progress Report. Final Report to U.S. Bureau of Reclamation, Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

*Ayers, A.D. and T. McKinney. 1996b. Lake Powell forebay and Glen Canyon Dam tailwater to Lee's Ferry during interim flows: Particulate organic matter transport, nutrient content, and periphyton standing stock. Final Report to U.S. Bureau of Reclamation, Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

Ayers, A.D. and T. McKinney. 1998. *Gammarus lacustris* Sars in the tailwaters of a regulated river. Journal of the Arizona-Nevada Academy of Science 32:83-96.

*Angradi, T.R., R. W. Clarkson, D.A. Kinsolving, D.M. Kubly and S.A. Morgensen. 1992. Glen Canyon Dam and the Colorado River: Response of the aquatic biota to dam operations. Report submitted to U.S. Bureau of Reclamation, Glen Canyon Environmental Studies. Flagstaff, AZ.

Benenati, P.L. 1998. Effects of regulation on the phytobenthic community in the Colorado River below Glen Canyon Dam. PhD. Dissertation, Northern Arizona University, Flagstaff, AZ.

Benenati, P.L., J. P. Shannon and D.W. Blinn. 1998. Desiccation and recolonization of phytobenthos in a regulated desert river: Colorado River at Lees Ferry, Arizona, USA. Regulated Rivers 14:519-532.

Benenati, E.P., J.P. Shannon, D.W. Blinn, K.P. Wilson and S.J. Hueftle. Reservoir-river linkages: Lake Powell and the Colorado River, Arizona. Journal of the North American Benthological Society. IN PRESS.

Blinn, D.W. and G.A. Cole. 1991. Algal and invertebrate biota in the Colorado River: Comparison of pre and post-dam conditions. *In*: Colorado River Ecology and Dam Management. (eds) Committee on Glen Canyon Environmental Studies. National Academy Press, Washington, D.C. pp. 102-123.

*Blinn, D.W., C.A. Pinney, R. Truitt and A. Pickart. 1986. Examination of the influence of elevated temperature on epiphytic species in the tailwaters of Glen Canyon Dam and the importance of these epiphytic diatoms in the diet of *Gammarus lacustris*. GCES Report, U.S. Bureau of Reclamation. Salt Lake City, UT.

*Blinn, D.W., J.P. Shannon, K.P. Wilson and L.E. Stevens. 1995. Interim flow effects from Glen Canyon Dam on the aquatic food base in the Colorado River in Grand Canyon National Park, Arizona. Cooperative Agreement CA 8024-8-0002.

Blinn, D.W., J.P. Shannon, K.P. Wilson, C. O'Brien and P.L. Benenati. 1999. Response of benthos and organic drift to a controlled flood. *In*: Webb, R., J.C. Schmidt, G.R. Marzolf, and R.A. Valdez (eds.), The Controlled Flood in Grand Canyon. Geophysical Monograph 110. pp. 259-272.

Blinn, D.W., J.P. Shannon, L.E. Stevens and J.P. Carder. 1995. Consequences of fluctuating discharge for lotic communities. Journal of the North American Benthological Society 14:233-248.

Blinn, D.W., J.P. Shannon, P.L. Benenati and K.P. Wilson. 1998. Algal ecology in tailwater stream communities: The Colorado River below Glen Canyon Dam, Arizona. Journal of Phycology 34:734-740.

*Blinn, D.W., L.E. Stevens and J.P. Shannon. 1992. Interim flow effects of Glen Canyon Dam on the aquatic food base in the Colorado River corridor in Grand Canyon, Arizona. Report No. CA-8009-8-0002, Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, AZ.

*Blinn, D.W., L.E. Stevens and J.P. Shannon. 1994. Interim flow effects of Glen Canyon Dam on the aquatic food base in the Colorado River corridor in Grand Canyon, Arizona. Report No. GCES II-02. Glen Canyon Environmental Studies, Bureau of Reclamation, Flagstaff, AZ.

Blinn, D.W., R. Truitt and A. Pickart. 1989. Response of epiphytic diatom communities from the tailwaters of Glen Canyon Dam, Arizona, to elevated water temperature. Regulated Rivers. 4:91-96.

Brock, J.T., T.V. Royer, E.B. Snyder, and S.A. Thomas. 1999. Periphyton metabolism: A chamber approach. *In*: Webb, R., J.C. Schmidt, G.R. Marzolf, and R.A. Valdez (eds.), The Controlled Flood in Grand Canyon. Geophysical Monograph 110. pp. 217-223.

Brouder, M.J., D.W. Speas, and T.L. Hoffnagle. 1999. Changes in number, sediment composition, and benthic invertebrates of backwaters. *In*: Webb, R., J.C. Schmidt, G.R. Marzolf, and R.A. Valdez (eds.), The Controlled Flood in Grand Canyon. Geophysical Monograph 110. pp. 241-248.

Carothers, S.W. and B.T. Brown. 1991. The Colorado River through Grand Canyon: Natural history and human change. The University of Arizona Press, Tucson.

*Carothers, S.W. and C.O. Minckley. 1981. A survey of the aquatic flora and fauna of the Grand Canyon. Final Report to USDI, Water and Power Research Service. Lower Colorado Region, Boulder City, Nevada. 401 pp.

*Cole, G. and D.M. Kubly. 1976. Limnologic studies on the Colorado River from Lees Ferry to Diamond Creek, Colorado River Research Series. Contributions, Grand Canyon National Park 37:1-88.

Czarnecki, D.B. and D.W. Blinn. 1977. Diatoms of the Lower Lake Powell and vicinity. Bibliotheca Phycologia 28:1-119.

Czarnecki, D.B. and D.W. Blinn. 1978. Diatoms of the Colorado River in Grand Canyon National Park and vicinity: Diatoms of southwestern USA. Bibliotheca Phycologia 38:1-182.

*Czarnecki, D.B., D.W. Blinn and T. Tompkins. 1976. A periphytic microflora analysis of the Colorado river and major tributaries in Grand Canyon National Park and vicinity. Colorado River Research Program Publication 6:1-106.

Haden, G.A. 1997. Benthic ecology of the Colorado River system through the Colorado Plateau region. MSc. Thesis. Northern Arizona University, Flagstaff, AZ.

*Haden, G.A., D.W. Blinn and J.P. Shannon. 1999. Food base studies and stable isotope analysis of the diet of humpback chub (Gila cypha) in the Little Colorado River, Coconino County, AZ. Final Report submitted to U.S. Fish & Wildlife Service.

Haden, G.A., D.W. Blinn, J.P. Shannon and K.P. Wilson. 1999. Driftwood: An alternative habitat for macroinvertebrates in a large desert river. Hydrobiologia 397:179-186.

*Haden, G.A., D.W. Blinn, J.P. Shannon, C. O'Brien and K.P. Wilson. 1997. Benthic ecology of the Colorado River system through the Colorado Plateau region of the Southwestern United States. Final Report submitted to the US Bureau of Reclamation, Salt Lake City, UT.

Haden, G.A., D.W. Blinn, J.P. Shannon and K.P. Wilson. 1999. Interference competition between the net-building caddisfly *Ceratopsyche oslari* and the amphipod *Gammarus lacustris*. Journal of Freshwater Ecology 14:277-280.

Hardwick, G.C., D.W. Blinn and H.D. Usher. 1992. Epiphytic diatoms on *Cladophora glomerata* in the Colorado river, Arizona: Longitudinal and vertical distribution in a regulated river. The Southwestern Naturalist 37:148-156.

*Haury, L.R. 1981. *Cladophora* drift and plankton crustaceans in the Colorado River: Lees Ferry to Diamond Creek. Report submitted to the Museum of Northern Arizona.

Hofknecht, G. 1981. Seasonal community dynamics of aquatic invertebrates in the Colorado River and its tributaries within Grand Canyon, Arizona. MSc. Thesis, Northern Arizona University, Flagstaff, AZ.

Leibfried, W.C. 1988. Utilization of *Cladophora glomerata* and epiphytic diatoms as a food source by rainbow trout in the Colorado river below Glen Canyon Dam, Arizona. MSc. Thesis, Northern Arizona University, Flagstaff, AZ. 41 pp.

*Leibfried, W.C. and D.W. Blinn. 1986. The effects of steady versus fluctuating flows on aquatic macroinvertebrates in the Colorado River below Glen Canyon Dam, Arizona. Glen Canyon Environmental Studies Report No. 15, National Technical Information Service: No. PB88-206362/AS. United States Department of Commerce, Springfield, VA. 58 pp.

*Maddux, H.R., D.M. Kubly, J.C. DeVos, Jr, W.R. Persons, R. Staedicke and R.L. Wright. 1987. Effects of varied flow regimes on aquatic resources of Glen and Grand Canyons. Final Report to the GCES. Arizona Department of Game and Fish, Phoenix, AZ.

Marzolf, G.R. 1999. Effects of flooding on plant production downstream from Glen Canyon Dam. USGS Fact Sheet 060-99. U.S. Geological Survey. 2 pp.

Marzolf, G.R., C.J. Bowser, R. Hart, D.W. Stephens and W.S. Vernieu. 1999. Photosynthetic and respiratory processes: An open stream approach. *In*: Webb, R., J.C. Schmidt,, G.R. Marzolf, and R.A. Valdez (eds.), The Controlled Flood in Grand Canyon. Geophysical Monograph 110. pp. 205-215.

McKinney, T., A.D. Ayers and R.S. Rogers. 1999. Macroinvertebrate drift in the tailwaters of a regulated river below Glen Canyon Dam, Arizona. Southwestern Naturalist 44:205-242.

*McKinney, T. and W.R. Persons. 1999. Rainbow trout and lower trophic levels in the Lee's Ferry tailwater below Glen Canyon Dam, Arizona: A review. Report to U.S. Bureau of Reclamation, Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

*McKinney, T., D.W. Speas, R.S. Rogers and W.R. Persons. 1999. Rainbow trout in the Lee's Ferry recreational fishery below Glen Canyon Dam, Arizona, following establishment of minimum flow requirements. Final Report to U.S. Bureau of Reclamation, Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

*McKinney, T., R.S. Rogers, A.D. Ayers and W.R. Persons. 1996. Effects of experimental flooding on algae, macrophytes, macroinvertebrates, rainbow trout and flannelmouth sucker in the Glen Canyon Dam tailwater. Final Report to U.S. Bureau of Reclamation, Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

McKinney, T., R.S. Rogers, A.D. Ayers, and W.R. Persons. 1999. Lotic community responses in the Lees Ferry reach. *In*: Webb, R., J.C. Schmidt,, G.R. Marzolf, and R.A. Valdez (eds.), The Controlled Flood in Grand Canyon. Geophysical Monograph 110. pp. 249-258.

*McKinney, T., R.S. Rogers and W.R. Persons. 1997. Lee's Ferry reach: Lower trophic levels and rainbow trout--1997 Annual Report. Final Report to U.S. Bureau of Reclamation, Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

McKinney, T. , R.S. Rogers and W.R. Persons. 1999. Effects of flow reductions on aquatic biota of the Colorado River below Glen Canyon Dam, Arizona. North American Journal of Fisheries Management 19:984-991.

*Montgomery, W.L., W.C. Leibfried, K. Gooby and P. Pollack. 1986. Feeding by rainbow trout on *Cladophora glomerata* at Lee's Ferry, Colorado River, AZ. The roles of *Cladophora* and epiphytic diatoms in trout nutrition. Preliminary report to the Bureau of Reclamation, Flagstaff, AZ.

Oberlin, G.A., J.P. Shannon and D.W. Blinn. 1999. Watershed influence on the macroinvertebrate fauna of ten major tributaries of the Colorado River through Grand Canyon, Arizona. Southwestern Naturalist 44:17-30.

Pilsbry, H.A. and J.H. Ferriss. 1911. Mollusca of the southwestern states, V: The Grand Canyon and northern Arizona. Proceedings of the Academy of Natural Sciences, Philadelphia 63:174-199.

Pinney, C.A. 1991. The response of *Cladophora glomerata* and associated epiphytic diatoms to regulated flow and the diet of *Gammarus lacustris*, in the tailwaters of Glen Canyon Dam. MSc. Thesis, Northern Arizona University, Flagstaff, AZ.

Polhemus, J.T. and M.S. Polhemus. 1976. Aquatic and semi-aquatic Heteroptera of the Grand Canyon (Insect: Hemiptera). Great Basin Naturalist 36:221-226.

Pollack, P.E. 1984. Sources of nutrition at Lee's Ferry on the Colorado River. Unpubl. Report. Northern Arizona University, Flagstaff, AZ.

Pomeroy, K., J.P. Shannon and D.W. Blinn. Leaf breakdown in a desert regulated river: Colorado River, Arizona. Hydrobiologia. IN PRESS.

Shannon, J.P. 1992. The effects of Glen Canyon Dam on the Colorado River ecosystem through Grand Canyon National Park. MSc. Thesis. Northern Arizona University, Flagstaff, AZ.

Shannon, J.P., D.W. Blinn and L.E. Stevens. 1994. Trophic interactions and benthic animal community structure in the Colorado River, Arizona, USA. Freshwater Biology 31:213-220.

Shannon, J.P., D.W. Blinn, E.P. Benenati, K.P. Wilson and C. O'Brien. Aquatic food base response to the 1996 spike flow below Glen Canyon Dam: Colorado River, Arizona. Ecological Applications. IN PRESS.

*Shannon, J.P., D.W. Blinn, K.P. Wilson, K.E. Pomeroy, G.A. Haden and E. P. Benenati. 1999. Monitoring the aquatic food base in the Colorado River, Arizona during fiscal year 1999. Final Report submitted to Glen Canyon Environmental Studies, Flagstaff, AZ.

*Shannon, J.P., D.W. Blinn, K.P. Wilson, P.L. Benenati and G.E. Oberlin. 1998a. 1997-1998 responses of the aquatic food base to elevated discharges and three-day low flows in the Colorado River below Glen Canyon Dam, Arizona. Final Report submitted to Grand Canyon Monitoring and Research Center. Flagstaff, AZ.

*Shannon, J.P., D.W. Blinn, K.P. Wilson, P.L. Benenati and G.E. Oberlin. 1996. Interim flow and beach building spike flow effects from Glen Canyon Dam on the aquatic food base in the Colorado River in Grand Canyon National Park, Arizona. Final Report submitted to Grand Canyon Monitoring and Research Center. Flagstaff, AZ.

*Shannon, J.P., D.W. Blinn, K.P. Wilson, P.L. Benenati, G.A. Haden and K.E. Pomeroy. 1998b. Monitoring the aquatic food base in the Colorado River, Arizona during fiscal years 1998 and 1999. Final Report submitted to Grand Canyon Monitoring and Research Center. Flagstaff, AZ. Flagstaff, AZ.

*Shannon, J.P., D.W. Blinn, P.L. Benenati, C. O'Brien, J.Hagen and K.P. Wilson. 1997. 1997 monitoring of the aquatic food base under modified fluctuating flows in the Colorado River through Grand Canyon. Final Report submitted to Grand Canyon Monitoring and Research Center. Flagstaff, AZ.

Shannon, J.P., D.W. Blinn, P.L. Benenati and K.P. Wilson. 1996. Organic drift in a regulated desert river. Canadian Journal of Fisheries and Aquatic Sciences 53:1360-1369.

Shaver, M.L. 1995. Turbidity and desiccation structuring of benthic communities in the tailwaters of Glen Canyon Dam, Arizona. MSc. Thesis, Northern Arizona University, Flagstaff, AZ.

Shaver, M.L., J.P. Shannon, K.P. Wilson, P.L. Benenati and D.W. Blinn. 1997. Effects of suspended sediment and desiccation on the benthic tailwater community in the Colorado River, USA. Hydrobiologia 357:63-72.

Stevens, L.E., J.E. Sublette and J.P. Shannon. 1998. Chironomidae (Diptera) of the Colorado River, Grand Canyon, Arizona, USA: Factors influencing distribution. Great Basin Naturalist 58:147-155.

Stevens, L.E., J.P. Shannon and D.W. Blinn. 1997. Colorado River benthic ecology in Grand Canyon, Arizona, USA: Dam, tributary and geomorphological influences. Regulated Rivers 13: 129-149.

Sublette, J.E., L.E. Stevens and J.P. Shannon. 1998. Chironomidae (Diptera) of the Colorado River, Grand Canyon, Arizona, USA. I. Systematics and Ecology. Great Basin Naturalist 58:97-146.

Usher, H.D. 1987. *Cladophora glomerata* in the Colorado River through Glen and Grand Canyons: Distribution and tolerance to exposure. MSc. Thesis, Northern Arizona University, Flagstaff, AZ.

Usher, H.D. and D.W. Blinn. 1990. Influence of various exposure periods on the biomass and chlorophyll *a* of *Cladophora glomerata* (Chlorophyta). Journal of Phycology 26:244-249.

*Yard, M.D. and D.W. Blinn. 1998. Factors influencing benthic algal standing mass in the Colorado River: Light, drift, and velocity. Cooperative Agreement 98-FC-40-0540. Annual Report to Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

*Yard, M.D. and D.W. Blinn. 1999. Factors influencing benthic algal standing mass in the Colorado River: Light, drift, and velocity. Cooperative Agreement: 98-FC-40-0540. Annual Report to Glen Canyon Monitoring and Research Center, Flagstaff, AZ.

*Yard, M.D., G.A. Haden and W.S. Vernieu. 1995. Photosynthetically available radiation (PAR) in the Colorado River: Glen and Grand Canyon. Glen Canyon Environmental Studies, Flagstaff, AZ.

Wilson, K.P., J.P. Shannon and D.W. Blinn. 1999. Effects of suspended sediment on biomass and cell morphology of *Cladophora glomerata* (Chlorophyta) in the Colorado River, Arizona. Journal of Phycology 35:35-41.

Woodbury, A.M., S. Flowers, D.W. Lindsay, S.D. Durrant, N.K. Dean, A.W. Grundman, J.R. Crook, W.H. Behle, H.G. Higgins, G.R. Smith, G.G. Musser and D.B. McDonald. 1959. Ecological studies of the flora and fauna in Glen Canyon. University of Utah Anthropological Papers 40:1-229.

NORTHERN
ARIZONA
UNIVERSITY

TRADITION • INNOVATION

DEPARTMENT OF
BIOLOGICAL
SCIENCES

RECEIVED GCMRC
OFFICIAL FILE COPY

RESPONSE
RESP. DATE
CNTL #
FOLDER # 60946-2
CLASS CODE PCJ-2.00-Unsch

| DATE | TO | INITIALS |
|---|---|---|
| 7/18/00 | GCMRC 720 | cc BR |
| 8/24 | 782 | Library |
| | | |
| | | |

17 July 2000

Dr. Barbara Ralston
Biological Program Manager
Grand Canyon Monitoring and Research Center
2255 N. Gemini Dr., Rm 341
Flagstaff, AZ 86001-1673

Dear ~~Dr. Ralston~~ Barbara,

Enclosed please find two copies of our preliminary report titled, "Environmental Conditions Associated with *Cladophora glomerata*, *Oscillatoria* spp., and Miscellaneous Algae, Macrophytes, and Bryophytes, MAMB" for the first deliverable on the extended GCMRC Contract Agreement No. 1425-98FC-22590. This report synthesizes the habitat requirements for various constituents of the phytobenthic community below Glen Canyon Dam. It also provides an updated literature list of all research conducted on the phytobenthic community in the tailwaters of Glen Canyon Dam.

Our next report will include the use of *Cladophora* as an indicator of "stream health" below Glen Canyon Dam

Please contact me if you have any questions.

Cordially,

Dean

Dean W. Blinn

Grand Canyon Monitoring
and Research Center

JUL 18 2000

Received
Flagstaff, AZ

PO Box 5640
Flagstaff, AZ 86011-5640
(520) 523-2381 fax (520) 523-7500