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

by

Chris A. Pinney

A Thesis
Submitted in Partial Fulfillment
of the Requirements for the Degree of
Master of Science in Biology

Northern Arizona University
December 1991

Approved:
Dean W. Blinn
RR Johnson
J. Norman Grim

ABSTRACT

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

CHRIS A. PINNEY

The biomass of the filamentous green alga Cladophora glomerata and the species composition of the associated epiphytic diatom community were analyzed over a 12 month period in the tailwaters of Glen Canyon Dam, Arizona to determine their response to regulated flow. C. glomerata biomass was significantly higher during periods of steady flow compared to periods of fluctuating flow. Of the 94 diatom species identified as epiphytic to C. glomerata at Lees Ferry, four co-dominant species comprised 78.6 to 95.2% of the species composition from September 1985 through August 1986. Diatoma vulgare and Cocconeis pediculus were the two co-dominant species most affected by decreases in the host Cladophora biomass due to desiccation from exposure. Fluctuating flows had less effect on the diatom Rhoicosphenia curvata standing crop. Achnanthes affinis-minutissima standing crop responded stochastically regardless of flow regime. These findings may have significant management implications for the Lees Ferry rainbow trout fishery.

The freshwater amphipod, *Gammarus lacustris* proved to be an opportunistic forager feeding on the four co-dominant epiphytic species associated with *Cladophora*. These diatoms numerically comprised >93% of the amphipod's diet at Lees Ferry. Ivlev's (1961) Electivity Index (EI) suggested that *Gammarus* utilize diatoms based upon the epiphyte's physiognomy. The more upright, loosely attached chain-forming *D. vulgare* and the mucilage stalk-forming *Rhoicosphenia curvata* were more readily ingested. The tightly adnate *C. pediculus* was difficult for the amphipod to manipulate and ingest. *Gammarus* was mobile during changing flow regimes and continued to utilize the four co-dominant epiphytic species in similar patterns. In all cases, *D. vulgare* dominated the amount ingested probably due to its greater cell volume. These data suggested that *Gammarus* commonly grazed selectively on the epiphytic diatoms without ingesting the host substrate, *Cladophora* cells. The relatively small frustule dimensions and volume of *A. affinis-minutissima* may increase its susceptibility to invertebrate grazing.

ACKNOWLEDGEMENTS

Most importantly, this thesis is dedicated to Judy, Rebekah, and Emily Rose. My family sacrificed the most in recreational time and household care while I grumbled over a computer terminal. Their support never foundered throughout my entire graduate career, and for this dedication I am the most grateful.

May this study serve as a memorial to M.C. (Marble Canyon), the family's longtime canine companion whose love for watery environments will never be forgotten. Rest in peace, girl!

Special thanks to my committee members, Drs. Dean Blinn, Norman Grim, and C. Dan Johnson for their support, advice, and patience through the duration of this study. I am indebted to Dean for his continual inspiration and persistance throughout my graduate career, and to Norm for contributing time from his sabbatical.

Partial funding for this project was provided by the Arizona Game and Fish Department as part of the Glen Canyon Environmental Studies, Phase I and a research assistantship from Northern Arizona University. Thanks to Dave Wegner of GCES for technical review of the first draft and to the diversity of river people who make working the Colorado so gratifying.

I am grateful to Howie Usher and Bill Leibfried for valuable assistance during those incredibly enduring hours spent either in the field or the laboratory.

Thanks to Heather Green for allowing me the freedom with my schedule at the Mormon Lake Ranger District to complete my analysis and writing of this thesis.

Lastly, my most sincere appreciation to Dr. Stanley Wilkes, who started me on this course of aquatic zoological inquiry. Thanks for the many trips to Cholla Bay where the importance of field investigation was nutured. Thanks for those grueling, under appreciated invertebrate and ichthyology courses. And from some of us from the Class of '82, thanks for the enthusiasm and contacts that enabled us to initiate our professional careers with the Japanese fishermen working off the coast of Alaska.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The free-flowing nature of rivers in the United States has been modified over the past century through the construction of dams (Benke 1990). Since the 19th century dams have been constructed for flood control, water storage, and hydroelectric power generation, in addition to creating a wide diversity of recreational opportunities in fishing and boating (Smith 1971). Sportfishermen have taken advantage of the formation of both lentic warm-water and lotic cold-water fisheries as a result of dam construction (Ward and Stanford 1979). Native fish species adapted to natural pulse stabilization patterns of pre-dam lotic ecosystems usually suffer from the effects of modified flows on the dynamics of their food chain and reproductive habitat (Maddux et al. 1987). Modified flows also affect the production of the food web components important to introduced game fish (Usher et al. 1986, Leibfried and Blinn 1986).

The Glen Canyon Dam on the Colorado River is one of these multipurpose structures. Upon completion in 1963, the bypass tunnels were closed to store water for hydroelectric power generation, incidental to delivery for consumptive use downstream and flood control. The regulation of flow of the Colorado River was a primary purpose and result. The constantly cold hypolimnetic releases into the Colorado River were suitable for the production of rainbow trout, Oncorhynchus mykiss, in the tailwaters of Glen Canyon Dam (Arizona Game and Fish Department 1968).

The operation of Glen Canyon Dam has dramatically changed many of the physical characteristics of the Colorado River in response to allocated water delivery and seasonal peaking power demands within the Colorado River Storage Project system. These flows changed the aquatic ecosystem downstream (Glen Canyon Environmental Studies 1989).

Pre-dam flows in the Colorado River were characterized by seasonal changes in magnitude, turbidity, and temperature (GCES 1989). Low steady flows occurred during the fall and winter. Seasonal high water transported sediments primarily associated with the summer monsoons and spring runoff. Water temperature ranged from near $0^{\circ}C$ in the winter to $27^{\circ}C$ in the summer (GCES 1989).

Post-dam flows in the Colorado River fluctuated in frequency and magnitude in response to seasonal consumer demand. Reduced flows dominated during the filling period (1963-1980) of Lake Powell, exceeding 16,000 cubic feet per second (cfs) 29% of the time (GCES 1989). Daily fluctuations exceeding 10,000 cfs in magnitude occurred 78% of the time during this reservoir filling period. In addition, the annual spring flood spate characteristic to the seasonal dynamics of the pre-dam river was virtually eliminated until the 1983 high water year. Flood releases were estimated to average once every four years under full reservoir conditions. This regulation of discharge allowed the development of an "intertidal" zone along the Colorado River. The pre-dam spring scour zone was invaded by riparian and herbaceous vegetation during this period. Since 1983, high flows exceeding 16,000 cfs occurred 83% of the time. Periods of stable flow increased the habitat for algae and invertebrates available to foraging trout. Flood releases greater than 45,000 cfs lasting longer than a month became more common during the summer. Daily fluctuations greater than 10,000 cfs in magnitude occurred 31% of the time.

The majority of the sediment historically transported by the Colorado River is now deposited in Lake Powell, drastically reducing the turbidity in the tailwaters of Glen Canyon Dam. The hypolimnial release from Lake Powell has also elevated nutrient levels and decreased water temperature to a constant $10 \pm 2^{\circ}C$ irrespective of the season (GCES 1989). One result of these physio-chemical changes in the tailwater of Glen Canyon Dam has been the prolific growth of the filamentous green alga, *Cladophora glomerata* Kutz.

Whitton (1970) provided the first review on the biology of *Cladophora*. Additional studies have addressed the ecology of *Cladophora* in marine systems or the Great Lakes (Storr and Sweeney 1971, Adams and Stone 1973, Ronnberg and Lax 1980, Graham et al. 1982, Lowe et al. 1982, Stevenson and Stoermer 1982). The effect of desiccation on *Cladophora* in lotic systems, especially in response to regulated flows in the tailwater of a dam, was relatively unstudied until Usher et al.

(1986). They discovered that exposure periods >12h reduced the biomass of Cladophora by 40%.

The mucilage free, profusely branched filaments of Cladophora provide an excellent substrate for the attachment of epiphytic diatoms. Four co-dominant diatom taxa grow epiphytically on C. glomerata in the tailwater of Glen Canyon Dam (Usher et. al 1986). These include Diatoma vulgare Bory, Rhoicosphenia curvata (Kutz.), Cocconeis pediculus Ehr., and the Achnanthes affinis-minutissima complex. Previous studies hypothesized that this algal assemblage is an important food source for rainbow trout in the Colorado River and may be responsible for the "Blue Ribbon" status of the Lees Ferry fishery (Bancroft and Sylvester 1978, Carothers and Minckley 1981, Pollack 1984, Leibfried and Blinn 1986, Leibfried 1988). Trout digestive systems are characteristically not adapted to herbivory (Willers 1981), however Leibfried (1988) proposed that diatoms on C. glomerata provide rainbow trout with a nutrient supplement allowing the fish to conserve body protein for growth. Diatoms contain large amounts of soluble lipids making them a good energy source (LaLonde 1979, Watanabe et al. 1979, Hilton and Slinger 1981, Pollack 1984). Usher et al. (1986) determined that desiccation from winter and summer exposure periods negatively influenced diatom standing crop. However, they did not determine the effects of seasonality on diatom standing crop and species composition.

The mats and tufts of Cladophora glomerata were thought to provide a refugium and a food source for the freshwater amphipod Gammarus lacustris Sar (Haury 1981). Management agencies proposed that the high production of this crustacean in the tailwaters of Glen Canyon Dam was responsible for increasing the growth rates of rainbow trout (Bancroft and Sylvester 1978). Although the post-dam physico-chemical changes have created near optimal conditions for trout production, the near constant water temperature and modified flow regimes proved detrimental to pre-dam river invertebrate biomass and diversity (Stone 1964, 1972). Chironomids and oligochaetes were the only native invertebrates not adversely affected by the operation of the dam (Carothers and Minckley 1981, Persons et al. 1985). The Arizona Game and Fish Department introduced _G. lacustris_ and snails (_Physa_) to the tailwaters of Glen Canyon Dam in 1967 and 1968 to increase the production of rainbow trout (AGFD 1968). _G. lacustris_ readily adapted to the post-dam physico-chemical modifications.

Since the introduction of amphipods to Lees Ferry it was widely accepted among the management agencies that the most important food item in the diet of the tailwater rainbow trout fishery was _G. lacustris_. _C. glomerata_ was thought to provide an important refugium and relatively stable food source for maintaining the production of _Gammarus_. Bancroft and Sylvester (1978) showed that _G. lacustris_ comprised 44% of the diet of rainbow trout stomach contents and _C. glomerata_ accounted for 34% of the contents. The occurrence of _C. glomerata_ found in the stomachs of rainbow trout during creel surveys was thought to be incidental to the taking of _G. lacustris_. Carothers and Minckley (1981) were the first to report that _C. glomerata_ was ingested by rainbow trout in a 2:1 proportion over _G. lacustris_.

Subsequent studies (Leibfried 1988) identified a 30:1 Cladophora-Gammarus ratio. Leibfried and Blinn (1986) proposed that fluctuating flow fragmented C. glomerata from its attachment and increased Cladophora drift. Rainbow trout have apparently capitalized on the increased amount of algal drift available for food requiring reduced energy expenditure in searching for their nutrition.

It is evident that both the C. glomerata-epiphyte assemblage and G. lacustris are important food items of rainbow trout in the tailwaters of Glen Canyon Dam. If regulated flow regimes decrease the biomass of C. glomerata, as indicated by Usher and Blinn (1990), then this in turn would decrease the standing crop of the associated epiphyte assemblage and G. lacustris, both important to the production of rainbow trout. No previous research evaluated this relationship on an annual basis where the effects of seasonal dynamics could be separated from the effects of modified flow.

In addition, no previous research addressed the diets of freshwater gammarid amphipods in regulated rivers to support the hypothesis that nutrient-rich diatoms are important to G. lacustris. Species related to G. lacustris have been utilized for laboratory feeding experiments to examine the role of allochthonous leaf material and associated bacteria to stream productivity (Hynes 1963, Minckley 1963, Minshall 1967, Nilsson 1974, Barlocher and Kendrick 1973a, b, 1976, Monk 1977, Anderson and Sedell 1979, Marchant 1981, Marchant and Hynes 1981, Willoughby and Earnshaw 1982, Fuller et al. 1986). Gammarus was used because of its reputed role as a facultative shredder. Data were usually gathered on the rate of loss of a certain vegetative species and not the examination of Gammarus gut content. Deksbakh and Sokolova (1965) were the first to show that G. lacustris ingested macrophytic algae. Moore (1975, 1977b) had the most complete study utilizing dissected gut analysis from field collected Gammarus. In the laboratory, he showed that G. pulex and G. lacustris differentially ingested diatoms and avoided C. glomerata, however he did not analyze for selective preference or avoidance of certain diatom taxa in comparison to availability in the field.

Therefore the objectives of this study are: 1) to quantify the effects of regulated flow on Cladophora glomerata and the associated epiphytic assemblage in the tailwaters of Glen Canyon Dam, and 2) to quantify the utilization of the Cladophora glomerata-epiphyte assemblage by the detrital feeder Gammarus lacustris.

CHAPTER 2

METHODS

Lees Ferry is located 22.5 km downstream from Glen Canyon Dam on the Colorado River in the northeastern part of Arizona (111° 35" Latitude and 36°52" Longitude), at an elevation of 942 m.

Flow data were recorded in average daily cubic feet per second (cfs) from the U.S. Geological Survey gauging station at Lees Ferry (USGS 1987, unpubl. data, Flagstaff, Arizona). For the purpose of this study, fluctuating flow refers to flow that exceeded daily fluctuations of 10,000 cfs which occurred October 1985 through February 1986. Steady flow fluctuated less than 5,000 cfs daily which occurred March through June 1986 for this study.

U.S. Geological Survey (1987) flow data showed that the operation of Glen Canyon Dam during September 1985 through August 1986 resulted in periods of strongly fluctuating flow intersected by a period of steady high base flow following spring runoff (Fig. 1). During October 1985 through January 1986, daily fluctuations exceeded 10,000 cfs in magnitude within zone 2 under low base releases. Zone 1 was disproportionately exposed during this period. Fluctuations resulted in the partial rewetting of zone 1 about every 2 to 3 days on the average (USGS 1987). Zone 3 remained submerged all but 2 days when the upper 3m

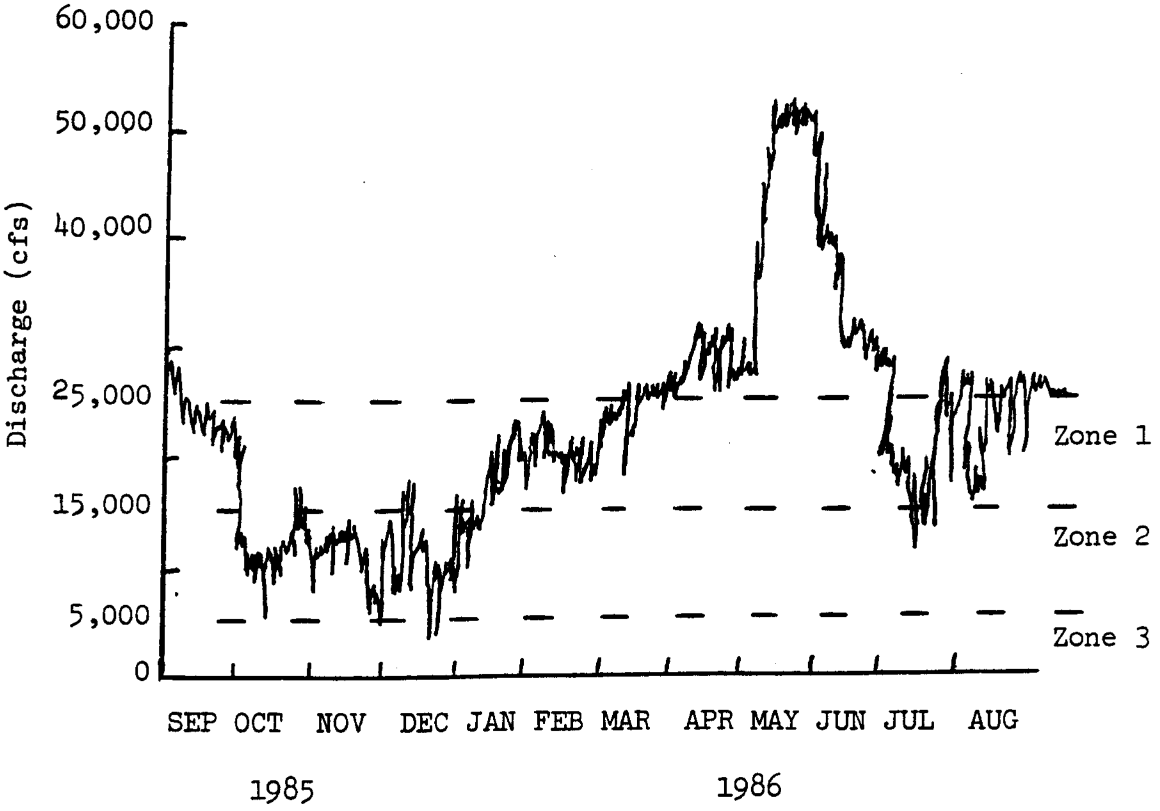

Figure 1. Representation of mean daily flow rates recorded at Lees Ferry, Arizona during September 1985 through August 1986 (USGS 1987). Note that September 1985 through February 1986 was a period of fluctuations greater than 10,000 cfs in magnitude at least once a day in depth zone 2 and zone 1 was greater than 90% exposed October through mid-January.

became exposed for less than 12h. The base flow began to rise to 20,000 cfs during late January 1986 exhibiting fluctuating flow in zone 1 until the end of February 1986. March through June 1986 was a period of steady flow with daily fluctuations less than 5,000 cfs within zones 1-3 as a result of high water releases. The base flow exceeded 25,000 cfs submerging all 3 zones until July 1986. In May 1986, the hollow jet valves of Glen Canyon Dam were opened to relieve flood potential resulting in hypolimnion releases greater than 50,000 cfs into the first week of June 1986. July and August 1986 returned to a period of fluctuating flow within zone 1. Zone 2 remained submerged under fluctuating flow in zone 1 greater than 75% of July and August 1986. Zone 3 was continually submerged during these two months.

Water temperature recorded at the U.S. Geological Survey's Lees Ferry gauging station indicated no discernable seasonal pattern throughout the study, typical of the relative constancy of hypolimnetic release dams. Figure 2 illustrates slight fluctuations in water temperature in response to changing water depth and velocity due to flow regime, varying $<4^{\circ}C$ throughout the study from a low of $8^{\circ}C$ in April 1986 to a high of $12^{\circ}C$ in December 1985.

Three depth zones were delineated at Lees Ferry for comparison sampling. The following zone boundaries were constant in relation to changing flow patterns. A debris and bank erosion line at the 25,000 cfs water mark served as the standard marker for the uppermost shoreline boundary of depth zone 1. Zone 1 extended in depth from the 25,000 cfs

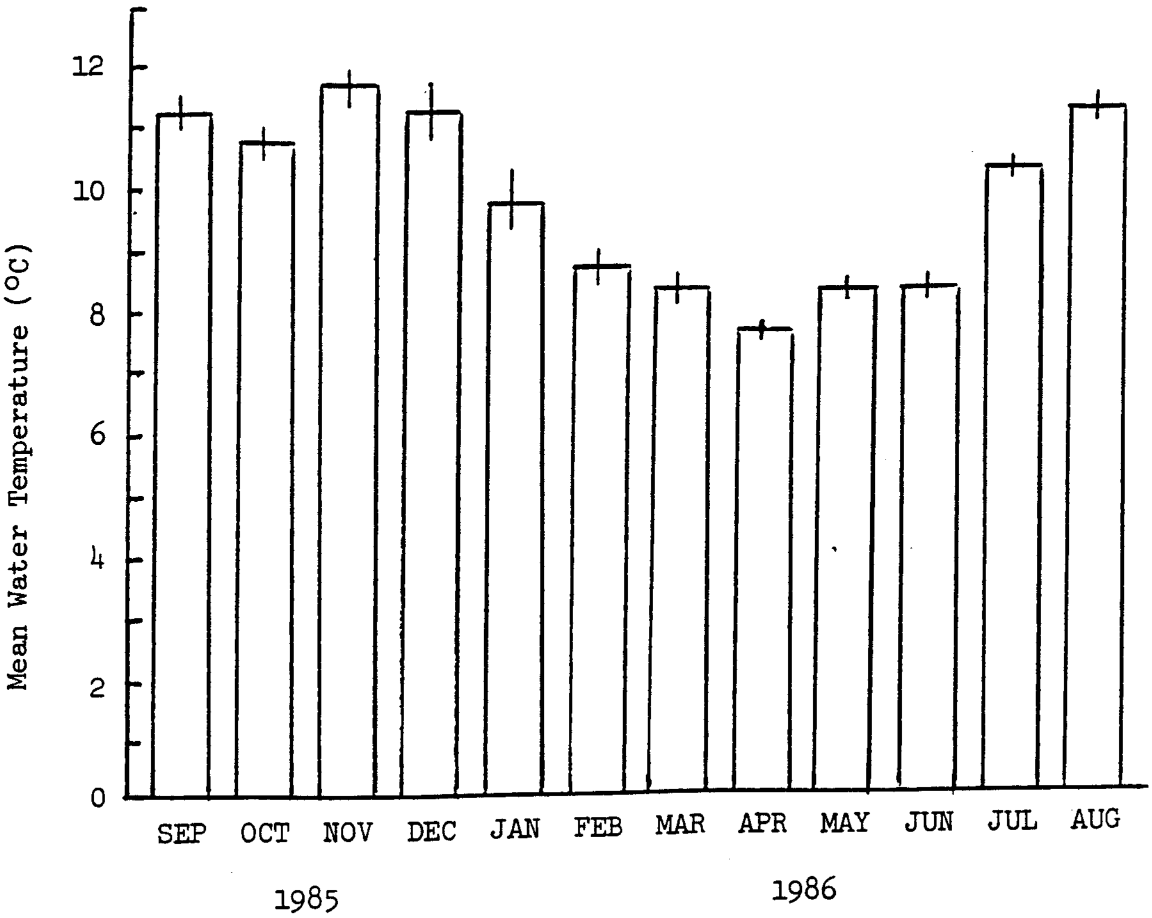

Figure 2. Mean daily water temperature at Lees Ferry, Arizona resulting from hypolimnetic releases of Glen Canyon Dam during September 1985 through August 1986 (USGS 1987).

to the 15,000 cfs water mark. Depth zone 2 extended from the 15,000 cfs to the 5,000 cfs water mark. Depth zone 3 extended from the 5,000 cfs to the 0 cfs water mark in the center of the channel. Zone 3 was continually submerged and served as the control zone in which to evaluate any natural seasonality patterns in *Cladophora* biomass. Theoretically little, if any, seasonality would be expected at Lees Ferry due to the relatively constant physico-chemical conditions of hypolimnetic releases from Glen Canyon Dam.

Cladophora Glomerata-Epiphyte Assemblage

Random samples consisting of individual 4cm^2 of the *Cladophora*-epiphyte assemblage were scraped from the substrate surface of 10 rocks within each depth zone at approximate monthly intervals from September 1985 through August 1986. Invertebrates were removed from the wet samples. The samples were immediately transferred to wire screen drying racks for transporting to the laboratory. They were allowed to air dry for at least 24h. In the laboratory, dried *C. glomerata* filaments were separated from silt and sand, placed in ceramic crucibles, and oven-dried for 12h at 100-105°C. Distinquishable sun-bleached filaments were separated from green filaments and analyzed separately when feasible. The dried samples were removed from the oven and weighed to the nearest 0.0001g on an analytical Mettler balance (Model #H20T) to achieve dry weights. The dry weight samples were ashed in a muffle furnace for one hour at 500°C (APHA 1975). The ash was weighed to the nearest 0.0001g on the analytical balance. The ashed weight was subtracted from the oven-dried weight to determine the ash-free dry weight for each sample (APHA 1975). Dry weights and ash-free dry weights calculated in g/cm^2 were converted to g/m^2 for ease of comparison.

One-half of the ash samples were oxidized by the 30% hydrogen peroxide-potassium dichromate method (van der Werff 1955) to remove the epiphytic diatom community from the assemblage. This provided a direct method of correlating the C. glomerata ash-free dry weight with the corresponding diatom standing crop and species composition from the same sample. The remaining one-half of the ash samples were placed in 4 dram vials and stored for backup or future enumeration. The oxidized samples were concentrated and cleaned through four repetitions of a centrifuge/decant/rinse series and brought to a constant volume of 10 ml. One-half of the cleared, homogenized, and concentrated sample was pipetted onto an 18 mm coverslip, evaporated over low heat, and the dried frustules were mounted in HYRAX media (Patrick and Reimer 1966).

Diatom species identifications were made at 1250x magnification using a Zeiss phase-constrast microscope with the aid of Patrick and Reimer (1966, 1975), Czarnecki and Blinn (1977), and Czarnecki (1978b) as primary taxonomic references. At least 500 valves were counted from each prepared slide and converted to diatom cells/cm^2 of sampled substrate area of C. glomerata . Relative cell volumes (um^3) were calculated by measuring the width, length, and height of a random sample of 50 individual cells of each of the four co-dominant diatom species (Moore 1975).

Community species diversity for the epiphytic diatoms was estimated for all samples using the Shannon and Weaver (1963) index:

$$H' = -\sum_{1}^{s} pi \log pi$$

where, s= the total number of species in a given sample, and pi= the proportion of the ith species in that respective sample. This diversity measure is appropiate for diatom studies where the total population is too large for all members to be counted (Pielou 1966). The number of taxa recorded for each sample was used for interpreting diversity (Czarnecki 1978a). A subsample of a given population was processed and the number of species present in any one given assemblage was assumed to be close to the total number of species actually present in the total community.

The difference in Cladophora biomass between the exposed depth zones 1-2 and the control depth zone 3 was determined for each month and a two-way analysis of variance (2x12 factorial design ANOVA) was conducted. The difference in epiphytic diatom species composition and standing crop between the period of fluctuating flow (159 days) when depth zone 1 was exposed and the period of stable high flow (123 days) when depth zone 1 was totally submerged was analyzed for each month. Two-way (5x12 factorial design) and one-way ANOVA tests for individual diatom species were conducted by month and flow regime. Subsequent

Mann-Whitney U and Kruskal-Wallis nonparametric tests were utilized when non-normalized distributions occurred. The Kruskal-Wallis test assigns ranks distributed as a chi-square (X^2). The probability acceptance level for the study was $p=.05$.

Sampling of Gammarus Lacustris Diet

Random samples of 20 individuals of the amphipod, *Gammarus lacustris* were collected from the Colorado River at Lees Ferry between 1200 hr and 1600 hr for March, April, August, and September 1986 and January 1987. Each of the 100 specimens were immediately preserved in Transeau's solution (Prescott 1962). In the laboratory, each amphipod's total length was measured to the nearest mm from the basal attachment of the antennae on the head to the terminal posterior of the telson. The complete digestive tract from the origin of the esophagus to the terminal posterior of the anus for each individual was removed manually. A wet mount of the entire tract for each amphipod was immediately prepared and the number of *C. glomerata* cells and other non-diatomaceous material (e.g. the red alga *Rhodochorton*, the cyanobacteria *Oscillatoria*, other cyanobacteria, and detrital fragments) were recorded. The entire sample was then brought to 10 ml of solution and oxidized in a 30% hydrogen peroxide-potassium dichromate solution (van der Werff 1955). This suspension was mounted in HYRAX for identification and enumeration of ingested diatoms following the same procedures described for the quantification of epiphyte species composition. Cell numbers of the dominant taxa *Diatoma vulgare*, *Rhoicospenia curvata*, *Cocconeis pediculus*, and *Achnanthes* affinis-minutissima were recorded. Residual diatom taxa were tallied and combined under a single group to be analyzed as pooled samples.

Ten random samples ($4cm^2$) of the C. glomerata-epiphyte assemblage were scraped from the substrate surface of rocks within the sample depth zones at Lees Ferry corresponding to the same time the random samples of G. lacustris were collected in order to determine the algal composition available to amphipod selection. The biomass of C. glomerata and the species composition of the associated epiphytes were determined by the same ash-free dry weight procedure previously described (van der Werff 1955). Again, those co-dominant diatom taxa mentioned previously were enumerated.

One-way and two-way analysis of variance (5x2 and 5x5 factorial design ANOVA) computations were supplemented with simple correlation tests to determine if G. lacustris selectively fed on specific diatom epiphytes in the tailwaters of Glen Canyon Dam. These analyses were based on the assumption that a low degree of variability in gut contents is indicative of a high degree of selectivity (Ricklefs 1979).

Ivlev's (1961) Electivity Index (EI) was applied to the digestive tract data to determine preference and/or avoidance for specific diatom species utilized by G. lacustris. The measure of electivity is,

$$\sum i = (ri-ni)(ri+ni)^{-1}$$

where ri and ni are percentages of diatoms type i in the amphipod's diet and diatoms type i in the environment, respectively. In Ivlev's

Electivity Index, values near 0 indicate a generalistic foraging pattern, while negative values approaching 1.0 suggest strong avoidance and positive values approaching 1.0 represent high selectivity.

In addition, Chesson's Alpha Index (1978) was used to compare the frequency of important diatom species within the digestive tract of each amphipod with the same diatom species epiphytic on *C. glomerata* in the environment. The measure of preference in this analysis is,

$$\sum_{i=1}^{m} ai = 1 \text{ where } rini^{-1} \left(\sum_{j=1}^{m} rjnj^{-1n}\right)^{-1},\ i = 1, \ldots, m.$$

where ri and ni are the number of diatoms type i in the amphipod's diet and environment, respectively. Alpha is expressed as a frequency of selection where the higher numerical value correlates with the greater the frequency in which *G. lacustris* selects for that diatom type.

CHAPTER 3

RESULTS

Cladophora Glomerata-Epiphyte Assemblage

The dry weight biomass of *Cladophora glomerata* in zone 1 was significantly higher (F= 20.881, df= 1,11, $p<0.01$) during the months of steady flow (588.9 g/m^2) than during the months of fluctuating flow (179.9 g/m^2). The dry weight biomass of *Cladophora* in zone 2 averaged 485.1 g/m^2 during months of steady flow to 284.6 g/m^2 during months of fluctuating flow although a one-way ANOVA showed no significant difference (F= 4.45, df= 1,9, $p>0.05$) between the pooled monthly data due to the high degree of variance (Fig. 3). *Cladophora* biomass in the continually submerged depth zone 3 showed no significant difference (F= 2.24, df= 1,8, $p>0.05$) between months of steady flow (407.3 g/m^2) and months of fluctuating flow (344.6 g/m^2).

An ANOVA conducted on mean dry weights of *Cladophora* in each depth zone during each of the 12 months showed a significant two-way interaction between zone and date of collection (F= 10.14, df= 8,16, $p<0.001$). This interaction indicated that *Cladophora* dry weight biomass varied with changing flow patterns in both fluctuating-versus-steady regimes and base flow (Fig. 4). Zone 1 dry weight biomass ranged from 450.0 g/m^2 during steady, high base flow in September

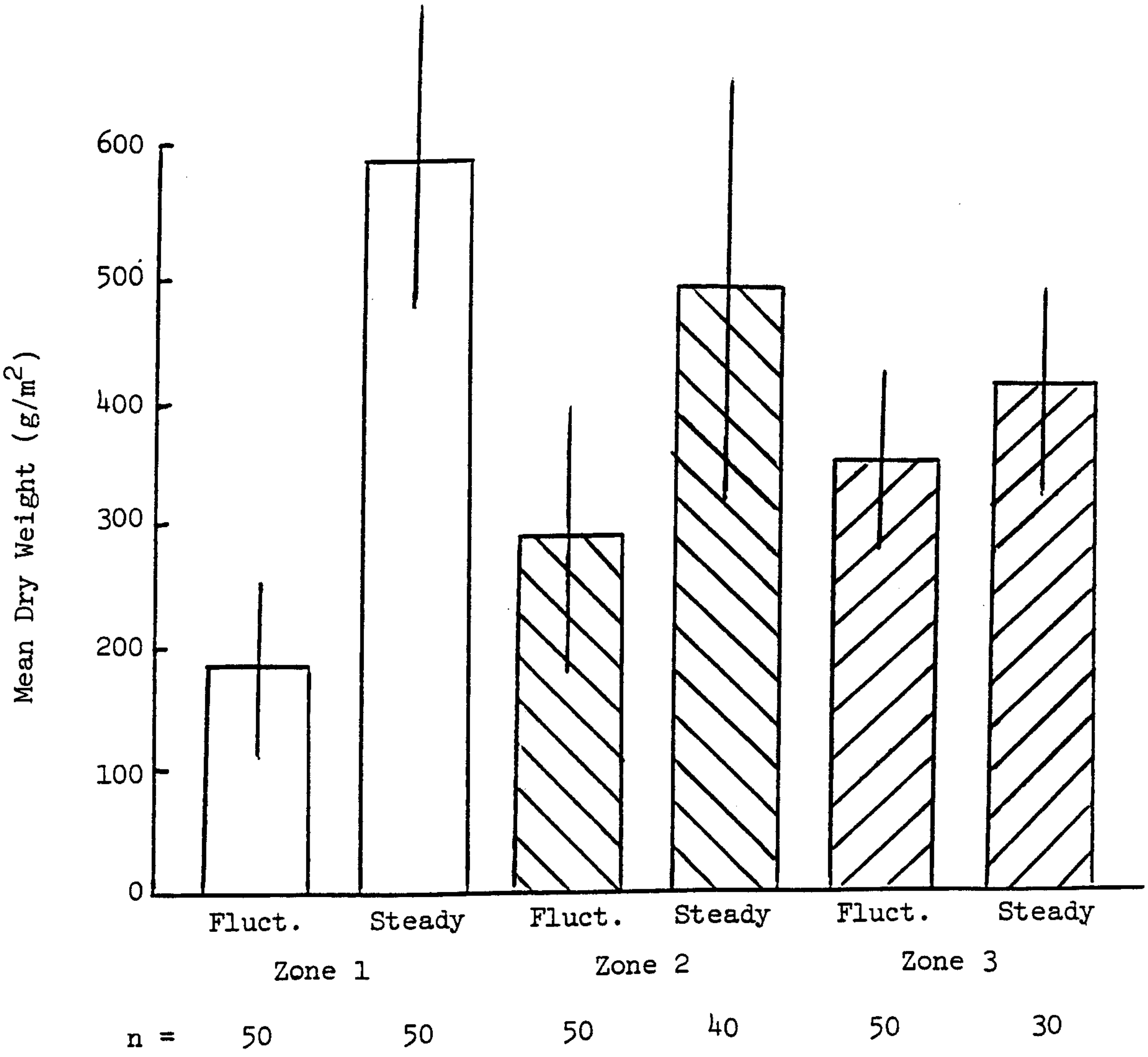

Figure 3. Mean dry weight standing crop of Cladophora glomerata (± s.e.) for depth zones 1-3 at Lees Ferry, Arizona. For periods of fluctuating-versus-steady flow, zone 1 dry weights were significantly different at $p < 0.01$. Zones 2 and 3 dry weights were not significantly different at $p > 0.05$.

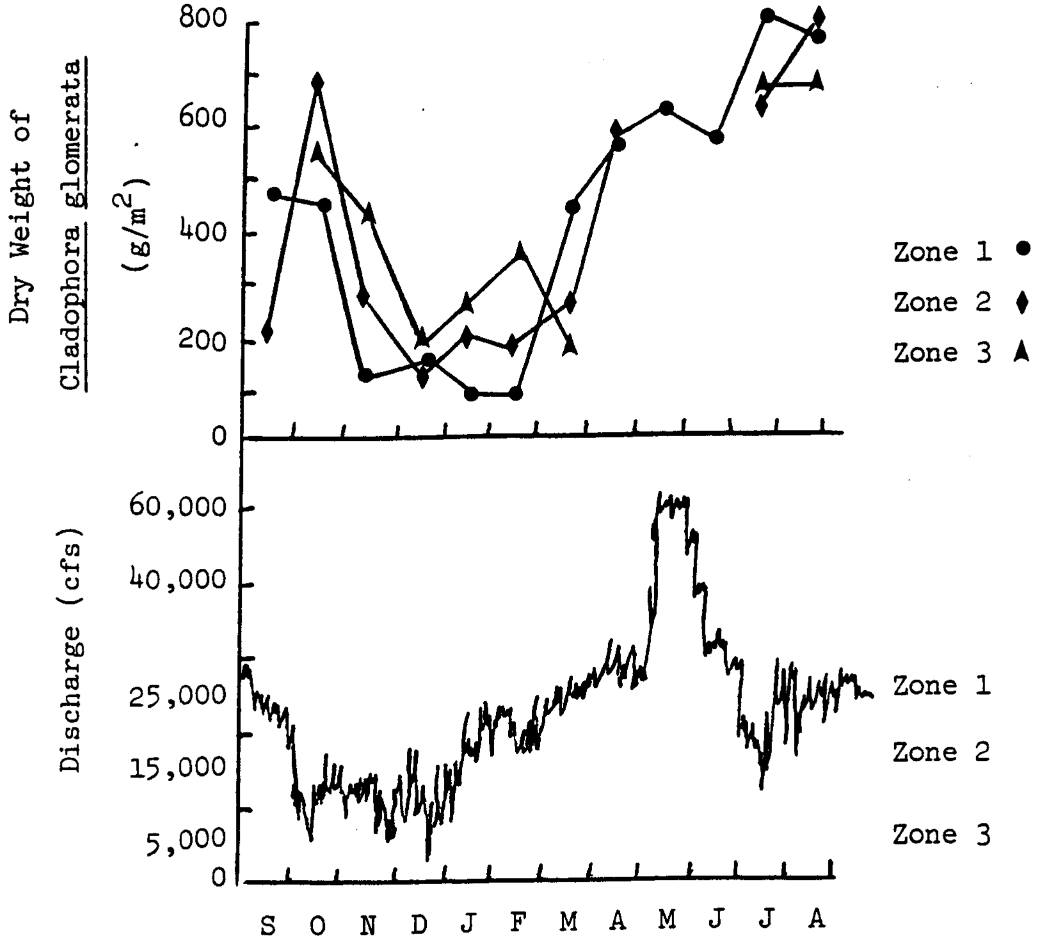

Figure 4. Mean monthly dry weight standing crop estimates (g/m^2) of *Cladophora glomerata* for depth zones 1-3 collected at Lees Ferry, Arizona during September 1985 through August 1986. For comparison purposes the graph representing mean daily flow rates is included.

1985 to a low of 84.5 g/m^2 following 3 months of relatively continuous exposure as a result of fluctuating flow. Cladophora dry weight increased dramatically to 415.0 g/m^2 in less than a month with the onset of steady flow and increased base flow in March 1986. Dry weights continued to increase under high steady flow, peaking in mid-July 1986 at 802.5 g/m^2, until strong fluctuating flow in zone 1 resulted in decreased dry weights to 747.3 g/m^2. Cladophora dry weight in zone 2 followed the same general pattern with two exceptions. First, dry weights dramatically increased to 685.3 g/m^2 with the onset of fluctuating flow below the zone 2 water mark in October 1985 from 202.5 g/m^2 under high steady flow in September 1985 (Fig. 4). During this time a portion of zone 2 remained rewetted for up to 12 h. Dry weights drastically decreased to 255.0 g/m^2 in November 1985 under continued fluctuating flow. The second exception was a dramatic increase of dry weight to 801.8 g/m^2 in August 1986 from 620.0 g/m^2 in July 1986. Although the flow was strongly fluctuating in zone 1, zone 2 remained submerged >90% of the time during July and August 1986. Even though zone 3 remained totally submerged, the effects of shallow water due to fluctuations in zone 2 appeared to influence the growth of Cladophora in zone 3 (157.5 g/m^2 in December 1985 decreased from 552.8 g/m^2 in October 1985). Dry weights in zone 3 increased to 359.8 g/m^2 in February 1986 in relation to increased base flow above the zone 2 water mark resulting in decreased light intensities reaching zone 3. Cladophora dry weight in zone 3 decreased to 152.0 g/m^2 in March 1986 perhaps reaching a tolerance limit in respect to light penetration with the onset of high steady flow in zones 1 and 2. Dry weights remained relatively constant at 662.5 to 677.5 g/m^2 during July and August 1986 when the flow was fluctuating within zone 1 and above both the zone 2 and 3 water mark.

An ANOVA conducted on mean ash-free dry weights of the Cladophora-epiphyte assemblage in each depth zone during each of the 12 months indicated a significant two-way interaction between zone and date of collection (Fig. 5; F= 17.96, df= 8,16 and F= 24.63, df= 2,16, $p<0.001$). Subsequent one-way ANOVAs indicated that ash-free dry weight values for months exhibiting steady flow were significantly greater than months exhibiting fluctuating flow (Fig. 5) for zone 1 (F= 6.56, df= 1,11, $p<0.05$) and zone 2 (F= 5.87, df= 1,9, $p<0.05$), but not for the control zone 3 (F= 4.08, df= 1,8, $p>0.05$). These interactions are shown graphically in Figure 6. The mean ash-free dry weight curves for zones 1 and 2 closely mimic the peaks and troughs of the base flow discharged through Glen Canyon Dam. The greatest decrease in ash-free dry weight occurred between mid-October and late-November, declining from 58.7 to 14.5 g/m^2 in zone 1 and 82.8 to 53.5 g/m^2 in zone 2 shortly after strongly fluctuating flow (Fig. 6). The lowest ash-free dry weight in zone 1 was 6.8 g/m^2 in February 1986 after the base flow rose above the 15,000 cfs water mark defining zone 1. The flow in zone 1 continued to fluctuate strongly while Cladophora was recovering from 3 months of exposure with a low frequency of rewetting. The ash-free dry weight in zone 1 did not increase significantly until the

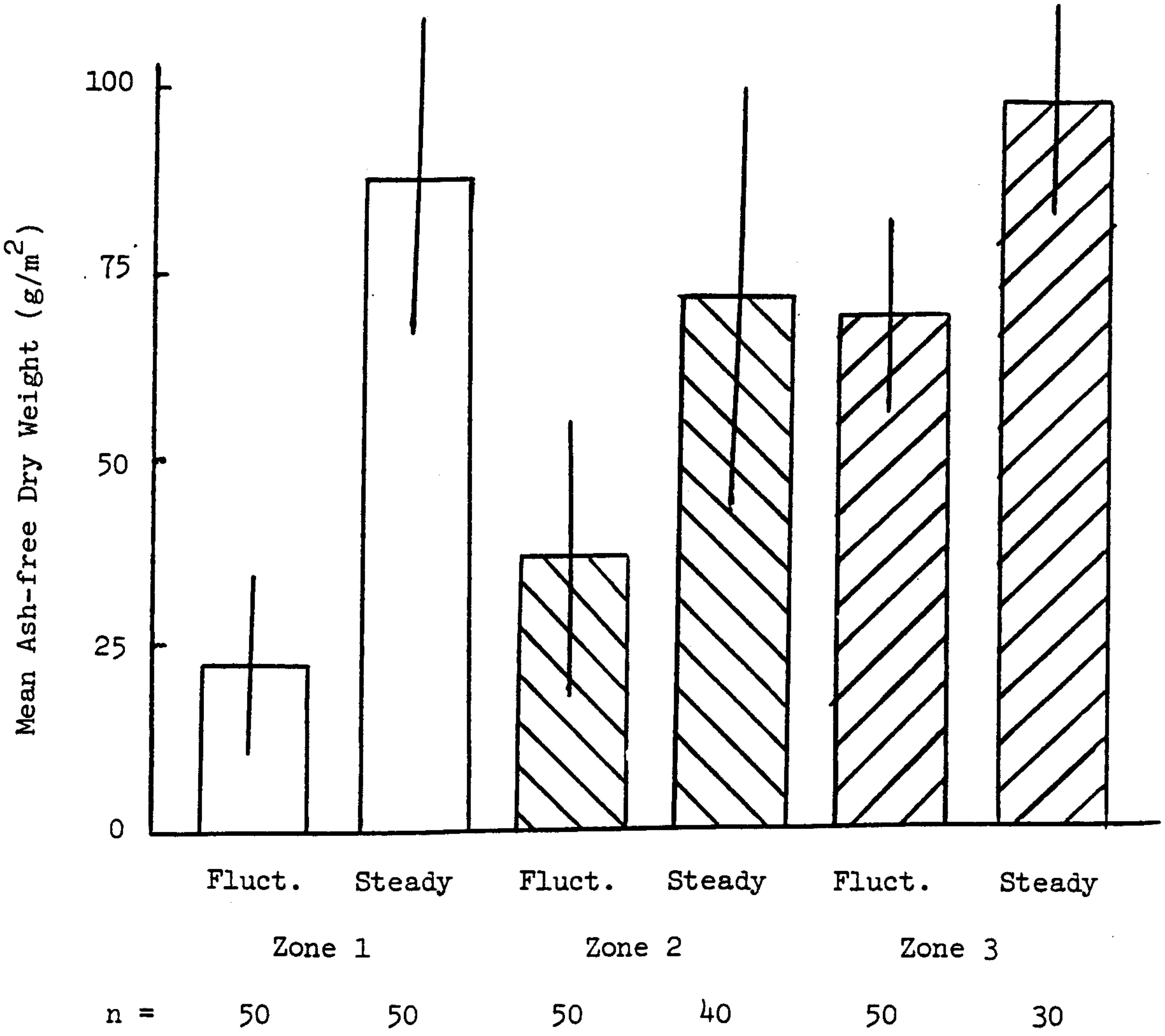

Figure 5. Mean ash-free dry weight standing crop of <u>Cladophora glomerata</u> (± s.e.) for depth zones 1-3 at Lees Ferry, Arizona comparing periods of fluctuating-versus-steady flow. Zones 1 and 2 significantly different at $p < 0.05$, zone 3 not significantly different at $p > 0.05$.

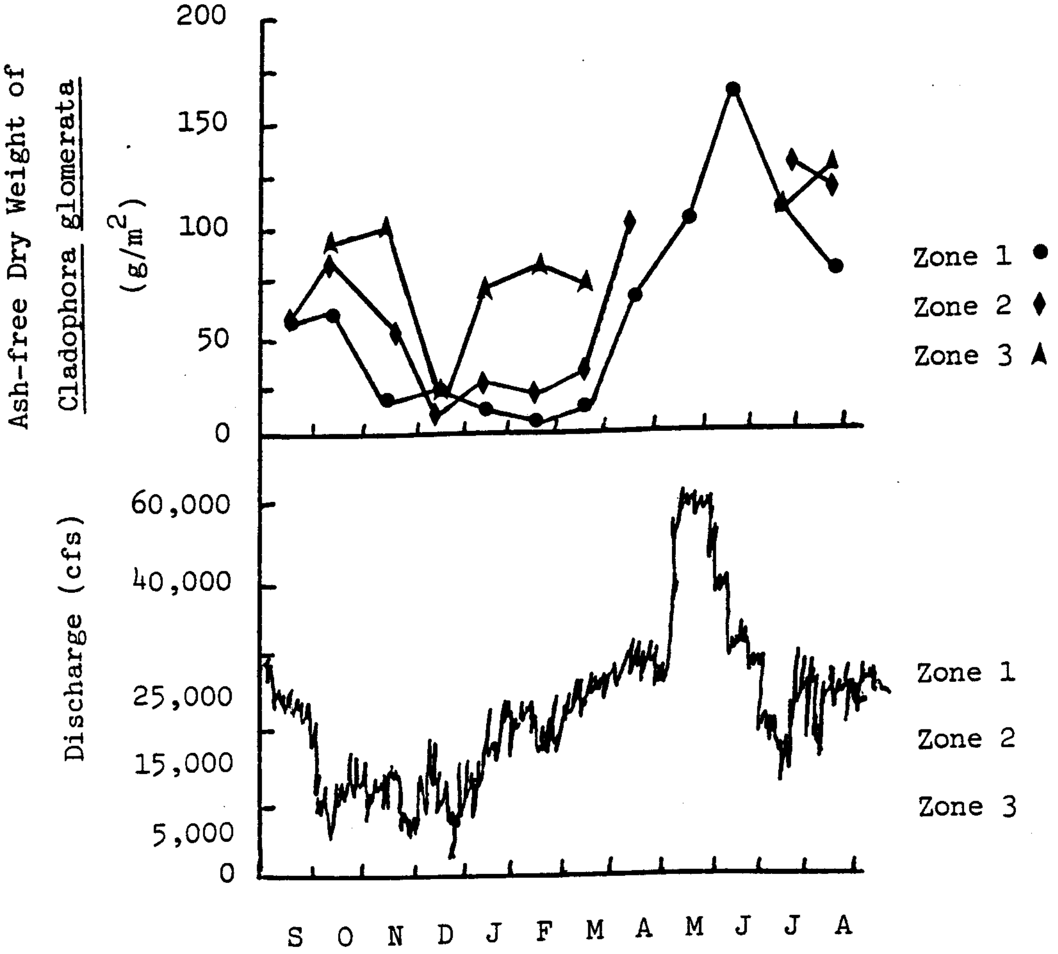

Figure 6. Mean monthly ash-free dry weight estimates (g/m^2) of Cladophora glomerata for depth zones 1-3 collected at Lees Ferry, Arizona during September 1985 through August 1986. For comparison purposes the graph representing daily flow rates is included.

onset of steady flow in late-March 1986. Ash-free dry weights peaked in June 1986 at 168.7 g/m^2 following a month of floodlike discharges greater than 50,000 cfs. The lowest ash-free dry weight in zone 2 was 8.2 g/m^2 in December 1985 during the most dramatic period of fluctuating flow under low base discharge from Glen Canyon Dam.

Ash-free dry weights were relatively stable under rising base flow until the onset of steady flow above the 15,000 cfs water mark in late-March 1986. The ash-free dry weight increased dramatically in zone 2 to 99.8 g/m^2 during late-March and April 1986. Ash-free dry weights were assumed to peak in zone 2 during June 1986 when sampling became physically limited. This assumption is based on the response of zone 1 values for the same month when flood releases greater than 50,000 cfs occurred. Resumed sampling in July 1986 resulted in decreasing ash-free dry weight from 134.1 to 117.6 g/m^2 in response to a month of strong fluctuating flow in zone 1. The Cladophora ash-free dry weights for zone 3 varied slightly when analyzed by collection date and were not significant ($F= 1.68$, $df= 1,8$, $p>0.05$). The mean ash-free dry weight for the continually submerged zone 3 remained greater than either zones 1 and 2 under fluctuating flow regimes. The curve for zone 3 closely mimic the increases and decreases of base flow discharges under fluctuating flow. The ash-free dry weight dropped dramatically from 100.1 g/m^2 in November 1985 to 18.1 g/m^2 in December 1985 in apparent response to an increased magnitude of fluctuations in zone 2 (Fig. 6). January 1986 values increased to 69.0 g/m^2 likely in response to a dramatic increase in base flow above the 15,000 cfs water mark. Ash-free dry weights leveled in February 1986, then decreased to 71.9 g/m^2 in March 1986 with high, steady flow greater than 25,000 cfs resulting from flood stage releases. A period of fluctuating flow in zone 2 returned during July 1986 resulting in an increase in ash-free dry weight from 112.0 to 132.7 g/m^2 (Fig. 6).

Ninety-three (93) different diatom species were identified in zone 1 as epiphytic to Cladophora glomerata at Lees Ferry during this study (Table 1). Four species were considered co-dominants and comprised 78.6% to 95.2% of the species composition from September 1985 through August 1986 (Table 2, Fig. 7). Pooled data for the co-dominant species annual mean (89.9%) were distributed as Diatoma vulgare 27.5%, Rhoicospenia curvata 26.5%, Cocconeis pediculus 21.3%, and Achnanthes affinis-minutissima 14.6% (Table 2).

An ANOVA conducted on mean diatom cells x $10^4/cm^2$ showed a significant two-way interaction between the individual co-dominant species during months with fluctuating-versus-steady flow (Fig. 8, F= 4.57, df= 1,8, $p<0.05$). Kruskal-Wallis non-parametric tests determined that all diatom species except A. affinis-minutissima were significantly different within species by sample date (Fig. 9, calculated value= 5.33, $p<0.05$). A. affinis-minutissima was the only co-dominant epiphyte that significantly correlated with the other three co-dominant species (49, 35, and 42%, respectively for D. vulgare, R. curvata, and C. pediculus, df= 98, $p<0.0001$).

Table 1. List of diatoms epiphytic on Cladophora glomerata collected at Lees Ferry, Arizona during September 1985 through August 1986.

Phylum Chrysophyta
  Sub-Phylum Bacillariophyceae
    Class Centrobacillariophyceae
      Order Eupodiscales
        Family Coscinodiscaceae

- *Cyclotella michiganiana* Skv.
- *Melosira granulata* (Ehr.) Ralfs
- *M. varians* Ag.

    Class Pennatibacillariophyceae
      Order Fragilaiales
        Family Fragilariaceae

- *Asterionella formosa* Hass.
- *Diatoma hiemale* var. *mesodon* (Ehr.) Grun.
- *D. vulgare* Bory
- *Fragilaria construens* var. *venter* (Ehr.) Grun.
- *F. crotonensis* Kitton
- *F. leptostauron* (Ehr.) Hust.
- *F. leptostauron* var. *dubia* (Grun.) Hust.
- *F. vaucheriae* (Kutz.) Peters
- *Synedra acus* Kutz.
- *S. rumpens* Kutz.
- *S. ulna* (Nitz.) Ehr.

      Order Achnanthales
        Family Achnanthaceae

- *Achnanthes affinis-minutissima* complex
- *A. clevei* Grun.
- *A. flexella* (Kutz.) Brun
- *A. lanceolata* (Breb.) Grun.
- *A. lanceolata* var. *dubia* Grun.
- *A. lanceolata* var. *omissa* Reim.
- *A. linearis* (W. Sm.) Grun.
- *Cocconeis pediculus* Ehr.
- *C. placentula* var. *euglypta* (Ehr.) Cl.
- *Rhoicosphenia curvata* (Kutz.) Grun. *ex* Rabh.

Table 1 continued.

Order Naviculales
Family Gomphonemaceae

Gomphonema affine Kutz.
G. olivaceum (Lyngb.) Kutz.
G. parvulum Kutz.
G. subclavatum (Grun.) Grun.
G. truncatum Ehr.
Gomphoneis herculeana (Ehr.)

Family Cymbellaceae

Amphora coffeiformis (Ag.) Kutz.
A. ovalis (Ehr.) Kutz.
A. ovalis var. pediculus (Kutz.) V.H. ex Det.
A. perpusilla (Grun.) Grun.
Cymbella affinis Kutz.
C. amphicephala Naeg. ex Kutz.
C. cistula (Ehr.) Kirchn.
C. laevis Naeg. ex Kutz.
C. microcephala Grun.
C. microcephala var. crassa Reim.
C. minuta Hilse ex Rabh.
C. prostrata (Berk.) Cl.
C. pusilla Grun.
C. sinuata Greg.
C. tumidula Grun. ex A.S.

Family Naviculaceae

Amphipleura pellucida Kutz.
Anomoeoneis vitrea (Grun.) Ross
Caloneis bacillum (Grun.) Cl.
Diploneis puella (Schum.)
Mastogloia smithii Thwaites ex W. Sm.
M. smithii var. amphicephala Grun.
M. smithii var. lacustris Grun.
Navicula arvensis Hust.
N. cari Ehr.
N. cryptocephala Kutz.
N. cryptocephala f. minuta Boye-P.
N. cryptocephala var. veneta (Kutz.) Rabh.
N. cuspidata var. major Meist.
N. decussis Ostr.
N. exigua Greg. ex Greg.
N. graciloides Mayer

Table 1 continued.

Order Naviculales
Family Naviculaceae

Navicula minima Grun.
N. miniscula Grun.
N. pseudoreinhardtii Patr.
N. pupula var. rectangularis (Greg.) Grun.
N. radiosa Kutz.
N. radiosa var. tenella (Breb. ex Kutz.) Grun.
N. secreta var. apiculata Patr.
N. subtilissima Cl.
N. tripunctata (Mull.) Bory
Nedium binode (Ehr.) Hust.
Pinnularia substomatophora Hust.
Stauroneis anceps Ehr.

Order Epithemiales
Family Epithemiaceae

Denticula elegans Kutz.
D. rainierensis Sov.
Epithemia turgida (Ehr.) Kutz.
Rhopalodia gibberula var. vanheurckii O. Mull.

Order Bacillariales
Family Nitzschiaceae

Bacillaria paradoxa Gmelin
Hantzschia amphioxys (Ehr.) Grun.
Nitzschia amphibia Grun.
N. bicrena Hohn & Heller
N. capitellata Hust.
N. denticula Grun.
N. dissipata (Kutz.) Grun.
N. fonticola Grun.
N. frustulum (Kutz.) Grun.
N. frustulum var. perpusilla (Rabh.) Grun.
N. hungarica Grun.
N. kutzingiana Hilse
N. palea (Kutz.) W. Sm.
N. viridula
N. vermicularis (Kutz.) Grun.

Order Surirellales
Family Surirellaceae

Surirella ovata Kutz.

Table 2. Relative abundance (%) with the percent co-dominant diatoms, species diversity (H'), and diatom species richness (# TAXA) epiphytic on *Cladophora glomerata* in depth zone 1 at Lees Ferry, Arizona. Acaf-mi= *Achnanthes affinis-minutissima*, Divu= *Diatoma vulgare*, Rhcu= *Rhoicosphenia curvata*, Cope= *Cocconeis pediculus*, Other= misc. diatom species other than the four co-dominant species.

	Acaf-mi	Divu	Rhcu	Cope	Other	% Co-Dominant	H'	#TAXA
SEP	16.3	17.5	30.4	30.2	5.6	94.4	2.4	38
OCT	7.5	14.9	37.8	34.0	5.8	94.2	2.2	28
NOV	23.3	5.3	28.4	34.1	8.9	91.1	2.4	30
DEC	24.0	8.8	34.0	23.4	19.8	90.2	2.6	34
JAN	18.8	18.5	33.6	23.5	5.6	94.4	2.3	19
FEB	25.0	34.6	18.9	2.3	19.2	80.8	2.9	46
MAR	11.5	22.3	38.7	6.5	21.0	79.0	2.9	37
APR	20.2	23.9	21.9	12.6	21.4	78.6	3.2	48
MAY	3.7	45.1	21.0	25.4	4.8	95.2	2.0	29
JUN	9.3	33.6	21.7	28.7	6.7	93.3	2.4	28
JUL	4.4	48.9	16.2	24.2	6.3	93.7	2.1	29
AUG	11.1	56.0	14.8	10.3	7.8	92.2	2.1	37
ANNUAL MEAN	14.6	27.5	26.5	21.3		89.9		

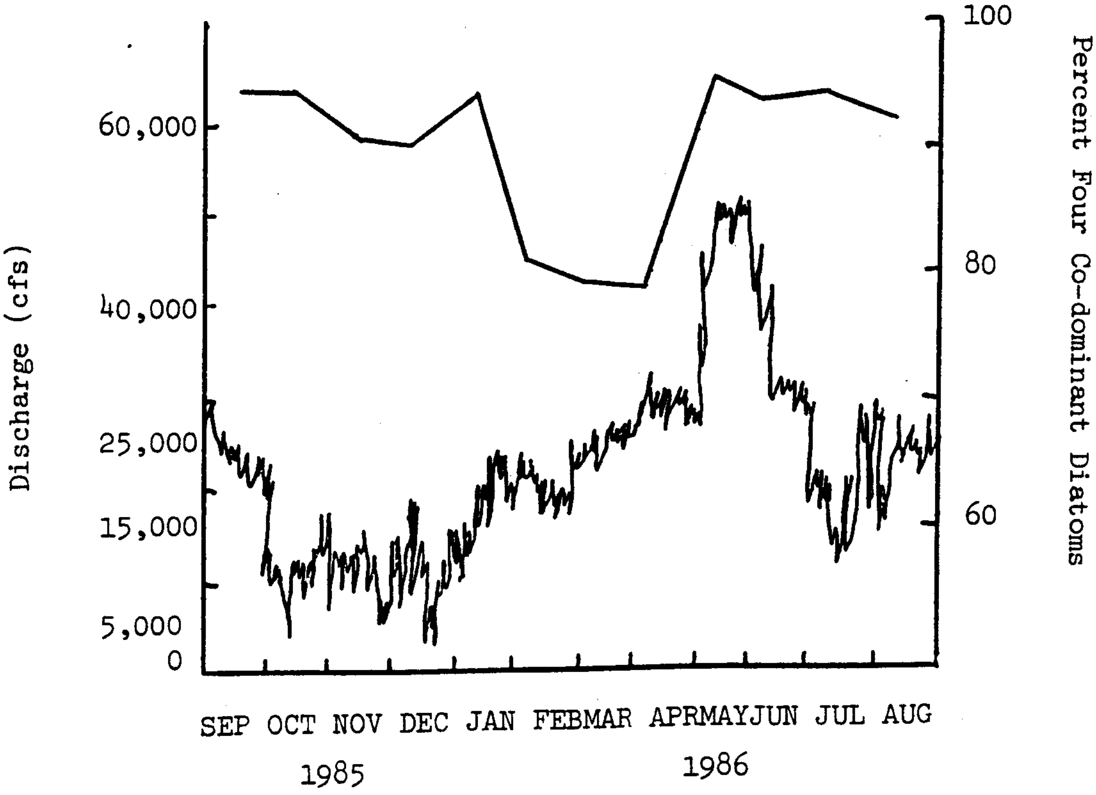

Figure 7. Percent change of the four co-dominant epiphytic species in relation to the mean daily flow at Lees Ferry, Arizona during September 1985 through August 1986.

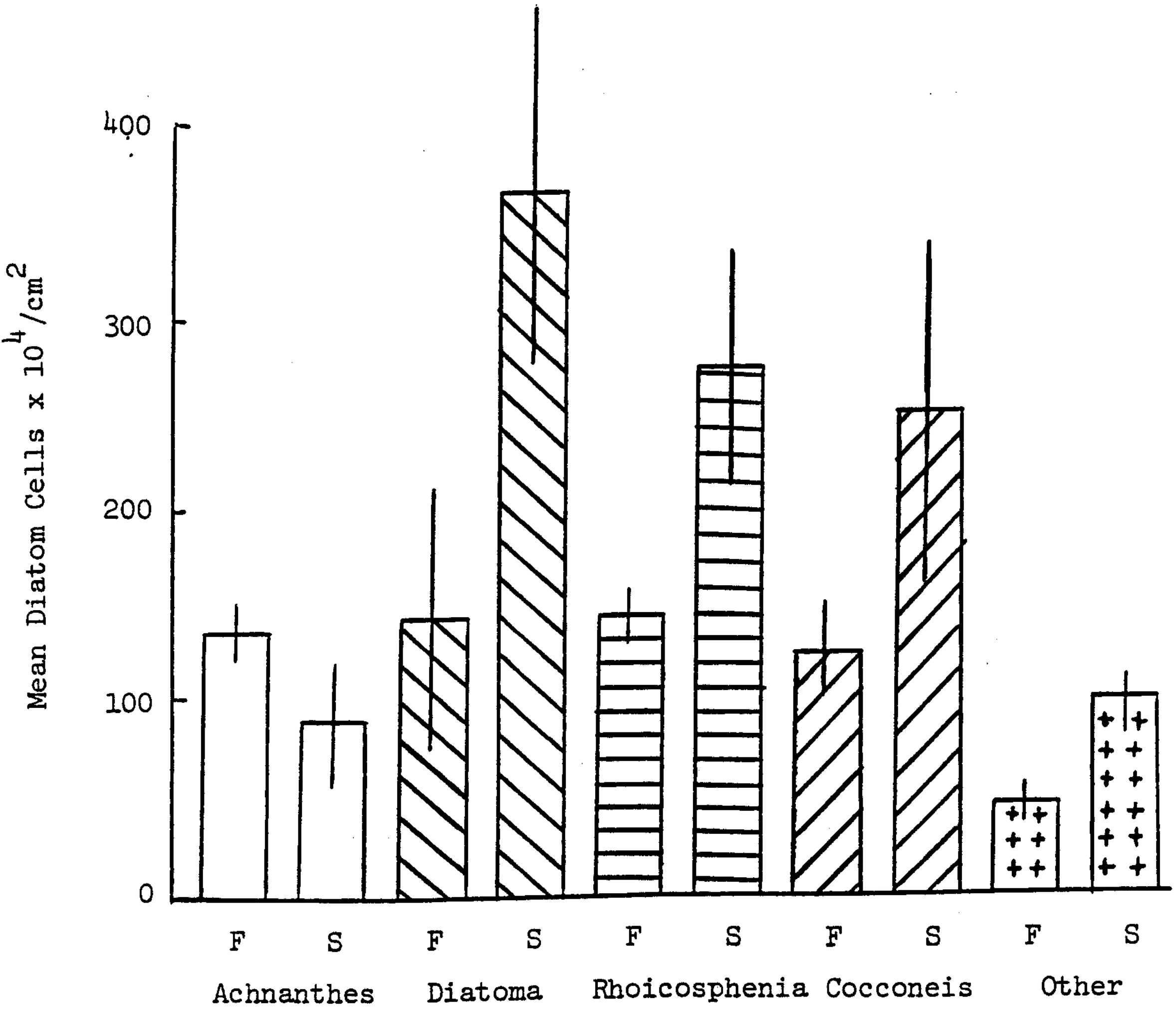

Figure 8. Standing crop (mean cells x $10^4/cm^2$) of diatoms epiphytic on <u>Cladophora glomerata</u> at Lees Ferry, Arizona during September 1985 through August 1986 ($\pm$ s.e.). All species distributions significantly different at $p < 0.05$.

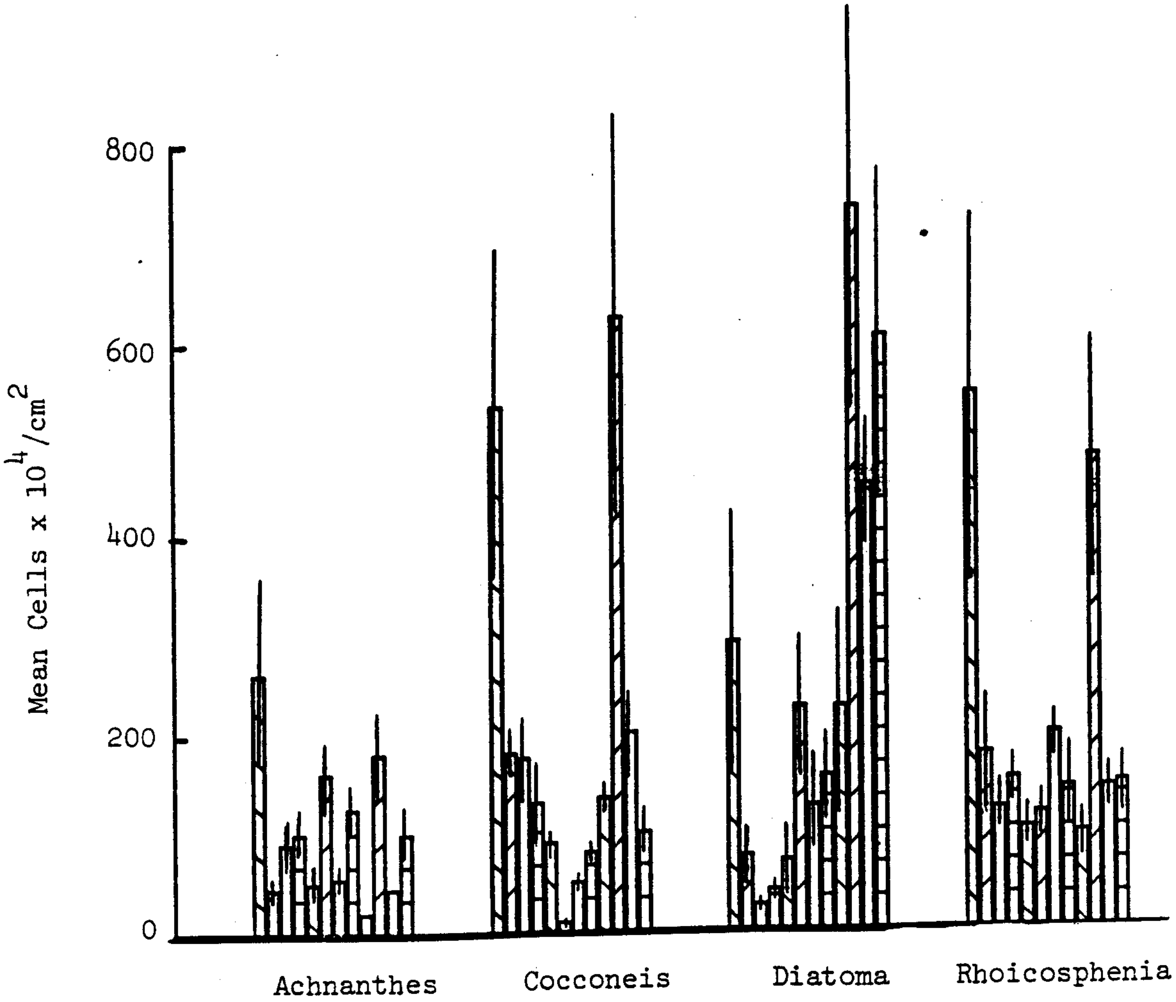

Figure 9. Standing crop (mean cells x $10^4/cm^2$) of the four co-dominant epiphytes on Cladophora glomerata ($\pm$ s.e.) collected at Lees Ferry, Arizona during September 1985 through August 1986. Cocconeis pediculus, Diatoma vulgare, and Rhoicosphenia curvata distributions significant at $p < 0.05$.

The data also suggested that D. vulgare and C. pediculus were the co-dominant diatoms most effected by changes in Cladophora biomass influenced by regulated flow. The monthly standing crop of D. vulgare mimic the changes in Cladophora dry weight exhibited during low base fluctuating flow versus high base steady flow. D. vulgare exhibited its lowest standing crop at 24.4 cells x $10^4/cm^2$ in November 1985 during the first period of greatest exposure of the Cladophora bed as a result of fluctuating flow. In contrast, D. vulgare reached its maximum standing crop at 732.0 cells x $10^4/cm^2$ following >1 month of flood releases >50,000 cfs. The monthly standing crop of C. pediculus steadily decreased with increased time of exposure related to fluctuating flow. The lowest value for C. pediculus (16.2 cells x $10^4/cm^2$) occurred during February 1986 and positively correlated with the lowest dry weight and ash-free dry weight values for Cladophora during the same month (Figs. 5 and 6). Standing crop values for C. pediculus steadily increased with rising steady base flow and peaked at 625.3 cells x $10^4/cm^2$ in June 1986 after greater than one month of flood releases (Fig. 9). This increase correlated well with the maximum ash-free dry weight value for Cladophora during June 1986.

Achnanthes affinis-minutissima standing crop responded stochastically regardless of flow regime by exhibiting high values during both fluctuating flow periods in February 1986 (173.2 cells x $10^4/cm^2$) and June 1986 (202.2 cells x $10^4/cm^2$) and steady flow periods in September 1985 (282.5 cells x $10^4/cm^2$) and April 1986 (135.4 cells x $10^4/cm^2$). The mean pooled data for the individual standing crops of the other 3 co-dominant epiphytic species decreased below 150 cells x $10^4/cm^2$ with fluctuating flow (Fig. 8). Mean Achnanthes standing crops were highest at 136.4 cells x $10^4/cm^2$ under fluctuating flow resulting in periods >12h of exposure (Fig. 8). With the onset of high base steady flow, mean pooled A. affinis-minutissima standing crop decreased to 91.4 cells x 10^4 $/cm^2$ (Fig. 8). In contrast, the other 3 co-dominant species nearly doubled their mean pooled standing crop to greater than 250 cells x $10^4/cm^2$ under high base flow that mimic a steady regime. Diatoma vulgare responded the most dramatically by increasing from 150.0 to 355.6 cells x $10^4/cm^2$ (Fig. 8).

The monthly standing crop of Rhoicosphenia curvata remained greater than the standing crop of Diatoma vulgare throughout the months of fluctuating flow, where the opposite trend existed under months of steady flow (Fig. 9). The change in dominance occurred in late January through mid-March 1986 during a period of transition in flow regime from strong fluctuating flow below 15,000 cfs (zone 2) to a rise in base flow above 15,000 cfs (zone 1). An ANOVA conducted on the relative abundance of the 4 co-dominant species in relation to all diatom species at Lees Ferry indicated that this interaction was significant (F= 74.04, df= 1,11, $p<0.01$).

The relative abundance of the 4 co-dominant species decreased from 94.4% in January 1986 to 80.8% in February 1986 during periods of rising water (Table 2). Sloughing of the co-dominant epiphytic species along with the fragmenting of Cladophora was visually evident in the field after extended periods of exposure at Lees Ferry. The relative abundance values equalling <80% of the 4 co-dominant epiphytic species continued into April 1986 when the flow increased above 25,000 cfs. The continuous inundation of zone 1 above 25,000 cfs corresponded with the relative abundance of the 4 co-dominant species above 90% from May to August 1986 (Table 2).

Analysis of diatom species diversity (H') showed the same trends as the relative abundance of the 4 co-dominant species (Table 2). The transition period of rising base flow exhibiting a strong fluctuations in zone 1 from February through April 1986 resulted in an increase in H' to 3.2 in January 1986. Continuous inundation of zone 1 after May 1986 resulted in a decrease of H' to 2.0.

Composition of Epiphytes in the Diet of Gammarus Lacustris

Gammarus lacustris readily ate the diatoms epiphytic to Cladophora in the tailwaters of Glen Canyon Dam. Diatoms numerically comprised >93.0% of the diet of these amphipods during all 5 months examined (Tables 3 and 4). Typically, over 75±10% of the diatom frustules observed in the guts of G. lacustris were emptied suggesting that diatom cell contents had been digested by amphipods. Insignificant amounts of sand particles and minute cell fragments of Cladophora, the red alga Rhodochorton, and the cyanobacteria Oscillatoria were also observed in the digestive tract of G. lacustris during all months examined (Tables 3 and 4).

Table 3. Mean cell number (± s.e.) of co-dominant diatoms, *Cladophora glomerata*, red alga *Rhodochorton*, and cyanobacteria *Oscillatoria* in the entire gut of *Gammarus lacustris* with the co-dominant diatom standing crop from the field expressed as cells x $10^4/cm^2$ (± s.e.) collected at Lees Ferry, Arizona. Gut values represent 20 animals. Acaf-mi= *Achnanthes affinis-minutissima*, Divu= *Diatoma vulgare*, Rhcu= *Rhoicosphenia curvata*, Cope= *Cocconeis pediculus*, Other= misc. diatom species other than the four co-dominant species.

	Acaf-mi	Divu	Rhcu	Cope	Other	Clgl	Rhodo	Oscill
MAR								
Field	.15	2.55	2.79	8.59				
	(±.00)	(±.05)	(±.05)	(± .02)				
Gut	650	1230	90	5	2	1	2	2
	(±6.8)	(±10.6)	(±1.0)	(± .1)	(± .7)	(± .3)	(± .6)	(± .6)
APR								
Field	2.84	80.67	12.06	15.95				
	(±.04)	(±1.72)	(±.20)	(±.36)				
Gut	20	355	165	5	1	12	8	2
	(± .2)	(± 2.6)	(± 1.0)	(± .1)	(±1.5)	(±3.3)	(±4.3)	(± .8)
AUG								
Field	2.89	125.39	15.30	9.38				
	(±.05)	(±2.59)	(±.29)	(±.20)				
Gut	85	410	305	155	2	5	1	3
	(± .7)	(±1.9)	(±1.9)	(±2.4)	(± .5)	(±1.8)	(± .7)	(±1.8)
SEP								
Field	10.49	34.38	41.39	23.42				
	(±2.36)	(±6.77)	(±9.40)	(±4.32)				
Gut	505	6345	1435	325	3	15	2	2
	(± 5.3)	(±57.7)	(±14.9)	(±2.7)	(± .2)	(±4.3)	(± .9)	(±1.0)
JAN								
Field	7.08	18.34	12.44	9.19				
	(±1.39)	(±3.41)	(±2.76)	(±2.35)				
Gut	6	43	12	2	3	2	1	2
	(± 1.0)	(±8.8)	(±2.1)	(± .5)	(±1.0)	(± .4)	(± .3)	(±1.8)

Table 4. Mean percent frequency (± s.e.) of co-dominant diatoms epiphytic on Cladophora glomerata compared to percent frequency of diatoms and other algal food items in the entire guts of Gammarus lacustris collected at Lees Ferry, Arizona. Acaf-mi= Achnanthes affinis-minutissima, Divu= Diatoma vulgare, Rhcu= Rhoicosphenia curvata, Cope= Cocconeis pediculus, Other= misc. diatom species other than the four co-dominant species.

	Acaf-mi	Divu	Rhcu	Cope	Other	Clgl	Rhodo	Oscill
MAR								
Field	2.3	40.2	44.0	13.5				
	(±.5)	(±8.0)	(±7.4)	(±2.0)				
Gut	32.8	62.1	4.5	.2	.1	.1	.1	.1
	(±4.6)	(±9.8)	(±1.1)	(±1.6)				
APR								
Field	2.6	72.3	10.8	14.3				
	(±.5)	(±9.9)	(±1.6)	(±6.6)				
Gut	3.5	62.5	29.1	.9	.1	2.1	1.4	.4
	(±1.3)	(±7.3)	(±6.3)	(± .2)				
AUG								
Field	1.9	82.0	10.0	6.1				
	(±.7)	(±8.2)	(± .3)	(±2.3)				
Gut	8.8	42.4	31.6	16.1	.2	.5	.1	.3
	(±3.5)	(±6.7)	(±4.7)	(±2.8)				
SEP								
Field	9.5	31.4	37.7	21.4				
	(±3.5)	(±2.8)	(±3.1)	(±3.0)				
Gut	5.8	73.5	16.7	3.8	.0	.2	.0	.0
	(±2.8)	(±7.0)	(±5.3)	(±3.9)				
JAN								
Field	15.1	39.0	26.4	19.5				
	(±3.0)	(±7.3)	(±0.0)	(±5.0)				
Gut	8.5	60.6	16.9	2.8	4.2	2.8	1.4	3.8
	(±1.0)	(±8.8)	(±2.1)	(±0.5)				
TOTAL								
Mean Field =	6.3	53.0	25.8	15.0				
	(±2.6)	(±13.2)	(±7.8)	(±3.6)				
Mean Gut =	11.9	60.2	19.8	4.8	1.0	1.0	.6	.8
	(±5.2)	(±12.3)	(±5.8)	(±2.8)				

An ANOVA conducted on the mean cell number of the four co-dominant epiphytic species ingested by Gammarus lacustris indicated a significant two-way interaction between the diatom species and the month sampled (F= 72.67, df= 3,12, $p<0.05$). The species composition of the four co-dominant diatom species available to Gammarus in the Cladophora algal mat at Lees Ferry were also significantly different with respect to the month sampled when analyzed by the mean cell number (Table 3, F= 15.21, df= 3,12, $p<0.05$). A similar ANOVA conducted on the percent relative abundance of the four co-dominant diatom species in the digestive tract of Gammarus showed no significant differences within the 5 months sampled (Table 4, F= 1.8, df= 3,4, $p>0.05$).

Based on these comparisons between diatom composition in the field and analysis of gut contents, G. lacustris utilized the more upright, loosely attached diatom species (chain-forming Diatoma vulgare and stalk-forming Rhoicosphenia curvata) and avoided or had difficulty in physically removing the more adnate Cocconeis pediculus (Tables 3, 4, and 5). A two-way ANOVA conducted between the different species of epiphytic diatoms indicated a significant difference between the four diatom species collected in the field versus the gut contents of G. lacustris (F= 57.75, df= 3,24, $p<0.05$). There were significantly fewer cells of the adnate C. pediculus in the guts of G. lacustris compared to the frequency of this species on Cladophora in the tailwaters of Glen Canyon Dam (Table 3; Mann-Whitney U, w= 26, $p<0.03$). The percent relative abundance of pooled data for the four co-dominant diatom epiphytes on Cladophora, thus available to G. lacustris in the

Table 5. Mean (± s.e.) percent relative abundance of co-dominant epiphytes on *Cladophora glomerata*; mean (± s.e.) percent relative abundance in *Gammarus lacustris* diet; mean (± s.e.) cell volume (um^3 x 10^2); Ivlev's Electivity Index; and Chesson's Alpha Index for the four co-dominant diatoms epiphytic on *Cladophora glomerata* at Lees Ferry, Arizona. Acaf-mi = *Achnanthes affinis-minutissima*, Divu= *Diatoma vulgare*, Rhcu= *Rhoicosphenia curvata*, Cope= *Cocconeis pediculus*.

Taxon	% Field	% Diet	Cell Volume	Ivlev's EI	Chesson's a
Acaf-mi	6.3 (± 2.6)	12.2 (± 5.2)	18.5 (±22.8)	.28	.407
Divu	53.0 (±13.2)	62.4 (±12.3)	77.3 (± 8.4)	.03	.242
Rhcu	25.8 (± 7.8)	20.6 (± 5.8)	50.6 (± 4.7)	-.04	.287
Cope	15.0 (± 3.6)	4.8 (±2.8)	64.3 (± 7.2)	-.53	.063

field,versus what was actually ingested by *G. lacustris* were positively correlated (r = .76, T= 3.64, p<.0024).

Ivlev's (1961) electivity index (EI) suggested that *G. lacustris* foraged opportunistically on the two upright diatom species, but had difficulty ingesting the adnate *Cocconeis pediculus* (Table 5). In this index, values near 0 indicate a more generalistic foraging pattern, while negative values approaching -1.0 suggest avoidance, and positive values approaching 1.0 represent high selectivity. Mean EIs for the 5 sampling months indicated a moderate preference for *Achnanthes affinis- minutissima* (0.28), slight preference for *Diatoma vulgare* (0.03), slight avoidance for Rhoicosphenia curvata (-0.04), and moderate avoidance for Cocconeis pediculus (-0.53).

Monthly EI values illustrate some interesting trends (Table 6). In every sampling period, for values determined either by cell number or cell volume, C. pediculus showed a negative value with an average EI value of -0.53 for the 5 sampling periods. G. lacustris did ingest more C. pediculus during a drawdown in August 1986 where the EI was less negative at -0.13 compared to the high avoidance range of -0.70 to -0.96 exhibited during high flow periods.

Table 6. Ivlev's Electivity Index, based on cell number (CN) and cell volume (CV) for the four co-dominant diatoms ingested by Gammarus lacustris at Lees Ferry, Arizona. Acaf-mi= Achnanthes affinis-minutissima, Divu= Diatoma vulgare, Rhcu= Rhoicosphenia curvata, Cope= Cocconeis pediculus.

	Acaf-mi		Divu		Rhcu		Cope	
	CN	CV	CN	CV	CN	CV	CN	CV
MAR	.87	.88	.13	.26	-.81	-.89	-.96	-.96
APR	.11	.21	-.05	-.02	.47	.50	-.88	-.87
AUG	.65	.73	-.31	-.17	.52	.62	-.13	-.04
SEP	-.24	-.31	.40	.33	-.39	-.45	-.70	-.65
JAN	-.21	-.90	.27	.30	-.15	-.39	-.76	-.81
TOTAL MEAN	.28	.48	.03	.14	-.04	-.12	-.53	-.67

The data suggest that Gammarus most commonly grazed on the upright epiphytic diatoms without ingesting the host Cladophora cells, even though Cladophora was extremely abundant in the tailwaters of Lees Ferry (Usher and Blinn 1990). This observation was based on the relative low numbers of both Cladophora cells and frustules of C. pediculus in the gut of Gammarus when compared to the numbers of C. pediculus estimated on Cladophora cells in the field (Table 3, Mann-Whitney U, w= 26.0, $p<0.03$).

In all cases, Diatoma vulgare dominated the number of cells (by species) ingested by G. lacustris (Table 3). A significant correlation indicated that G. lacustris found D. vulgare associated with patches of Cladophora ($p<0.04$). The EI for D. vulgare was negative in April (-0.05) and August (-0.31) during periods when the standing crop for D. vulgare in the field was at its highest level (Table 3). Gammarus was able to switch epiphyte species ingestion according to that epiphyte's abundance in the field. In general, when the EI was negative for D. vulgare, the EI was positive for Rhoicosphenia curvata, and vice versa. Furthermore, the negative EIs always occurred when the standing crop for that respective species was greater than the standing crop for the other species exhibiting the positive EI (Tables 3 and 6).

The ingestion of Achnanthes affinis-minutissima by Gammarus indicated a strong positive EI for months with fluctuating flow (March= 0.87 and August= 0.65) and slightly positive (April= 0.11) to moderately negative (September 1987= -0.24 and January 1987= -0.21) EIs for months with steady flow. The relatively small frustule size of A. affinis-minutissima in comparison to the other diatom species

(Table 5, cell volume estimates) and the accummulation of A. affinis-minutissima in the mucilage of the two upright co-dominant species may explain the "apparent" selectivity for this species in the guts of G. lacustris. Significant correlations of A. affinis-minutissima with each of the other 3 co-dominant epiphytic species in the guts of Gammarus and in the field at Lees Ferry support this hypothesis of "hitch-hiking" by Achnanthes (0.49 for Diatoma, 0.35 for Rhoicosphenia, and 0.42 for Cocconeis; all $p<0.001$).

For comparison, Chesson's alpha index (1978) showed similar trends for diatom selectivity as Ivlev's EI (Table 5). In this index, alpha is expressed as a frequency. The higher the numerical value towards 1.0 (100%) correlates with the greater the frequency in which Gammarus lacustris selected for that diatom species.

Alpha values for the 4 co-dominant epiphyte species ranged from 0.407 for Achnanthes to 0.063 for Cocconeis. The mean relative proportions of the four co-dominant species were significantly higher in the gut of Gammarus compared to their proportions in the tufts of Cladophora ($T= 3.64$, $p<0.002$). Relatively low proportions of the "other" species category in the guts of Gammarus were much less than their proportions collected in the field (Table 4). The long chains of D. vulgare and the stalk-forming R. curvata had similar alpha values (0.242 and 0.287, respectively) suggesting moderate selectivity dependent on flow regime and the amphipod's ability to switch resource patches ($T= 14.64$, $p<0.0007$). The slight dominance of R. curvata over D. vulgare in alpha values was in contrast to

Ivlev's EI values where D. vulgare was the slightly dominant species (Table 5). This was most likely a product of the indeces. Chesson's alpha accounts for the presence of all other diatom species in relation to the species in question and the replacement of that species in question as it is removed from the community. Ivlev's EI accounts for only the relationship between the numbers of frustules of the diatom species in question from the field and within the gut. A. affinis-minutissima exhibited the highest alpha value (0.407) suggesting the "apparent" high selectivity probably as a result of the species small frustule size and "hitch-hiking" nature previously described. The closely adnate C. pediculus exhibited the lowest alpha value (0.063) suggesting either avoidance or difficulty for Gammarus to physically manipulate or ingest this species.

CHAPTER 4

DISCUSSION

Regulated Flow on the Cladophora Glomerata-Epiphyte Assemblage

This study suggests that daily fluctuations in flow (>10,000 cfs) have negative effects on the standing crop of Cladophora glomerata and associated diatom epiphytes at Lees Ferry. Periods of exposure at Lees Ferry over a 12 month period resulted in significant decreases of up to 19% in Cladophora biomass during months of fluctuating flow, while periods of steady flow resulted in significant increases of up to 105% in biomass following three months of exposure. The magnitude of decrease in Cladophora biomass in the respective depth zones correlated with the magnitude of fluctuations in association with the base flow. The shallow and middle zones (1 and 2) were subjected to the greatest amount of exposure and exhibited the greatest amount of variation in biomass.

Data from this study support the laboratory experiments on Cladophora glomerata by Usher and Blinn (1990). Their study showed that significant decreases in biomass occurred from exposure periods >12 hours. They also demonstrated that in situ Cladophora biomass dramatically decreased as the result of a one-time exposure period lasting 3 days during an experimental draw-down to <5,000 cfs in October 1984.

The predominant Cladophora die-off at Lees Ferry during my study occurred during late fall as a result of repeated exposure due to fluctuating flow (Fig. 4). This observation was in contrast to normal seasonal growth patterns described for Cladophora. The common annual growth pattern of Cladophora glomerata in both lotic and lentic systems include short periods of intensive growth in the spring and fall, with sharp decreases in mid-summer (Chudyba 1965, Bellis and McLarty 1967, Wood 1968, Herbst 1969, Moore 1977a, Wong et al. 1978, Manatai 1982). During my study the spring period of increased growth for Cladophora coincided with a rising base flow that approached a steady regime. Manatai (1982) proposed that the midsummer die-off was due to a negative energy balance as a result of increasing water temperatures. In contrast to normal seasonality, my data demonstrated that during the midsummer, Cladophora was prolific under relatively constant temperature ($10 \pm 2^{\circ}C$) in the shallower zones 1 and 2 of Lees Ferry, apparently in response to hypolimnetic floodstage releases through Glen Canyon Dam.

The Colorado River at Lees Ferry is characteristically stenothermic ($10 \pm 2^{\circ}C$, Fig. 2), as is typical of tailwater sections below hypolimnetic release dams (Ward and Stanford 1979). The absence of seasonal and diurnal water temperature fluctuations in the tailwaters of Glen Canyon Dam suggest that changes in light intensity modified by changing flow levels and frequencies are the most important regulators of Cladophora biomass at Lees Ferry. The natural seasonal dynamics of the pre-dam system appeared to be stabilized by cold hypolimnetic water withheld, then released by the operation of Glen Canyon Dam for consumptive distribution, including hydroelectric generation.

The natural effects of water depth on Cladophora biomass and epiphyte cell densities were modified by flow regime and periodicity (Fig. 4). All three depth zones responded in some way to the frequency and/or magnitude of regulated flow. Cladophora biomass and diatom densities decreased following periods of exposure or shallow water conditions resulting from fluctuating flow. Usher et al. (1986) observed a positive correlation between Cladophora biomass and increased depth at Lees Ferry. Both studies support previous literature on Cladophora's adaptation to relatively low light conditions (Neel 1968, Wood 1968, Adams and Stone 1973, Graham et al. 1982).

Freshwater species of Cladophora commonly reproduce asexually by simple fragmentation when light and temperature conditions are optimal (Mason 1965). Based upon the large amount of Cladophora in the drift at Lees Ferry (Haury 1981, Leibfried and Blinn 1986), fragmentation is probably the most common form of reproduction in the tailwater of Glen Canyon Dam. Many factors can effect the rate of fragmentation in Cladophora. Repeated periods of desiccation in zones 1 and 2 induced by fluctuating flow resulted in significant losses of Cladophora biomass due to fragmentation (pers. obs., Leibfried and Blinn 1986). There is experimental evidence that the increased degree of exposure to damaging unfiltered ultraviolet light is probably one of the most important regulators for the rate of fragmentation. Based on Calkins and Thordardottier's (1980) studies of closely related algae, ultraviolet light may affect Cladophora by physically weakening the filaments near their holdfast. The growth of mucilage producing epiphytic diatoms may provide protection to the host Cladophora thalli from ultraviolet light and desiccation. In contrast, Stevenson and Stoermer (1982) suggested that epiphytic diatoms common on Cladophora may form a "nutrient shield" causing filaments to weaken, thus increasing the rate of fragmentation.

Lamberti and Resh (1983) suggest that increased fragmentation can increase productivity by removing decadent filaments and allowing younger, fast-growing filaments to proliferate as light is allowed to penetrate to newly exposed thalli. In contrast, my biomass estimates collected during periods of fluctuating flow suggest that fragmentation probably does not enhance productivity at Lees Ferry. Long-term increased productivity would require relatively steady flow or fluctuations of such low frequency as to mimic steady flow. This hypothesis is supported by data for March 1986 when biomass recovered in all zones following steady flows. In addition, Cladophora biomass dramatically increased with the inundation of zone

1 because of steady flow >20,000 cfs. This increase in biomass followed a period of inhibited growth resulting from three months of repeated exposure under strong fluctuating flow.

Few studies address the impacts of exposure on algal populations in regulated rivers. Past studies typically address the changes in algal communities that result from modified physico-chemical parameters below reservoirs (Lawson and Rushford 1975, Lowe 1979, Marcus 1980, Holmes and Whitton 1981, Ward 1982, Dufford et al. 1987, Blinn et al. 1989). Lowe (1979), in addition to Usher and Blinn (1990) suggested that widely fluctuating flow decrease algal standing crop. Peterson (1987) found that diatom communities inhabiting sheltered habitats below Hoover Dam were less resistant to desiccation than communities inhabiting more rigorous flows.

Exposure of algae has been studied in relation to marine or Great Lake littoral forms. Algae exposed during intertidal fluctuations demonstrated adaptations to resist desiccation. Commonly, forms adapted to intertidal zones have thicker cell walls, produce more mucilage, or increase their saturated lipid content (Zaneveld 1937, 1969, Johnson et al. 1974, Wiltens et al. 1978, Schonbeck and Norton 1979, Jones and Norton 1979, Dromgoole 1980, Lobban et al. 1985).

Intertidal marine algae exhibit adaptations to tolerate periods of exposure because they occupy habitats subjected to regular submergence-emergence regimes over evolutionary time. In comparison, the construction of dams on major rivers is a relatively recent human activity (Smith 1971) that usually results in the development of lotic intertidal zones maintained by regulated flows. Significant impacts on resident freshwater algal populations in regulated rivers probably occur because these populations lack evolutionary adaptations to desiccation resulting from exposure.

Some forms of Cladophora occur in the littoral zones of freshwater lakes (Bellis and McLarty 1967, Blum 1982, Lorenz and Herdendorf 1982) and marine environments (Round 1981). Adaptations to intermittent exposure in these habitats may have pre-conditioned C. glomerata evolutionarily for the submergence-emergence regimes of regulated rivers. Similar mitotic divisions described for C. glomerata (McDonald and Pickett-Heaps 1976) and the marine C. flexuosa (Scott and Bullock 1975) suggest that C. glomerata is a marine invader of freshwater systems (Graham et al. 1982).

C. glomerata exhibits few adaptations to tolerate the strong fluctuating flow regimes caused by Glen Canyon Dam. The cell walls of C. glomerata are relatively thick, constructed partly by cellulose and silicon (Bold and Wynne 1985). Similar to some intertidal marine macroalgae (Evans 1959, Jones and Norton 1979, Quadir et al. 1979, Schonbeck and Norton 1979, Dromgoole 1980, Hodgson 1981). The filaments of Cladophora collapse on themselves as the river initially falls, efficiently trapping water for up to 12h (pers. obs.). The overlying filaments are subjected to the damaging effects of the sun while providing a shield for the underlying filaments. The basal holdfast of one tuft is protected by the overlying filaments of a neighbor. The exposed filaments near the holdfast of the Cladophora tuft typically dry first. The weakened filaments are easily broken as the river rises resulting in the drift of viable terminal tufts with damaged filaments. If repeated cycles of desiccation occur over extended periods of time, the tufts in the shallower sections of the river bed would be reduced. Repeated exposure of the riverbed may damage the holdfast to the point of inhibiting growth of Cladophora in the exposed zones until steady flow can restore a continual supply of nutrients and act to buffer potential negative effects of ultraviolet light.

Field observations suggest that Cladophora glomerata at Lees Ferry reguires a minimum 0.5 meter of water coverage for maintenance of growth irrespective of flow regime. Zone 1 achieved maximum biomass values under high base steady flow while zone 3 achieved maximum biomass values under continual inundation of low base flow that fluctuated in zones 1 or 2. The fluctuations that occurred in zones 1 and 2 likely allowed optimal light penetration into zone 3 due to reduced depth. While zone 3 was productive during this time, zones 1 and 2 continued to experience declines in biomass due to exposure.

Cladophora maintained low, but declining biomass in zone 1 following 3 months (October through December 1985) of nearly 100% exposure. This low biomass was probably a result of the mitigating climate during the fall when atmospheric temperatures are lower and humidities are higher (Arizona Climatological Data 1985, 1986), even though shorter daylengths during the fall would cause decreased light available for photosynthesis. *Cladophora* typically exhibits periods of intensive growth in both lotic and lentic systems during the fall (Chudyba 1965, Bellis and McLarty 1967, Wood 1968, Herbst 1969, Moore 1977a, Wong et al. 1978, Manatai 1982). Freezing temperatures during winter exposure was shown to have no adverse effect on related intertidal marine macroalgae (Kanwisher 1957, Biebl 1962, Schonbeck and Norton 1979). In contrast, Usher et al. (1986) found that 12h of exposure under freezing temperatures on cloudless winter nights resulted in significant losses of *Cladophora* biomass. My data indicated that *Cladophora* biomass did steadily decline with extended time of exposure during late fall-early winter, suggesting that near-freezing temperatures had a negative effect on *Cladophora* growth.

To produce electricity for peaking power demands hydroelectric generating facilities typically release water through their generators during daylight hours and withhold water at night. As a result of the peaking power operation of Glen Canyon Dam, periods of greatest exposure for *Cladophora* near Lees Ferry occurred during the night when atmospheric conditions were more hospitable. Usher and Blinn (1990) found that experimental exposures as short as 12h conducted during summer nights showed no significant loss of *Cladophora*, while similar summer daytime exposure periods did have a significant effect on biomass. Their data indicated that high water during the day and low water as a result of fluctuating flow during the night appeared to mitigate the hot daytime temperatures capable of exceeding $38^{o}C$ (Arizona Climatological Data 1986), high ultraviolet light, low humidity, and warm winds that occur during summer days in northern Arizona. Exposure periods during daylight hours result in higher evaporation rates because of increased atmospheric temperature and light (Usher and Blinn 1990).

Studies of marine intertidal algae suggest that seasonal atmospheric microconditions such as cloud cover, high humidity, mild temperatures, or breezes transporting spray from breaking waves act to increase boundary layer humidities of exposed plants, thus decreasing the rate of desiccation and the extent of damage resulting from a given period of exposure (Jenik and Lawson 1967, Jones and Norton 1979, Dromgoole 1980, Dring and Brown 1982). The effect of atmospheric conditions on Cladophora exposed for periods shorter than 12h has not been experimentally tested although field observations during the summer indicate that the basal holdfast can dry following periods of exposure as short as four hours (pers. obs.).

Increased ultraviolet light may also inhibit physiological activity by damaging photosynthetic pigments (Graham et al. 1982). Damage to the pigments could limit the cell's ability to effectively conduct photosynthesis following rewetting. Graham et al. (1982) suggested that the photosynthetic efficiency of Cladophora glomerata decreases above 400 $uE/m^2/sec$. On a cloudy winter day at Lees

Ferry this light value would likely exceed the range of average measurements (GCES data for July 1986). Light intensities would far exceed 400 uE/m^2/sec on summer days in shallow water resulting in extreme inhibition of physiological activity in even moist tufts of *Cladophora glomerata*.

Dawes et al. (1978) found that *Cladophora repens*, a closely related intertidal marine species to *C. glomerata*, exhibited very low photosynthetic rates when exposed and very poor recovery following re-immersion. The same low tolerance to exposure is probably true for *Cladophora glomerata* at Lees Ferry.

The lack of mucilage production in *Cladophora glomerata* allows for the profuse colonization of a diverse epiphytic diatom community. The thick growth of epiphytes on *Cladophora* filaments can compete with the host thalli for nutrients resulting in stress to the host (Stevenson and Stoermer 1982). The physical attachment of diatom cells to the filament can cause structural damage to the *Cladophora* cell wall (Stevenson and Stoermer 1982) possibly causing the weakened host filament to become detached. *Cladophora* is capable of supporting epiphytic diatom populations whose densities are so great that the green color of the host can be masked by the brown pigmentation of the diatoms. *Cladophora* can support 1.32×10^4 diatom cells/mm^2 (Lowe et al. 1982). Usher et al. (1986) found densities as high as 8.0×10^2 cells/mm^2 in October 1985 compared to the 5.1×10^2 cells/mm^2 density I collected during the same month. I found the lowest standing crop (3.56×10^2 cells/mm^2)

during January 1986 and the highest standing crop (21.78×10^2 cells/mm^2) during June 1986. January 1986 was a period of rising fluctuating flow from zone 2 to zone 1 where the sloughing of stressed Cladophora was very high due to 3 months of wintertime exposure. The June 1986 standing crop occurred after 2 months of flood releases which inundated zone 1 under >2 meters of water. The fucoxanthin pigment has allowed diatoms to adapt to utilize relatively low light conditions (Prescott 1962, Poff et al. 1990).

Cladophora is incapable of producing mucilage as a protective mechanism from desiccation. The dense growth of epiphytic diatoms among Cladophora tufts do secrete mucilage and probably provide a moisture retaining protective layer against desiccation, in addition to sheilding exposed tufts from damaging ultraviolet light (Berquist 1957, Evans 1959, Jones and Norton 1979, Stevenson and Stoermer 1982). Peterson (1984) suggested that enhanced diatom species diversity occurred below Hoover Dam as a result of increased production of mucilage by resident species subjected to fluctuating flow regimes. He proposed that this greater amount of mucilage provided additional substrate for new species to colonize.

Epiphytic species diversity (H') at Lees Ferry remained low throughout the 12 months (Table 2). Four co-dominate species consistantly comprised >90% of the standing crop in 9 of the 12 months sampled during this study. These species, Diatoma vulgare, Rhoicosphenia curvata, Cocconeis pediculus, and Achnanthes affinis-minutissima are the most common epiphytes found on Cladophora glomerata in the Grand Canyon (Czarnecki 1978). Usher et al. (1986) found that >80% of the epiphytic standing crop consisted of the same four co-dominant species. Low species diversity was attributed to the relative constancy of the physico-chemical parameters found below hypolimnetic release dams (GCES 1989). This stability appeared to remain under steady flow, but was modified with the scouring effects of fluctuating flow that can physically remove loosely attached growth forms (Table 2).

Cocconeis pediculus, Diatoma vulgare, and Rhoicosphenia curvata occur as dominant epiphytic diatoms on Cladophora in a variety of habitats (Chudyba 1965, Ronnberg and Lax 1980, Sheath and Morison 1982, Lowe et al. 1982). As the effects of fluctuating flow and duration of exposure on Cladophora become more prevalent into the winter, species diversity (H') of the associated diatom community increased until it peaked at 3.2 in April 1986 (Table 2). In support of Peterson's (1984) theory that diatom species diversity can be enhanced as a result of increased mucilage production initiated by fluctuating flow, species adapted to colonize disturbed-sites, especially Achnanthes affinis-minutissima, increased among the epiphytic community at Lees Ferry. A. affinis-minutissima is physically much smaller than the other three co-dominant species (Table 4) and was found inhabiting the mucilage produced by the larger co-dominants at Lees Ferry. In comparison, the relative abundance of co-dominant species decreased below the characteristic

90% value to a low of 78.6% in April 1986. Fluctuating flow increased diatom species diversity by decreasing the abundance of the system's numerically co-dominant species opening habitat for pioneer species to colonize. The effect of rising base flow in association with fluctuating flow increased the effects of scouring that removed viable and nonviable frustules of the co-dominant epiphyte species. Extended exposure periods tended to dismantle the relative constancy of the physico-chemical parameters in which Diatoma and Rhoicosphenia are adapted. The immigration of Achnanthes and related species adapted to the rapid re-colonization of disturbed sites appeared to increase with ecosystem instability.

The relatively stable physico-chemical conditions at Lees Ferry resulting from hypolimnetic releases from Glen Canyon Dam provided an opportunity to examine the relationship between light and temperature on diatom diversity and succession in the inundated depth zones. Seasonal patterns in diatom periodicity result from the integration of light, temperature, nutrient concentrations, and biological interactions (Hutchinson 1967, Round 1971, 1981), as well as the frequency of rewetting observed in regulated systems such as the tailwaters of Glen Canyon. Ecologists typically find it difficult to interpret the independent role of each variable in most natural systems since these variables interact both temporally and spatially to varying degrees. Aquatic habitats that have exhibited some degree of constancy for the major regulating variables are found in lakes of equatorial regions. These ecosystems typically have relatively low biological diversity and high biomass for a few dominant species throughout the year (Ganf and Viner 1973, Ganf 1974). Temperate lakes commonly have greater diversity and variation in seasonal abundance attributed to greater seasonal amplitudes of change in light and temperature (Round 1971, Wetzel 1983). Boucher et al. (1984) examined a stenothermic limestone sink located in temperate northern Arizona. They found that the total seasonal phytoplankton density was correlated with the regional incident light at Montezuma Well. The relatively constant water temperature and nutrient concentrations maintained a relatively constant species composition, except during the annual monsoon season when nutrients became diluted with increased water input from atmospheric precipitation.

The data collected at Lees Ferry suggested that the tailwater ecosystem below Glen Canyon Dam is a temperate lotic ecosystem that could be compared favorably to physico-chemical constant lentic ecosystems. Commonly, diatom succession and abundance are highly dynamic in natural unrestricted lotic ecosystems similar to those described for lentic systems. Hypolimnetic release dams characteristically maintain low temperatures and high nutrient concentrations. The stability of these two physico-chemical variables at Lees Ferry has resulted in low species diversity dominated by high standing crops of the four species better adapted to these conditions (Fig. 6). Typical incident light regulated by the temperate seasons and the changing water volumes due to flow regime acted to regulate the standing crops of the individual diatom species (Fig. 6). Steady flow at Lees Ferry optimized the physico-chemical constancy maintaining peak co-dominant diatom species standing crop. In contrast, fluctuating flow acted to increase diversity by allowing pioneer species like Achnanthes affinis-minutissima to increase in abundance as the fragmentation rate of the host Cladophora increases. Achnanthes abundance was not dependent on the amount of Cladophora as a host substrate. The abundance of Cladophora as a substrate was more important to the other three co-dominant epiphytic species (Fig. 6), although the relative abundance of the three larger co-dominant epiphytes never decreased below 78%.

Epilimnetic releases from Glen Canyon Dam would likely change the species composition of diatoms. Experimentation in the laboratory showed that increased water temperatures >18°C would favor the dominance of the adnate Cocconeis pediculus over the other co-dominant species (Blinn et al. 1986, Blinn et al. 1989). Decreased nutrients would further restrict Diatoma vulgare abundance, in addition to Cladophora glomerata biomass (Whitton 1970). Diversity would remain low because the lake water ecosystem would maintain relatively constant water temperature and nutrient concentrations. Fluctuating flow would likely affect diversity to a less degree than with the colder hypolimnetic releases.

The diatoms epiphytic on Cladophora formed a three-dimensional community structure. C. pediculus is an adnate (closely appressed) form with curved valves that adhere so tightly to *Cladophora* thalli, that even though the epitheca may be dislodged, the hypotheca usually remains attached (Lowe et al. 1982). This close adherence provides protection against grazing on *C. pediculus* by macroinvertebrates (Patrick 1948). The adherence qualities of *C. pediculus* also allowed the species protection from the scouring effects of increased current velocities reulting from rising fluctuating flow levels.

Although *Cocconeis* was probably the most tolerant of the co-dominant epiphytes to direct desiccation due to the thickness of its cell wall, the species relative abundance declined in response to fluctuating flow. *Cocconeis pediculus* was found to be closely associated with changes in *Cladophora* biomass as the green alga responded to regulated flow. The negative effects that fluctuating flow imposed upon *Cladophora* adversely affected *C. pediculus* (Figs. 4 and 6). The lowest *C. pediculus* standing crop value positively correlated with the lowest dry weight and ash-free dry weight for *Cladophora glomerata* following a short lagtime for colonization. In addition, the increase of *Cocconeis* standing crop with the rising base and steady flow correlated well with the maximum ash-free dry weight for *Cladophora*. This standing crop peaked after >1 month of flood releases >50,000 cfs. This observation was in contrast to another study, which characterized *C. pediculus* as a shallow water epiphyte adapted to high light (Czarnecki 1978a).

The effects of fluctuating flow on the epiphytic community at Lees Ferry was evident (Fig. 8). *A. affinis-minutissima* was the only co-dominant epiphyte that did not dramatically increase under steady flow (Fig. 6). *A. affinis-minutissima* responded stochastically throughout the sampling year irrespective of flow regime, which supports the hypothesis that this species is adapted to colonize disturbed sites.

Diatoma vulgare standing crop appeared to be associated with the shading and filtering of light more then any of the four co-dominants. These light parameters were inturn influenced by the flow regime (Fig. 6). *D. vulgare* dominated the epiphytic community during months of high steady flow that occurred March through June 1986. *D. vulgare* standing crop peaked following >1 month of flood releases >50,000 cfs. This observation was consistant with the fall epiphytic collections of Usher et al. (1986) and compares favorably with the literature stating that *Diatoma* is adapted to deeper water habitats with lower light conditions (Czarnecki 1978a).

In contrast to the dominance of *Diatoma vulgare* during high steady flow, *Rhoicosphenia curvata* dominated the epiphytic community during months of prolonged fluctuating flow that occurred October 1985 through January 1986. *R. curvata* appeared to be more tolerant of exposure than *D. vulgare* due to its wider physiological tolerances and adaption to shallow, higher light conditions (Ronnberg and Lax 1980). *R. curvata* exhibited a community dichotomy with dominance in both epilithic and epipelic communities in the stenothermic lentic ecosystem of Montezuma Well, Arizona (Czarnecki 1978a). As an epilith the species exhibited seasonal preferences for light. In contrast, as an epipel the species did not indicate any seasonal preferences for light.

Importance of Epiphytes in the Diet of Gammarus Lacustris

Epiphytic diatoms are probably the most important component of energy flow to the rainbow trout fishery at Lees Ferry. Diatoms are among the most efficiently assimilated foods for a variety of heterotrophs including protozoa, rotifers, insects, and fish (Phillips 1969, Lowe et al. 1982, Stevenson and Stoermer 1982, Leibfried 1988).

The co-dominant diatoms epiphytic on Cladophora at Lees Ferry formed a three-dimensional community structure. Diatoma vulgare attaches by a short mucilage pad and formed a loosely arranged, multicellular, zig-zag chain upon cell division. Rhoicosphenia curvata attaches by a short mucilage stalk (Lowe et al. 1982). The loose attachment of these two species made them highly accessible to grazing macroinvertebrates and trout (Blinn et al. 1986, Leibfried 1988). The Achnanthes affinis-minutissima complex was also highly accessible to grazing due to the species' small physical size and high relative abundance attributable to pioneering adaptations. In contrast, the cup-shaped frustule of Cocconeis pediculus is adapted to tightly adhere to the host Cladophora filament. This adaptation has made C. pediculus relatively inaccessible to grazing macroinvertebrates.

The most important potential impact to the epiphytes on Cladophora resulting from fluctuating flow may be a shift in species composition towards the dominance of closely attached forms like C. pediculus or epilithic forms like Gomphonema parvulum that could potentially replace the loosely growing forms like D. vulgare and R. curvata through scouring. This shift in species composition would be a function of increased current velocities during fluctuating flow and high ramping magnitudes which would remove the loosely attached diatoms from their host substrate. In addition, warmer water at the littoral zone can reach 21°C during the summer (GCES 1989) and would favor eurythermal forms that could successfully compete for nutrients (Blinn et al. 1989). Cocconeis pediculus, Cymbella affinis, and Achnanthes affinis-minutissima are better adapted to these conditions and would likely dominate. If water temperatures are elevated beyond 20°C, overall diatom density would be reduced and/or epiphytic diatoms may be replaced by green algae or cyanobacteria (Blinn et al. 1989). Under this scenerio rainbow trout (Leibfried 1988) and Gammarus lacustris (present study) that utilize the lipid-rich epiphytes would have to search out other components of the food web for nutritional substitutes. Trout would become more dependent on Gammarus directly as they did historically (Bancroft and Sylvester 1978), thus potentially decreasing their energetic efficiency as a result of increased searching activity for a less abundant nutrient source.

Gammarus lacustris readily utilized the epiphytic diatoms on Cladophora at Lees Ferry. Diatoms numerically comprised at least 95% of the diet of the amphipods during all 5 months examined. Typically over 75% of the diatom frustules observed in the digestive tracts of G. lacustris were empty suggesting that the cell contents were digested by the amphipods. Insignificant amounts of sand particles and cell fragments of Cladophora, the red alga Rhodochorton, and the cyanobacteria Oscillatoria were ingested secondarily by G. lacustris. The amphipod stomach consists of a gastric mill with chitinous teeth and setae capable of opening the siliceous frustules of diatoms (for a review, see Hickman 1973), allowing the cytoplasm to be released for digestion into the amphipod body.

Gammarid amphipods are generally described as bottom dwelling scavengers (Hickman 1973) that inhabit both lotic and lentic habitats. Riverine gammarids are well known as shredders that feed continuously on allochthonous detritus derived from deciduous leaves (Hynes 1954, Moore 1975, Willoughby and Sutcliffe 1976). Marchant and Hynes (1981) determined that the feeding rate of G. pseudolimnaeus was independent of physical size. They suggested that assimilation efficiencies may increase with lower temperatures due to the longer period in which the food remains in the gut for the digestive process. The relatively low temperature maintained at Lees Ferry would favor the optimization of assimilation in G. lacustris.

Efficiences were also found to increase in Hyalella azteca (Hargrave 1970) that fed on algae.

Gammarus lacustris is reported as an opportunistic species adapted to streams with low water temperature (Hynes and Harper 1972). The species' primary diet usually consists of algae (Moore 1977b). They are also reported to feed on chironomids (Menon 1966), scavenge on their own fecal pellets in laboratory tanks, and cannibalize their own weak individuals during molting. These observations of gammarid behaviour led Newman and Waters (1984) to criticize management agencies that proposed gammarids in general ate whatever was present or introduced into a particular ecosystem. This was logically the reason for the introduction of the slow water adapted G. lacustris into the Lees Ferry rainbow trout fishery dominated by Cladophora. The relatively abundant biomass of Cladophora was accepted as a readily accessible food source for Gammarus while overlooking the utilization of the diatoms.

Moore (1975) found that diatoms accounted for at least 80% of the diet of a closely related European riverine form, G. pulex. The balance of the diet consisted of cyanobacteria. G. pulex did not ingest the Cladophora that was abundant in the system. This finding was consistent with my observations on G. lacustris at Lees Ferry. Less than 0.1% of all digestive tracts sampled contained minute fragments of Cladophora. G. pulex ingested Rhoicosphenia curvata the greatest numerically. Some degree of selectivity by G. pulex was observed for numerically rare species found in the environment during the sampling season, including Diatoma vulgare.

Both Ivlev's (1961) electivity index and Chesson's (1978) alpha index suggested that G. lacustris at Lees Ferry fed opportunistically with respect to the two upright diatom species (Diatoma vulgare and Rhoicosphenia curvata) and avoided the more closely attached Cocconeis pediculus. G. lacustris probably could not physically break and ingest whole Cladophora cells in that their feeding appendages are not adapted for mastigating food items, although small refactory fragments were rarely observed in the digestive tracts. These fragments were probably ingested secondarily along with sand particles during foraging in the detritus for epiphytes. There were significantly fewer cells of the adnate C. pediculus in the guts of Gammarus compared to the frequency of Cocconeis on Cladophora in the tailwaters of Glen Canyon Dam. This suggested that C. pediculus was more difficult to remove from Cladophora thalli than the upright forms. This observation would be important to the management of Lees Ferry. If water from the epilimnion of Lake Powell was released through Glen Canyon Dam the elevated water temperature near 18^{o}C would cause C. pediculus to become the dominant species in the epiphytic community (Blinn et al. 1989). This scenario would affect the energy flow of the tailwater ecosystem by reducing the number of readily available loosely attached epiphyte species and replacing them with tightly adhering species that are difficult for macroinvertebrates to manipulate or ingest.

Achnanthes affinis-minutissima was ingested by *G. lacustris* in relatively large amounts. The vulnerability of this species due to its small cell size and habit of epiphytically colonizing the mucilage of the two larger upright species explains the "apparent" selectivity for *A. affinis-minutissima* by a forager evolutionarily adapted to collecting food items. Moore (1975) reported that *G. pulex* ingested *Achnanthes* species in greater proportion to cell densities in the field during the spring, summer, and autumn months in four separate British river systems.

The epiphytic diatoms ingested by *Gammarus* supply the amphipod with lipids that may allow protein sparing similar to that proposed for other crustacea (Roman 1984) and trout (Watanabe et al. 1979). Protein sparing can occur when low quality food (cellulose from *Cladophora*) can be used for an organism's energy requirements allowing high protein foods (diatoms) to be used primarily for growth (Roman 1984). Pollack (1984) demonstrated that *Gammarus* tissue collected from Lees Ferry contained significant amounts of lipids. The same 16-chain fatty acid found in the epiphytic diatoms were identified in *G. lacustris*. Other freshwater and marine crustacea store lipids as energy reserves (Tessier and Goulden 1982, Hakanson 1984, Wirsen and Jannasch 1983). The high growth rates of the rainbow trout at Lees Ferry may also be indirectly related to high diatom production, mediated by *Gammarus* (Leibfried 1988). Both the diatomic 16-chain fatty acid and an 18-chain fatty acid tracable to Gammarus and Cladophora through gas chromotagraphy were found in rainbow trout tissue (Pollack 1984).

Diatom fatty acid production was found to be highest in the intermediate water levels of the Colorado River (Pollack 1984) where Gammarus prefer to forage (Leibfried and Blinn 1986). Cladophora was prolific at these intermediate depths under steady flow regimes, as well as the shallower water habitats (Fig. 3). Gammarus gain better refuge from trout predation at these shallower depths. This behaviour necessitates movement between depth zones by Gammarus to feed, thus increasing their vulnerability to dislodgement into the river current (Waters and Hokenstrom 1980), especially when the flows fluctuate widely. Trout commonly feed in the intermediate depth zones that exhibit a high degree of drift (Willers 1981), thus minimizing energy expended to acquire nutrition. Vulnerability to drift and trout predation both are probably regulatory mechanisms on the amphipod population. Feeding on Gammarus by trout would likely maintain amphipod production at a level near the ecosystem's carrying capacity for invertebrate production (Waters and Hokenstrom 1980).

Gammarus may have a similar regulatory effect on epiphytic diatom production by their selective removal of the upright and early successional species. In addition, rainbow trout potentially remove large amounts of the Cladophora-epiphyte assemblage as they actively pursue Gammarus. These processes may serve in maintaining the epiphytic diatom species distribution as Gammarus selectively graze patches of loosely attached diatoms (Hudon 1983).

Management Recommendations

To mitigate the effects of fluctuating flow on Cladophora and the associated epiphytic community, Glen Canyon Dam should be operated in a manner that emphasizes the suitable habitat for Cladophora production. This operational schedule would mitigate the effects on the subsequent food web links (epiphytes and Gammarus) important for resident fish. Minimum flow below 8,000 cfs that would expose a substantial portion of Cladophora habitat for periods >6 hrs should be avoided, especially during summer days and winter nights. Prolonged flood releases exceeding 35,000 cfs for greater than two weeks should be avoided because zone 3 production would potentially stagnate as a result of light limitation. In addition, the resultant impact due to scouring of suitable Cladophora substrate could be substantial.

Seasonal disturbance is a natural component of lotic ecosystems that act to regulate successional processes. Diversity of successional species adapted to changing habitat is important for overall community "health". As long as the management emphasis remains centered around the productivity of the rainbow trout fishery while limiting the impacts of peaking power releases through Glen Canyon Dam, diversity would have to be enhanced by a seasonal inflow-outflow operational scenario that emphasizes minimal daily fluctuations. This scenario would re-establish pre-dam timing of seasonal flooding and low flow patterns potentially maximizing the amount of riverbed available for the stable colonization of *Cladophora*. This seasonally stable community of *Cladophora* could then support prolific production of epiphytic diatoms and aquatic macroinvertebrates. Re-establishment of seasonality would increase species diversity in both diatom and macroinvertebrate communities that are currently adapted to the regional pre-dam successional processes regulated by temperature, light, and flow regimes. Increased species diversity would be beneficial to managed trout populations, as well as decreasing impacts to native fish populations, by broadening the components of the food web.

CHAPTER 5

SUMMARY

The results of this study demonstrate that fluctuating flow negatively impact the growth and extent of Cladophora glomerata and its associated epiphytic diatom community, which indirectly affects Gammarus lacustris. The operation of Glen Canyon Dam as a peaking power facility releasing daily fluctuations of 5,000 to 25,000 cfs, as those experienced in the fall of 1985, could have severe long-term repercussions on the Colorado River aquatic ecosystem through Glen Canyon. A breakdown or uncoupling of the present aquatic ecosystem due to extended periods of fluctuating flow would disrupt the introduced trout populations of the river. Cladophora glomerata and its associated epiphytes are the foundation of the aquatic food web utilized by both Gammarus lacustris and rainbow trout inhabiting Glen Canyon. When repeated or prolonged exposures decreased the biomass of Cladophora, a negative dominoe effect appeared to occur. The nutrient-rich co-dominant diatom species that utilize Cladophora for attachment decreased with the reduction in Cladophora biomass. In turn, Gammarus lacustris abundance and productivity would decrease as the amphipod's food source, the epiphytes, were directly removed by scour or indirectly depleted by fragmenting *Cladophora*. Under optimal conditions for *Cladophora* productivity trout would likely minimize energy required searching for nutrition.

The effects of fluctuating flow would likely have similar results on trout physical condition dependent on the magnitude and periodicity of the fluctuations. Recent research has demonstrated that the physical conditions of rainbow trout diminished after three days of atmospheric exposure to *Cladophora* (D. Kubly, pers. comm.).

In either case, negative changes in the abundance of the two primary food items (*C. glomerata*-diatom epiphyte assemblage and *Gammarus lacustris*) utilized by trout at Lees Ferry could have negative repercussions on the physical condition of trout. *G. lacustris* provides protein and an important source of energy to trout in the tailwaters of Glen Canyon. Epiphytes likely provide lipid derived fatty acids used for protein sparing that allow individual fish to acheive increased body weights.

Post-dam conditions have resulted in cool stenothermic conditions condusive to algal, gammarid, and rainbow trout productivity. An increase in water temperature would result in the decrease of readily available epiphytic species and the increase in the relatively unavailable *Cocconeis* due to its adhesive growth form. The "Blue Ribbon" body weights of the rainbow trout that makes Lees Ferry popular among sportfishermen would likely suffer as a result of the decrease in the epiphytic nutrient exchange.

LITERATURE CITED

Adams, M. S. and W. Stone. 1973. Field studies on photosynthesis of Cladophora glomerata (Chloropyta) in Green Bay, Lake Michigan. Ecology 54: 853-62.

American Public Health Association. 1975. Standard Methods for the Examination of Water and Wastewater. American Public Health Association Inc., New York, 1193 pp.

Anderson, N. H. and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Ann. Review Entomol. 351-77.

Arizona Climatological Data. 1985, 1986. National Oceanic and Atmospheric Administration. National Climatic Data Center. Ashville, N.C. Vol. 89, 90.

Arizona Game and Fish Department. 1968. Glen Canyon tailwater fishery investigation, in-house report. AZ Game and Fish Dept.

Bancroft, D. C. and K. Sylvester. 1978. The Colorado River Glen Canyon Tailwater Fishery. Ann. Rept. July 1977- June 1978. AZ Game and Fish Dept.

Barlocher, F. and B. Kendrick. 1973a. Fungi in the diet of G. pseudolimnaeus (Amphipoda). Oikos 24: 295-300.

_____. 1973b. Fungi and food preference of G. pseudolimnaeus. Arch. Hydrobiolo. 72: 501-16.

_____. 1976. Hyphomycetes as intermediaries of energy flow in streams. Pages 435-46 in E. B. Gareth Jones, ed. Recent Advances in Aquatic Mycology. Elek, London.

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

Benke, A. C. 1990. A perspective on America's vanishing streams. J. N. Am. Benthol. Soc. 9(1): 77-88.

Berquist, P. L. 1957. Some factors in brown algal zonation. MSc. Thesis, Univ. of Auckland. 331 pp.

Biebl, R. 1962. Seaweeds. pp 799-815 in Ed. Lewin, R. A. Physiology and Biochemistry of Algae. Academic Press, New York.

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, Utah, USA. 19 pp.

_____, 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. 9: 1-6.

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

Bold, H. C. and M. J. Wynne. 1985. Introduction to the Algae. Prentice-Hall, Inc. Englewood Cliffs, New Jersey. 720 pp.

Boucher, P., D. W. Blinn, and D. B. Johnson. 1984. Phytoplankton ecology in an unusually stable environment (Montezuma Well, Arizona, U.S.A.). Hydrobiol. 119: 149-60.

Calkins, J. and T. Thordardottier. 1980. The ecological significance of solar UV radiation on aquatic organisms. Nature. 283: 563-66.

Carothers, S. W. and C. O. Minckley. 1981. A survey of the fishes, aquatic invertebrates and aquatic plants of the Colorado River and selected tributaries from Lees Ferry to Separation Rapids. Contract No. 7-07-30-X0026, U. S. Bureau of Reclamation, Boulder City, Nevada. 401 pp.

Chesson, J. 1978. Measuring preference in selective predation. Ecology 59(2): 211-15.

Chudyba, H. 1965. Cladophora glomerata and accompanying algae in the Skawa River. Acta. Hydrobiol. 7, Suppl.(1): 92-126.

Czarnecki, D. B. 1978a. Diatoms of Northern Arizona- Their distribution, ecology, and taxonomy- Including notes on successional patterns in Montezuma Well and morphological variability in Navicula cuspidata (Kutz.) Kutz. Ph.D. Dissertation. Northern Ariz. Univ., Flagstaff, Arizona, USA. 135 pp.

Czarnecki, D. B. 1978b. Diatoms of the Colorado River in Grand Canyon National Park and Vicinity. (Diatoms of Southwestern USA III). Biblio. Phycol. 38: 1-181.

Dawes, C. J., R. E. Moon, and M. A. Davis. 1978. The photosynthetic and respiration rates and tolerances of the benthic algae from a mangrove and salt marsh estuary: a comparative study. Estuarine and Coastal Marine Sci. 6: 175-85.

Deksbakh, N. K. and G. A. Sokolova. 1965. Biology of _Gammarus lacustris_ Sars in some lakes of the central Urals (feeding). Trudy sverdlovsk sel-khoz Inst. 12: 475-80.

Dring, M. J. and F. A. Brown. 1982. Photosynthesis of intertidal brown algae during and after periods of emersion: a renewed search for physiological causes of zonation. Mar. Ecol. Prog. Serv. 8: 301-08.

Dromgoole, F. I. 1980. Desiccation resistance of intertidal and subtidal algea. Bot. Mar. 23: 149-59.

Dufford, R. G., H. J. Zimmerman, 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, New York. pp. 383-90.

Evans, J. H. 1959. The survival of freshwater algae during dry periods. II. Drying experiments. III. Stratification of algae in pond margin litter and mud. J. Ecol. 47: 55-81.

Fuller, R. L., J. L. Roelofs, and T. J. Fry. 1986. The importance of algae to stream invertebrates. J. N. Am. Benthol. Soc. 5(4): 290-296.

Ganf, G. G. 1974. Phytoplankton biomass and distribution in a shallow eutrophic lake (Lake George, Uganda). Oecologia 16: 9-29.

_____ and A. B. Viner. 1973. Ecological stability in a shallow equatorial lake (Lake George, Uganda). Proc. r. Soc. 184: 321-46.

Glen Canyon Environmental Studies. 1989. Final Report. United States Department of the Interior, Bureua of Reclamation, Upper Colorado Region Report No. GCES/01/87. Salt Lake City, Utah, USA. 287 pp.

Graham, J. M., M. T. Auer, R. P. Canale, and R. P. Hoffmann. 1982. Ecological studies and mathematical modelling of *Cladophora* in Lake Huron: 4. Photosynthesis and respiration as functions of light and temperature. J. Great Lakes Res. 8: 100-11.

Hakanson, J. L. 1984. The long and short term feeding condition in field caught *Calanus pacificus*, as determined from the lipid content. Limnol. and Oceanogr. 29(4): 794-804.

Haury, L. R. 1981. *Cladophora* drift and planktonic crustaceans in the Colorado River: Lees Ferry to Diamond Creek. Special Report. 24 pp.

Hargrave, B. T. 1970. The utilization of benthic microflora by *Hyalella azteca* (Amphipoda). J. Anim. Ecol. 39: 427-37.

Herbst, R. P. 1969. Ecological factors and the distribution of *Cladophora glomerata* in the Great Lakes. Am. Mid. Nat. 82: 90-98.

Hickman, C. P. 1973. Biology of the Invertebrates. 2nd Ed. The C.V. Mosby Company. St. Louis, Missouri, USA. 757 pp.

Hilton, J. W. and S. J. Slinger. 1981. Nutrition and feeding of rainbow trout. Can. Special Publ. Fish Aquatic Sci. 55: 15-28.

Hodgson, L. M. 1981. Photosynthesis of the red alga, *Gastroclonium coutteri* (Rhodophyta) in response to changes in temperature, light intensity, and desiccation. J. Phycol. 17: 37-42.

Holmes, N. T. W. and B. A. Whitton. 1981. Phytobenthos of the River Tees and its tributaries. Freshwat. Biol. 11: 139-63.

Hudon, C. 1983. Selection of unicellular algae by the littoral amphipods *Gammarus oceanicus* and *Calliopius laevuisculus* (Crustacea). Mar. Biol. 78(1): 59-67.

Hutchinson, G. E. 1967. A Treatise on Limnology. 2 John Wiley & Sons, Inc. New York. 2: 1115 pp.

Hynes, H. B. N. 1954. The ecology of *Gammarus duebeni* Lilljeborg and its occurrence in freshwater in Western Britain. J. Anim. Ecol. 23: 38-84.

______. 1963. Imported organic matter and secondary productivity in streams. 16th Int. Congr. Zool. Washington. 4: 324-9.

______. and F. Harper. 1972. The life histories of *Gammarus lacustris* and *Gammarus pseudolimnaeus* in Southern Ontario. Crustac. 3: 329-41.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Connecticut, USA.

Jenik, J. and G. W. Lawson. 1967. Observations on water loss of seaweeds in relation to microclimate on a tropical shore (Ghana). J. Phycol. 3: 113-116.

Johnson, W. S., A. Gigon, S. L. Gulmon, and H. A. Mooney. 1974. Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. Ecology. 55: 771-81.

Jones, H. G. and T. A. Norton. 1979. Internal factors controlling the rate of respiration from fronds of some intertidal algae. New Phytol. 83: 275-85.

Kanwisher, J. 1957. Freezing and drying in intertidal algae. Biol. Bull. 113: 275-285.

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. J. Chem. Ecol. 5: 371-81.

Lamberti, G. A. and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64: 1124-35.

Lawson, L. L., and S. R. Rushforth. 1975. The diatom flora of the Provo River, Utah, U.S.A. Bibliotheca Phycologia 17: 1-149.

Leibfried, W. C. 1988. The utilization of Cladophora glomerata and epiphytic diatoms as a food resource by rainbow trout in the Colorado River below Glen Canyon Dam. MSc. Thesis. Northern Ariz. Univ., Flagstaff, Arizona. 36 pp.

______ 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 Technical Report No. B-8. Bureau of Reclamation, Salt Lake City, Utah.

Lobban, C. S., P. J. Harrison, and M. J. Duncan. 1985. The Physiological Ecology of Seaweeds. Cambridge University Press, Cambridge. 242 pp.

Lorenz, R. C. and C. E. Herdendorf. 1982. Growth dynamics of Cladophora glomerata in western Lake Erie in relation to some environmental factors. J. Great Lakes Res. 8: 42-53.

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, New York. pp. 25-34.

______, B. H. Rosen, and J. C. Kingston. 1982. A comparison of epiphytes on Bangia atropurpurea (Rhodaphyta) and Cladophora glomerata (Chlorophyta) from Northern Lake Michigan. J. Great Lakes Res. 8(1): 164-68.

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, Arizona.

Manatai, K. E. 1982. Energy relationships of Cladophora glomerata. Plant Physiol. 69 (4 Suppl.): 103.

Marchant, R. 1981. The ecology of Gammarus in running water. in M. A. Lock and D. D. Williams (eds), Perspectives in Running Water Ecology. Plenum Press, New York. pp. 225-49.

Marchant, R. and H. B. N. Hynes. 1981. Field estimates of feeding rate for Gammarus pseudolimnaeus (Crustacea: Amphipoda) in the Credit River, Ontario. Freshw. Biol. 11: 27-36

Marcus, M. D. 1980. Periphytic community response to chronic nutrient enrichment by a reservoir discharge. Ecology 61: 387-99.

McDonald, K. L. and J. D. Pickett-Heaps. 1976. Ultrastructure and differentiation in Cladophora glomerata. I. Cell division. Am. J. Bot. 63: 592-601.

Menon, P. S. 1966. Population ecology of Gammarus lacustris lacustris Sars in Big Island Lake. Ph.D. Thesis, Univ. of Alberta, Edmonton, Alberta. 109 pp.

Minckley, W. L. 1963. The ecology of a spring stream Doe Run, Meade County, Kentucky. Wildl. Monogr. Chestertown. 11: 1-124.

Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology. 48: 139-49.

Monk, D. C. 1977. The digestion of cellulose and other dietary components and pH of the gut of the amphipod Gammarus pulex (L.). Freshwat. Biol. 7: 431-40.

Moore, J. W. 1975. The role of algae in the diet of Asellus aquaticus L. and Gammarus pulex L. J. Anim. Ecol. 44: 719-30.

______. 1977a. Seasonal succession of algae in a eutrophic stream in Southern England. Hydrobiol. 53(2): 181-92.

______. 1977b. Importance of algae in the diet of subarctic populations of Gammarus lacustris and Pontoporeia affinis. Can. J. Zool. 55: 637-41.

Neel, J. K. 1968. Seasonal succession of benthic algae and their macro-invertebrate residents in a headwater limestone stream. J. Wat. Poll. Control Fed. 40: R10-R30.

Newman, R. M. and T. F. Waters. 1984. Size-selective predation on Gammarus pseudolimnaeus by trout and sculpins. Ecology 65(5): 1535-45.

Nilsson, L. M. 1974. Energy budget of a lboratory population of Gammarus pulex (Amphipoda). Oikos 25: 35-42.

Patrick, R. 1948. Factors affecting the distribution of diatoms. Bot. Rev. 14: 473-524.

______. and C. W. Reimer. 1966. The Diatoms of the United States. Volume 1. Acad. Nat. Sci. Phil. 688 pp.

Patrick, R. and C. W. Reimer. 1975. The diatoms of the United States. Volume II, Part I. Acad. Nat. Sci. Philadelphia Mono. No. 13. 213 pp.

Persons, W. R., K. McCormack, and T. McCall. 1985. Fishery investigations of the Colorado River from Glen Canyon Dam to the confluence of the Paria River: assessment of the impact of fluctuating flows on the Lee's Ferry Fishery. Federal Aid in Sport Fish Restoration Dingell-Johnson Project F-14-R-14. Arizona Department of Game and Fish.

Peterson, C. G. 1984. Benthic diatom community dynamics in the Colorado River: Interactive effects of periodic desiccation and current regime. MSc. Thesis. Univ. Nev. Las Vegas. Las Vegas, Nevada, USA. 140 pp.

______. 1987. Influence of flow regime on development and desiccation response of lotic diatom communities. Ecology 68: 946-54.

Phillips, G. L. 1969. Diet of the minnow Chrosomus erythrogaster (Cyprinidae) in a Minnesota stream. Am. Mid. Nat. 82: 99-109.

Pielou, E. C. 1966. The measurement of diversity of different types of biological conditions. J. Theoret. Biol. 13: 137-44.

Poff, N. L., N. J. Voelz, J. V. Ward, and R. E. Lee. 1990. Algal colonization under four experimentally-controlled current regimes in a high mountain stream. J. N. Am. Benthol. Soc. 9(4): 303-18.

Pollack, P. E. 1984. Sources of nutrition at Lee's Ferry on the Colorado River. Unpubl. Report. Northern Ariz. Univ., Flagstaff, Arizona, USA. 20 pp.

Prescott, G. W. 1962. Algae of the Western Great Lakes Region. W. C. Brown Co., Dubuque, Iowa.

Quadir, A., P. J. Harrison, and R. E. DeWreede. 1979. The effects of emergence on the photosynthesis and respiration of marine macrophytes. Phycologia. 18: 83-88.

Ricklefs, R. E. 1979. Ecology. 2nd Ed. Chiron Press, Inc. New York. 966 pp.

Roman, M. R. 1984. Utilization of detritus by the copepod, *Acartia tonsa*. Limnol. and Oceanogr. 29(5): 949-59.

Ronnberg, A. S. and P. Lax. 1980. Influence of wave action on morphology and epiphytic diatoms of *Cladophora glomerata* (L.) Kutz. Ophelia (Suppl.) 1: 209-18.

Round, F. E. 1971. The growth and succession of algal populations in freshwater. Mitt. int. Ver. Limnol. 19: 70-99.

______. 1981. The Ecology of Algae. Cambridge University Press, Cambridge. 653 pp.

Schonbeck, M. W. and T. A. Norton. 1979. An investigation of drought avoidance in intertidal fucoid algae. Bot. Mar. 31: 303-13.

Scott, J. L. and K. W. Bullock. 1975. Ultrastructure of cell division in the haploid generation of *Cladophora flexuosa*. Can. J. Bot. 54: 1546-60.

Shannon, C. E. and W. Weaver. 1963. The Mathematical Theory of Communication. Univ. Illinois Press, Urbana.

Sheath, R. G. and M. O. Morison. 1982. Epiphytes on *Cladophora glomerata* in the Great Lakes and St. Lawrence seaway with particular reference to the red alga *Chroodactylon ramosum* (= *Asterocystis smargdina*). J. Phycol. 18: 385-91.

Smith, N. 1971. A History of Dams. Peter Davies, London. 279 pp.

Stevenson, R. J. and E. F. Stoermer. 1982. Seasonal abundance patterns of diatoms on Cladophora in Lake Huron, USA. J. Great Lakes Res. 8(1): 169-83.

Stone, J. L. 1964. Limnological study of Glen Canyon tailwater area of the Colorado River. Arizona Department of Game and Fish, Colorado River Storage Project, P.L. 485, Sec. 8. 23 pp.

______. 1972. Tailwater fisheries investigations- creel census and biological study of the Colorado River below Glen Canyon Dam, July 1, 1971- June 30, 1972. Arizona Department of Game and Fish, Colorado River Storage Project, P.L. 485, Sec 8. 23 pp.

Storr, J. F. and R. A. Sweeney. 1971. Development of a theoretical seasonal growth response curve of Cladophora glomerata to temperature and photoperiod. pp. 119-27 in Proc. 14th Conf. Great Lakes Res., Internat. Assoc. Great Lakes Res.

Tessier, A. J. and C. E. Goulden. 1982. Estimating food limitation in cladoceran populations. Limnol. and Oceanogr. 27(4): 707-17.

U.S. Geological Survey. 1987. Unpubl. Flow Data from Lees Ferry Gauging Station- Draft. Flagstaff, Arizona, USA. 2 pp.

Usher, H. D., D. W. Blinn, G. C. Hardwick, and W. C. Leibfried. 1986. Cladophora glomerata and its diatom epiphytes in the Colorado River through Glen and Grand Canyons: Distribution and desiccation tolerance. GCES Report #B-8. 73 pp.

Usher, H. D. and D. W. Blinn. 1990. Influence of various exposure periods on the biomass and chlorophyll A of Cladopora glomerata (Chlorophyta). J. Phycol. 26: 244-249.

van der Werff, A. 1955. A new method of concentrating and cleaning diatoms and other organisms. Verhand. Inter. Ver. Limnol. 12: 276-77.

Ward, J. V. 1982. Ecological aspects of stream regulation: response in downstream lotic reaches. Water Pollut. Manage. Rev. 2: 1-26.

______ and J. A. Stanford. 1979. The Ecology of Regulated Streams. Plenum Press. New York and London. pp. 35-55.

Watanabe, T., T. Takeuchi, and C. Ogino. 1979. Studies on the sparing effects of lipids on dietary protein in rainbow trout (Salmo gairdneri). in Ed. Halver, J. E. and K. Tiens. Proc. World Symp. on Finfish, Nutrition and Fishfeed Technology. vl. Berlin Heeneman.

Waters, T. F. and J. C. Hokenstrom. 1980. Annual production and drift of stream amphipod Gammarus pseudolimnaeus in Valley Creek, Minnesota. Limnol. and Oceanogr. 24(4): 700-10.

Wetzel, R. G. 1983. Limnology. 2nd Ed. W. B. Saunders Co. Philadelphia. 767 pp.

Whitton, B. A. 1970. Biology of Cladophora in freshwaters. Water Res. 4: 457-76.

Willers, W. B. 1981. Trout Biology. Univ. Wisc. Press. Wisc. 206 pp.

Willoughby, L. G. and R. Earnshaw. 1982. Gut passage times in Gammarus pulex (Crustacea: Amphipoda) and aspects of summer feeding in a stony stream. Hydrobiol. 97: 105-17.

______. and D. W. Sutcliffe. 1976. Experiments on feeding and growth of the amphipod Gammarus lacustris (L.) related to its distribution in the River Duddon. Freshw. Biol. 6: 577-86.

Wiltens, J., V. Schrieder, and W. Vidaver. 1978. Chlorophyll flourescence induction: An indicator of photosynthetic activity in marine algae undergoing desiccation. Can. J. Bot. 56: 2754-87.

Wirsen, C. O. and H. W. Jannasch. 1983. In situ studies on deep-sea amphipods and their intestinal microflora. Mar. Biol. 78(1): 69-73.

Wong, S. L., B. Clark, M. Kirby, and R. F. Kosciaw. 1978. Water temperature and seasonal periodicity of Cladophora glomerata and Potamogeton pectinaus in shallow rivers. J. Fish. Res. Bd. Can. 35: 866-70.

Wood, K. G. 1968. Photosynthesis of Cladophora under unnatural conditions. pp 121-133 in Ed. Jackson, D. F. Algae, Man and Environment. Syracuse Univ. Press. Syracuse, New York, USA.

Zaneveld, J. S. 1937. The littoral zonation of some Fucaceae in relation to desiccation. J. Ecol. 25: 431-68.

______. 1969. Factors controlling the delimitation of littoral benthic marine algae. Am. Zool. 9: 367-91.

BIOGRAPHICAL INFORMATION

NAME OF AUTHOR: Chris Allen Pinney

PLACE OF BIRTH: Huntington, Indiana

DATE OF BIRTH: 15 June 1958

EDUCATIONAL INSTITUTIONS ATTENDED:
Northern Arizona University, B.S. Zoology, 1982
Northern Arizona University, M.Sc. Biology, 1991.

PROFESSIONAL POSITIONS HELD:
Coconino National Forest, Mormon Lake Ranger District,
Wildlife Biologist, 1990 to Present.
Kaibab National Forest, Supervisor's Office,
Wildlife Biologist, 1989 to 1990.
Northern Arizona University,
Research Assistant, 1984 through 1986.
National Marine Fisheries Service (Alaska),
Foreign Fisheries Biologist, 1982 through 1983.