THE SOUTHWESTERN NATURALIST 37(2):148-156 JUNE 1992

EPIPHYTIC DIATOMS ON *CLADOPHORA GLOMERATA* IN THE COLORADO RIVER, ARIZONA: LONGITUDINAL AND VERTICAL DISTRIBUTION IN A REGULATED RIVER

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ABSTRACT—Seventy-eight taxa of diatoms were identified from the epiphytic community of *Cladophora glomerata* in the Colorado River through Glen and Grand Canyons. *Achnanthes affinis, Cocconeis pediculus, Diatoma vulgare,* and *Rhoicosphenia curvata* made up 80% of the diatom epiphyton community within 15 km of Glen Canyon Dam, Arizona. However, these taxa made up only 33% of the periphyton community 354 km downstream. Mean total diatom density associated with *Cladophora glomerata* was significantly reduced at each sequential station downstream. Diatom density decreased and community composition of diatoms changed with increasing water depth in the river channel. Cell densities of *D. vulgare, C. pediculus,* and *R. curvata* decreased markedly at Lees Ferry following a 3-month period of fluctuating flow during October through December 1985.

Several studies on the algal communities in the Colorado River through Glen and Grand Canyons, Arizona, were conducted prior to the completion of Glen Canyon Dam near Page, Arizona, in 1963. Flowers (1959) observed 52 taxa of algae, including 29 taxa of diatoms in Glen Canyon, and Woodbury et al. (1959) were the first to report *Cladophora glomerata* (L.) Kütz., now the dominant filamentous alga in the mainstream of the Canyon system (pers. obser.). Williams and Scott (1962) and Weber (1966, pre-dam data) listed the dominant species of diatoms at a water quality surveillance station near Page, Arizona.

A few algal surveys have been conducted in the Colorado River since the completion of Glen Canyon Dam in 1963. Crayton and Sommerfeld (1978) examined the planktonic algal species in the main river and concluded that many of the planktonic species were attached forms that had been dislodged by the current. S. W. Carothers and C. O. Minckley (in litt.) listed total numbers of epilithic diatom species for several major tributaries to the Canyon system. Czarnecki et al. (1976) studied the periphyton in the seeps and at the mouths of tributaries in the Grand Canyon and reported that *C. glomerata* was the dominant, attached green alga in the Canyon system, especially at the mouths of major tributaries. Czarnecki and Blinn (1978) reported a total of 235 taxa of diatoms from the Grand Canyon system. Their study showed that *Diatoma vulgare, Cocconeis placentula,* and *Rhoicosphenia curvata* were the dominant taxa of diatoms. Peterson (1987) studied the importance of desiccation on the structure of diatom communities in the tailwaters of Lake Mead in the Colorado River. He reported that biomass and density were reduced by desiccation on sheltered substrata, as a function of regulated flow. Blinn et al. (1989*a*) examined the importance of water temperature on the composition of tailwater (Glen Canyon Dam to Lees Ferry) diatom communities and found that relative frequencies of *R. curvata* and *D. vulgare* decreased when water temperature was >18°C. The relative abundance of *Cocconeis pediculus* increased at elevated water temperatures.

This paper presents a preliminary study on the composition of diatoms epiphytic on *C. glomerata* in the mainstream of the Colorado River through Grand Canyon. *Cladophora* represents a major biotic substrate for epiphytic diatoms throughout the Grand Canyon system (Czarnecki et al., 1976; Usher and Blinn, 1990). Furthermore, by using a common algal host substrate, i.e., *C. glomerata,* throughout the Grand Canyon system the study design has minimized variability due to substrate type. Diatom composition and densities were examined as functions of distance downstream of Glen Canyon Dam and of increasing water depth. We also compared assemblages of epiphytic diatoms following relatively steady flows and fluctuating flows at Lees Ferry.

MATERIALS AND METHODS—*Cladophora glomerata* typically is most abundant on rock bars at the mouths of tributaries throughout the Grand Canyon system (Czarnecki et al., 1976; Usher and Blinn, 1990). Furthermore, preliminary observations indicated that assemblages of epiphytic diatoms on *Cladophora* at the mouths of tributaries are similar to the epiphytic assemblages on *Cladophora* in other nearby regions of the Colorado River system. Therefore, the sampling sites were selected at major tributaries throughout the Colorado River during July 1985 to examine the longitudinal distribution of epiphytic diatoms on *Cladophora*. All samples were taken at depths of <0.3 m in the mainstream of the Colorado River because sites downstream commonly did not have *C. glomerata* at deeper depths. Tailwater sites upstream of the Paria River (the first major suspended sediment source) included 12.1 km below Glen Canyon Dam and Lees Ferry (river kilometer, RK, 0.0). Downstream sampling sites were located near Nankoweap Creek (RK 84.5), Bright Angel Creek (RK 141.1), Kanab Creek (RK 230.9), and RK 354.

Three water depth zones, based on the 708-m^3/s water level, were established at Lees Ferry to examine the vertical distribution of epiphytic diatoms in the river channel. The discharge of 708 m^3/s was selected to establish the depth zones, because this was the approximate mean flow discharged from Glen Canyon Dam during 1984 (Bureau of Reclamation, United States Department of the Interior). Depth zone I extended from the waters edge to 0.3 m deep, zone II ranged from 0.3 to 1.2 m, while depth zone III was 1.2 to 2.5 m deep.

Three random samples of *C. glomerata* with a basal attachment area of 4 cm^2 each were collected from each water depth zone at Lees Ferry in October 1984, October 1985, and December 1985. These samples included only the section of *Cladophora* filaments included in the 4 cm^2 when the alga was out of the water (stranded), i.e., primarily the basal portion of the filaments. This procedure provided uniformity in examining primarily the mature basal sections of the plant. The collections taken during December 1985 followed 3 months of fluctuating flows. These samples were compared to collections from October 1985 which followed 4 months of relatively stable flows. Diatom collections were also taken from depth zone I during January 1987 to compare the winter epiphytic diatom community under relatively steady flows with winter diatom communities under fluctuating flows (i.e., December 1985). Flows during the 3-month period prior to January 1987 fluctuated <145 m^3/s in a 24-h period (Bureau of Reclamation, United States Department of the Interior). Similar depth zones and sampling design were employed at Nankoweap in October 1984. Scuba-diving was employed for some collections in zone III.

Diatom samples were oxidized by the peroxide-dichromate method, and prepared slides were mounted in Hyrax mounting medium. At least 200 diatom valves were counted from each slide. Population densities of diatoms were calculated on the basis of cells per square centimeter of the basal attachment system of *C. glomerata*. One-way analysis of variance (ANOVA) was used to examine the longitudinal distribution of diatom population density through the Canyon system, while two-way ANOVA (3 × 3 design) was used to examine the vertical distribution of diatom cell density for the three water depths at Lees Ferry.

RESULTS—*Longitudinal Distribution of Diatoms*—Seventy-eight taxa of diatoms (20 genera) were identified from the epiphytic community on *C. glomerata* in the Colorado River at six sites between Glen Canyon Dam and RK 354 (Table 1). Twenty-eight of these taxa were found only in the tailwaters (Glen Canyon Dam to Paria River), and 10 taxa were restricted to the Colorado River below the confluence of the Paria River (RK 1.2). *Achnanthes affinis, C. pediculus, D. vulgare,* and *R. curvata* composed at least 80% of the epiphyton in the tailwaters. *Cyclotella michiganiana* and *Fragilaria crotonensis,* both considered remnant species from the upstream Lake Powell plankton community (Stewart and Blinn, 1976; Czarnecki and Blinn, 1977), were present in the tailwaters between Glen Canyon Dam and Lees Ferry but quickly disappeared at downstream stations.

There was a notable downstream decrease in the relative proportions of the four dominant taxa (Fig. 1). At Lees Ferry, these four taxa composed 80% of the epiphyton, while, at RK 354, these species represented only 33% of the epiphyton. *Diatoma vulgare* showed the least change in relative abundance throughout the Canyon (Fig. 1). *Achnanthes affinis, C. pediculus,* and *R. curvata* were replaced by *Gomphonema olivaceum, Cymbella affinis,* and *Nitzschia dissipata* as dominants in the downstream sites (Kanab Creek and RK 354). The latter three taxa composed 25% of the "other" category at Kanab and 58% at RK 354.

There was a significant decrease in the mean total diatom density during July 1985 for sites between Glen Canyon Dam and RK 354 (F =

TABLE 1—List of epiphytic diatoms on *Cladophora glomerata* in the Colorado River in Glen and Grand Canyons, Arizona. Taxa are marked (X) to indicate presence only in the tailwaters (T, above the Paria River), only downstream of the tailwaters (D, below the Paria River), or throughout the river system (RS).

Taxon	T	D	RS
Coscinodiscaceae			
Cyclotella michiganiana Skv.			X
Melosira varians Ag.			X
Fragilariaceae			
Diatoma hiemale var. *mesodon* Ehr. Grun.	X		
Diatoma tenue Ag.	X		
Diatoma vulgare Bory			X
Fragilaria construens var. *venter* (Ehr.) Grun.	X		
Fragilaria crotonensis Kitton	X		
Fragilaria leptostauron (Ehr.) Hust.			X
Fragilaria vaucheriae (Kütz.) Peters			X
Opephora anasata Hohn et Hellerm.		X	
Synedra acus Kütz.	X		
Synedra incisa Boyer		X	
Synedra ulna (Nitz.) Ehr.			X
Achnanthaceae			
Achnanthes affinis Grun.			X
Achnanthes clevei Grun.	X		
Achnanthes flexella (Kütz.) Brun.	X		
Achnanthes lanceolata (Breb.) Grun.	X		
Achnanthes lanceolata var. *omissa* Reim.	X		
Achnanthes linearis (W. Sm.) Grun.		X	
Achnanthes microcephala (Kütz.) Grun.			X
Achnanthes minutissima Kütz.			X
Cocconeis pediculus Ehr.			X
Cocconeis placentula var. *euglypta* (Ehr.) Cl.			X
Rhoicosphenia curvata (Kütz.) Grun. *ex* Rabh.			X
Gomphonemaceae			
Gomphonema affine Kütz.	X		
Gomphonema olivaceum (Lyngb.) Kütz.			X
Gomphonema parvulum Kütz.			X
Gomphonema subclavatum (Grun.) Grun.			X
Cymbellaceae			
Amphora coffeiformis	X		
Amphora ovalis (Ehr.) Kütz.	X		
Amphora ovalis var. *pediculus* (Kütz.) V.H. *ex* Det.		X	
Amphora perpusilla (Grun.) Grun.			X
Cymbella affinis Kütz.			X
Cymbella amphicephala Naeg. *ex* Kütz.			X
Cymbella microcephala Grun.	X		
Cymbella microcephala var. *crassa* Reim.			X
Cymbella minuta Hilse *ex* Rabh.			X
Cymbella prostrata (Berk.) Cl.			X
Cymbella pusilla Grun.	X		
Cymbella sinuata Greg.			X
Cymbella tumidula Grun. *ex* A.S.	X		
Naviculaceae			
Anomoeoneis vitrea (Grun.) Ross	X		
Caloneis bacillum (Grun.) Cl.	X		

TABLE 1—Continued.

Taxon	T	D	RS
Caloneis hyalina Hust.	X		
Diploneis smithii Thwaites *ex* W. Sm.	X		
Mastogloia smithii var. *lacustris* Grun.	X		
Navicula arvensis Hust.	X		
Navicula confervacea (Kütz.) Grun.		X	
Navicula cryptocephala Kütz.	X		
Navicula cryptocephala f. *minuta* Boye-P.			X
Navicula cryptocephala var. *veneta* (Kütz.) Rabh.			X
Navicula cuspidata var. *minor* Meist			X
Navicula decussis Ostr.	X		
Navicula exigua Greg. *ex* Greg.	X		
Navicula miniscula Grun.			X
Navicula mutica Kütz.		X	
Navicula pseudoreinhardtii Patr.			X
Navicula pupula var. *rectangularis* (Greg.) Grun.			X
Navicula radiosa Kütz.			X
Navicula radiosa var. *tenella* (Breb. *ex* Kütz.) Grun.			X
Navicula tripunctata (Mull.) Bory			X
Navicula zanoi Hust.		X	
Epithemiaceae			
Denticula elegans Kütz.			X
Rhopalodia gibberula var. *vanheurckii* O. Mull.		X	
Nitzschiaceae			
Nitzschia amphibia Grun.			X
Nitzschia bicrena Hohn et Hellerm.	X		
Nitzschia capitellata Hust.			X
Nitzschia denticula Grun.			X
Nitzschia dissipata (Kütz.) Grun.			X
Nitzschia fonticola Grun.	X		
Nitzschia frustulum (Kütz.) Grun.			X
Nitzschia frustulum var. *perpusilla* (Rabh.) Grun.			X
Nitzschia gracilis Hantzs.		X	
Nitzschia hungarica Grun.	X		
Nitzschia kutzingiana Hilse			X
Nitzschia linearis W. Sm.		X	
Nitzschia palea (Kütz.) W. Sm.			X
Nitzschia romana Grun.	X		

7.2; *d.f.* = 5,18; $P < 0.01$). This pattern was most dramatic when comparing tailwater sites with sites below the Paria River (i.e., first major source of suspended sediment below Glen Canyon Dam). Mean diatom community density in depth zone I (0.0 to 0.3 m) averaged 315 × 10^4 cells/cm^2 (*SE* = 93) at sites between Glen Canyon Dam and Lees Ferry and only 75 × 10^4 cells/cm^2 (*SE* = 3.2) at the four sites below the Paria River.

Diatom Distribution with Water Depth—Another trend observed on three sampling dates (October 1984, October 1985, and December 1985) at Lees Ferry was a significant decrease (F = 18.2; *d.f.* = 2,21; $P < 0.01$) in mean diatom community density with increased water depth. During October 1984, the mean total community density declined from 302 × 10^4 cells/cm^2 in the shallow zone I to 157.9 × 10^4 cells/cm^2 in depth zone II, and 46 × 10^4 cells/cm^2 in the deepest water zone (Fig. 2). During October 1985, diatom community densities decreased from 800 × 10^4 cells/cm^2 in zone I to 269 × 10^4 cells/cm^2 in zone II, and 166 × 10^4 cells/cm^2 in zone III. A similar pattern with respect to water depth oc-

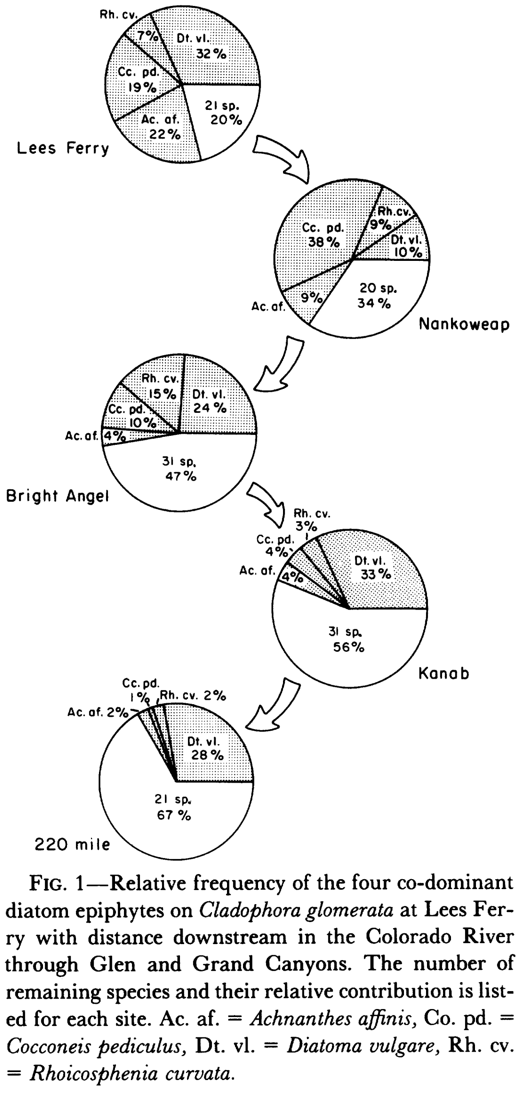

FIG. 1—Relative frequency of the four co-dominant diatom epiphytes on *Cladophora glomerata* at Lees Ferry with distance downstream in the Colorado River through Glen and Grand Canyons. The number of remaining species and their relative contribution is listed for each site. Ac. af. = *Achnanthes affinis*, Co. pd. = *Cocconeis pediculus*, Dt. vl. = *Diatoma vulgare*, Rh. cv. = *Rhoicosphenia curvata*.

curred during December 1985 with 103 × 10^4 cells/cm^2 in zone I, 75 × 10^4 cells/cm^2 in zone II, and 16 × 10^4 cells/cm^2 in zone III.

A decrease in mean diatom community density with increasing depth was also apparent at Nankoweap during October 1984. However, the greatest decrease in diatom density at this downstream site occurred between the two shallowest depth zones (Fig. 2). Mean diatom density decreased from 283 × 10^4 cells/cm^2 in the shallow water zone to 42.8 × 10^4 and 39 × 10^4 cells/cm^2 in zones II and III, respectively (Fig. 2). *Cocconeis pediculus* was the dominant epiphytic diatom in all depth zones at Nankoweap. This closely adnate diatom species contributed 78% of the mean diatom community density in zone I, 27% of the mean diatom community density in zone II, and 44% in the deepest water (zone III).

Diatom Composition Following Steady and Fluctuating Flows—The samples from October 1985 reflected 4 months of relatively high, stable flows. During the 4 months prior to October 1985, flows fluctuated <227 m^3/s (8,000 feet^3/s) over 24 h, and water levels did not change dramatically (W. C. Leibfried and D. W. Blinn, in litt.). *Diatoma vulgare, C. pediculus,* and *R. curvata* composed nearly 77% of the epiphytic diatoms in all depth zones during October 1985 following relatively high and stable flows (Fig. 3).

The diatom community in December 1985 reflected highly variable flows that fluctuated as much as 510 m^3/s (18,000 feet^3/s) in <2 h. These flow regimes occurred from mid-October through December 1985 and frequently exposed all of depth zone I and occasionally the intermediate depth zone (W. C. Leibfried and D. W. Blinn in litt.). The deepest zone was not exposed during any of these fluctuating flow regimes between mid-October through December.

Following the 3-month period of fluctuating flows, there was a marked decrease in three of the four dominant epiphytic diatom species at Lees Ferry. *Diatoma vulgare, R. curvata,* and *C. pediculus* made up <24% of the diatom composition in the two shallow depths (Fig. 3). The deepest and unexposed zone (1.2 to 2.5 m) showed high proportions (75%) of *D. vulgare, C. pediculus,* and *R. curvata* during December 1985, i.e., similar to the values found for all depths during the collections in October 1985 under relatively steady flows (Fig. 3). *Achnanthes affinis, Gomphonema affine,* and *G. olivaceum* made the greatest contribution to the diatom community in the two shallow zones during December 1985 following fluctuated flows.

When epiphytic diatoms were examined during January 1987 at Lees Ferry (winter period following steady flows), *D. vulgare, C. pediculus,* and *R. curvata* made up an average of 76.9% of the epiphytic diatoms, while *A. affinis* composed 23.1% of the diatom community (C. Pinney, pers. comm.).

DISCUSSION—The increased suspended sediment load at downstream sites in the Grand Canyon probably caused the reduction in mean community density of diatom epiphytes on *C.*

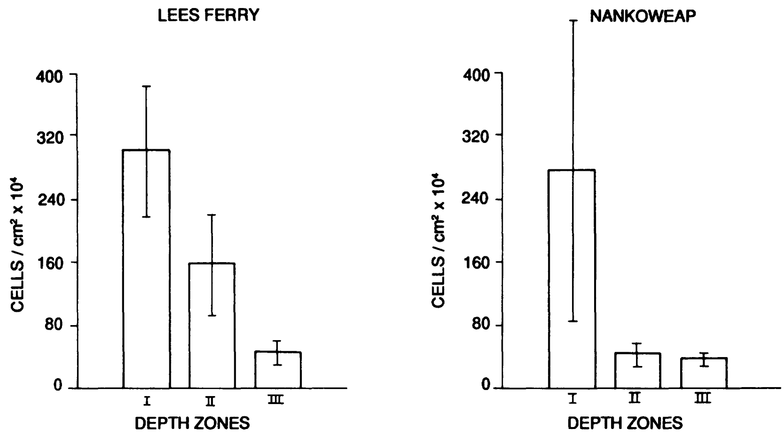

FIG. 2—Average standing crop of epiphytic diatoms on *Cladophora glomerata* in depth zones I to III at Lees Ferry and Nankoweap during October 1984. Vertical lines represent ±1 *SE*. Depth zone I extended from the waters edge to 0.3 m deep, zone II ranged from 0.3 to 1.2 m, and depth zone III was 1.2 to 2.5 m deep.

glomerata. Two major sediment sources in the Colorado River system are the Paria River (RK 1.2) just downstream from Lees Ferry and the Little Colorado River at RK 99 (Cole and Kubly, 1976; (United States Geological Survey, 1984, 1985, 1986). Suspended sediment values below these two tributaries at Bright Angel Creek (888 mg/l) were over 85-fold higher than suspended sediment at Lees Ferry (8 to 12 mg/l^2) during the July 1985 period (United States Geological Survey, 1985). Furthermore, the reduction in epiphytic diatom community density on *Cladophora* below the Paria and Little Colorado River tributaries corresponds with decreases in standing crop of *C. glomerata* (Usher and Blinn, 1990) and invertebrates (W. C. Leibfried and D. W. Blinn, in litt.) in the lower Grand Canyon. It is, therefore, possible that the growth rate and physiological state of *Cladophora* at the various sites may influence the patterns of distribution of diatoms downstream. Stevenson and Stoermer (1982) reported that only selected diatom populations colonized the active *Cladophora* thallus in Lake Huron. The interactions between epiphyton and *Cladophora* need further study.

The replacement of the three dominant taxa of diatoms at Lees Ferry (*C. pediculus, R. curvata,* and *A. affinis*) by *G. olivaceum, C. affinis,* and *N. dissipata* at the Kanab Creek and RK 354 sites (Fig. 1) is perhaps also due to the various effects of increased suspended sediment. In July 1985, when this trend was observed, Secchi disc values decreased from 5.8 m at Lees Ferry to 0.75 m at RK 322 (H. R. Maddux et al., in litt.). The effects associated with suspended sediments are many and include decreased light penetration and abrasion by the sediment. Bahls et al. (1984) characterized *N. dissipata* as tolerant of large amounts of suspended sediment and reported the other two replacement taxa as tolerant to some suspended sediment.

Nutrient enrichment could also favor the replacement of *C. pediculus, R. curvata,* and *A. affinis*. H. R. Maddux et al. (in litt.) reported an increase in total phosphorus (290 ug/l) near the tributary of Kanab Creek and near RK 354. Lowe (1974) considers *G. olivaceum* and *N. dissipata,* two of the replacement taxa, as indicators of eutrophic conditions.

Water temperature is probably not an important variable in modifying the epiphyton community in downstream sites because it showed only minor increases throughout the Grand Canyon system. Average water temperature ranged from 9.7°C at Lees Ferry (RK 0.0) to 11.5°C near Diamond Creek (RK 363) during the period of study (H. R. Maddux et al., in litt.). Furthermore, Blinn et al. (1989*a*) reported marked changes in the epiphyton community at Lees Ferry only after water temperature in a laboratory stream tank was >18°C.

Reduction in total diatom community density with increasing depth was gradual at Lees Ferry. The decline in diatom community density with depth cannot be attributed to suspended sediment because there are minimal sediment inputs above

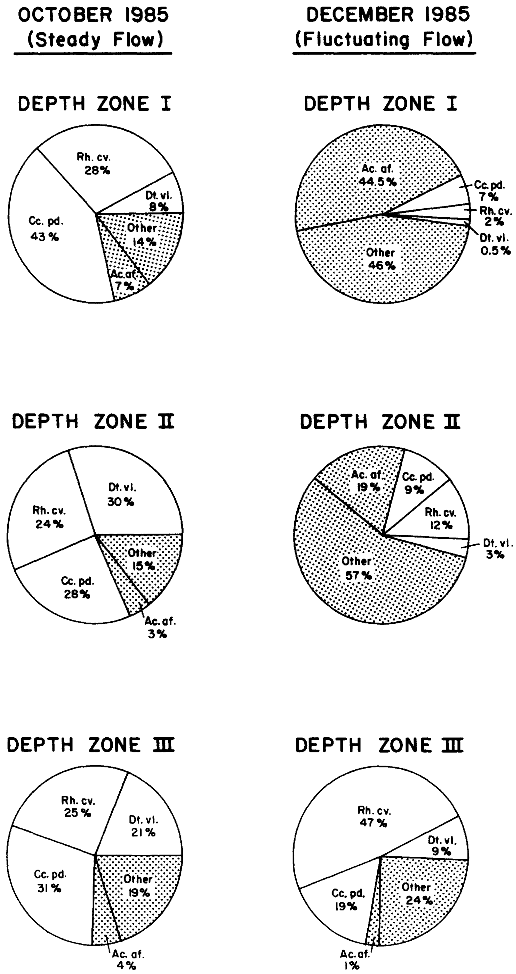

FIG. 3—Relative frequency of the four co-dominant diatom epiphytes on *Cladophora glomerata* at Lees Ferry after relatively steady flow (October 1985) and fluctuating flows (December 1985). Ac. af. = *Achnanthes affinis,* Co. pd. = *Cocconeis pediculus,* Dt. vl. = *Diatoma vulgare,* Rh. co. = *Rhoicosphenia curvata.*

Lees Ferry. Suspended sediment at Lees Ferry ranges from 5 to 12 mg/l (United States Geological Survey, 1985). Furthermore, the reduction in epiphytic diatoms at Lees Ferry cannot be attributed to reductions in *Cladophora* because *Cladophora* increased with depth at Lees Ferry (pers. obser.). The vertical zonation of epiphytic diatoms at Lees Ferry is probably a result of light attenuation with increasing depth. Duncan and Blinn (1989) recently reported on the importance of seasonal changes in light energy in determining the density and composition of diatom communities in a heavily shaded stream in north-central Arizona.

The pattern of decreased diatom community density with depth was considerably more dramatic at Nankoweap than at Lees Ferry (Fig. 2). Both of the deeper stations at Nankoweap were significantly reduced from the shallow station (0 to 0.3 m), which infers a reduction in light transmission due to heavy suspended sediment originating from the Paria River. The dominance of *C. pediculus* at all three depths at Nankoweap is probably due to its tolerance to low light energy. Robinson and Rushforth (1987) also found *Cocconeis pediculus* to be a shade tolerate species in an Idaho stream. The adnate mode of attachment of *C. pediculus* may also reduce scouring by suspended sediment.

The change in the epiphytic diatom community at Lees Ferry following fluctuating flows is likely attributable to the disturbance of flow fluctuation rather than seasonality. Changes in water temperature at the Lees Ferry site are minimal throughout the year (United States Geological Survey, 1986), and canopy cover is negligible. The duration and extent of shading by cliffs and the incipient light angle are the only naturally occurring seasonal variables apparent in the reach of the Colorado River oriented northeast to southwest. Furthermore, epiphyton communities at Lees Ferry during the winter (January 1987) were similar to epiphyton communities during the period of steady flow in the fall (October 1985).

Diatom assemblages in the deepest depth zone in December 1985 (following fluctuating flows) were similar to the diatom assemblages following near steady flows (October 1985) at Lees Ferry (Fig. 3). The deepest zone was the least impacted during fluctuating flows while the highest and intermediate zones were frequently exposed. The dominance of *A. affinis* in zones I and II following fluctuating flows suggests its tolerance to disturbance at the upper depths. Robinson and Rushforth (1987) found diatoms with horizontal growth such as *Achnanthes* predominate on highly disturbed substrates. They suggest that frequent disturbance can maintain the diatom community in an early successional stage made up of adnate, horizontal forms. Duncan and Blinn (1989) also reported that *Achnanthes minutissima* is a primary colonizer following disturbance resulting from spates in Oak Creek, Arizona.

The replacement of larger upright diatoms with smaller or adnate diatoms due to regulated flow and suspended sediment may be important in food transfer to higher trophic levels within the Colorado River ecosystem. The upright diatoms are commonly more easily grazed (Colletti et al., 1987; Steinman et al., 1987; Blinn et al., 1989*b*), and, therefore, are important food items for macroinvertebrates and fish populations.

In summary, our study demonstrates a decrease in total diatom cell numbers and a change in diatom community structure associated with *C. glomerata* downstream of the Paria and Little Colorado Rivers, which are major sources of suspended sediment. We also noted a decrease in diatom cell density with increased depth, with a pronounced decrease in cell density in reaches with elevated suspended sediment. Disturbance by fluctuating flow in the tailwaters of Glen Canyon Dam has the potential of reducing loosely attached upright diatom forms and dislodging *Cladophora* substrata through "stranding" (Usher and Blinn, 1990). Reductions in diatom cell density and changes in diatom community structure may have important ramifications on the diet of macroinvertebrate and fish populations in the Colorado River.

This study was supported in part by funds from the Arizona Game and Fish Department subcontracted from the Bureau of Reclamation (Contribution #GCES 05/88 of the Glen Canyon Environmental Studies). We especially thank D. Wegner and R. Hardwick for their critical review of an earlier version of the manuscript. The staff of the Glen Canyon Environmental Study, Flagstaff Office were helpful in obtaining flow data. We also thank B. Leibfried for assistance with the diatom collections and the Secchi disc readings during July 1985.

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