

565 GCES #12  
ENV-4.0  
C719  
18226

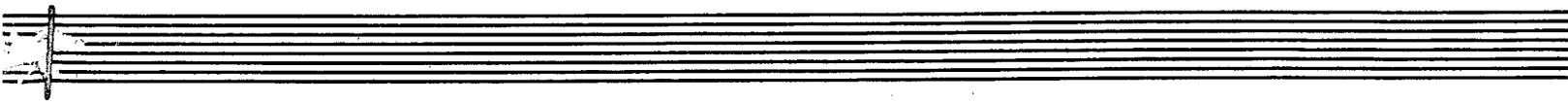
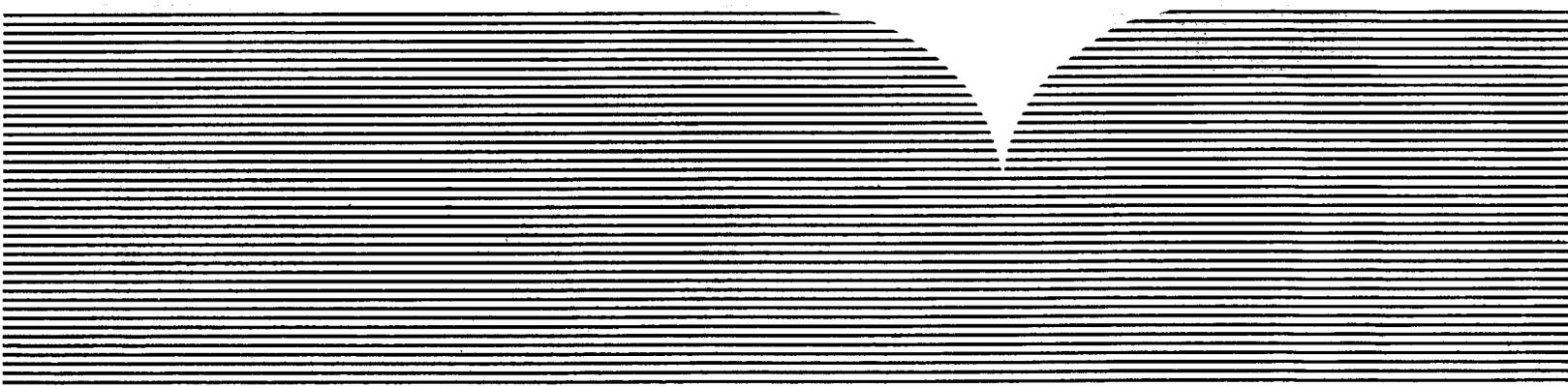
PB88-183454

Cladophora glomerata and Its Diatom  
Epiphytes in the Colorado River through  
Glen and Grand Canyons  
Distribution and Desiccation Tolerance

(U.S.) Glen Canyon Environmental Studies  
Flagstaff, AZ

**GCES OFFICE COPY  
DO NOT REMOVE!**

Sep 87



7

**U.S. DEPARTMENT OF COMMERCE  
National Technical Information Service**



565.00  
ENV-4.00  
C719  
18226 c.i. AQU404

AQU404

CLADOPHORA GLOMERATA AND ITS DIATOM EPIPHYTES  
IN THE COLORADO RIVER THROUGH GLEN AND GRAND CANYONS:  
DISTRIBUTION AND DESICCATION TOLERANCE

Contract No.: 6400042

Submitted by:

H.D. Usher, D.W. Blinn, G.G. Hardwick and W.C. Leibfried  
Department of Biological Sciences  
Northern Arizona University  
Flagstaff, Arizona  
86011

Submitted to:

Mr. James deVos and Mr. Henry Maddox  
Arizona Game and Fish Department  
Phoenix, Arizona  
85023

Final Report  
Glen Canyon Environmental Studies

September 1987



## ABSTRACT

Standing crop of Cladophora glomerata in the Colorado River through Glen and Grand Canyons decreases significantly with distance downstream of Glen Canyon Dam. Standing crop of Cladophora also shows a significant increase with increasing depth. Density of epiphytic diatoms on Cladophora decreases significantly with distance downstream of Glen Canyon Dam. The density of epiphytic diatoms also decrease significantly with increasing depth. Composition of epiphytic diatoms on Cladophora change with distance downstream of Glen Canyon Dam. Achnanthes affinis-minutissima, Cocconeis pediculus, Diatoma vulgare and Rhoicosphenia curvata decreased in importance with distance downstream of Glen Canyon Dam.

Laboratory experiments and field observations show that exposure and desiccation of Cladophora and its epiphytes, result in a significant decrease of standing crop and cell density. Depending on local atmospheric conditions, exposures of 12 hours in duration can result in significant reductions in standing crop of Cladophora. One time exposure and repeated cycles of exposure and rewetting both result in a significant decrease in standing crop of Cladophora. Over a two week period a comparison of one time exposures to repeated cycles of exposure and rewetting, the repeated cycles showed greater losses.

Daily fluctuations from 5,000 cfs to 25,000 cfs, with exposure periods of 12 hours or more, should be avoided. Glen Canyon Dam should be operated in such a manner as to minimize daily fluctuations. Investigations of the effects of exposure periods of less than 12 hours in duration should be conducted to determine their impact on the standing crop of Cladophora below Glen Canyon Dam.

#### ACKNOWLEDGEMENTS

The authors of this report would like to acknowledge those people whose help made this study possible. While on collecting trips, both at Lees Ferry and downstream in Grand Canyon, Chris Pinney, Behrooz Dehdashti, Jane Ayers, Roland Wass, Peggy Pollak, Matthew Tallarovic and the Humphrey Summit crew provided valuable field assistance. The Glen Canyon National Recreation Area and Grand Canyon National Park provided the necessary collecting permits and Tom Workman, Patty Horn and John Dick, of the National Park Service, provided us with access to our study area at Lees Ferry. Behrooz Dehdashti, Chris Pinney, Jane Ayers and Deb Comly also provided assistance in the lab, processing Cladophora samples, monitoring desiccation experiments and/or doing statistical analysis. Lane Krahl built the dryer that was used to air dry Cladophora before processing in the lab. Oars Inc., Wilderness World Inc. and SWCA helped in the transport of Colorado River water from Lees Ferry to our experimental stream tanks at Northern Arizona University. Chris Sacchi and Ken Paige were consulted on the statistical analysis of the data. The illustrations were done by Ruth Ann Border of NAU University News and Publications, Gloria Judges Edwards and the graphic arts staff at the Bilby Research Center. We would also like to thank Dave Wegner, Glen Canyon Environmental Studies manager, and the Bureau of Reclamation for the loan of a second artificial stream tank which enabled us to increase our sample size during later desiccation experiments. We also acknowledge and appreciate the invaluable encouragement and support which Dave Wegner and his office provided throughout the course of this study. Finally, this research was conducted under contract (#6400042) with the Arizona Game and Fish Department as a part of the Glen Canyon Environmental Studies which was sponsored by the U. S. Bureau of Reclamation.

## TABLE OF CONTENTS

	PAGE
List of Tables . . . . .	ii
List of Figures . . . . .	iv
List of Plates . . . . .	v
Chapter One: Introduction . . . . .	1
Chapter Two: Objectives . . . . .	3
Chapter Three: <u>Cladophora glomerata</u> : A Literature Review . . . . .	4
Life History, Reproduction and Seasonality . . . . .	4
Nutrients . . . . .	6
Temperature . . . . .	8
Light . . . . .	10
Desiccation . . . . .	12
Epiphytes. . . . .	16
Summary . . . . .	20
Literature Cited . . . . .	23
Chapter Four: Methods and Materials . . . . .	32
A. <u>Cladophora glomerata</u> ; Distribution and Standing Crop . . . . .	32
B. Epiphytes; Standing Crop, Composition and Distribution. . . . .	33
C. Desiccation Tolerance of <u>Cladophora glomerata</u> ; Laboratory Experiments . . . . .	33
Chapter Five: Results . . . . .	35
A. <u>Cladophora glomerata</u> ; Distribution and Standing Crop . . . . .	35
B. Epiphytes; Standing Crop, Composition and Distribution. . . . .	36
C. Desiccation Tolerance of <u>Cladophora glomerata</u> ; Laboratory Experiments . . . . .	37
Chapter Six: Discussion . . . . .	68
Chapter Seven: Conclusions and Operating Criteria . . . . .	74
Chapter Eight: Research Report; Literature Cited . . . . .	77

## LIST OF TABLES

	PAGE
Table 1. Seasonal standing crop (gm/m <sup>2</sup> ; dry weight) estimates of <u>Cladophora glomerata</u> at selected reaches in the Colorado River through Grand Canyon National Park. . . . .	39
Table 2. ANOVA Table of three-way interactions between collection site (site), depth cell (cell) and date of collection (date) with <u>Cladophora</u> biomass as the dependent variable. . . . .	41
Table 3. ANOVA Table of two-way interactions between collection site (site) and depth cell (cell) with percent ash free dry weight as the dependent variable. . . . .	43
Table 4. Ash-free dry weight/dry weight (AFDW/DW) of <u>Cladophora glomerata</u> at selected sites in the Colorado River during 21-23 October 1984. . . . .	44
Table 5. One-way ANOVA table for <u>Cladophora</u> biomass by collection site . . . . .	45
Table 6. One-way ANOVA table for <u>Cladophora</u> biomass against date of collection. . . . .	45
Table 7. ANOVA Table of two-way interactions between depth cell (cell) and collection date (date) at Lees Ferry with <u>Cladophora</u> biomass as the dependent variable. . . . .	47
Table 8. List of epiphytic diatoms identified from <u>Cladophora glomerata</u> samples collected in October 84. . . . .	50
Table 7. Mean densities for dominant epiphytic diatom species (cells x 10 <sup>4</sup> /cm <sup>2</sup> ) at selected sites along the Colorado River. . . . .	53
Table 10. One-way ANOVA table for total epiphyte diatom cell density by collection site. . . . .	55
Table 11. Total mean densities of epiphytic diatoms (cells x 10 <sup>4</sup> /cm <sup>2</sup> ) at selected sites along the Colorado River. . . . .	56
Table 12. ANOVA Table of three-way interactions between collection site (site), depth cell (cell) and dominant diatom species (spp) with diatom cell density as the dependent variable. . . . .	57

	PAGE
Table 13. ANOVA Table of three-way interactions between collection date (date), depth cell (cell) and dominant diatom species (spp) with diatom cell density as the dependent variable. . . . .	59
Table 14. ANOVA Table of the two-way interactions between the two summer test runs (run) and all six experimental test regimes (regime) with <u>Cladophora</u> biomass as the dependent variable. . . . .	62
Table 15. Atmospheric conditions at the top of the Northern Arizona University Biological Sciences Building during experimental stranding of <u>Cladophora glomerata</u> . . . . .	64
Table 16. Results of the Orthogonal Contrast Analysis comparing <u>Cladophora</u> standing crop (gm/m ; final/initial) of the control and the different exposure periods during laboratory desiccation experiments ( acceptance at P=0.05 for all contrasts; computer P levels are provided). . . . .	65
Table 17. ANOVA tables showing the effect of repeated wetting and drying on <u>Cladophora</u> with biomass as the dependent variable. . . . .	67

LIST OF FIGURES

	PAGE
Figure 1. Standing crop of <u>Cladophora glomerata</u> at Lees Ferry during October 1984 in depth cells 1-3. . . . .	42
Figure 2. Standing crop of <u>Cladophora glomerata</u> at selected sites in the Colorado River through Glen and Grand Canyons during July 1985. . . . .	46
Figure 3. Standing Crop of <u>Cladophora glomerata</u> at Lees Ferry from October to December 1985. . . . .	47
Figure 4. Standing crop of <u>Cladophora glomerata</u> at Lees Ferry during October 1985 and in depth cells 1-3. . . . .	49
Figure 5. Frequency of the Lees Ferry four co-dominant epiphytic diatoms and remaining diatoms epiphytic to <u>Cladophora glomerata</u> with distance downstream from Glen Canyn Dam. . . . .	54
Figure 6. Standing crop of diatoms epiphytic to <u>Cladophora glomerata</u> at Lees Ferry in depth cells 1-3 during July. . . . .	58
Figure 7. Standing crop of diatoms epiphytic on <u>Cladophora glomerata</u> at Lees Ferry following steady flows (Oct 1985) and regulated flows (Dec 1985) in depth cells 1-3. . . . .	60
Figure 8. Standing crop of the four Lees Ferry co-dominant epiphytic species at Lees Ferry following steady flows (Oct 1985) and regulated flows (Dec 1985). . . . .	61
Figure 9. Percent standing crop following experimental exposures. . . . .	63
Figure 10. Percent standing crop after two week period at repeated cycles of exposure and rewetting. . . . .	66

LIST OF PLATES

PAGE

Plate 1. Bleached (presumably non-viable) filaments  
near the basal holdfast and viable green filaments  
at the terminal tufts. . . . . 71

## CHAPTER ONE: INTRODUCTION

Early in 1963 the floodgates of Glen Canyon Dam were closed and the ecology of the Colorado River through Grand Canyon was set on a new course. The onset of regulated flow initiated diurnal fluctuations of cool, clear water from the bottom of Glen Canyon Dam. These new conditions provided suitable habitat for the establishment of the filamentous green alga Cladophora glomerata as well as the introduction of both an amphipod, Gammarus lacustris, and rainbow trout.

The Lees Ferry and Glen Canyon Dam tailwater fishery which has developed is considered to be one of the Southwest's "blue ribbon" fisheries. For a long time many have believed that the most important food item in the diets of trout in this fishery was Gammarus and that Cladophora only provided an important refugium for the Gammarus. The occurrence of Cladophora in the diets of trout was initially thought to be only incidental to the taking of Gammarus (Bancroft and Sylvester 1978). Recently however, it has been suggested that diatoms epiphytic to Cladophora may be providing the trout with a nutritional supplement (Carothers and Minckley 1981). Although many factors regulate the condition of a fish species, it may be that reductions in the condition of mainstream trout downstream of Lees Ferry are a result of decreased food supplies (C.O. Minckley, personal communication), possibly due to a decrease in Cladophora and its epiphytes.

Whitton (1970) provided a review on the biology of Cladophora. Nowhere in this review, or anywhere else in the literature, is there any quantification of Cladophora distribution or seasonality in the Colorado River through Glen and Grand Canyons. Since the completion of his review additional studies have been directed toward understanding the ecology of Cladophora, particularly in marine systems and 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). In none of these studies however, is the effect of exposure (desiccation) on Cladophora or the biology of Cladophora in a dam tailwater ever discussed. In light of the potential importance of Cladophora and its epiphytic diatoms to the fishery below Glen Canyon Dam this report attempts to address these two issues, particularly the problem of fluctuating flow and the effect of exposure on Cladophora and its epiphytes. Although the effect of seasonality may be important in the interpretation of field data, under fluctuating flow conditions it is impossible to determine its effect. For the purpose of this report fluctuating flows will refer, but not be limited, to flows that approach daily fluctuations of approximately 20,000 cubic feet per second (cfs); such fluctuations were observed during the experimental period beginning in October 1985 and carrying on through January 1986. Chapter Three of this report provides an up-date of Whitton's 1970 review and the succeeding chapters deal with field observations of the distribution of Cladophora as well as field and laboratory studies of the effects of exposure and desiccation on Cladophora glomerata. Two

literature cited sections are included in this report; one at the end of Chapter Three, the literature review, and another, Chapter Eight, for the remaining chapters of the report.

## CHAPTER TWO: OBJECTIVES

The objectives of this study are:

1. Conduct a thorough literature review on the ecological tolerances of Cladophora glomerata and associated epiphytes on those factors potentially significant in regulated rivers (e.g. desiccation, temperature, light, nutrient requirements and discharge). The life history strategies and resistant stages of Cladophora glomerata are also reviewed.
2. Determine the standing crop of Cladophora glomerata along various reaches of the Colorado River through Glen and Grand Canyons.
3. Quantify the standing crop and composition of the epiphytic diatom assemblage on Cladophora glomerata along the same reaches of the Colorado River.
4. Measure the influence of various desiccation regimes on the standing crop of Cladophora glomerata in the laboratory.
5. Examine the influence of desiccation on the standing crop and composition of the epiphytic diatoms.

CHAPTER THREE: CLADOPHORA GLOMERATA; A LITERATURE REVIEW

Cladophora glomerata is a highly branched filamentous green alga that attaches by rhizoidal cells to a wide range of substrates in current swept or wave-washed alkaline waters. According to Whitton (1970), activities of man have played a major role in the success of this alga throughout the world. One such activity, the construction of Glen Canyon Dam near Lees Ferry, has resulted in diurnal fluctuations in water level as well as a reduction in suspended sediment and water temperature. A consequence of this change in physical habitat has been the prolific growth of C. glomerata.

Based on previous studies (Moffett 1942, Mullan et al. 1976, Bancroft & Sylvester 1978, Carothers & Minckley 1981), C. glomerata appears to be an important food item for rainbow trout in the Colorado River and may be partially responsible for the Blue Ribbon status of the Lees Ferry fishery. Mats and tufts of Cladophora also provide a refugium for many small invertebrates (Haury 1981) and possibly play a fundamental role in the food web in the tailwaters of Glen Canyon Dam (Persons et al. 1985), by providing a substrate for the growth of a myriad of energy-rich microscopic plants, especially diatoms. Due to the potential importance of Cladophora, fisheries and resource managers have developed a great deal of interest in the status and ecology of this alga throughout the world. In fact, one entire issue of the Journal of Great Lakes Research (Vol. 8, No. 1, 1982) was recently devoted to filamentous algae, with the major emphasis on Cladophora. Even so, in the 24 years since the construction of Glen Canyon Dam there has been no quantification of distribution, seasonality or desiccation tolerance of Cladophora glomerata in the Colorado River through Glen and Grand Canyons.

The present literature review addresses those environmental parameters considered to be most important to the development of the C. glomerata population in the tailwaters of Glen Canyon Dam and in the Colorado River through Grand Canyon National Park. Particular emphasis will be given to those physical parameters (i.e. temperature, light, and desiccation) that are influential during drawdown periods when tufts of Cladophora are stranded. The nutrient requirements, reproductive strategies and resistant stages of this alga also will be addressed. Finally, the diatom epiphytes commonly associated with Cladophora, and their importance, will be examined. The conditions discussed for each parameter will be compared with the environmental regimes found within the Colorado River below Glen Canyon Dam. A discussion of the potential fate of C. glomerata populations resulting from the modification of these variables will be incorporated for each environmental parameter.

LIFE HISTORY, REPRODUCTION AND SEASONALITY.

It is generally accepted that marine species of Cladophora glomerata exhibit a diplobiontic alternation of generations (ie

have two free-living generations) with isomorphic sporophyte (2N) and gametophyte (1N) stages (Wik-Sojostedt 1970, Bold & Wynne 1985). However, freshwater species of Cladophora rarely produce functional gametes but commonly reproduce asexually by simple fragmentation, akinete formation or zoospore production (Mason 1965, Pantastico & Zenaida 1971). Production of swimming biflagellate or quadriflagellate zoospores is the least common mode of reproduction in C. glomerata (Mason 1965, Bold & Wynne 1985). Although zoospore production may be initiated by low light, they appear to be most common in some systems during May and June as light increases (Mason 1965) and as late as October in other systems (Chudyba 1965). Hoffman (1979), studying effects of various levels of temperature and light intensity on zoospore production in C. glomerata, found that a short-day photoperiod (8 hrs light and 16 hrs dark) was most optimum.

Fragmentation of vegetative branches is apparently the most common form of reproduction in C. glomerata (Mason 1965). As the dense tufts of Cladophora fragment, light reaches new branches which in turn increases the growth potential of these once shaded cells. Fragmentation of Cladophora filaments can be facilitated by a number of processes. There is evidence suggesting that epiphytic assemblages common on Cladophora may form a "nutrient shield" which could weaken filaments and increase the rate of fragmentation (Stevenson & Stoermer 1982). In addition, repeated periods of desiccation can weaken Cladophora filaments as well, further increasing the rate of fragmentation.

Akinetes are resting spores characterized by increased levels of reserve storage products, increased dry matter content and reduced metabolic activity (O'Neal & Lembi 1983). These structures are not nearly as common in Cladophora as they are in Pithophora, a closely related genus, still they are formed under some situations. Akinete formation appears to be induced by very low light conditions and with advanced age (Mason 1965, Pantastico & Suayan 1971, 1973a). Prolonged illumination with red light hastens the ageing process and increases the rate of akinete formation (Pantastico & Suayan 1973b). This may explain why Mason (1965) observed more akinetes in Cladophora filaments taken from shallow water than from deeper water. Red light is rapidly absorbed and does not penetrate far into the water column. Although light intensities at the surface may be too high to induce akinete formation the amount of red light penetrating the surface water may be sufficient to increase ageing to such an extent that akinete formation will be more common.

One study suggests that akinete formation may also be a function of nutrient depletion and/or the result of desiccation due to fluctuating water levels (Rosemarin 1985). If this is the case, then fluctuating flows from Glen Canyon Dam may have a dramatic effect on the life history and reproduction of Cladophora at Lees Ferry.

The common annual growth pattern of C. glomerata in both lotic and lentic systems includes short periods of intensive growth in the spring and fall, with sharp decreases in mid-summer (Chudyba 1965, Bellis & McLarty 1967, Wood 1968, Herbst 1969, Moore 1976, Wong et al. 1978, Mantai 1982). The fall period of

growth typically yields less total biomass than the spring. Evidence also supports a late spring-early summer unimodal growth peak (Blum 1982). Mantai (1982) proposed that a negative energy balance, due to increasing water temperatures and declining light in Lake Erie, caused cells to deteriorate resulting in the midsummer die-off.

Several authors believe that initial growth in the spring originates from overwintering basal holdfasts and that the vegetative development appears to be stimulated by increasing day length (Bellis & McLarty 1967, Blum 1983). Moore (1976) concluded that day length was primarily responsible for the onset of a spring bloom of Cladophora in the River Avon, England. This conclusion was based on a rapid increase in day length while nutrients and water temperature remained stable and relatively high.

#### Tailwater Summary.

Based on the large amount of Cladophora biomass in the drift at Lees Ferry (Hauray 1981, personal observations) it appears that fragmentation may be the most common form of reproduction of this alga in the Colorado River through Grand Canyon. With increased diel fluctuations of the River, desiccation of Cladophora filaments may increase the rate of fragmentation. Although basal regeneration, production of zoospores and/or formation of akinetes may occur, none have been observed in the Colorado River. A cursory examination to detect these processes provided no data to support their occurrence. Whether these contribute much to the proliferation of Cladophora in this system is unknown. With continued fluctuating flows due to hydroelectric generation at Glen Canyon Dam, akinete formation may increase in importance as a mode of Cladophora reproduction in the Colorado River through Grand Canyon.

Seasonal growth patterns of Cladophora in the Colorado River are not yet fully understood. One might assume that the seasonal standing crop of C. glomerata would be relatively constant in the tailwaters due to the near-constant temperature conditions. The dramatic reduction in Cladophora biomass at Lees Ferry following the October 1984 test flow of 5000 cfs may have resulted from desiccation or seasonal die-off (see Chapter Four of this study). Investigations concerning seasonal growth patterns are in progress but their results will be difficult to interpret due to the irregular flows and the lack of baseline information prior to fluctuating flow regimes. If a seasonal growth pattern does exist the main seasonal growth regulator may be light or nutrient load rather than temperature in that water temperature remains relatively constant year round.

#### NUTRIENTS

Well developed growths of Cladophora have been associated with areas of moderate to high nutrient concentration and therefore the alga is thought to be favored by such environments (Herbst 1969, Whitton 1970, Pitcairn & Hawkes 1973, Lowe 1979, Jackson & Hamdy 1982, Wharfe et al. 1984). In most of these cases the high nutrient levels have been a function of human

activity such as urbanization and agriculture. These activities have artificially elevated phosphorous (P) and nitrogen (N) levels through sewage effluent and agricultural runoff.

Phosphorous has been identified as the major nutrient contributing to overgrowths of Cladophora downstream of sewage effluents (Pitcairn & Hawkes 1973) and the major limiting nutrient in other systems as well (Bolas & Lund 1974, Thomas et al. 1979, Jackson & Hamdy 1972, Neil & Jackson 1982). Pitcairn and Hawkes (1973) confirmed the importance of P by showing that growth of Cladophora in waters upstream of sewage discharges could be increased to downstream growth levels by the addition of P.

Many studies on limiting nutrient levels have been conducted which have resulted in much controversy and a wide range of P concentrations considered to be critical to the growth of Cladophora. Using flask cultures, Pitcairn and Hawkes (1973) reported that growth was significantly reduced by levels below 1.0 mg/l total phosphorous (TP) and that 0.5 mg/l TP was limiting. Wong and Clark (1976) observed a direct relationship between P concentration in the water and the P content of the Cladophora tissue and reported a much lower growth limiting P concentration of 0.06 mg/l TP for six streams in northern Ontario. This lower critical concentration may be a function of flowing water reducing the diffusion gradient between waste material in the cells and nutrients in the water (Whitford 1960, Whitford & Schumacher 1961).

Eichenberger (1967 a, b) found that Cladophora grew best at intermediate nutrient levels. These findings appear to be supported by Pitcairn and Hawkes (1973) who reported maximum growth of Cladophora at 1.5 mg/l TP with no significant increase in growth above that concentration. In addition they reported that P levels above 3.0 mg/l inhibited growth. On the other hand, Thomas (1975) reported prolific growth in areas with 15 ug/l (0.015 mg/l) TP. This may suggest that the interaction of P with some other physical-chemical parameter(s) is important.

Unlike P, the N content of water alone does not show a significant correlation with growth of Cladophora (Wong & Clark 1976, Mantai et al. 1982, Manuel-Faler et al. 1984). In association with P, however, the importance of N becomes significant. The effects of N and P on Cladophora growth are not independent and the ratio (P:N) of one to the other, appears to be very important (Whitton 1970, Pitcairns & Hawkes 1973). Whitton (1970) suggests that high P:N favors growth of Cladophora while Neil and Jackson (1982) suggest that high N:P (150:1) may be limiting. Based on the work of Pitcairn and Hawkes (1973) it is quite clear that some interactions do exist. Exactly what the relationship is between N, P and Cladophora is not yet completely understood.

Very little work has been done on the importance of trace elements with regard to growth and distribution of Cladophora. Whitton (1970) indicated that Cladophora is sensitive to high concentrations of heavy metals, particularly zinc and copper. It is interesting to note that silicon is present in the cell walls of C. glomerata and an essential nutrient to this species (Moore & Traquair 1976).

### Tailwater Summary.

Total phosphorus analyzed from river water taken in the Lees Ferry area, by the U.S. Bureau Reclamation (USBUREC data) showed little spatial variation in ambient concentration from the Glen Canyon Dam to the confluence with the Paria River (unpublished USBUREC data) for any season. In another study Cole and Kubly (1976) showed dramatic seasonal differences in phosphorus concentrations. In their study total phosphorus concentrations ranged from 9.8 ug/l (0.01 mg/l) in June and August to 234.7 ug/l (0.24 mg/l) in March. If we accept Wong and Clark's (1976) estimate of the critical limiting concentration (0.06 mg/l) of TP for Cladophora, then Cole and Kubly's (1976) data indicate that critical TP levels are reached in the Lees Ferry area in the late spring (61.9 ug/l) (0.062 mg/l) in April and May and remains well below critical levels throughout the summer. In addition, unpublished Bureau of Reclamation data (1984, 1985) suggest that TP during October and January falls well below critical levels, 0.026 and 0.011 mg/l, respectively.

Personal observations suggest that these low levels of TP are not limiting to Cladophora in the Colorado River near Lees Ferry. Two reasons may account for this. First, larger algae such as Cladophora have a large intracellular nutrient storage capacity which may provide nutrients during periods of low ambient nutrient concentration. Based on this ability it is uncertain that lowering available nutrients will reduce plant growth (Wong and Clark 1976). Second, as indicated earlier, algae in flowing water systems have the ability to function successfully at lower nutrient concentrations than algae in standing bodies of water. This is due to current providing a constant supply of nutrients while washing away metabolic wastes therefore reducing the diffusion gradient between the algal cells and the surrounding environment (Whitford 1960, Whitford and Schumacher 1961). There is no indication to date to suggest that fluctuating flows will have any major effect on nutrient availability below Glen Canyon Dam.

### TEMPERATURE

Cladophora glomerata has been reported from a wide range of temperature conditions throughout the world (Whitton 1970) and frequently dominates the cool nutrient-rich tailwaters of dams (Lowe 1979). Field observations have suggested that C. glomerata has a bimodal growth pattern with maximal growth associated with water temperatures at 15 C and 4 C, which corresponds to its peak growth during late spring and fall with a minimum during the period of highest water temperatures in the summer (Herbst 1969, Bellis & McLarty 1967).

Based on the literature, it appears that optimum temperature for measurable growth of Cladophora, as determined by cell measurements and standing crop, is between 10 C (50 F) and 30 C (86 F). Whitton (1967) found that rapid growth of this alga took place in the River Wear between 15 C (59 F) and 25 C (77 F), with 6 C (42.8 F) and 30 C (86 F) the lower and upper limits, respectively, for measurable growth. Bellis (1968) found that laboratory cultures of C. glomerata collected from Midway Creek,

Ontario, grew best at 15 C (59 F) and 30 C (86 F), with no growth at 5 C (41 F) and only slight growth at 10 C (50 F). Vegetative cells were killed when exposed to temperatures over 30 C (86 F) and overnight freezing temperatures of -5 C (23 F). Storr and Sweeney (1971) reported that the optimal temperature for growth of C. glomerata in Lake Ontario was 18 C (64.4 F) and that growth stopped at 25 C (77 F). Moore (1978) noted the appearance of C. glomerata in Lake Erie at 11 C (51.8 F) with optimum growth at 26 C (78.8 F). In a flowing water system in Ontario, Wong et al. (1978) identified the temperature limits for the growth of Cladophora as 11 C (51.8 F) to 23 C (73.5 F). There has been one unusual report where C. glomerata was collected from a cooling tower that was approaching 40 C (104 F) (Sladeckova 1969).

There has been an interest in determining the role of temperature on certain metabolic processes of Cladophora (i.e. photosynthesis and respiration). Experimental studies of this type may in fact be more valuable in determining the true role of temperature on this alga in the natural environment since these processes are directly responsible for the rate of measurable growth. Adams and Stone (1973) reported that highest rates of in situ photosynthesis occurred between 19 C (66.2 F) and 24 C (75.2) at a productive site in Lake Michigan. Graham et al. (1982) found that cultures of C. glomerata isolated from Lake Huron showed somewhat lower maxima, between 13 C (55.4 F) and 17 C (62.6 F) for optimum photosynthesis. No positive net photosynthesis was measured at 35 C (95 F), however, they did note positive photosynthesis at 2 C (35.6 F) at high light levels between 150-300 uE/m<sup>2</sup>. This low temperature is considerably below the minimum field temperature (6 C, 42.8 F) for measurable growth reported by Whitton (1967) and Bellis (1968).

#### Tailwater Summary

Regulated flow can potentially cause fluctuations in water temperature in rivers as a result of reduced water volume in the channel (Usher et al. 1984). However, if the water continues to be released from the hypolimnion then the temperature regime in the Glen Canyon area should not be affected to any extent. The mean annual water temperature in the tailwaters of Glen Canyon Dam is about 10 C +/- 1 C. Based on the literature, this temperature is within the reported range necessary for both metabolism and growth of C. glomerata; standing crop estimates for C. glomerata were over 225 g/m<sup>2</sup> in the tailwaters of Glen Canyon dam at a depth of one to two meters during October 1984 (unpublished data). This value equals or surpasses the mean annual standing crop estimates for many of the nutrient enriched sites in the Great Lakes (Millner et al. 1982, Neil & Jackson 1982, Lorenz & Herdendorf 1982).

Based on the literature it appears that increases in water temperature up to 20 C (68.0 F) would not significantly reduce the standing crop of C. glomerata in the tailwaters of Glen Canyon Dam. There is a good chance, however, that it might alter the potentially important epiphytic diatom assemblages attached to C. glomerata. Significant changes in assemblages of epiphytic diatoms do occur between 10 C (50 F) and 20 C (68 F) (Patrick 1977). If in fact these diatoms, particularly the loosely

attached Diatoma vulgare and Rhoicosphenia curvata species are an important food source for either Gammarus or rainbow trout, then changes in temperature that modify the epiphyton assemblages to species which are less palatable or more closely attached, become an important consideration.

### LIGHT

Solar radiation is an important ecological factor with respect to the growth and periodicity of C. glomerata. Experimentally, light intensity and photoperiod have received less attention than temperature. Whitton (1970) suggested that C. glomerata is favored by high light intensities. A number of reports support this statement. Jaag (1938) indicated that a series of cloudy days was enough to reduce this alga in the Upper Rhine. Blum (1957) asserts that the mid-season decline of C. glomerata in the Saline River could be related to the reduction in light intensity caused by the leafing out of overhanging vegetation.

Other studies have suggested that Cladophora is adapted to relatively low light habitats where the photosynthetic efficiency decreases above 400 micro Einsteins ( $\mu\text{E}$ )/ $\text{m}^2/\text{sec}$  (Neel 1968, Wood 1968, Adams & Stone 1973, Hoffman 1979, Graham et al. 1982). Neel (1968) found that summer growth of C. glomerata in a Kentucky stream was restricted to shaded situations. Adams and Stone (1973), using the light-and-dark bottle method to measure primary production, noted little relation between light intensity and photosynthetic rate at irradiance levels above 70 watts/ $\text{m}^2$  ( $700 \mu\text{E}/\text{m}^2/\text{sec}$ ). This suggests that photosynthetic activity of C. glomerata saturates at low light intensities. Verduin (1959), Mantai (1974) and Wood (1975) showed that photosynthesis studied by the oxygen evolution method under completely natural conditions, yielded rates two to four times higher than those reported from light-and-dark bottle studies. In comparison, Mantai (1974), using oxygen evolution method at the same sites used by Adams and Stone (1973), noted saturation levels for C. glomerata averaging 92 watts/ $\text{m}^2$  ( $920 \mu\text{E}/\text{m}^2/\text{sec}$ ) between May and October. Lester et al. (1974) found that photosynthesis for C. glomerata from Green Bay reached light saturation levels ranging from 345 to 1125  $\mu\text{E}/\text{m}^2/\text{sec}$ . Along open reaches of Sycamore Creek, Arizona, Busch and Fisher (1981) recorded in situ summer photosynthetic rates of C. glomerata that were inversely related to algal biomass. They attributed this to self-shading. In addition, they noticed that the assimilation efficiency of photosynthesis was inversely related to the light intensity.

In a closely controlled laboratory study, Graham et al. (1982) found that the optimum light intensity for C. glomerata isolated from Lake Huron fell within the range of 300 to 600  $\mu\text{E}/\text{m}^2/\text{sec}$  at 15 C (59 F). At 20 to 25 C (68-77 F) the net photosynthetic rate declined with light intensities above 300  $\mu\text{E}/\text{m}^2/\text{sec}$  and became negative with increasing light at 30 C (86 F). From their data they calculated an optimum photosynthetic light intensity of 400  $\mu\text{E}/\text{m}^2/\text{sec}$  at 15 C (59 F). At temperatures less than 3 C (37.4 F) or greater than 30 C (86 F), optimum net photosynthesis occurred at 150  $\mu\text{E}/\text{m}^2/\text{sec}$ . Lower light limits for

C. glomerata growth may therefore be considerably below those reported by Whitton (1967, 1970), Mantai (1974) and Wood (1975).

Adaptation to shade environments has been exhibited in closely related freshwater Cladophora species. Jonasson (1979) and Hunding (1979) showed that isolated colonies of C. aegagrophila had higher rates of primary production at the lowest light intensities in response to 190 days of ice cover per year in Lake Myvatn, Iceland. Van Den Hoek (1963) also concluded that C. basiramosa was shade loving in Lake Takern, Sweden.

#### Tailwater Summary

The believed absence of dramatic seasonal and diurnal temperature fluctuations in the tailwaters of Glen Canyon Dam suggest that seasonal changes in light and photoperiod may be the most important regulators of Cladophora in the Grand Canyon. If reduced flows cause appreciable fluctuations in the water temperature then the system may be adversely impacted by the effects of direct sunlight. Even so the general seasonal periodicity should remain in cycle.

In relation to light, the greatest impact of reduced or fluctuating flows on the C. glomerata community in the tailwaters of Glen Canyon Dam is the exposure to direct (unfiltered) sunlight. Wood (1968) reported that the intensity of direct sunlight inhibited the photosynthesis of Lake Erie C. glomerata during July. Van Den Hoek (1963) found that exposure of C. glomerata to strong sunlight diminished the cell diameter and the density of chloroplast reticulum. The visually evident high percentage of bleached filaments of Cladophora stranded at Lees Ferry during the 3-day drawdown in October 1984 (personal observations) agrees with their observations. The extent of impact would be dependent on the duration of the drawdown as well as the time of day, season and amount of cloud cover. The exposure of stranded C. glomerata to the full intensity of the sun, especially in the late spring and summer months, will probably result in detrimental effects from ultraviolet light. The effects of unfiltered UV light on Cladophora have not been studied to any extent. Calkins and Thordardottier (1980), however, studied Rhizoclonium, a closely related filamentous alga in the same family. They observed that Rhizoclonium inhabiting temperate high elevation waters demonstrated little or no capacity to withstand increased UV radiation.

C. glomerata appears to be well adapted to the relatively low illuminated habitats found within the shaded channel of the tailwaters of Glen Canyon Dam. The literature suggests that the photosynthetic efficiency of C. glomerata decreases above 400  $\mu\text{E}/\text{m}^2/\text{sec}$  (Graham et al. 1982). On a cloud covered day in the winter at Lees Ferry this intensity would most likely fall within the range of average measurements. On the other hand, during the summer or on cloudless winter days, the light intensity would far exceed 400  $\mu\text{E}/\text{m}^2/\text{sec}$  resulting in extreme inhibition of physiological activity of even moist tufts of stranded C. glomerata.

## DESICCATION

There is a paucity of studies pertaining to the desiccation of Cladophora and other filamentous freshwater algae. However, there are a number of studies concerning the desiccation of marine intertidal algae. This section will provide a review of this work and discuss how the results relate to C. glomerata in the Colorado River near Lees Ferry.

Early studies indicated that the vegetative stages of most algae are unable to tolerate severe desiccation and only specially adapted resting spores, such as akinetes, can survive such harsh conditions (Evans 1958). Other workers (Zanefeld 1937, 1969; Wiltens et al. 1978, Jones & Norton 1979, Dromgoole 1980) have gone to some length to elucidate the factors which help the vegetative stages of various intertidal algae cope with desiccation. The mechanisms which provide algae with the means to cope with longer periods of exposure and desiccation include characteristics which increase the resistance to water loss or enhance the plants tolerance to dehydration (Wiltens et al. 1978, Jones & Norton 1979).

The most significant difference between resistance and tolerance is not the actual changes that take place but the ability of an individual to recover to normal or near normal levels of physiological activity after rehydration (Wiltens et al. 1978). Although desiccation resistance is important it appears that desiccation tolerance is more so. This is illustrated by species of two intertidal genera which were able to survive after desiccation of 96% of their initial water content (Schonbeck & Norton 1979). In addition, Johnson et al. (1974) showed that periods of exposure were not simply tolerated but in some cases were a time of active primary production with photosynthetic rates higher than during periods of submergence. This ability to maintain a positive net rate of photosynthesis during periods of exposure and then recover initial rates after rehydration, is more complete in species which grow in the higher intertidal regions (Johnson et al. 1974, Dring & Brown 1982).

Most algae have neither the thick cuticle nor the stomata of higher plants for controlling the flux of water from metabolically active tissue. Cladophora does, however, exhibit a pseudocuticle (Bold & Wynne 1985) as well as a number of other adaptations which provide desiccation resistance. These adaptations can be classified as morphological, physiological or behavioral.

Early studies stressed the importance of morphological aspects of desiccation resistance. Zanefeld (1937) observed that intertidal Fucaceae (rockweed) inhabiting the upper tidal zones started out periods of desiccation with a greater percent water content and exhibited a slower rate of desiccation than did Fucaceae inhabiting the lower zones. This he attributed to characteristics of the cell wall. He observed that fucoids of the higher zones had a thicker cell wall and that a large portion of the water lost was from the cell wall and not necessarily from the protoplasm. Although C. glomerata has not been studied through a similar gradient it does exhibit the pseudocuticle as a part of its cell wall which is thicker than most other cell walls

found in filamentous green algae (Prescott 1978). The diameter of the cell wall of the Fucoids studied by Zanefeld (1937), decreased at a rate which coincided with the rate of water loss. After the first three hours both the rate of cell wall shrinkage and the rate of water loss decreased appreciably. Therefore, the thick cell wall of these plants in the higher tidal zones appears to act as a buffer against desiccation of cytoplasmic water.

Other authors have also recognized the importance of the cell wall (Jenik & Lawson 1967, Jones & Norton 1979, Dromgoole 1980). However, they made no correlations between cell wall thickness and desiccation resistance. These studies indicated the importance of tissue structure and physiological adaptations. Zanefeld (1937, 1969) acknowledged that the cell wall in Fucus acts in a manner similar to a colloid gel and that differences in resistance to desiccation are possibly due to biochemical or biophysical differences in protoplasm, such as increased lipid and fatty acid accumulation (McLean 1967, Wiltens et al. 1978).

The role of colloids in the cell wall may be of support, maintaining structural organization during desiccation (Dromgoole 1980). Water loss continues until the colloids of the cell wall have lost so much water that their surface is essentially dry. At this point evaporation almost reaches zero as the loss of water is stopped by a swelling of the gel. This swelling provides an impervious layer to water flow and adds structural support to the cell.

Jones and Norton (1979) suggested an alternate hypothesis. They contend that as water is lost, tissue shrinks causing a reduction in evaporative surface. Although this hypothesis appears to be in direct opposition to the previous one, both may be working simultaneously (but in different species). Whether either hypothesis applies to C. glomerata is presently unknown.

Based on the idea of an impervious layer to evaporation, several additional factors which contribute to desiccation resistance have been suggested. These include strategies which could alter the permeability of the thallus by precipitation of salts during evaporation (McCully 1968) or by the presence of a protective layer of mucilage (Berquist 1957, Evans 1959, Jones & Norton 1979). Jones and Norton (1979) observed an impervious skin formed on the mucilage of intertidal Laminaria and Fucus during periods of desiccation. They also noted that those species most resistant to water loss excreted the most mucilage. In order to conduct an independent test they put mucilage from Laminaria on wet filter paper and exposed it to desiccation. The results of this test showed a decrease in conductance as relative water content fell. These results are similar to the observations concerning biocolloids (Zanefeld 1937, 1969, Jones & Norton 1979). On the other hand, Dromgoole (1980) challenged the observations of Berquist (1957) that mucilage retarded the dehydration of Ecklonia. In repeated experiments with washed and unwashed blades, there was no difference in desiccation rate recorded. These findings are in accord with Edwards (1951) who suggested that mucilage is a selective barrier to macromolecules, but is very permeable to water. It is important to note that although C. glomerata does not exhibit a mucilage layer it does host a dense layer of epiphytic diatoms which do secrete

mucilage. In addition, a thin layer of salt precipitate has been observed on some exposed C. glomerata filaments during our current study.

Many terrestrial plants avoid drought by adopting a low surface area to mass ratio. For young fucoid algae, Schonbeck and Norton (1979) recorded a progressive decrease in ratio of surface area to volume from the lower tidal species to the upper species. They also noted a close correlation between percent dry matter of the thallus and the amount of bound water, but in contrast to earlier studies of plants with high water content (Zanefeld 1937, 1969), there was not a tendency for greater desiccation resistance. Dromgoole (1980) agreed that the rate of desiccation is related to the ratio of the evaporating surface area to volume of the thallus and to a lesser extent by the water content.

For Cladophora there is a conflict when it comes to the surface area to volume ratios. Although a high surface area to volume ratio increases the rate of desiccation it is also important for nutrient exchange and light absorption as well as reabsorption of water upon submergence after desiccation. To some extent, Cladophora and many intertidal algae have overcome this dilemma by adopting a complement of branched thalli. While submerged, the plant is displayed for maximum light reception and nutrient exchange but when dewatered it collapses in on itself with overlapping fronds and branches which protect each other from desiccation (Evans 1959, Jones & Norton 1979, Quadir et al. 1979, Schonbeck & Norton 1979, Dromgoole 1980, personal observations). In natural stands of intertidal algae, branch overlap was estimated to reduce the area of exposed thalli to only 20% of that exposed by isolated plants (Schonbeck & Norton 1979). In addition, field results showed that the exposed upper portions of plants were subjected to faster desiccation rates than the lower portions. In effect, the holdfast of one individual was being protected by the fronds of its neighbor (Hodgson 1981).

Environmental conditions and period of day have also been studied with regard to algal desiccation. Factors which correlate with increased rates of desiccation include, exposure during daylight hours, ambient temperature, relative humidity, shading and wind speed (Jenik & Lawson 1967, Zanefeld 1969, Schonbeck & Norton 1978, Quadir et al. 1979). The results obtained by Jenik and Lawson (1967) showed much greater algal desiccation during daytime hours. Zones were periodically thinned on days when neap tides coincided with drying conditions such as high ambient air temperatures, low humidity and brisk wind (Zanefeld 1937, 1969, Schonbeck & Norton 1978). In contrast, on days with cloud cover mild temperatures, high humidity or with breeze carrying spray from breaking waves, less desiccation will occur. From these observations Jenik and Lawson (1967) concluded that nocturnal exposure of intertidal algae during neap tides is not a limiting factor.

Although Wiebe (1966) indicated that freezing may alter the moisture release curves of cytoplasmic colloids, Schonbeck and Norton (1978) suggested that cold temperatures and prolonged frost had no adverse effects. Additional evidence to support

this claim is provided by Kanwisher (1957) who observed Fucus vesticulosus photosynthesizing after having been frozen at  $-40^{\circ}\text{C}$  and by Biebl (1962) who reported 13 littoral species which survived ambient air temperatures of  $-8^{\circ}\text{C}$ .

The microclimate, including thallus temperature and boundary layer humidity, are also important in desiccation rate (Jones & Norton 1979, Dromgoole 1980, Dring & Brown 1982). Thallus temperature is lower than that of the surrounding air at high levels of hydration but can become greater than air temperature as desiccation proceeds, resulting in a slight potential increase in desiccation rate (Dromgoole 1980). In one experiment with Fucus serratus, photosynthesis was measured for 10 hours in 100% humidity at the boundary layer. No decline in photosynthetic rate was observed (Dring & Brown 1982).

#### Tailwater Summary

This section has covered principles developed in studies of marine intertidal algae. Cladophora in the tailwaters of Glen Canyon Dam inhabits a freshwater intertidal zone and therefore these principles should have relevance here as well. Also several species of Cladophora inhabit the spray zone in marine systems. Several of these desiccation resistant adaptations are found in C. glomerata at Lees Ferry. First, C. glomerata is a filamentous green alga which grows in tufts. Although its surface area to volume ratio is undoubtedly high, its tufted filamentous nature collapses in on itself and its neighbors, forming an overlapping mat of filaments and tufts to provide protection against desiccation. As do some intertidal algae, C. glomerata has a thick cell wall. Cladophora does not produce mucilage, however, it does support a dense growth of epiphytic diatoms. Although the benefit gained by these two adaptations is debatable, the diatom assemblage may provide an additional layer of protection against desiccation and the thick cell wall might supply structural support to cells with lowered water content during exposure.

To our knowledge, no physiological studies concerning desiccation tolerance have been completed on C. glomerata. However, a marine representative of the genus, Cladophora repens, exhibited very low photosynthetic rates when exposed and a very poor recovery rate after rewatering (Dawes et al. 1978). This may indicate a very low tolerance to desiccation for C. repens and, disregarding possible physiological variability between the two closely related species, one might speculate the same to be true for C. glomerata.

During the spring and summer, Glen and Grand Canyons provide a harsh, inhospitable environment for exposed algae. Based on peaking power demand at Glen Canyon Dam, periods of greatest exposure for C. glomerata in the vicinity of Lees Ferry, where it is most prolific, would occur during the night when the conditions should be less harsh. Such a flow pattern would mitigate the hot daytime temperatures, low humidity and warm breezes occurring during the day. Whether this mitigation would be sufficient to maintain the present Cladophora community is not known. Downstream low flow periods do not always coincide with nighttime hours because of the lag-time between release at Glen

Canyon Dam and appearance at a given location. As a result, some areas would be subjected to severe desiccation conditions and possible reduction of biomass. During the winter, occasional freezing temperatures at night should have damaging effects on exposed Cladophora, however, the cool temperatures, lower light and long canyon shadows during the day would result in relatively hospitable conditions to exposed C. glomerata.

#### EPIPHYTES

The mucilage free filaments of C. glomerata provide an excellent substrate for the attachment of various groups of epiphytic algae. In addition, its thick growths and highly branched nature provide a refuge from the disruptive forces of current and wave action. Cladophora can support populations of epiphytes whose densities are so great that the green color of the alga is masked, and quantification is difficult. In comparison to 1.2 epiphytic algal cells/mm on Bangia, a mucilage producing red alga, Cladophora can support as many as  $1.32 \times 10^6$  cells/mm<sup>2</sup> (Lowe et al. 1982). In one case, epiphytic diatoms made up over 60% of the biomass of the Cladophora-epiphyte assemblage observed in Lake Huron (Stevenson & Stoermer 1982).

The epiphytes found on Cladophora form an important, diverse and structurally complex group of microscopic algae. This three dimensional community is comprised of adnate (closely appressed) forms as well as cells that attach by means of a mucilage stalk or loose filamentous colonies. These colonies attach to the Cladophora host by means of a small mucilage pad on the basal cell.

These epiphytes are important components of energy flow in aquatic systems. Epiphytic 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 & Stoermer 1982). One amphipod in particular, Gammarus pulex L., a close relative of G. lacustris L. in the Colorado River at Lees Ferry, has been reported grazing on diatoms from Cladophora filaments in several rivers (Moore 1975).

As many as 245 algal taxa have been reported as epiphytes on Cladophora (Stevenson & Stoermer 1982). Of this community, diatoms are by far the most common group making up as much as 95% of the total non-filamentous epiphytic algae (Parker & Brown 1982). The diatoms (Bacillariophyceae) are followed in importance by green algae (Chlorophyta), and blue-green algae (Cyanobacteria) (Chudyba 1965, Czarnecki et al. 1976, Moore 1977, Stevenson & Stoermer 1982). Species of Chrysophyta, Euglenophyta, Rhodophyta and Xanthophyta have also been identified as epiphytic on Cladophora, but these groups do not appear to play a major role in the community (Chudyba 1965, Moore 1977). In a number of studies on diatoms epiphytic on Cladophora, three species reoccur as dominant members of the community. They are Cocconeis pediculus Ehr., Diatoma vulgare Bory and Rhoicosphenia curvata (Kutz.) Grun. (Chudyba 1965, Ronnberg & Lax 1980, Sheath & Morison 1982, Lowe et al. 1982). These diatoms are also included on a list of the most common and

probably most important epiphytes of Cladophora glomerata in the Grand Canyon (Czarnecki & Blinn 1978). Peterson (1984) also found these 3 species to be important in the tailwaters of Hoover Dam. Cocconeis pediculus is adnate with curved valves that adhere so well to Cladophora filaments that even though the epitheca (top valve) may get dislodged, the hypotheca (bottom valve) will most often remain attached (Lowe et al. 1982). Such a close adherence to the filament provides a protection against grazing (Patrick 1948) which decreases the availability of this species as a food item. Diatoma vulgare attaches by a short mucilage pad and then divides, forming a loosely arranged, multicellular, zig-zag chain. Rhoicosphenia curvata is attached to Cladophora filaments by a short mucilage stalk (Lowe et al. 1982). Due to the loose attachment of these two species, particularly D. vulgare, they may be important food to grazing macroinvertebrates and possibly rainbow trout.

Czarnecki and Blinn (1978) described each of these diatoms as preferring cool flowing water. Both C. pediculus and D. vulgare are alkaliphilous and common epiphytes of Cladophora in Grand Canyon. Rhoicosphenia curvata on the other hand, can tolerate a wide range of ionic compositions and conductivities and is normally epilithic (attached to rock substrates) in Grand Canyon (Czarnecki & Blinn 1978), even though it has been observed in large numbers as an epiphyte on Cladophora (personal observations).

Czarnecki et al. (1976) also reported a number of green and blue-green algae that are common epiphytes on Cladophora in Grand Canyon. The common taxa of green algae include Mougeotia spp., Oedogonium spp. and Spirogyra spp. while the common blue-green taxa include Lynxbya perelegans Lemmerman, L. aeruginocaerulea (Kutz.) Gomont, Oscillatoria rubescens De Candolle and O. subbrevis Schmidle. These taxa generally prefer warmer water near tributary confluences and are not common in the Lees Ferry area.

In a number of diverse systems (marine, lentic and lotic), epiphyte diversity and abundance has shown definite seasonal fluctuations (Chudyba 1965, Ronnberg & Lax 1980, Stevenson & Stoermer 1982, O'Quinn & Sullivan 1983). In all four studies cited, diatom epiphytes showed two peaks; one in May and a second in September (Ronnberg & Lax 1980, Stevenson & Stoermer 1982) or October (Chudyba 1965, O'Quinn & Sullivan 1983). In addition, studies showed a definite summer decline during June and July. In the Skawa River of Poland the summer decline is dominated by green and blue-green algae with water temperatures ranging above 18-20 C (Chudyba 1965). During the Spring and Fall peaks diatoms dominate the system at water temperatures of 2-16 C (Chudyba 1965).

Most authors agree that water temperature is the most important factor controlling seasonal fluctuations of epiphytes of C. glomerata (Chudyba 1965, Moore 1977, Stevenson & Stoermer 1982, O'Quinn & Sullivan 1983). Chudyba (1965) observed that the most abundant diatom development in the Skawa River occurred at water temperatures of 4-11 C and then decreased at temperatures exceeding 18 C. Certain green and blue-green algae will replace diatoms in warmer water (Cairns 1972, Vannote et al. 1980).

Seasonal changes in photoperiod may also be an important regulator of epiphyte seasonality (Ronnberg & Lax 1980, Stevenson & Stoermer 1982, O'Quinn & Sullivan 1983). The influence of light and temperature are very closely related and difficult to separate. Moore (1977) agrees that light influences epiphyte seasonality but states that it is of less importance than temperature. O'Quinn and Sullivan (1983) compared epilithic and epiphytic community structure in shaded and unshaded areas and observed identical species patterns in all cases. Based on these findings they reported that light intensity and substrate type had little effect on diatom distributions but that diatom seasonality was probably a function of seasonal changes in temperature and light.

O'Quinn and Sullivan (1983) further reported no apparent interaction between attached diatoms and their substrate, however, Stevenson and Stoermer (1982) indicated that the summer decline in epiphytes may be a result of nutrient limitation as a function of competition with Cladophora. They go on to say that low diatom epiphyte abundance and diversity in the summer indicates that Cladophora was the better competitor. This observation is supported by the findings of Fitzgerald (1969) who reported that low epiphyte standing crop in low nitrogen water was due to the ability of Cladophora to act as a nitrogen sink. Other epiphyte-host studies exclusive of Cladophora have documented nutrient and dissolved organic carbon exchange between the host and its epiphytes (Allen 1971, Harlin 1973, McRoy & Goering 1974, Penhale & Thayer 1980). Wong and Clark (1976) indicated that Cladophora is capable of "luxury consumption" of nutrients. This in conjunction with its thick cell walls may account for the lack of nutrient exchange with its epiphytes and its superior competitive ability.

Other host-epiphyte interactions have been suggested which appear to increase the rate of filament fragmentation. It has been reported that the best epiphyte development occurs at the basal portion of older Cladophora filaments (Kociolek et al. 1983). Stevenson and Stoermer (1982) suggested that these epiphytes may cause physical damage to the Cladophora cell walls and that they shield the Cladophora from sunlight and nutrients. Graham and co-workers (1982) have shown that growth of Cladophora is a direct function of light intensity at optimal temperatures. The shading and nutrient deficiency may physiologically weaken the basal portion of the filaments. Tension on the Cladophora cells from wave action and current velocity should be greatest near the base of the filaments where the greatest epiphyte development occurs. These phenomena working independently or in combination could easily enhance fragmentation rate of Cladophora and therefore increase downstream drift.

Contrary to the inference of Stevenson and Stoermer (1982), that wind induced wave action could rinse epiphytes from Cladophora, other authors agree that current and wave action are important to well developed diatom communities (Chudyba 1965, Horner & Welch 1981, Korte & Blinn 1983). When describing C.pediculus, D.vulgare and R.curvata, Czarnecki and Blinn (1978) refer to each as a rheophil (current lover). Chudyba (1965) suggested that a "medium current" of 25-30 cm/sec was important

for epiphyte development. Furthermore, Ronnberg and Lax (1980) observed the best diatom development at sites open to natural and artificial (boat wake) wave action. Chudyba (1965) did however, observe that a rise in current velocity above average, as a result of increasing flow, caused an intermediate drop in epiphyte density.

In a recent study by Peterson (1984) in the tailwaters of Hoover Dam, benthic diatom communities in sheltered, eddy environments were more fragile and exhibited both lower resistance and less resilience to fluctuating flows than diatom communities developed in fast current. He also found that fluctuating flow enhanced diatom species diversity as a result of increased production of mucilage by resident species subjected to fluctuating flow regimes. He proposed that the increased production of mucilage provides additional substrate for species to colonize.

### Tailwater Summary

Water released from Glen Canyon Dam during 1984-1985 maintained a relatively constant temperature which, in the Lees Ferry area, stayed at about 9-10 C (48.0-50.0 F)(unpublished provisional data, U.S. Geological Survey). If water temperature is the most important regulator of seasonal changes in epiphyte composition and density, then epiphytes in the Lees Ferry area should remain relatively constant. In addition, temperatures of 9-10 C (48.0-50.0 F) fall within the optimum range for epiphytic diatoms reported by Chudyba (1965). This temperature regime favors diatoms over green and blue-green algae and provides a good year-round food source for organisms such as Gammarus lacustris. If on the other hand, epiphyte seasonality is shown to occur, then it is probably not regulated by temperature, but possibly by light and/or some internal periodicity as suggested by Ronnberg and Lax (1980).

If competition for nutrients does exist between Cladophora and its epiphytes as Stevenson and Stoermer (1982) suggested, then it should be of little consequence near the dam but increase in importance downstream. Based on the available nutrient data (Cole & Kubly 1978, U.S. Bureau of Reclamation 1984, 1985), some seasonality in competition might be expected as nutrient concentrations become reduced in the summer. Stevenson and Stoermer (1982) reported that Cocconeis pediculus is a good competitor for nutrients with Cladophora. If this is true then Cocconeis pediculus should increase in dominance in the summer and downstream from the dam as nutrients are assimilated and reduced. Due to its tight adherence to Cladophora, C. pediculus is not as readily available as a food item (Patrick 1948) as the loosely attached D. vulgare. Therefore this might indicate a decrease in food quality downstream.

The greatest potential for epiphytes appears to exist upstream near the dam where optimum nutrient concentrations and temperature conditions exist. If epiphytes increase the fragmentation rate of Cladophora by creating a light and nutrient shield and by damaging the cell wall, like some authors suggest, then the fragmentation rate should be greatest near the dam. Fragmentation in this area would provide a source of drifting

Cladophora heavily laden with epiphytes. If this drifting Cladophora-epiphyte assemblage is an important food item for trout, then fish many miles downstream of the dam may benefit because Cladophora and its epiphytes have been observed in some quantity many miles downstream of Lees Ferry (Haury 1981, personal observations).

Fluctuating flows as a result of hydroelectric power demands might affect the Cladophora-epiphyte assemblage in two ways. First, changes in flow will affect current velocity across the entire river channel. As flow increases current velocity will change. As a result, loosely attached diatoms such as D. vulgare may be washed away. In stronger currents, diatom species which are closely appressed like C. pediculus or firmly attached by flexible mucilage like R. curvata, may be favored (Ronnberg & Lax 1980). Secondly, water temperature near shore is generally warmer than in the main current. During some seasons, near shore water temperature may reach 21 C (personal observations). These elevated water temperatures would favor the development of green and blue-green algae (Chudyba 1965). These two groups are not easily assimilated food items in comparison to diatoms. As the river level fluctuates, a wider band of Cladophora may be subjected to warmer temperatures favorable to these two algal groups. In either case, elevated temperature or current velocity, the results of fluctuating flows appear to be detrimental to the growth and persistence of easily acquired and assimilated diatom epiphytes such as D. vulgare.

#### SUMMARY

In this review we have discussed each parameter separately. In nature no one parameter works independently, but all interact to create an environment in which the biota exists. In this section we will provide a summary of the interaction of the previously discussed parameters and how the interaction of these parameters may affect the presence of Cladophora and its epiphytes in the tailwaters of Glen Canyon Dam.

Two possible ramifications of fluctuating flows in the Lees Ferry area include a potential increase in the rate of fragmentation of Cladophora and a change in the community structure of the associated epiphytic diatoms on Cladophora. Many different factors affect the fragmentation rate. During periods of desiccation one of the most important regulators is increased exposure to unfiltered solar radiation (i.e., U.V. light) This ultraviolet light effects the Cladophora in two ways which combine to weaken the filaments near the holdfast and increase the rate of fragmentation. First, the increased light inhibits physiological activity and may irreparably damage the photosynthetic pigments. The damage to the pigments may seriously limit the ability of the cell to effectively conduct photosynthetic activity when rewetted. Second, this period of exposure results in a higher evaporation rate in the daylight than in the dark (personal observations). Drying occurs much faster at the base of exposed filaments than in the thick terminal tufts which are better able to hold water. These two factors in combination tend to weaken the Cladophora filaments,

particularly at their base, and therefore increase the rate of fragmentation and downstream drift. In some cases, following prolonged periods of exposure, the Cladophora becomes matted with a thin layer of bleached filaments overlying a thicker layer of green filaments (personal observation). Even though the bleached layer of filaments is obviously damaged, this mat does not appear to fragment as readily and stays attached to the stream bottom for some time. It is not clear whether the green filaments below survive when rewetted, however it is assumed that eventually the bleached filaments break up and are carried away by the current. In any case, repeated periods of exposure could result in the total eradication of Cladophora in the shallow marginal zone.

In addition to exposure as a function of regulated flow, two other factors may also effect the fragmentation rate; nutrient stress and epiphytes. Nutrient stress can be a function of two factors, nutrient seasonality and competition for nutrients with other algae. Although one would expect a constant flow of nutrients from a hypolimnion release dam, this does not appear to be the case in the Lees Ferry area. Seasonality in nutrient concentrations, particularly in phosphorus has been reported below Glen Canyon Dam. In addition, the thick growth of epiphytic diatoms associated with the Cladophora filaments may compete for nutrients. This competition may result in nutrient stress during some periods and weaken the Cladophora host. Furthermore, the mere attachment of diatom cells to the filament can cause physical damage to the Cladophora cell wall. Both nutrient stress and physical damage from epiphyte attachment may further increase fragmentation.

An increase in the fragmentation rate of Cladophora has a number of important implications; both positive and negative. It has been suggested that for Cladophora, the most common form of reproduction is by fragmentation (Mason 1965), therefore an increased rate of fragmentation may enhance downstream colonization of both the Glen Canyon Dam tailwaters and suitable areas below the confluence of the Paria River in Grand Canyon. In addition, increased fragmentation may increase productivity due to cropping (Lamberti and Resh 1983); removing older slow growing filaments and leaving younger fast growing filaments. Increased rates of fragmentation mean increased drift of Cladophora and its associated invertebrate fauna. This may be important to the trout fishery. Increased drift may provide trout with enhanced accessibility to an important food source. On the other hand, fragmentation may result in the disruption of habitat for diatom epiphytes and the associated invertebrate fauna. It has been shown that colonization and growth of epiphytic diatoms are inhibited on young rapidly growing filaments (Kociolek et al. 1983). It has been shown that Gammarus lacustris, another important food item in the diet of rainbow trout (Bancroft & Sylvester 1978, Carothers & Minckley 1981), feed on the diatoms epiphytic to Cladophora (Blinn et al. 1986). If epiphytic diatom habitat is lost due to increased fragmentation of Cladophora then a breakdown in the present trophic structure may follow. Perhaps, most important to the fishery at Lees Ferry are the epiphytic diatoms. This stems from the fact that Gammarus lacustris feed on the diatoms epiphytic to

Cladophora (Blinn et al. 1986) and in turn are fed upon by the rainbow trout (Bancroft & Sylvester 1978, Carothers & Minckley 1981). The most important potential impact to the epiphytes resulting from fluctuating flows may be a shift in species composition to more closely attached forms like Cocconeis pediculus and Achnanthes spp. and fewer loosely attached forms such as Diatoma vulgare and Rhoicosphenia curvata. This shift in species composition may potentially be a function of increased current velocities during rising flows which could wash away loosely attached diatoms. In addition, warm water at the margins may favor eurythermal forms that could compete well for nutrients. The closely attached C. pediculus and Achnanthes spp. are better adapted to accommodate these conditions and are most likely to persist. Furthermore, if water temperatures are elevated beyond 20 C, overall diatom density may be reduced and/or epiphytic diatoms may be replaced by green and blue-green algae. If this is the case and if Gammarus prefer the loosely attached epiphytic diatoms like D. vulgare and R. curvata for food, then it is possible that the Gammarus, and possibly the fish, may have to look elsewhere for a food substitute.

Finally, seasonal growth patterns of Cladophora in the Glen Canyon Dam tailwaters are not yet fully understood. One might assume that the seasonal standing crop of C. glomerata would be relatively constant in the tailwaters due to the near-constant temperature conditions. The dramatic reduction in Cladophora biomass at Lees Ferry following the low water of October 1984 and the experimental fluctuations of late 1985 (see Chapter Five: Results) may have resulted from desiccation or seasonal die-off. Investigations concerning seasonal growth patterns are in progress but their results will be difficult to interpret due to the irregular flows and the lack of baseline information prior to fluctuating flow regimes. If a seasonal growth pattern does exist the main regulator may be light or nutrient load rather than temperature in that water temperature remains relatively constant year round.

For the present, these statements are simply inferences and projections as to what might occur, based on previous studies of Cladophora and its relatives in systems other than the Colorado River. In some cases the work may have been conducted in rivers similar to the Colorado River. However, most of this review is based on studies conducted in freshwater lakes and marine systems. It is quite clear that in order to understand the ecology and life history of Cladophora glomerata and associated epiphytes in the Colorado River below Glen Canyon Dam, additional studies of nutrient availability and uptake, temperature tolerance and seasonal growth patterns are necessary.

LITERATURE CITED

- Adams, M.S. and W. Stone. 1973. Field studies on photosynthesis of Cladophora glomerata (Chlorophyta) in Green Bay, Lake Michigan. *Ecology* 54:853-862.
- Allen, H.L. 1971. Primary productivity, chemoorganotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. *Ecol. Monogr.* 41:97-127.
- Bancroft, D.C. and K. Sylvester. 1978. The Colorado River Glen Canyon Tailwater Fishery. Ann. Rept. July 1977-June 1978. Arizona Game and Fish Department.
- Bellis, V.J. 1968. Unialgal cultures of Cladophora glomerata (L.) Kutz. 1. Response to temperature. *J. Phycol.* 4:19-23.
- Bellis, V.J. and D.A. McLarty. 1967. Ecology of Cladophora glomerata (L.) Kutz. in southern Ontario. *J. Phycol.* 3:57-63.
- Berquist, P.L. 1957. Some factors in brown algal zonation. MS thesis, Univ. of Auckland. 331 pp.
- Biebl, R. 1962. Seaweeds. pp 799-815 In: R.A. Lewin (ed), Physiology and Biochemistry of Algae. Academic Press, New York.
- Blinn, D.W., C.A. Pinney, R. Truitt and A. Davis. 1986. The influence of elevated water temperatures on epiphytic diatom species in the tailwaters of Glen Canyon Dam and the importance of these epiphytic diatoms in the diet of Gammarus lacustris. Final report to the Glen Canyon Environmental Studies, U.S. Bureau of Reclamation, Flagstaff, AZ. 19 pp.
- Blum, J.L. 1957. An ecological study of the algae of the Saline River, Michigan. *Hydrobiologia* 9:361-408.
- Blum, J.L. 1982. Colonization and growth of attached algae at the Lake Michigan water line. *J. Great Lakes Res.* 8:10-15.
- Bolas, P.M. and J.W.G. Lund. 1974. Factors affecting the growth of Cladophora glomerata in the Kentish Stour. *Wat. Treat. Exam.* 23:25-51.
- Bold, H.C. and M.J. Wynne. 1985. Introduction to the Algae. Prentice-Hall, Inc., Englewood Cliffs, N.J. 720 pp.
- Busch, D.E. and S.G. Fisher. 1981. Metabolism of a desert stream. *Freshwater Biol.* 11:301-308.

- Cairns, J. Jr. 1972. Coping with heated waste water discharges from steam electric power plants. *BioScience* 22:411-420.
- Calkins, J. and T. Thordardottier. 1980. The ecological significance of solar UV radiation on aquatic organism. *Nature* 283:563-566.
- Carothers, S.W. and C.O. Minckley. 1981. A survey of the aquatic flora and fauna of the Grand Canyon. Final Report to U.S.D.I., Water and Power Res. Serv., Lower Colorado Region, Boulder City, Nevada. 401 pp.
- Chudyba, H. 1965. Cladophora glomerata and accompanying algae in the Skawa River. *Acta. Hydrobiol.* 7, Suppl.(1):92-126.
- Cole, G. and D.M. Kubly. 1976. Limnologic studies on the Colorado River from Lees Ferry to Diamond Creek. Technical Report #8. Colorado River Research Program, Grand Canyon National Park. 83 pp.
- Czarnecki, D.B. and D.W. Blinn. 1978. Diatoms of the Colorado River in Grand Canyon National Park and Vicinity (Diatoms of southwestern USA III). *Biblio. Phycol.* 38:1-181.
- Czarnecki, D.B., D.W. Blinn, and T. Tompkins. 1976. A periphytic microflora analysis of the Colorado River and major tributaries in Grand Canyon and vicinity. Colorado River Res. Program, Tech. Rept. No. 6, 106 pp.
- Dawes, C.J., R.E. Moon, and M.A. Davis. 1978. The photosynthetic and respiratory rates and tolerances of the benthic algae from a mangrove and salt marsh estuary: a comparative study. *Estuarine and Coastal Marine Sci.* 6:175-185.
- 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. Ser.* 8:301-308.
- Dromgoole, F.I. 1980. Desiccation resistance of intertidal and subtidal algae. *Bot. Mar.* 23:149-159.
- Edwards, J. 1951. Is mucus a selective barrier to macromolecules? *British Med. Bull* 34:55-56.
- Eichenberger, E. 1967a. Okologische Untersuchungen an Mosellfliessengewassern. I. Die Jahreszeitliche Verteilung der bestandesbildenden pfkanzichen Organismen bei verscheidener Abwasserbelastung. *Schweiz. Z. Hydrol.* 29:1-31.
- Eichenberger, E. 1967b. Okologische Untersuchungen an Modellfliessgewassern. II. Jahreszeitliche Veranderungen der Biomassebildung bei verschieden abwasserbelastungen. *Schweiz. Z. Hydrol.* 29:32-52.

- Evans, J.H. 1958. The survival of freshwater algae during dry periods. I. An investigation of the algae of five small ponds. *J. Ecol.* 46:149-167.
- 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.
- Fitzgerald, G.P. 1969. Some factors in the competition or antagonism among bacteria, algae, and aquatic weeds. *J. Phycol.* 5:351-359.
- Graham, J.M., M.T. Auer, R.P. Canale, and J.P. Hoffman. 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.* 8:100-111.
- Harlin, M.N. 1973. Transfer of products between epiphytic marine algae and host plants. *J. Phycol.* 9:234-248.
- Hauray, L.R. 1981. Cladophora drift and planktonic crustaceans in the Colorado River: Lees Ferry to Diamond Creek. Special Report to the Museum of Northern Arizona, Flagstaff. 24 pp.
- Herbst, R.P. 1969. Ecological factors and the distribution of Cladophora glomerata in the Great Lakes. *Amer. Mid. Nat.* 82:90-98.
- Hodgson, L.M. 1981. Photosynthesis of the red alga, Gastroclonium couteri (Rhodophyta) in response to changes in temperature, light intensity, and desiccation. *J. Phycol.* 17:37-42.
- Hoffman, J.P. 1979. Evidence for photosynthetic control of reproduction in the nuisance alga Cladophora glomerata, Chlorophyceae, Cladophorales. Meeting of the Phycological Society of America, Stillwater, Okla. USA, Aug. 12-16, 1979. *J. Phycol.* 15 (Suppl.) 1979.
- Horner, R.R. and E.B. Welch. 1981. Stream periphyton development in relation to current velocity and nutrients. *Can. Fish. Aquat. Sci.* 38:449-457.
- Hunding, C. 1979. The oxygen balance of Lake Myvatn, Iceland. *Oikos* 32:139-150.
- Jaag, O. 1938. Die Kryptogamenflora des Rheinfalls und des Hochrheins von Stein bis Eglisau. *Mitt. Naturf. Ges. Schaffhausen* 14:1-158.
- Jackson, M.B. and Y.S. Hamdy. 1982. Projected Cladophora growth in southern Georgian Bay in response to proposed municipal sewage treatment plant discharges to the Mary Ward Shoals. *J. Great Lakes Res.* 8:153-163.

- 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* 55:771-781.
- Jonasson, P.M. 1979. The Lake Myvatn ecosystem, Iceland. *Oikos* 32:289-305.
- Jones, H.G. and T.A. Norton. 1979. Internal factors controlling the rate of respiration from fronds of some intertidal algae. *New Phytol.* 83:275-285.
- Kanwisher, J. 1957. Freezing and drying in intertidal algae. *Biol. Bull.* 113:275-285.
- Kociolek, J.P., M.A. Lamb, and R.L. Lowe. 1983. Notes on the growth and ultrastructure of Biddulphia laevis Ehr. (Bacillariophyceae) in the Maumee River, Ohio. *Ohio J. Sci.* 83:125-130.
- Korte, V.L. and D.W. Blinn. 1983. Diatom colonization on artificial substrata in pool and riffle zones studied by light and scanning electron microscopy. *J. Phycol.* 19:332-341.
- Lamberti, G.A. and V.H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. *Ecology* 64:1124-1135.
- Lester, W.W., M.S. Adams, and E.H. Deltmann. 1974. Light and temperature effects on photosynthesis of Cladophora glomerata (Chlorophyta) from Green Bay, Lake Michigan: Model analysis of seasonal productivity. Masters thesis, Univ. of Wisconsin, Dept. of Botany.
- Lorenz, R.C. and C.E. Herndendorf. 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.) pp 25-34. The Ecology of Regulated Streams. Plenum Press, Corp., N.Y.
- Lowe, R.L., Rosen, B.H. and J.C. Kingston. 1982. A comparison of epiphytes on Bangia atropurpurea (Rhodophyta) and Cladophora glomerata (Chlorophyta) from northern Lake Michigan. *J. Great Lakes Res.* 8:164-168.
- Mantai, K.E. 1974. Some aspects of photosynthesis in Cladophora glomerata. *J. Phycol.* 10:288-291.

- Mantai, K.E. 1982. Energy relationships of Cladophora glomerata. Plant Physiol. 69 (4 Suppl):103.
- Mantai, K.E., P.E. Garwood, and L.E. Peglowski. 1982. Environmental factors controlling physiological changes in Cladophora in Lake Erie. J. Great Lakes Res. 8:61-65.
- Manuel-Faler, C.Y., G.W. Minshall, R.W. Dunn, and D.A. Bruns. 1984. In situ nitrogen enrichment experiments in two Idaho (U.S.A.) streams. Environ. Monit. Assess. 4:67-79.
- Mason, C.P. 1965. Ecology of Cladophora in farm ponds. Ecology 46:421-428.
- McCully, M.E. 1968. Histological studies on the genus Fucus. III. Fine structure and possible functions of the epidermal cells of the vegetative thallus. J. Cell Sci. 3:1-16.
- McLean, R.J. 1967. Desiccation and heat resistance of the alga Spongiochloris typica. Can. J. Botany 45:1933-1939.
- McRoy, C.P. and J.J. Goering. 1974. Nutrient transfer between Seagrass, Zostera marina and its epiphytes. Nature 248:173-174.
- Millner, G.C.R., A. Sweendy, and V.R. Frederick. 1982. Biomass and distribution of Cladophora glomerata in relation to some physical-chemical variables at two sites in Lake Erie. J. Great Lakes Res. 8:35-41.
- Moffett, J.W. 1942. A fishery survey of the Colorado River below Boulder Dam. Calif. Fish & Game 28:76-86.
- Moore, J.W. 1975. The role of algae in the diet of Asellus aquaticus and Gammarus pulex. J. Anim. Ecol. 44:719-730.
- Moore, J.W. 1976. Seasonal succession of algae in rivers. Part 1: Examples from the Avon River, England: A large slow flowing river. J. Phycol. 12(3):342-349.
- Moore, J.W. 1977. Seasonal succession of planktonic and epiphytic algae in a canal in southern England. Hydrobiol. 53:213-220.
- Moore, L.F. 1978. Attached algae at thermal generating stations-the effect of temperature on Cladophora. Verh. Internat. Verin. Limnol. 20:1727-1733.
- Moore, L.F. and J.A. Traquair. 1976. Silica, a required nutrient for Cladophora glomerata (L.) Kutz. Planta 128:179-182.
- Mullan, J.W., V.J. Starostka, J.L. Stone, R.W. Wiley, and W. Wiltzius. 1976. Factors affecting upper Colorado River Reservoir tailwater trout fisheries. In: Instream Flow needs. J.F. Osbourne and C.H. Allman (Eds.), Vol. 2. Am. Fish. Soc., Wash. D.C. pp. 405-427.

- 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.
- Neil, J.H. and M.B. Jackson. 1982. Monitoring Cladophora growth conditions and the effect of phosphorous additions at a shoreline site in northwestern Lake Erie. *J. Great Lakes Res.* 8:30-34.
- O'Neal, S.W. and C.A. Lembi. 1983. Physiological changes during germination of Pithophora oedogonia (Chlorophyta) akinetes. *J. Phycol.* 19:193-199
- O'Quinn, R. and M.J. Sullivan. 1983. Community structure dynamics of epilithic and epiphytic diatoms in a Mississippi, USA, stream. *J. Phycol.* 19:123-128.
- Pantastico, J.B. and Z.A. Suayan. 1973a. Akinete differentiation in Cladophora sp. Part 2: Interaction among light photoperiod and growth regulators. *Kalikasan Philipp. J. Biol.* 2:39-40.
- Pantastico, J.B. and Z.A. Suayan. 1973b. Akinete differentiation in Cladophora sp. Part 3: Effects of aging and related factors. *Philipp. Agric.* 57:305-312.
- Pantastico, J.B. and Z.A. Suayan. 1971. Effects of Gibberellic acid and IAA on branching and akinete formation in Cladophora sp. and Pithophora sp. *Philipp. Agric.* 54:402-413.
- Parker, R.D.R. and D.B. Brown. 1982. Effects of phosphorus enrichment and wave simulation on populations of Ulothrix zonata from northern Lake Superior. *J. Great Lakes Res.* 8:16-26.
- Patrick, R. 1948. Factors affecting the distribution of diatoms. *Bot. Rev.* 14:473-524.
- Patrick, R. 1971. The effects of increasing light and temperature on the structure of diatom communities. *Limnol. Oceanogr.* 16:405-421.
- Penhale, P.A. and G.W. Thayer. 1980. Uptake and transfer of carbon and phosphorus by eelgrass (Zostera marina L.) and its epiphytes. *J. Exp. Mar. Biol. Ecol.* 42:113-123.
- 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. *Az. Game & Fish. Dept., Phoenix, Az.* 93 pp.

- Peterson, C.G. 1984. Benthic diatom community dynamics in the Colorado River: Interactive effects of periodic desiccation and current regime. M.S. thesis, Univ. Nev. Las Vegas. 140 pp.
- Phillips, G.L. 1969. Diet of the minnow Chrosomus erythrogaster (Cyprinidae) in a Minnesota stream. Am. Mid. Nat. 82:99-109.
- Pitcairn, C.E. and H.A. Hawkes. 1973. The role of phosphorous in the growth of Cladophora. Water Res. 7:159-171.
- Prescott, G.W. 1978. How To Know the Freshwater Algae. Wm. C. Brown, Co., Dubuque, Ia. 293 pp.
- 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.
- Ronnberg, O. and P. Lax. 1980. Influence of wave action on morphology and epiphytic diatoms of Cladophora glomerata (L.) Kutz. Ophelia (Suppl) 1:209-218.
- Rosemarin, A.S. 1985. Reproductive strategy in the filamentous green alga Cladophora glomerata (L.) Kutz.-An explanation for its widespread distribution. Verh. Internat. Verin. Limnol. 22:2872-2877.
- Schonbeck, M.W. and T.A. Norton. 1978. Factors controlling the upper limits of Furoid algae on the shore. J. Exp. Mar. Biol. Ecol. 31:303-313.
- Schonbeck, M.W. and T.A. Norton. 1979. An investigation of drought avoidance in intertidal furoid algae. Bot. Mar. 31:303-313.
- 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 smaragdina). J. Phycol. 18:385-391.
- Sladeckova, A. 1969. Control of slimes and algae in cooling systems. Verh. Internat. Verin. Limnol. 17:532-538.
- Stevenson, R.J. and E.F. Stoermer. 1982. Seasonal abundance patterns of diatoms on Cladophora in Lake Huron. J. Great Lakes Res. 8:169-183.
- Storr, J.F. and R.A. Sweeney. 1971. Development of a theoretical seasonal growth response curve of Cladophora glomerata to temperature and photoperiod. In: Proc. 14th Conference on Great Lakes Research. Internat. Assoc. Great Lakes Research, Lake Ontario, Oswego. pp.119-127.

- Thomas, N.A. 1975. Physical-chemical requirements. In: Cladophora in the Great Lakes. H. Shear and D.E. Konasewich (eds). Internat. Joint Commission, Windsor, Ontario. pp. 81-82.
- Thomas, N.A., Robertson, A. and W.C. Sonzogni. 1979. Review of control objectives, new target loads and input controls. Great Lakes Environmental Planning Study, Contribution No. 9. In: Proc. of a Conference on Phosphorous Management Strategies for the Great Lakes. Internat. Joint Commission, Windsor, Ontario.
- USBUREC 1984. Chemical analysis of water samples. Unpublished Report.
- USBUREC 1985. Chemical analysis of water samples. Unpublished Report.
- Usher, H.D., W.C. Leibfried, D.W. Blinn, and S.W. Carothers. 1984. A survey of the aquatic and terrestrial habitats of Roaring Springs, Bright Angel, Garden and Pipe Creeks, Grand Canyon National Park. Final Report to U.S. Dept. Interior, N.P.S. Western Region, San Francisco, Ca., Contract No. CX 8000-9-0032.
- Van Den Hoek, C. 1963. Revision of the European species of Cladophora. E.J. Brill, Leiden.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing. 1980. The River Continuum Concept. Can. J. Fish. Aquat. Sci. 37:130-137.
- Verduin, J. 1959. Photosynthesis by aquatic communities in northwest Ohio. Ecology 40:377-383.
- Warfe, J., K.S. Taylor, and H.A.C. Montgomery. 1984. The growth of Cladophora glomerata in a river receiving sewage effluent. Wat. Res. 18:971-979.
- Whitford, L.A. 1960. The current effect and growth of freshwater algae. Trans. Am. Microsc. Soc. 79:302-309.
- Whitford, L.A. and G.J. Schumacher. 1961. Effect of current on mineral uptake and respiration by a freshwater alga. Limnol. Oceanogr. 6:423-425.
- Whitton, B.A. 1967. Studies on the growth of riverine Cladophora in culture. Archiv. fur Mikrobiologie 58:21-29.
- Whitton, B.A. 1970. Biology of Cladophora in freshwaters. Water Res. 4:457-476.
- Wiebe, H.H. 1966. Matric potential of several plant tissues and biocolloids. Plant Physiol. 41:1439-1442.

- Wik-Sjostedt, A. 1970. Cytogenic investigations in Cladophora. Hereditas 66:233-262.
- Wiltens, J., V. Schreider, and W. Vidaver. 1978. Chlorophyll fluorescence induction: An indicator of photosynthetic activity in marine algae undergoing desiccation. Can. J. Bot. 56:2754- 2787.
- Wong, S.L. and B. Clark. 1976. Field determination of the critical nutrient concentrations for Cladophora in streams. J. Fish. Res. Bd. Can. 33:85-92.
- Wong, S.L., B. Clark, M. Kirby, M., and R.F. Kosciaw. 1978. Water temperature and seasonal periodicity of Cladophora glomerata and Potamogeton pectinatus in shallow rivers. J. Fish. Res. Bd. Can. 35:866-870.
- Wood, K.G. 1968. Photosynthesis of Cladophora under unnatural conditions. In: Algae, Man and Environment. D.F. Jackson (ed). Syracuse Univ. Press, Syracuse, N.Y. pp. 121-133.
- Wood, K.G. 1975. Photosynthesis of Cladophora in relation to light and CO<sub>2</sub> limitation; CaCO<sub>3</sub> precipitation. Ecology 56:479-484.
- Zanefeld, J.S. 1937. The littoral zonation of some Fucaceae in relation to desiccation. J. Ecol. 25:431-468.
- Zanefeld, J.S. 1969. Factors controlling the delimitation of littoral benthic marine algae. Amer. Zool. 9:367-391.

## CHAPTER FOUR: METHODS

### A. CLADOPHORA GLOMERATA; DISTRIBUTION AND STANDING CROP

During October of 1984 an experimental drawdown from approximately 25,000 cfs to nearly 5,000 cfs was conducted in the Colorado River below Glen Canyon Dam. During this drawdown four collection sites were selected based on suitability for the growth of Cladophora (ie presence of rock substrate for attachment), accessibility and time availability while on downriver collecting trips.. These sites were 7.5 mile (below Glen Canyon Dam), Lees Ferry, Paria and Nankoweap. The zero shoreline was surveyed at the 25,000 cfs water level. Three depth zones at each collection site were established; Cells 1, 2 and 3. Cell 1 extended from the waters edge to one foot in depth, Cell 2 ranged from one to four feet in depth and Cell 3 was greater than four feet in depth. These cells were stationary and did not move with fluctuating flow, therefore Cell 1 was dry during much of the fluctuating period of 1985. Lees Ferry and Nankoweap were sampled five times during the study, 7.5 mile was sampled three times and the Paria was sampled once. Depth cells at each site were sampled according to river level and accessibility.

In order to determine standing crop of Cladophora a random sample of 30 4 cm biomass samples was taken from each cell for a total of 90 samples from each site. In every case throughout this study random samples were collected according to standard random number tables and predetermined grids. Only 15 samples were taken from the Paria site. Samples were transported to the lab where they were air dried for at least 24 hours. Cladophora filaments were then separated from silt and sand, placed in ceramic crucibles and oven dried for 12 hours at 100-104 C. When feasible bleached filaments were separated from green filaments and analyzed separately. Although this method was the most desirable it was only possible on those occasions when white and green filaments were clumped and could be separated reliably. The dried samples were removed from the oven and weighed to the nearest 0.0001 gram on an analytical Mettler balance (Model #H20T). Ash-free dry weight was determined for samples taken during the October 1984 drawdown. Following the procedures outlined above, each sample was ashed in a muffle furnace for one hour at 500 C (American Public Health Association 1976). The weighed ash was subtracted from the oven dried weight to determine the ash-free weight for each sample. Statistical analyses included analysis of variance (ANOVA) and orthogonal contrast analysis. The probability rejection level for the study was set at  $P=.05$ , however in the text print out probabilities are included.

In addition to the above, Northern Arizona University personnel accompanied four Arizona Department of Game and Fish river trips; December 1984, July, October, and December 1985. During these trips additional sites and depth cells were sampled according to time and accessibility. Samples were collected according to the procedures discussed above and sample sizes varied according to time availability at each site.

## B. EPIPHYTES; STANDING CROP, COMPOSITION AND DISTRIBUTION

Field collection of the epiphytic diatoms followed the procedures outlined for Cladophora biomass. As described above, a random sample of 30 4 cm of Cladophora was collected from each depth cell at a given site, preserved in AFA (49%, 95% ethyl alcohol; 39%, distilled water; 10% formalin; 2% acetic acid) and transported to the lab for analysis.

In the lab, diatom samples were oxidized by the peroxide-dichromate method according to Van der Werff (1955). The samples were concentrated by centrifugation and brought to a constant volume (20 ml). One-half ml of cleared, homogenized and concentrated sample was placed on an 18 mm coverslip and evaporated over low heat. Each coverslip was then mounted in HYRAX mounting media (Patrick & Reimer 1966).

Diatom species identifications were made at 1250X magnification using a Zeiss phase-contrast microscope. Taxonomic references used for identification included Czarnecki and Blinn (1977, 1978) and Patrick and Reimer (1966, 1975). At least 200 diatom cells were identified and counted from each slide. Number of cells/Whipple grid was converted to a value representing diatom cells/cm<sup>2</sup>. These numbers were used to arrive at relative abundance values. It is important to note that diatoms were enumerated as number of cells per 4 cm<sup>2</sup> of basal attachment area of Cladophora and not by volume. This may be a potential source of bias in the interpretation of the results.

## C. DESICCATION TOLERANCE OF CLADOPHORA GLOMERATA; LABORATORY EXPERIMENTS

Experimental studies of the desiccation tolerance of Cladophora were conducted in the lab with Frigid Unit "Living Stream" Systems (Model#LSW-700) as holding tanks. Experiments were conducted on four occasions to provide replicate winter runs (March and April 1985) and replicate summer monsoon runs (July and September 1985). During each test, samples of Cladophora were subjected to four different experimental regimes and a control. These experimental regimes included exposure periods of 12 hours in the dark (night), 12 hours in the light (day), one day and two days. These exposure periods were selected to resemble actual conditions in the field. In addition during the March and September runs a fifth regime or three day exposure period was included to simulate in the lab the observed field results of the October 1984 drawdown.

A random sample of Cladophora colonized rocks was collected from Cell 2 at the Lees Ferry site for each experiment. The number of rocks collected for each run depended on the extent of Cladophora development and the carrying capacity of the stream tank. Rocks were transported back to the lab in large coolers filled with river water. In the lab the rocks were placed into the stream tank which had been filled with river water collected from Lees Ferry. The Cladophora was allowed to acclimate in the tank for two days at ambient water temperatures as measured at Lees Ferry.

Following the acclimation period a random sample of rocks

was selected for each experimental regime and the control. At the start of each run a random sample of three or four (depending on the run) 4 cm<sup>2</sup> biomass samples was collected from each rock to determine the initial biomass. The experimental rocks were then placed on the roof of the NAU Biological Science building and subjected to atmospheric conditions for the designated period of time. During the exposure period, light intensity, temperature and relative wind speed were monitored at regular intervals from sunrise through sunset. Due to the lack of funding and manpower environmental conditions were not monitored during the night.

Following exposure the experimental rocks were removed from the roof and placed back into the stream tank for a two week incubation period. Based on field observations a two week incubation period appeared to be a sufficient time to observe the effects of a given exposure period on Cladophora. After the incubation period a final random sample of 4 cm<sup>2</sup> biomass measurements was taken and the experiment was terminated.

One additional experiment was conducted to determine the effect of repeated desiccation on a regular cycle. Procedures followed those described above with the only difference being the exposure and incubation periods. Eight Cladophora covered rocks were subjected to one of two regimes and were compared to eight control rocks left in the tank for the duration of the experiment. The first regime consisted of a 12 hour exposure followed by 12 hours of submergence in the stream tank repeated continually over a two week period. The second regime was a 24 hour exposure followed by 24 hours of submergence in the tank repeated continually over the same two week period. Final biomass measurements were taken at the end of the experimental period with no further incubation.

Statistical analysis included ANOVA and orthogonal contrasts run against the ratio of initial to final biomass as the dependent variable with run and regime as the independent variables. The rejection level was set at  $P=.05$  however, computer generated probabilities are included in the text.

In addition to these experiments field observations at Lees Ferry also gave some indication of the effects of exposure on Cladophora biomass; in particular the October 1984 drawdown and the experimental fluctuating flow period in late 1985. In October of 1984 the Colorado River below Glen Canyon Dam was lowered from approximately 25,000 cfs to nearly 5,000 cfs for a three day period. In October 1985 the Bureau of Reclamation initiated an experimental fluctuating flow period which lasted through December 1985. Collections at the beginning and end of each of these periods were analyzed statistically to determine changes in Cladophora biomass. For the fluctuating flow period of 1985 the initial sample was taken early in October prior to the onset of any effects of exposure and the final sample was taken in December, after three months of daily fluctuations with high flows ranging from 20,000 to 25,000 cfs and lows of approximately 2,000 to 5,000 cfs.

## CHAPTER FIVE: RESULTS

### A. CLADOPHORA GLOMERATA; DISTRIBUTION AND STANDING CROP

Mean Cladophora standing crop (biomass in  $\text{gm/m}^2$ ) at each site and in each cell is summarized for each sampling period in Table 1. Of the stations sampled at the beginning of this study, Lees Ferry supported the greatest standing crop of Cladophora with a site average of  $179.0 \text{ g/m}^2$ . In comparison, the site at Nankoweap supported the least at only  $34.0 \text{ g/m}^2$ . The maximum standing crop observed during the study was  $351.5 \text{ g/m}^2$  during the October, 1985, sampling period in Cell 2 at Lees Ferry. During this same period Cell 1 at Lees Ferry supported  $314.7 \text{ g/m}^2$  which compared to  $60.1 \text{ g/m}^2$  in Cell 1 at Nankoweap  $35.9 \text{ g/m}^2$  in Cell 1 at 220 mile (Table 1).

An ANOVA (Table 2) indicated that there was a significant depth effect on the standing crop of Cladophora ( $F_{2,17}=4.902$ ,  $P<.008$ ). The general pattern observed during this study was that of an increase in Cladophora biomass with an increase in depth (Figure 1). Only twice during the study did we observe a deviation from this pattern. The first time was at the start of the study in October, 1984, in the silt laden waters of Nankoweap and the second was near the end of the study, at Lees Ferry in October, 1985.

Ash free dry weight (AFDW) of Cladophora was measured once during the study; October, 1984. During this period, an ANOVA (Table 3) based on the relationship between AFDW and dry weight (DW) (i.e. percent organic carbon or food quality) showed a significant two-way interaction between site and cell ( $F_{6,11}=8.358$ ,  $P<.001$ ) which suggests that the cells respond differently at different sites. Inspection of the data indicates a decrease of AFDW/DW in Cell 1 below the 7.5 mile station while Cells 2 and 3 remain relatively constant throughout the sites (Tables 3 and 4). In Cell 1 at the 7.5 mile station organic carbon was 61.7 % while at the site downstream it was never greater than 40.0 % (Table 4). Cells 2 and 3 remained relatively constant with percent organic carbon ranging from 61.4 % to 70.9 %.

Based on a one-way ANOVA of Cladophora biomass collected from Cell 1 at eight sites during July, 1985, we observed a significant site effect ( $F=9.483$ ,  $df=7$ ,  $P<.001$ ) (Table 5). A trend of decreasing biomass with distance downstream from Glen Canyon Dam (Figure 2) was suggested by an orthogonal contrast which followed the ANOVA. Sites above the confluence of the Paria River (i.e. Lees Ferry and 7.5 mile) supported significantly greater Cladophora standing crop than did sites downstream ( $T=4.997$ ,  $df=27.1$ ,  $P<.001$ ). The standing crop observed at Kanab is an anomaly for which there is no apparent explanation. The pattern in Figure 1 appears true of each sampling period except the December, 1984, through January, 1985, period which followed the October, 1984, drawdown (Table 1).

A one-way ANOVA of Cladophora standing crop in Cell 2, sampled at Lees Ferry during eight periods throughout the study

showed a significant effect based on the date of collection ( $F=23.901$ ,  $df=7$ ,  $P<.001$ ) (Table 6). An orthogonal contrast analysis which followed indicated a decrease in biomass following the October, 1984, drawdown ( $T=4.454$ ,  $df=38.9$ ,  $P<.001$ ) and the fluctuating flow period during the end of 1985 ( $T=9.875$ ,  $df=34.0$ ,  $P<.001$ ) (Figure 3). The apparent effect of the fluctuating flow period at the end of 1985 at Lees Ferry was a reduction in mean standing crop in all cells combined, from  $303.9 \text{ g/m}^2$  in October, 1985, to  $113.7 \text{ g/m}^2$  in December, 1985. An ANOVA (Table 7) conducted on mean biomass in each cell during these two periods showed a significant two-way interaction between depth cell and date of collection ( $F_{2,5}=7.978$ ,  $P<.001$ ). This interaction is shown graphically in Figure 4. In October the greatest biomass was sampled in Cells 1 and 2. However, following three months of fluctuating flow Cell 3 had 24% more Cladophora biomass than Cells 1 and 2 combined. Following this period of fluctuating flow, numerous bleached filaments (presumably nonviable) were observed in these two cells. This observation may indicate that the loss of viable Cladophora there was greater than the numbers indicate.

#### B. EPIPHYTES; STANDING CROP, COMPOSITION AND DISTRIBUTION

During the course of this study 90 different diatom species were identified as epiphytic to Cladophora in the Colorado River below Glen Canyon Dam (Table 8). Of these species 32 taxa were restricted to the tailwaters of Glen Canyon Dam and only 13 were unique to the Colorado River below the confluence of the Paria River. Four species were considered co-dominants at the Lees Ferry site: Achnanthes affinis, Cocconeis pediculus, Diatoma vulgare and Rhoicosphenia curvata. Mean densities of these species at selected sites along the Colorado River through Glen and Grand Canyons are provided in Table 9. During July of 1985 these four species made up 80% of the community at Lees Ferry but declined in importance with distance downstream from the dam (Figure 5). By river mile 220 these species made up only 33% of the epiphytic community. Although Diatoma vulgare remained a dominant member of the community throughout the system it still decreased dramatically in density with distance downstream from Glen Canyon Dam. In July of 1985 Diatoma vulgare in Cell 1 at Lees Ferry was found at a density of  $70.6 \times 10^7$  cells/cm<sup>2</sup> and was found at a density of only  $25.5 \times 10^4$  cells/cm<sup>2</sup> in Cell 1 at river mile 220 (Table 9).

Two trends were observed in the total density of diatoms epiphytic to Cladophora. First, in July of 1985 a significant site effect explaining the distribution of total cell density was observed ( $F=6.506$ ,  $df=5$ ,  $P<.002$ ) (Table 10). A contrast analysis following the ANOVA showed a significant decrease in epiphytic diatom density downstream of Lees Ferry ( $T=3.381$ ,  $df=3.5$ ,  $P<.043$ ). Mean total cell density ranged from  $629.3 \times 10^4$  (7.5 mile) to  $217.7 \times 10^4$  cells/cm<sup>2</sup> (Lees Ferry) in Cell 1 above the confluence of the Paria River and only  $92.1 \times 10^4$  (220 mile) to  $35.0 \times 10^4$  cells/cm<sup>2</sup> (Bright Angel) below the confluence (Table 11). This trend was also observed between Lees Ferry and Nankoweap in October of 1984 but was not significant during this

period ( $F_{1,23}=.100$ ,  $P<.753$ )(Table 12).

Second, mean total cell density was significantly affected by depth ( $F_{2,23}=3.417$ ,  $P<.038$ )(Table 12). This trend was observed at both Lees Ferry and Nankoweap (Figure 6). At Lees Ferry mean total cell density in October 1984 declined from  $302.3 \times 10^4$  (Cell 1) to  $46.2 \times 10^4$  cells/cm<sup>2</sup> (Cell 3) and at Nankoweap from  $282.8 \times 10^4$  (Cell 1) to  $38.0 \times 10^4$  cells/cm<sup>2</sup> (Cell 3)(Table 11). This trend was also observed and found to be statistically significant at Lees Ferry during October and December of 1985 ( $F_{2,23}=21.816$ ,  $P<.001$ )(Table 13). Differences among the dominant diatom species in the relationship between depth and cell density were not analyzed.

In addition to these trends a dramatic decrease in mean total cell density was observed at Lees Ferry between October and December of 1985 during the period of fluctuating flow. The difference in mean cell density from October to December was significant ( $F_{1,23}=65.488$ ,  $P<.001$ )(Table 13). In Cell 1 the mean cell density dropped from nearly  $800 \times 10^4$  cells/cm<sup>2</sup> in October to approximately  $100 \times 10^4$  cells/cm<sup>2</sup> in December (Figure 7). Three-way analysis of variance also indicated a significant three-way interaction between date, depth and diatom species ( $F_{6,23}=5.402$ ,  $P<.001$ )(Table 13) suggesting that each species is affected differently by the fluctuating flows. Of the four dominants at Lees Ferry Cocconeis pediculus, Diatoma vulgare and Rhoicosphenia curvata were virtually eliminated following three months of fluctuating flows (Figure 8). Achnanthes affinis, on the other hand was not so severely affected and was found in much greater densities after the three months of fluctuating flows than the other three co-dominants (Figure 8). This may be due to the fact that Achnanthes affinis is known as a weedy species which is capable of rapidly colonizing disturbed areas.

#### C. DESICCATION TOLERANCE OF CLADOPHORA GLOMERATA; LABORATORY EXPERIMENTS

An ANOVA was used to test for differences between the two winter runs and the two summer monsoon runs. There was no significant difference between the two summer monsoon runs ( $F_{1,9}=1.67$ ,  $P<.205$ )(Table 14). Based on this analysis the monsoon runs were combined for further study.

These desiccation experiments showed that one time exposures of Cladophora glomerata, for as little as 12 hours, can result in a reduction of standing crop. During each test the control rocks showed measurable growth ranging from 15-36% of the original standing crop. Nearly all the exposure periods resulted in reductions of standing crop. The greatest amount of decrease, approximately 84%, occurred as a result of the three day exposure during the Winter 1 test run. Twelve hour exposures generally resulted in reductions which ranged from 57% (Winter 1) to as little as four percent (Monsoon) (Figure 9). One exception to this was the unexpected increase in standing crop following the 12 hour night exposure during the Winter 1 test run. The one day exposures resulted in standing crop decreases ranging from 62% (Winter 1) to as little as 25% (Winter 2) (Figure 9). Two and three day exposures showed results similar to the one day

exposures. These results may have been affected by local atmospheric conditions (Table 15).

In order to test for significant differences between the exposure periods, Orthogonal Contrast Analysis was used. This analysis showed that, with the exception of the second winter run, the control rocks had significantly greater Cladophora standing crop than did those rocks exposed to a one day exposure period (Table 16). There was no significant difference found between the standing crop after one day exposure in comparison to the rocks exposed for three days. The results of the contrasts comparing the control rocks to the rocks exposed for 12 hours during the day or night were variable and no particular pattern was observed during the winter runs.

A one-way ANOVA conducted on the repeat exposure experiments suggests that repeated exposure of either a 12 hour or 24 hour cycle will have detrimental effects on the standing crop of Cladophora. During the course of this experiment, exposure resulted in the bleaching of many of the Cladophora filaments. If the bleached filaments are accepted as viable, and included in the measurement of biomass there is only a 22% decrease as a result of the exposures (Figure 10). This decrease is not significantly different from the five percent increase in biomass of the control ( $F_{2,21}=1.263$ ,  $P<.304$ ) (Table 17). On the other hand, if these bleached filaments, which have lost their chlorophyll and therefore their ability to carry out photosynthetic activity, are considered dead and only viable green filaments are included in the analysis then the decrease is as much as 75% which is significantly different from the increase of the control ( $F_{2,21}=10.032$ ,  $P<.001$ ) (Table 17).

TABLE 1. Seasonal Dry Weight Standing Crop Estimates (g/m<sup>2</sup>) of Cladophora glomerata at Selected Reaches in the Colorado River through Grand Canyon National Park. Standard deviations are given in parentheses.

SAMPLE STATION	21-23 Oct 84			20 Dec 84- 17 Jan 85	5-11 July 85	
	I	CELL II	III	CELL I	I	II
7.5 Mile	55.7 n=30 (44.9)	65.3 n=34 (43.8)	152.3 n=30 (122.1)	13.9 n=30 (19.9)	138.6 n=15 (143.9)	
Lees Ferry	90.3 n=30 (117.7)	195.0 n=30 (122.7)	240.9 n=30 (103.2)	17.3 n=30 (31.1)	144.6 n=25 (107.6)	175.5 n=15 (146.7)
Paria	11.5 n=15 (30.4)	33.5 n=15 (33.3)	164.9 n=15 (89.4)			
Nankoweap	46.1 n=30 (60.7)	58.9 n=30 (49.6)	18.4 n=30 (15.8)	30.6 n=30 (79.3)	27.2 n=12 (70.9)	
Bright Angel				29.1 n=30 (76.3)	23.7 n=15 (37.2)	
Crystal						
Tapeats				44.0 n=30 (46.8)	18.2 n=15 (32.1)	
Kanab					104.5 n=15 (101.6)	
National					<0.1 n=15 ( 0.1)	
220 Mile				2.4 n=30 ( 5.3)	8.8 n=15 (16.8)	

Table 1 (Cont.)

SAMPLE STATION	6-14 Oct 85			17-25 Dec 85		
	I	CELL II	III	I	CELL II	III
7.5 Mile						
Lees Ferry	314.7 n=30 (299.0)	351.5 n=30 (153.6)	245.3 n=30 (107.2)	*89.5 n=30 (168.6)	62.8 n=30 (45.4)	188.7 n=30 (86.2)
Paria						
Nankoweap	60.1 n=30 (62.1)	52.3 n=30 (175.5)	131.4 n=30 (109.1)	*25.0 n=30 (58.4)	*19.5 n=30 (34.7)	41.2 n=30 (63.9)
Bright Angel				**	*27.5 n=30 (35.3)	
Crystal	**	56.3 n=30 (74.8)				
Tapeats	**	34.0 n=30 (49.2)	58.3 n=30 (71.4)	**	*17.7 n=20 (31.9)	27.7 n=20 (42.8)
Kanab						
National						
220 Mile	35.9 n=30 (74.5)	22.7 n=30 (33.9)				

\* All white filaments (presumably nonviable).

\*\* Very little, if any, Cladophora seen in this cell at this site; no samples taken.

TABLE 2. ANOVA Table of three-way interactions between collection site (site), depth cell (cell) and date of collection (date) with Cladophora biomass as the dependent variable. DF= degrees of freedom.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARES	F	SIGNIF. OF F
MAIN EFFECTS	4467777.370	5	893555.469	61.020	.001
SITE	2929985.620	1	2929985.620	200.085	.001
CELL	144106.289	2	72053.141	4.920	.008
DATE	1393685.500	2	696842.750	47.587	.001
2-WAY INTERACTIONS	672502.500	8	84062.813	5.741	.001
SITE-CELL	46466.670	2	23233.335	1.587	.206
SITE-DATE	436920.670	2	218460.297	14.918	.001
CELL-DATE	189115.227	4	47278.807	3.229	.012
3-WAY INTERACTIONS	563878.875	4	140969.875	9.627	.001
SITE-CELL-DATE	563878.898	4	140969.719	9.627	.001
EXPLAINED	5701458.750	17	335538.750	22.914	.001
RESIDUAL	7644002.250	522	14643.682		
TOTAL	13348161.000	539	24764.677		

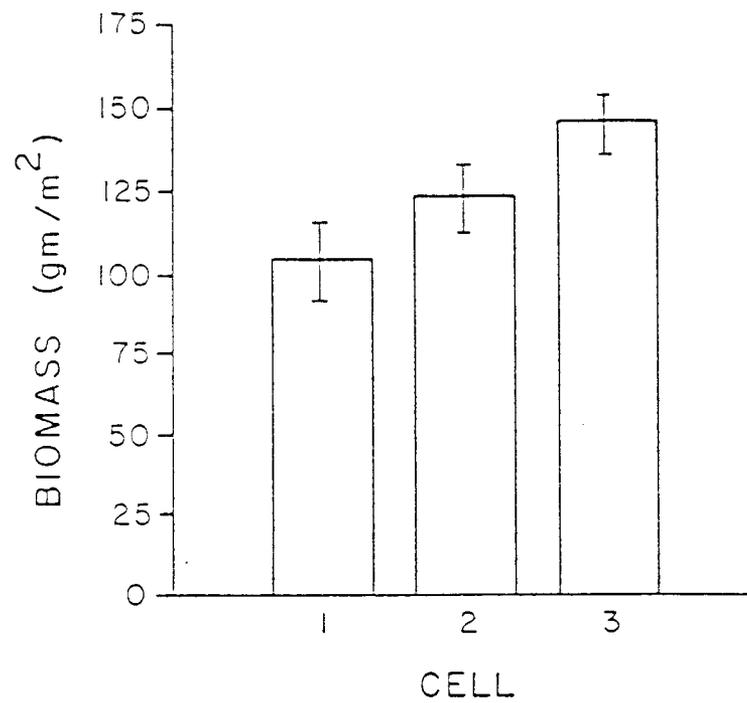


FIGURE 1. Standing crop of Cladophora glomerata at Lees Ferry during October 1984 in depth cells 1-3. Horizontal lines represent +/- one standard error of the mean.

TABLE 3. ANOVA Table of two-way interactions between collection site (site) and depth cell (cell) with percent ash free dry weight as the dependent variable. DF= degrees of freedom.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARES	F	SIGNIF. OF F
MAIN EFFECTS	28009.085	5	5601.817	36.414	.001
SITE	3440.724	3	1146.908	7.455	.001
CELL	24942.732	2	12471.366	81.069	.001
2-WAY INTERACTIONS	7714.583	6	1285.764	8.358	.001
SITE-CELL	7714.583	6	1285.764	8.358	.001
EXPLAINED	35723.667	11	3247.606	21.111	.001
RESIDUAL	40920.278	266	153.836		
TOTAL	76643.945	277	276.693		

TABLE 4. Ash-free dry weight/dry weight (AFDW/DW) of Cladophora glomerata at selected sites in the Colorado River during 21-23 October 1984. Standard error in parenthesis.

SITE	CELL DEPTH	AFDW/DW (%)	SAMPLE SIZE
7.5 mile			
	Cell 1	61.7 (2.55)	N = 25
	Cell 2	67.2 (2.77)	N = 31
	Cell 3	65.1 (2.45)	N = 30
Lees Ferry			
	Cell 1	40.0 (2.34)	N = 28
	Cell 2	63.7 (2.45)	N = 30
	Cell 3	70.9 (1.38)	N = 30
Paria River Confluence			
	Cell 1	31.1 (2.94)	N = 3
	Cell 2	61.9 (3.79)	N = 9
	Cell 3	61.4 (3.28)	N = 15
Nankoweap			
	Cell 1	37.0 (2.22)	N = 25
	Cell 2	64.8 (1.87)	N = 26
	Cell 3	67.8 (2.06)	N = 26

TABLE 5. Oneway ANOVA table for Cladophora biomass by collection site. DF= Degrees of Freedom.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARES	F	SIGNIF. OF F
BETWEEN GROUPS	.0719	7	.0103	9.483	.0000
WITHIN GROUPS	.1288	119	.0011		
TOTAL	.2007	126			

TABLE 6. Oneway ANOVA table for Cladophora biomass against date of collection. DF= Degrees of Freedom.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARES	F	SIGNIF. OF F
BETWEEN GROUPS	.2806	7	.0401	23.901	.0000
WITHIN GROUPS	.3623	216	.0017		
TOTAL	.6429	223			

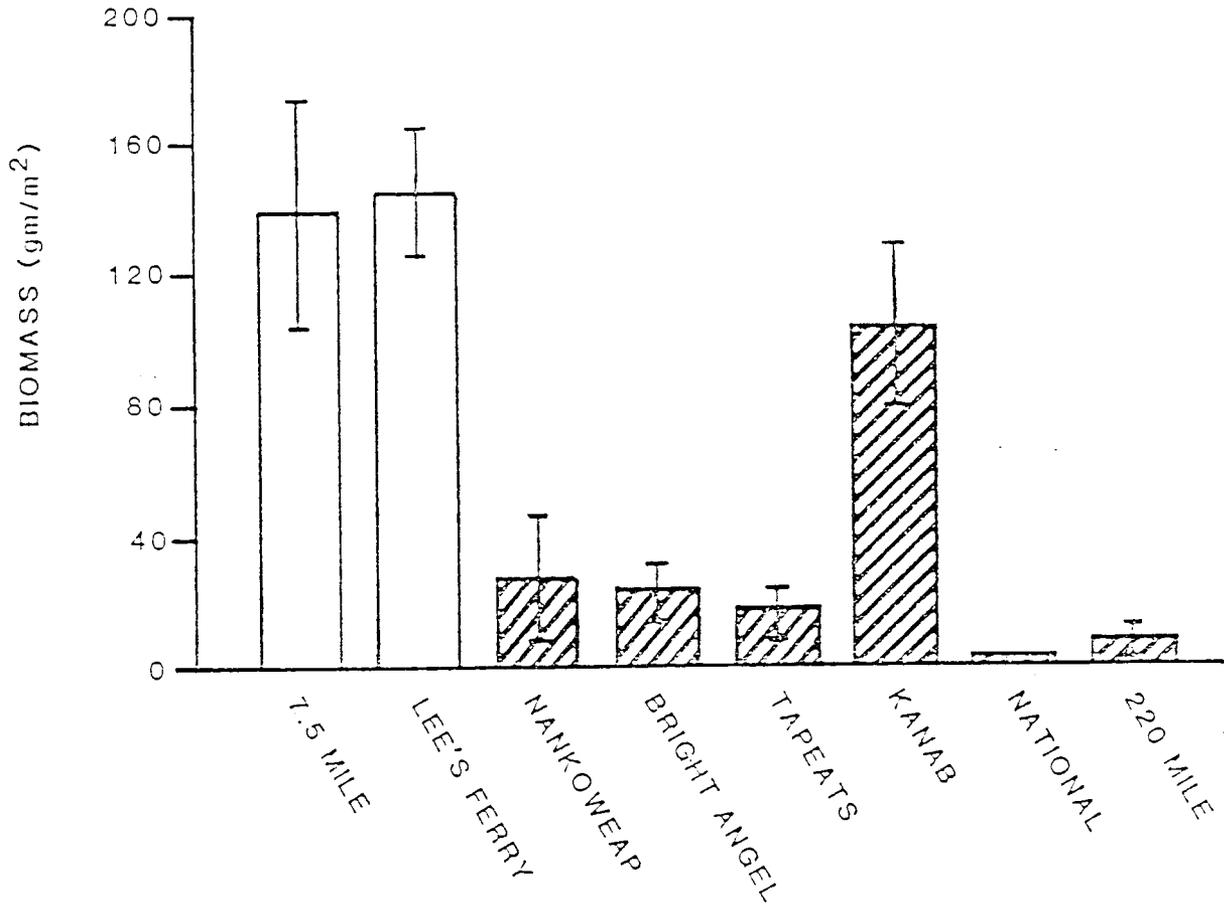


FIGURE 2. Standing crop of Cladophora glomerata from Cell 1 at selected sites in the Colorado River through Glen and Grand Canyons during July, 1985. Histograms with diagonal hatch lines represent sites with high suspended sediment. Horizontal lines represent +/- one standard error of the mean.

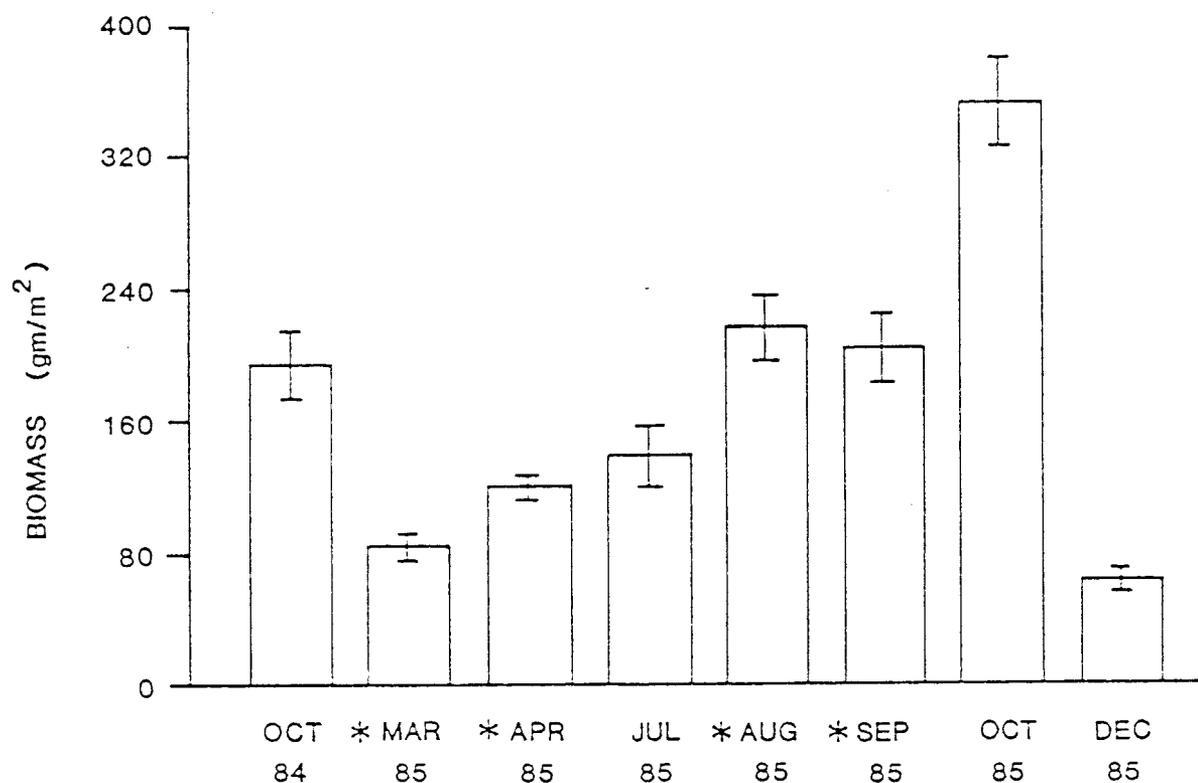


FIGURE 3. Standing crop of Cladophora glomerata in Cell 2 collected at Lees Ferry from October 1984 to December 1985. Notice the dramatic decrease in standing crop in March 1985 following the October 1984 drawdown and December 1985 following a period of fluctuating flow. Horizontal lines represent +/- one standard error of the mean.  
\* Data from these dates collected during trips to Lees Ferry to collect material for laboratory experiments.

TABLE 7. ANOVA Table of two-way interactions between depth cell (cell) and collection date (date) at Lees Ferry with Cladophora biomass as the dependent variable. DF= degrees of freedom.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARES	F	SIGNIF. OF F
MAIN EFFECTS	1634544.000	3	544848.000	20.133	.001
CELL	6865.504	2	3432.752	.127	.881
DATE	1627678.500	1	1627678.500	60.145	.001
2-WAY INTERACTIONS	431810.750	2	215905.375	7.978	.001
CELL-DATE	431810.750	2	215905.385	7.978	.001
EXPLAINED	2066354.750	5	413270.945	15.271	.001
RESIDUAL	4708902.370	174	27062.657		
TOTAL	6775257.120	179	37850.598		

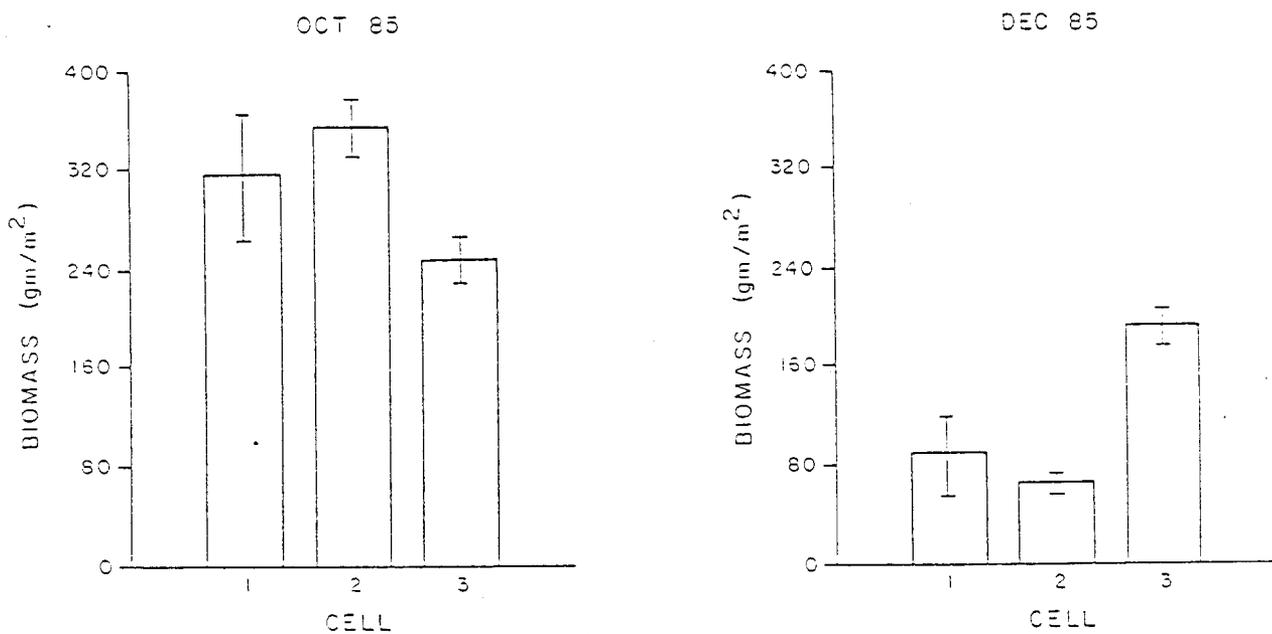


FIGURE 4. Standing crop of *Cladophora glomerata* at Lees Ferry following steady flows (October 1985) and fluctuating flows (December 1985) in depth cells 1-3. Horizontal lines represent +/- one standard error of the mean.

Table 8. List of epiphytic diatoms identified from Cladophora glomerata samples collected in October 1984; July, October, and December 1985. \* - taxa found only in tailwaters (7.5 mi. and/or Lees Ferry); # - taxa found only downstream of tailwaters; unmarked taxa found throughout river system.

COSCINODISCACEAE

- Cyclotella michiganiana Skv.  
Cyclotella sp.  
Melosira varians Ag.  
 \*Stephanodiscus sp.

FRAGILARIACEAE

- \*Diatoma hiemale var. mesodon (Ehr.) Grun.  
 \*D. tenue Ag.  
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  
Fragilaria sp.  
 #Opephora sp.  
 \*Synedra acus Kutz.  
 #S. incisa Boyer  
S. ulna (Nitz.) Ehr.

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.  
 #A. microcephala (Kutz.) Grun.  
Achnanthes sp.  
Cocconeis pediculus Ehr.  
C. placentula var. euglypta (Ehr.) Cl.  
Rhoicosphenia curvata (Kutz.) Grun. ex Rabh.

GOMPHONEMACEAE

- \*Gomphonema affine Kutz.  
G. olivaceum (Lyngb.) Kutz.  
G. parvulum Kutz.  
G. subclavatum (Grun.) Grun.

## 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. 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.
- #Cymbella sp.

## NAVICULACEAE

- \*Anomoeoneis vitrea (Grun.) Ross
- \*Caloneis bacillum (Grun.) Cl.
- \*C. hyalina Hust.
- Caloneis sp.
- \*Diploneis smithii Thwaites ex W. Sm.
- \*Mastogloia smithii var. lacustris Grun.
- \*Navicula arvensis Hust.
- #N. confervacea (Kutz.) Grun.
- \*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. miniscula Grun.
- #N. mutica Kutz.
- N. pseudoreinhardtii Patr.
- N. pupula var. rectangularis (Greg.) Grun.
- N. radiosa Kutz.
- N. radiosa var. tenella (Breb. ex Kutz.) Grun.
- N. tripunctata (Mull.) Bory
- #N. zanoi Hust.
- Navicula sp.
- \*Nedium sp.
- \*Pinnularia sp.
- \*Stauroneis sp.

## EPITHEMIACEAE

- Denticula elegans Kutz.
- #Rhopalodia gibberula var. vanheurckii O. Mull.

## NITZSCHIACEAE

- 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. gracilis Hantzsch.  
\*N. hungarica Grun.  
N. kutzingiana Hilse  
#N. linearis W. Sm.  
N. palea (Kutz.) W. Sm.  
\*N. romana Grun.  
Nitzschia sp.

TABLE 9. Mean densities for dominant epiphytic diatom species (cells x 10<sup>4</sup>/cm<sup>2</sup>) at selected sites along the Colorado River.

	CELL I	CELL II	CELL III
<u>OCTOBER 1984:</u>			
		7.5 Mile	
<u>Achnanthes affinis</u>	10.2	0.1	0.2
<u>Cocconeis pediculus</u>	22.2	1.6	4.1
<u>Diatoma vulgare</u>	28.9	2.2	2.2
<u>Rhoicosphenia curvata</u>	46.0	3.5	4.4
		Lees Ferry	
<u>Achnanthes affinis</u>	69.3	1.8	0.2
<u>Cocconeis pediculus</u>	75.5	18.7	12.1
<u>Diatoma vulgare</u>	31.7	46.5	3.8
<u>Rhoicosphenia curvata</u>	48.9	75.4	21.4
		Nankoweap	
<u>Achnanthes affinis</u>	0.9	0.1	1.1
<u>Cocconeis pediculus</u>	219.2	11.6	16.8
<u>Diatoma vulgare</u>	41.2	17.3	1.1
<u>Rhoicosphenia curvata</u>	15.3	8.3	4.3
<u>OCTOBER 1985:</u>			
		Lees Ferry	
<u>Achnanthes affinis</u>	55.9	7.4	7.1
<u>Cocconeis pediculus</u>	347.3	75.0	51.5
<u>Diatoma vulgare</u>	61.9	79.9	35.1
<u>Rhoicosphenia curvata</u>	221.4	64.8	40.7
<u>DECEMBER 1985:</u>			
		Lees Ferry	
<u>Achnanthes affinis</u>	46.0	13.9	0.2
<u>Cocconeis pediculus</u>	7.1	7.1	3.0
<u>Diatoma vulgare</u>	0.4	2.1	1.5
<u>Rhoicosphenia curvata</u>	1.9	8.6	7.5
		*   *   *	
<u>JULY 1985:</u>			
	7.5 Mile	Lees Ferry	Nankoweap
	Cell I	Cell I	Cell I
<u>Achnanthes affinis</u>	135.0	48.0	7.9
<u>Cocconeis pediculus</u>	10.6	41.2	34.9
<u>Diatoma vulgare</u>	213.3	70.6	9.2
<u>Rhoicosphenia curvata</u>	25.1	16.2	8.6
	Bright Angel	Kanab	220 Mile
	Cell I	Cell I	Cell I
<u>Achnanthes affinis</u>	1.5	3.0	1.8
<u>Cocconeis pediculus</u>	3.5	3.0	0.7
<u>Diatoma vulgare</u>	8.4	26.0	25.5
<u>Rhoicosphenia curvata</u>	5.4	2.9	1.9

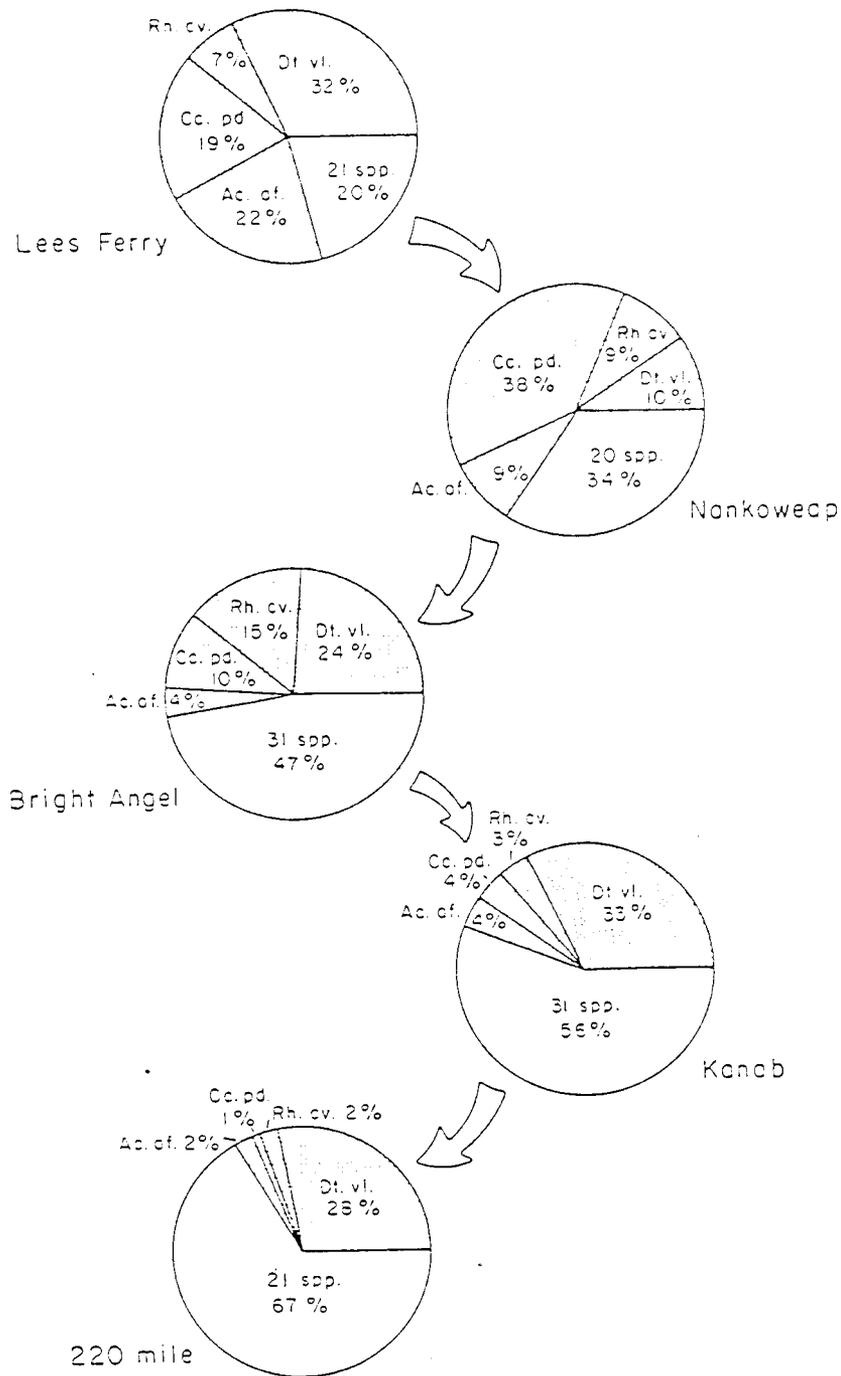


FIGURE 5. Frequency of the Lees Ferry four co-dominant epiphytic diatoms and remaining diatoms epiphytic to Cladophora glomerata with distance downstream from Glen Canyon Dam, July 1985. Notice the decrease in importance of the four Lees Ferry co-dominants at downstream sites. Rh. cv. = Rhoicosphenia curvata, Dt. vl. = Diatoma vulgare, Cc. pd. = Cocconeis pediculus, Ac. af. = Achnanthes affinis.

TABLE 10. Oneway ANOVA table for total epiphytic diatom cell density by collection site. DF= Degrees of Freedom.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARES	F	SIGNIF. OF F
BETWEEN GROUPS	1025919.9406	5	205183.9840	6.506	.002
WITHIN GROUPS	536169.1980	17	31539.3647		
TOTAL	1562089.1200	22			

Table 11. Total mean densities of epiphytic diatoms (Cells x  $10^4/\text{cm}^3$ ) at selected sites along the Colorado River. Values without data indicate that samples were not taken. Cell 1 through Cell 3 represents increasing depth in river channel. N = 3 collections for each value.

SITE	DATE			
	Oct 84	July 85	Oct 85	Dec 85
7.5 mi Cell 1	156.7	629.3	---	---
7.5 mi Cell 2	7.9	---	---	---
7.5 mi Cell 3	14.1	---	---	---
Lees Ferry Cell 1	302.3	217.7	800.2	103.0
Lees Ferry Cell 2	157.9	97.8	268.8	74.8
Lees Ferry Cell 3	46.2	---	165.5	15.9
Nankoweap Cell 1	282.8	91.7	---	---
Nankoweap Cell 2	42.8	---	---	---
Nankoweap Cell 3	38.0	---	---	---
Bright Angel Cell 1	---	35.0	---	---
Kanab Cell 1	---	79.1	---	---
220 Mile Cell 1	---	92.1	---	---

TABLE 12. ANOVA Table of three-way interactions between collection site (site), depth cell (cell) and dominant diatom species (spp) with diatom cell density as the dependent variable. DF= degrees of freedom.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARES	F	SIGNIF. OF F
MAIN EFFECTS	81059.742	6	13509.957	1.777	.116
SITE	758.623	1	758.623	.100	.753
CELL	51956.632	2	25978.316	3.417	.038
SPP	28344.491	3	9448.164	1.243	.301
2-WAY INTERACTIONS	88040.039	11	8003.640	1.053	.411
SITE-CELL	6198.790	2	3009.395	.408	.667
SITE-SPP	25472.042	3	8490.681	1.117	.348
CELL-SPP	56369.202	6	9394.867	1.236	.298
3-WAY INTERACTIONS	32828.461	6	5471.410	.720	.635
SITE-CELL-SPP	32828.466	6	5471.411	.720	.635
EXPLAINED	201928.242	23	8779.489	1.155	.314
RESIDUAL	547418.477	72	7603.034		
TOTAL	749346.719	95	7887.860		

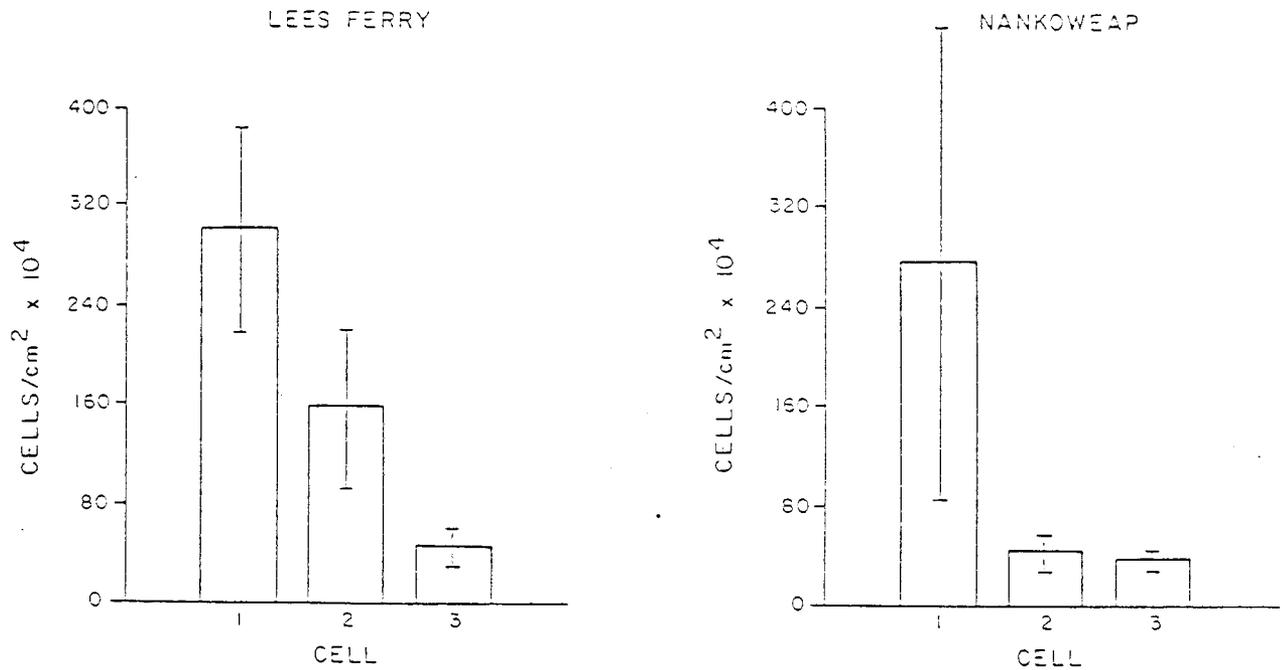


FIGURE 6. Standing crop of diatoms epiphytic to *Cladophora glomerata* at Lees Ferry and Nankoweap in depth cells 1-3 during October 1984. Horizontal lines represent +/- one standard error of the mean.

TABLE 13. ANOVA Table of three-way interactions between collection date (date), depth cell (cell) and dominant diatom species (spp) with diatom cell density as the dependent variable. DF= degrees of freedom.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARES	F	SIGNIF. OF F
MAIN EFFECTS	227924.719	6	37987.453	22.098	.001
DATE	112576.008	1	112576.008	65.488	.001
CELL	75003.305	2	37501.652	21.816	.001
SPP	40345.409	3	13448.469	7.823	.001
2-WAY INTERACTIONS	154830.078	11	14075.461	8.188	.001
DATE-CELL	56737.323	2	28638.662	16.503	.001
DATE-SPP	54467.956	3	18155.985	10.562	.001
CELL-SPP	43624.795	6	7270.799	4.230	.002
3-WAY INTERACTIONS	55717.320	6	9286.220	5.402	.001
DATE-CELL-SPP	55717.323	6	9286.220	5.402	.001
EXPLAINED	438472.117	23	19064.005	11.090	.001
RESIDUAL	82513.695	48	1719.035		
TOTAL	520985.812	71	7337.828		

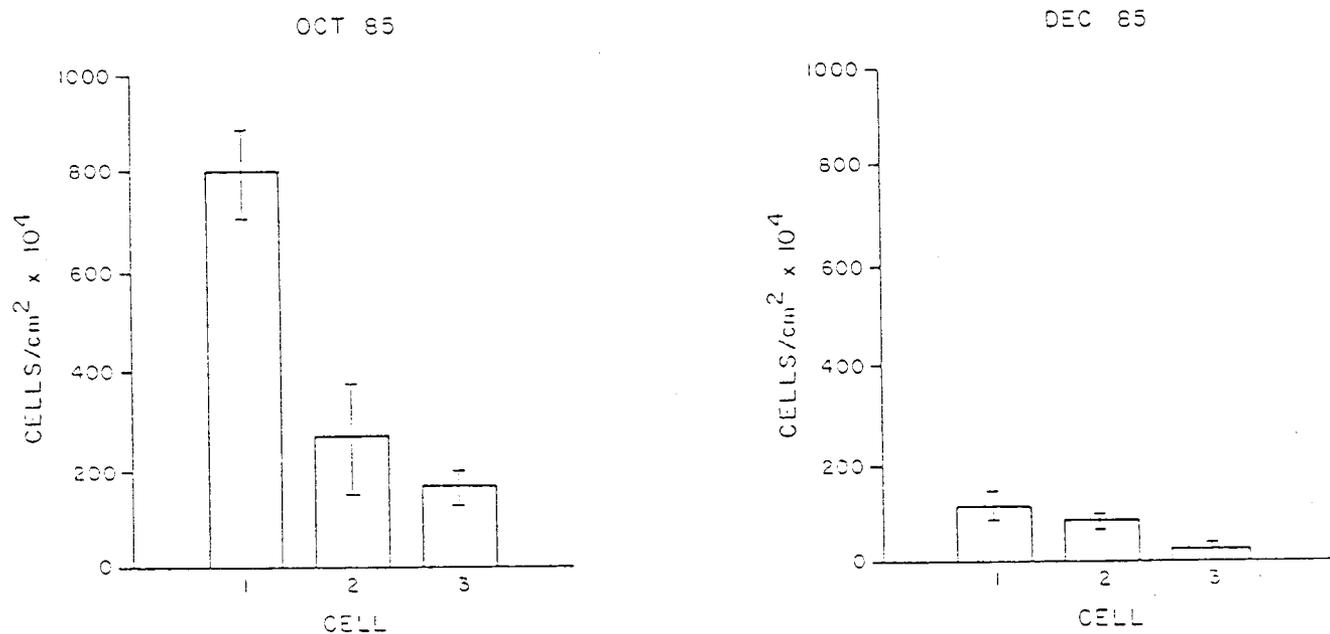


FIGURE 7. Standing crop of diatoms epiphytic to Cladophora glomerata at Lees Ferry following steady flows (October 1985) and fluctuating flows (December 1985). Horizontal lines represent +/- one standard error of the mean.

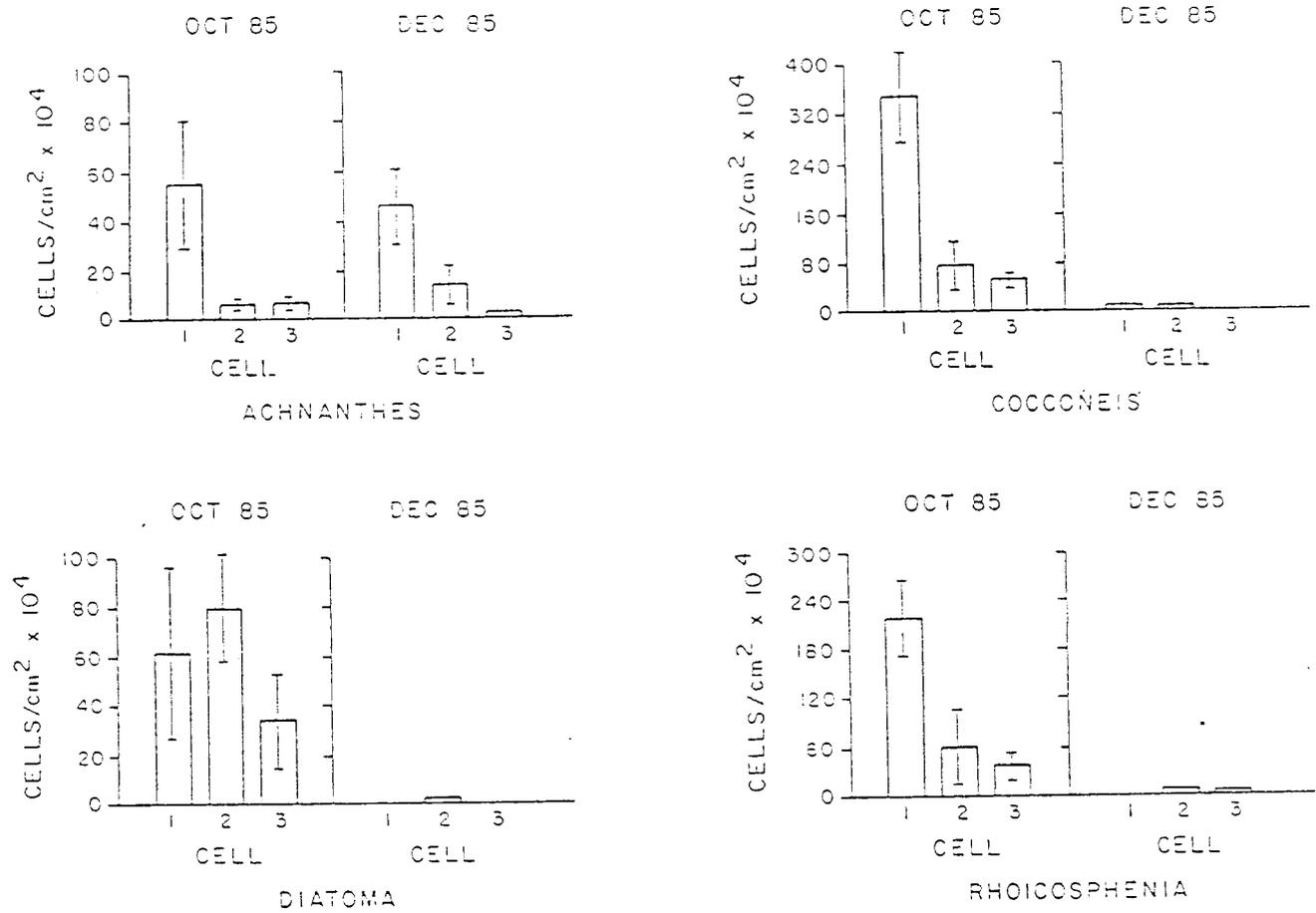


FIGURE 8. Standing crop of the four co-dominant epiphytic diatom species at Lees Ferry following steady flows (October 1985) and fluctuating flows (December 1985). Horizontal lines represent  $\pm$  one standard error of the mean.

TABLE 14. Two-way ANOVA Table of both monsoon test runs (run) and all six experimental regimes (regime) with Cladophora biomass as the dependent variable. .DF= degrees of freedom.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARES	F	SIGNIF. OF F
MAIN EFFECTS	4.901	5	.980	3.349	.014
RUN	.489	1	.489	1.670	.205
REGIME	4.412	4	1.103	3.769	.012
2-WAY INTERACTIONS	.199	4	.050	.170	.952
RUN-REGIME	.199	4	.050	.170	.952
EXPLAINED	5.099	9	.567	1.963	.079
RESIDUAL	10.243	35	.293		
TOTAL	15.342	44	.349		

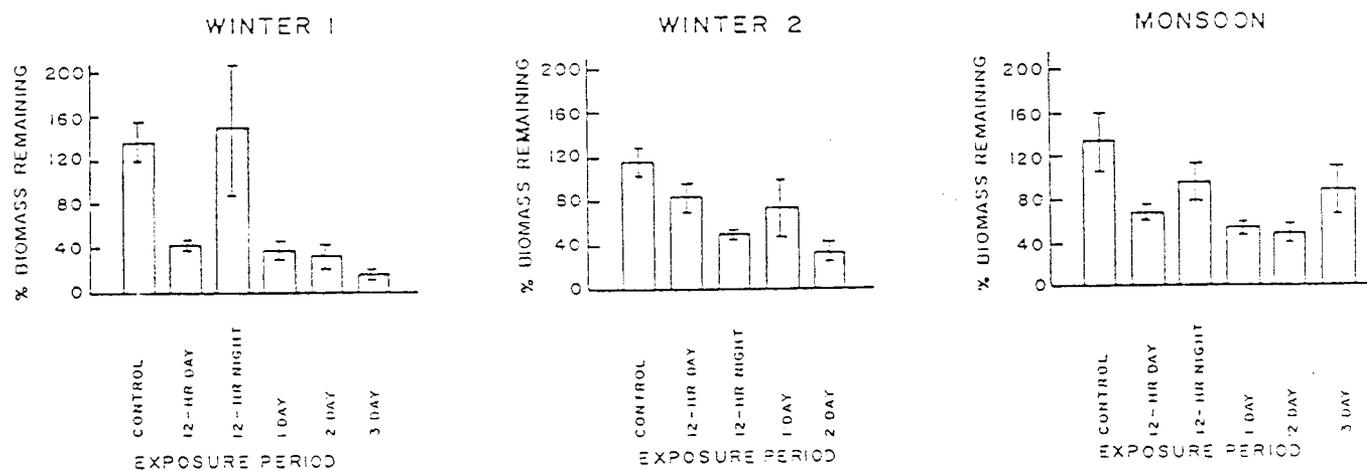


FIGURE 9. Percent standing crop of Cladophora glomerata remaining following experimental trials. Experimental exposures were for 12 hours during the day, 12 hours during the night, one day, two days and three days after which the exposed Cladophora was rewetted and allowed to incubate for two weeks in an artificial laboratory streamtank. Horizontal lines represent +/- one standard error of the mean.

Table 15. Atmospheric conditions at the top of the Northern Arizona University Biological Sciences Building during experimental stranding of Cladophora glomerata.

	TEMPERATURE (C)	LIGHT INTENSITY (uE/sec/m2)	RELATIVE HUMID.* (%)	COMMENTS
<u>WINTER 1</u> : start date 26 February 1985				
Range:	-5 - 23	925-2300	23-85	Little wind, rain or snow.
Mean:	9.0	1700	48.2	
S.D.:	8.5	546	19.1	
<u>WINTER 2</u> : start date 28 March 1985				
Range:	-12 - 14.5	2100-4300	30-82	Occasional strong wind and blowing snow.
Mean:	0.7	3017	56.8	
S.D.:	6.5	816	16.1	
<u>MONSOON 1</u> : start date 16 July 1985				
Range:	12 - 37	100-2500	29-78	Afternoon thunder showers.
Mean:	25.0	1711	54.4	
S.D.:	8.0	956	14.2	
<u>MONSOON 2</u> : start date 29 August 1985				
Range:	10 - 36	350-4200	25-77	Strong afternoon wind and thunder showers.
Mean:	21.5	2023	47.3	
S.D.:	7.5	1162	13.0	
<u>REPEAT DESICCATION</u> : start date 10 June 1985				
Range:	8 - 33.5	550-2700	11-74	Mostly clear.
Mean:	23.5	1964	24.2	
S.D.:	8.5	817	12.4	

\* Data collected from the Pulliam Airport weather station.

Table 16. Results of the Orthogonal Contrast Analysis comparing Cladophora standing crop (gms/m<sup>2</sup>; final/initial) of the control and the different exposure periods during laboratory desiccation experiments (acceptance at P=0.05 for all contrasts; computer P levels are provided).

CONTRAST	RUN		
	WINTER 1	WINTER 2	MONSOON
1 C>1 DAY	SIGNIFICANT (T=4.7, df=3.1, P=.01)	NOT SIGNIFICANT (T=1.3, df=4.4, P=.27)	SIGNIFICANT (T=2.6, df=8.6, P=.05)
2 1 DAY>3 DAY	NOT SIGNIFICANT (T=2.1, df=2.1, P=.17)	*	NOT SIGNIFICANT (T=-1.3, df=4.5, P=.2)
3 C>12 HR L	SIGNIFICANT (T=4.7, df=2.6, P=.02)	NOT SIGNIFICANT (T=1.5, df=6, P=.18)	SIGNIFICANT (T=2.1, df=9.4, P=.05)
4 C>12 HR D	NOT SIGNIFICANT (T=-.21, df=2.6, P=.85)	SIGNIFICANT (T=4.5, df=3.2, P=.02)	NOT SIGNIFICANT (T=1.1, df=13.4, P=.3)

1= Control greater than 1 day exposure; 2= 1 day exposure greater than 3 day exposure; 3= Control greater than 12 hour exposure in the light of day; 4= Control greater than 12 hour exposure in the dark of night; \*= No three day exposure conducted during this run.

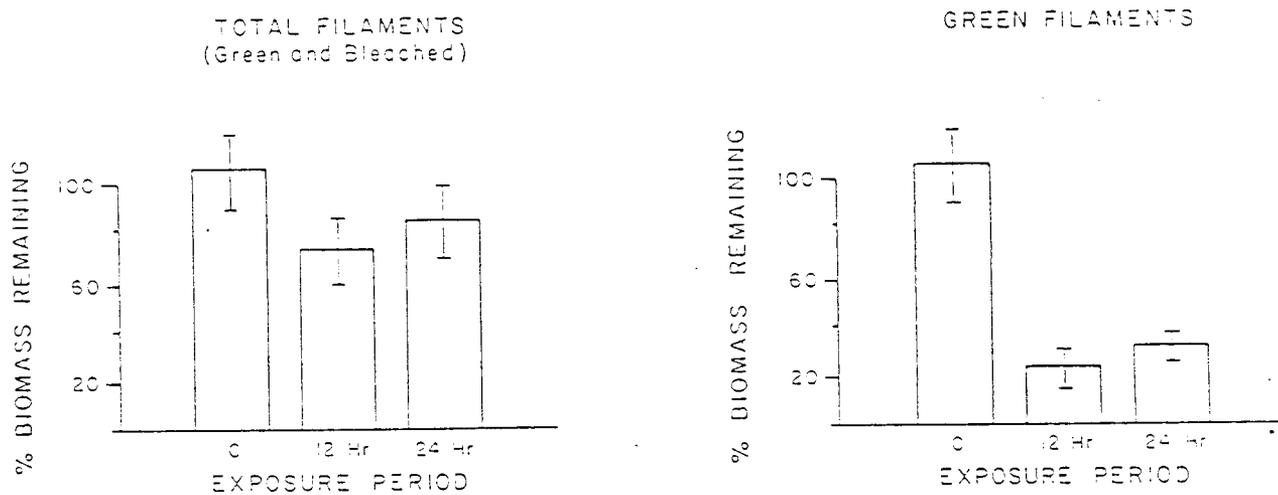


FIGURE 10. Percent standing crop of Cladophora glomerata remaining after a two week period of repeated cycles of exposure and rewetting. Two experimental cycles of 12 and 24 hours were compared to a control (C) which remained wetted in a streamtank for the entire two week period. Horizontal lines represent +/- one standard error of the mean. N=8.

TABLE 17. ANOVA Tables showing the effect of repeated wetting and drying on Cladophora with biomass as the dependent variable.  
DF= degrees of freedom.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARES	F	SIGNIF. OF F
<u>TOTAL FILAMENTS</u>					
MAIN EFFECTS	10483.898	2	5241.949	1.263	.304
TREATMENT	10483.898	2	5241.949	1.263	.304
EXPLAINED	10483.898	2	5241.949	1.263	.304
RESIDUAL	87185.031	21	4151.668		
TOTAL	97668.930	23	4246.475		
<u>GREEN FILAMENTS</u>					
MAIN EFFECTS	59845.259	2	29922.629	10.032	.001
TREATMENT	59845.259	2	29922.629	10.032	.001
EXPLAINED	59845.259	2	29922.629	10.032	.001
RESIDUAL	62635.233	21	2982.630		
TOTAL	122480.492	23	5325.239		

## CHAPTER SIX: DISCUSSION

The results of this study suggest that daily fluctuations in flow from the bottom of Glen Canyon Dam have a detrimental effect on the growth and standing crop of Cladophora glomerata and its epiphytes in the Glen Canyon Tailwaters and the Colorado River through Grand Canyon. The effects of exposure were observed in the field and in the laboratory and in both cases a decrease in biomass was the result. Our data could be explained in terms of seasonal growth patterns based on fluctuations in temperature, photoperiod and/or nutrient availability, however there is insufficient baseline data from which an accurate determination of seasonality based on any of these parameters can be discussed. With this in mind we have interpreted our data as follows:

Distribution of Cladophora and its epiphytes following periods of steady flow showed a significant decrease downstream from the dam. In addition, the common diatom epiphytes found on Cladophora in the Glen Canyon Dam Tailwaters above the confluence of the Paria River show a continual decrease in importance with distance downstream from the dam. This decrease in biomass and shift in epiphyte dominance is possibly the result of increased silt loads during certain periods of the year below the confluence of the Paria River (see Cole and Kubly 1976 for turbidity and secchi depth data). The silt has two effects on the Cladophora and its epiphytes. First, it physically abrades the algal cells much like a sand blaster. Second, it can totally block light from penetrating any deeper than several centimeters during periods of heavy silt loads, effectively shutting down photosynthesis and eliminating Cladophora from the area.

Cladophora biomass and epiphyte cell density are also affected by depth of the water. Cladophora shows a steady increase in biomass with greater depth. Light penetration decreases but is not eliminated with depth. The fact that Cladophora does so well in the dimly lighted water of the deeper zones supports the work of earlier authors who have suggested that Cladophora is adapted to relatively low light habitats (Neel 1968, Wood 1968, Adams and Stone 1973, Hoffman 1979, Graham et al. 1982). The diatom epiphytes show just the opposite trend; a decrease in cell density with an increase in depth. In addition, species dominance shifts with greater depth of water. Cocconeis and Rhoicosphenia dominate the shallow water zones and Diatoma dominates the deeper water.

It is on this background that the effects of desiccation and exposure were studied. The effects of desiccation were observed in three ways: 1) in situ following a three day drawdown to approximately 5,000 cfs, during October 1984, 2) in situ following a three month fluctuating flow period at the end of 1985 with flows ranging from approximately 5,000 to 25,000 cfs, and 3) in the lab with both single and repeated exposures. In every case a reduction of both Cladophora biomass and epiphyte cell density was observed. In situ observations showed that Cladophora and its epiphytes in the shallow and mid water zones, which were subjected to the greatest amount of exposure, were most severely impacted. It is important to note that even if Cells 1 and 2, the shallow and mid water zones, represent a small

portion of the wetted channel it is in these zones that epiphytic diatoms are most abundant (see Figure 6, Chapter Five). Loss of Cladophora in these zones means a loss of important substrate for the attachment of epiphytic diatoms. The diatoms are fed upon by the Gammarus (Blinn et al. 1986) which are in turn fed upon by the rainbow trout (Bancroft and Sylvester 1978, Carothers and Minckley 1981). Should the loss of Cladophora in these zones occur without the replacement of suitable conditions in the deeper zones then an important link in the aquatic food chain in the Glen Canyon Dam tailwaters may be lost.

Based on the laboratory experiments it was clear that an exposure period of as little as 12 hours could have significant effects. In addition, the effects of one time exposure differed from that of repeated exposures. Experiments involving repeated desiccations more accurately mimic natural conditions than do one time desiccation experiments (Hodgson 1981). The repeated experiments showed a much greater decline in Cladophora biomass after two weeks than did the one time exposure experiments. Following the two week incubation period the one time exposures of 12 hour duration resulted in losses ranging in severity of from four to 57% while the two weeks of repeated 12 hour exposures resulted in a loss of 67%. The extent of loss in both laboratory experiments and in situ observations may have been affected to some extent by the time of year and the immediate meteorological conditions.

Studies of marine intertidal algae suggest that the atmospheric microconditions surrounding exposed plants play an important role in rate of desiccation and the extent of damage resulting from a given period of exposure (Jones and Norton 1979, Dromgoole 1980, Dring and Brown 1982). This appeared to be the case during our studies as well. The shortest exposure period investigated during our experiments was 12 hours. The effect of this 12 hour exposure varied depending on time of day and the atmospheric microconditions which the Cladophora was subjected to. During this study atmospheric conditions were measured qualitatively and therefore the results are difficult to interpret. However, it does appear that freezing temperatures in the winter and slight breezes combined with hot, dry conditions in the summer can result in significant losses of Cladophora during an exposure period of 12 hours. The effect of these atmospheric conditions on Cladophora exposed for shorter periods has not been tested, however, field observations indicate that the basal holdfast can dry in the summer following periods of exposure as short as four hours in duration (personal observation).

When the river level falls, exposure produces a distinct drying pattern in Cladophora. The damage which follows results in the loss of viable as well as damaged filaments when the river level rises. As the river initially falls, the Cladophora filaments collapse on themselves with the long filaments overlapping each other, much like intertidal macroalgae (Evans 1959, Jones and Norton 1979, Quadir et al. 1979, Schonbeck and Norton 1979, Dromgoole 1980, Hodgson 1981), and efficiently trap water like a sponge. The long tufts effectively hold water for long periods (12 hours or more) and therefore are protected from

desiccation (Plate 1). The overlying filaments are however subjected to the damaging effects of the sun but do provide a shield for the underlying filaments. The basal holdfast of one tuft is generally protected by overlying filaments of a neighboring plant. The exposed filaments near the holdfast, which are the first parts of the Cladophora tuft to be exposed to the elements, are the first portion of the tuft to dry. These filaments are therefore most susceptible to desiccation and damage due to exposure. As the river begins to rise the weakened filaments are easily broken, resulting not only in the loss of the damaged filaments due to exposure, but also, in the loss of the viable terminal tufts as well. After repeated cycles of desiccation over long periods of time the long tufts in the shallower portions of the river bed may be totally eradicated exposing the basal holdfast. Repeated exposure of the riverbed may irreparably damage the holdfast and inhibit any recolonization of Cladophora in the exposed zones.

The diatom epiphytes are also reduced as a result of exposure. Initially the tufts of Cladophora which are torn off into the drift may be rich in epiphytes. However, with repeated exposure the density of diatoms epiphytic to attached Cladophora as well as drifting Cladophora is sure to decline. It has been suggested that diatom epiphytes do not do well on young rapidly growing host filaments (Kociolek et al. 1983). If any Cladophora remains after repeated exposures, it is likely that the filaments that remain will be of this type. If this is the case, then the habitat would be suboptimal for epiphyte growth and fewer diatoms could be expected. Our results show that, under steady flows the epiphytes are most abundant in the shallow zones and sharply drop-off in density with depth. These shallow zones are the zones which are most severely impacted by fluctuating flows. Therefore the decline in diatom density observed during this study is probably the result of damage due to exposure and a reduction in useable habitat. Our data do not suggest that the Cladophora in deep water will be colonized when the shallow water habitat is destroyed.

How will this affect the whole aquatic ecosystem of the Glen Canyon Dam Tailwaters and the Colorado River through Grand Canyon? Cladophora is at the base of the aquatic food chain in the Colorado River below Glen Canyon Dam, particularly in Glen Canyon. Cladophora provides an attachment site for epiphytic diatoms. Gammarus feed on these diatoms (Blinn et al. 1986) and in turn are fed upon by trout. Other important dietary components of trout and native fish, are a number of aquatic insect larvae (Carothers and Minckley 1981) which are commonly found in the Cladophora tufts. If the Colorado River below Glen Canyon Dam is subjected to fluctuating flows similar to those experienced late in 1985 (5000-25,000 cfs; USBuRec 1985) one might predict a disruption in the present aquatic ecosystem with potential adverse repercussions to the trout populations of the river. This conclusion is complicated by observations of the status of Cladophora glomerata and the Colorado River fishery prior to 1983. Before the construction of Glen Canyon Dam Cladophora did exist in Glen and Grand Canyons, found only in isolated patches in the silt laden water of the Colorado River

Rep. Plate 1 from  
Geol. Surv. Canada 1911

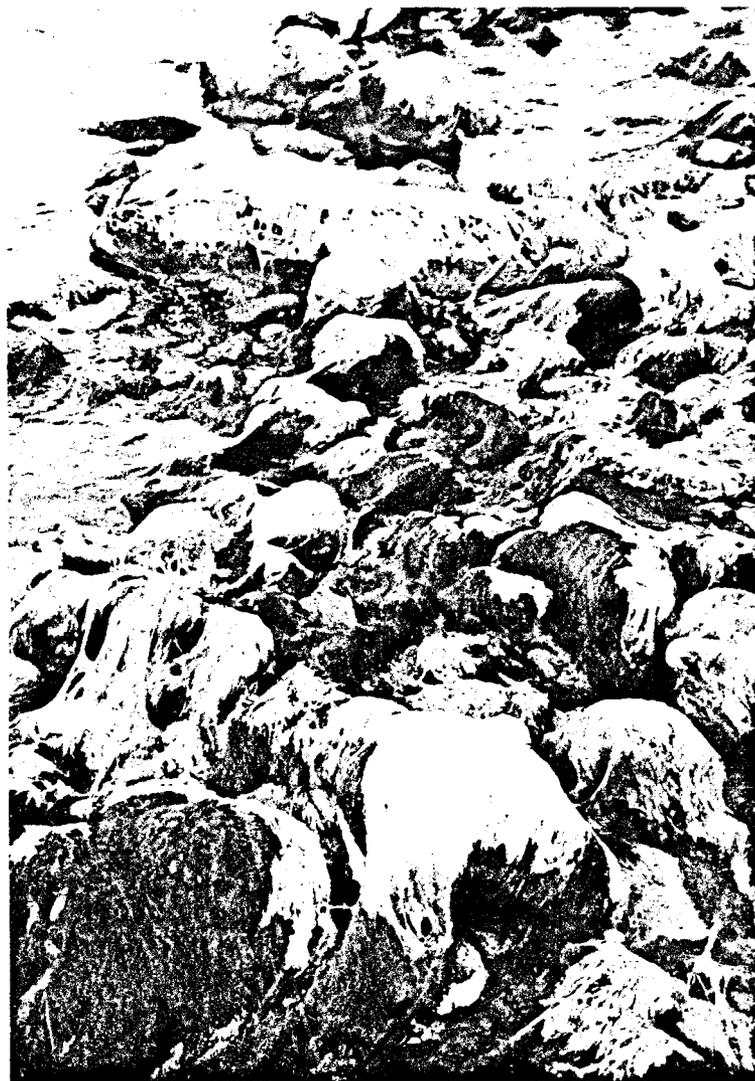


Plate 1. Bleached (presumably non-viable) filaments near the basal holdfast and viable green filaments at the terminal tufts.

(Woodbury et al. 1959). Prior to 1983 the Colorado River had been subjected to daily fluctuating flows. During at least part of this period (1977-1980) rainbow trout populations in the Glen Canyon Dam tailwaters and the Colorado River through Grand Canyon were relatively healthy and the area was considered one of the Southwest's blue ribbon trout fisheries (Carothers and Minckley 1981). The daily fluctuations in flow appeared to have no detrimental effects on the trout at that time. During this same period Cladophora was a major dietary item of rainbow trout (Carothers and Minckley 1981). The condition and extent of growth of Cladophora and its diatom epiphytes at the time is unknown however, Cladophora tufts were commonly seen drifting in the river (personal observation).

Several questions remain unanswered. The in situ observations of the effects of exposure were carried out during the fall of two successive years. The fall period is typically a period of growth (Chudýba 1965, Bellis and McLarty 1967, Wood 1968, Herbst 1969, Moore 1976, Wong et al. 1978, Mantai 1982), however during both periods we observed significant losses of Cladophora which is contrary to the reported pattern. At the present time we have no way of separating the effect of seasonal trends in the growth of Cladophora from the suspected effects of exposure. Although, it appears quite clear from both in situ and laboratory observations that exposure results in significant declines in standing crop of Cladophora, some of the decline may be due to seasonal trends. Following the 1984 drawdown, Cladophora showed a steady recovery and in one year had surpassed the initial standing crop measured at the out set of the study. Mason (1965) suggests that the most common form of reproduction in Cladophora is fragmentation. Observations of the post-drawdown recovery suggest that some form of reproduction other than fragmentation, perhaps sexual or asexual zoospore production or holdfast regeneration as suggested by Bellis and McLarty (1967) and Blum (1982), is important in the Glen Canyon Dam Tailwaters. If this is the case then it may have important ramifications concerning the recovery potential of Cladophora in exposed areas. Finally, Cladophora has been associated with areas of moderate to high nutrient concentrations (Whitton 1970). If this is the case, is the decrease in Cladophora downstream of the Paria River confluence a function of decreased light and abrasion or decreased nutrient loads? If decreased nutrient load is the answer then an increase in nutrients at the mouth of Kanab Creek may explain the large growth of Cladophora at that location.

The results of this study suggest that fluctuating flows are harmful to Cladophora and its diatom epiphytes. The operation of Glen Canyon Dam as a peaking power facility with daily fluctuations of 5000 to 25,000 cfs could have detrimental repercussions on the Colorado River aquatic ecosystem through Glen and Grand Canyons, particularly in the vicinity of Glen Canyon Dam and Lees Ferry. This study suggests that, depending on ambient atmospheric conditions, flows as low as 5,000 cfs with exposure periods as long as 12 hours can result in significant losses of Cladophora. In an effort to mitigate the effects of fluctuating flows on Cladophora and its diatom epiphytes we

recommend that Glen Canyon Dam be operated such that flows of approximately 5,000 cfs which expose of Cladophora glomerata for periods of 12 hours or more be avoided.

## CHAPTER SEVEN: CONCLUSIONS AND OPERATING CRITERIA

### CONCLUSIONS

- 1) Standing crop of Cladophora glomerata in the Colorado River above the confluence of the Paria River is significantly greater than in the Colorado River below the confluence.
- 2) Standing crop of Cladophora glomerata shows a significant increase with increasing depth during steady flow conditions at Lees Ferry.
- 3) Density of epiphytic diatoms on Cladophora glomerata in the Colorado River through Glen and Grand Canyons decreases significantly with distance downstream of Glen Canyon Dam.
- 4) The density of epiphytic diatoms on Cladophora glomerata decrease significantly with increasing depth during steady flow conditions at Lees Ferry.
- 5) Composition of epiphytic diatoms on Cladophora glomerata change with distance downstream of Glen Canyon Dam. Achnanthes affinis-minutissima, Cocconeis pediculus, Diatoma vulgare and Rhoicosphenia curvata decreased in importance with distance downstream of Glen Canyon Dam.
- 6) Laboratory experiments and field observations suggest that exposure and desiccation of Cladophora glomerata and its epiphytes, result in a significant decrease of standing crop and cell density.
- 7) Depending on local atmospheric conditions, exposures of 12 hours in duration can result in significant reductions in standing crop of Cladophora glomerata.
- 8) One time exposure and repeated cycles of exposure and rewetting both result in a significant decrease in standing crop of Cladophora glomerata. Over a two week period a comparison of one time exposures and repeated cycles of exposure and rewetting showed greater losses following the repeated cycles.

### OPERATING CRITERIA

Daily fluctuations of as much or more than 5,000 cfs to 25,000 cfs, with exposure periods of 12 hours or more, should be avoided. Investigations of the effects of exposure periods of less than 12 hours in duration should be conducted to determine their impact on the standing crop of Cladophora glomerata below Glen Canyon Dam. Seven potential flow scenarios have been tentatively proposed by the Bureau of Reclamation, Glen Canyon Environmental Studies office. The following is an evaluation of each alternative with respect to Cladophora glomerata and its diatom epiphytes:

Alternative Number One: Under this alternative of monthly base flow releases, there will be no daily fluctuations of flow levels. Flows will vary on a monthly basis ranging from 8,300 to 14,600 cfs. Even though this range of flows is much lower than what was observed during this project the relatively stable conditions which would prevail, should allow for the development of a relatively mature stand of Cladophora and diatom epiphytes. Cladophora standing crop and epiphyte density patterns, with respect to depth, may be similar to what was observed during this study.

Alternative Number Two: This scenario represents the classic daily fluctuations of a hydroelectric peak power facility. Fluctuations will vary with day, season and month and may be as great as 1,000 to 31,500 cfs each day. Fluctuations this great will certainly expose large portions of the wetted channel for 12 hours or more and result in a loss of Cladophora and epiphytes.

Alternative Number Three: This alternative is very similar to Alternative Number Two but the extent of daily fluctuation will be reduced. Daily fluctuations will be as much as 8,000 to 25,000 cfs. Fluctuations of this type will expose portions of the wetted channel for 12 hours or more and result in the loss of Cladophora and epiphytes, but to a lesser extent. Whether a stable Cladophora bed with a diverse diatom assemblage will develop below the lowest tide is unknown.

Alternative Number Four: Alternative Number Four represents an optimized situation for commercial river runners. Steady flows of 25,000 cfs will be maintained during the summer months with the remainder of the year subject to daily fluctuations of 1,000 to 31,500 cfs. This will result in the exposure of large portions of the wetted channel for periods of 12 hours or more during most of the year. Based on qualitative observations of the recovery of Cladophora following the October 1984 drawdown, a three month period of recovery may not be sufficient for the return of Cladophora to the previously exposed areas.

Alternative Number Five: This scenario releases water in order to maximize fish habitat during certain times of the year. Daily fluctuations are minimized (6,000 to 10,000 cfs) for five months during the fall and winter and then returned to maximum daily fluctuations (1,000-3,000 to 31,500 cfs) for the remainder of the year. During the major portion of the year large portions of the wetted channel will be exposed for 12 hours or more resulting in the loss of Cladophora and epiphytes from those areas. Whether the five months of reduced daily fluctuations will allow for the colonization of these areas by Cladophora and its epiphytes is unknown.

Alternative Number Six: This alternative proposes how to route water downstream during high runoff years if water needs to be bypassed. The effects of this alternative depend on the alternative flow patterns which precede and follow the bypass.

Alternative Number Seven: Alternative Number Seven suggests how to parcel water out during low water or drought years. If flows are maintained at low levels, with or without daily fluctuations, for extended periods Cladophora and epiphytes will be lost from the exposed areas. The recolonization of rewetted areas depends on the alternative flow pattern which follows the drought period.

CHAPTER EIGHT: RESEARCH REPORT; LITERATURE CITED

- Adams, M.S. and W. Stone. 1973. Field studies on photosynthesis of Cladophora glomerata (Chlorophyta) in Green Bay, Lake Michigan. *Ecology* 54:853-862.
- Bancroft, D.C. and K. Sylvester. 1978. The Colorado River Glen Canyon Tailwater Fishery. Ann. Rept. July 1977-June 1978. Arizona Game and Fish Department.
- American Public Health Association. 1976. Standard Methods for the Examination of Water and Wastewater. American Public Health Association, Inc., New York. 1193 pp.
- Bellis, V.J. and D.A. McLarty. 1967. Ecology of Cladophora glomerata (L.) Kutz. in southern Ontario. *J. Phycol.* 3:57-63.
- Blinn, D.W., C.A. Pinney, R. Truitt and A. Davis. 1986. The influence of elevated water temperatures on epiphytic diatom species in the tailwaters of Glen Canyon Dam and the importance of these epiphytic diatoms in the diet of Gammarus lacustris. Final Report to the Glen Canyon Environmental Studies, U.S. Bureau of Reclamation, Flagstaff, AZ. 19 pp.
- Blum, J.L. 1982. Colonization and growth of attached algae at the Lake Michigan water line. *J. Great Lakes Res.* 8:10-15.
- Carothers, S.W. and C.O. Minckley. 1981. A survey of the aquatic flora and fauna of the Grand Canyon. Final Report to U.S.D.I., Water and Power Res. Serv., Lower Colorado Region, Boulder City, Nevada. 401 pp.
- Chudyba, H. 1965. Cladophora glomerata and accompanying algae in the Skawa River. *Acta. Hydrobiol.* 7, Suppl.(1):92-126.
- Czarnecki, D.B. and D.W. Blinn. 1977. Diatoms of lower Lake Powell and vicinity. *Biblio. Phycol.* 28:1-119.
- Czarnecki, D.B. and D.W. Blinn. 1978. Diatoms of the Colorado River in Grand Canyon National Park and Vicinity (Diatoms of southwestern USA III). *Biblio. Phycol.* 38:1-181.
- 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. Ser.* 8:301-308.
- Dromgoole, F.I. 1980. Desiccation resistance of intertidal and subtidal algae. *Bot. Mar.* 23:149-159.

- Ivars, 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.* 47:55-61.
- Graham, J.M., M.T. Auer, R.P. Canale, and J.P. Hoffman. 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.* 8:100-111.
- Herbst, R.P. 1969. Ecological factors and the distribution of Cladophora glomerata in the Great Lakes. *Amer. Mid. Nat.* 82:90-98.
- Hodgson, L.M. 1981. Photosynthesis of the red alga, Gastroclonium couteri (Rhodophyta) in response to changes in temperature, light intensity, and desiccation. *J. Phycol.* 17:37-42.
- Hoffman, J.P. 1979. Evidence for photosynthetic control of reproduction in the nuisance alga Cladophora glomerata, Chlorophyceae, Cladophorales. Meeting of the Phycological Society of America, Stillwater, Okla. USA, Aug. 12-16, 1979. *J. Phycol.* 15 (Suppl.) 1979.
- Jones, H.G. and T.A. Norton. 1979. Internal factors controlling the rate of respiration from fronds of some intertidal algae. *New Phytol.* 83:275-285.
- Kociolek, J.P., M.A. Lamb, and R.L. Lowe. 1983. Notes on the growth and ultrastructure of Biddulphia laevis Ehr. (Bacillariophyceae) in the Maumee River, Ohio. *Ohio J. Sci.* 83:125-130.
- Mantai, K.E. 1982. Energy relationships of Cladophora glomerata. *Plant Physiol.* 69 (4 Suppl):103.
- Mason, C.P. 1965. Ecology of Cladophora in farm ponds. *Ecology* 46:421-428.
- Moore, J.W. 1976. Seasonal succession of algae in rivers. Part 1: Examples from the Avon River, England: A large slow flowing river. *J. Phycol.* 12(3):342-349.
- 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.
- Patrick, R. 1977. Ecology of the freshwater diatoms and diatom communities. In: Biology of the Diatoms, Vol. 13, Werner, D., ed. University of Calif. Press, Berkeley. pp 284-332.
- Patrick, R. and C.W. Reimer. 1966. The diatoms of the United States. Volume I. *Acad. Nat. Sci. Philadelphia Mono. No.* 13. 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.
- 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.
- Schonbeck, M.W. and T.A. Norton. 1979. An investigation of drought avoidance in intertidal fucoid algae. *Bot. Mar.* 31:303-313.
- USBUREC 1985. Glen Canyon Dam flow releases. Unpublished Report.
- Whitton, B.A. 1970. Biology of Cladophora in freshwaters. *Water Res.* 4:457-476.
- Wong, S.L., B. Clark, M. Kirby, M., and R.F. Kosciaw. 1978. Water temperature and seasonal periodicity of Cladophora glomerata and Potamogeton pectinatus in shallow rivers. *J. Fish. Res. Bd. Can.* 35:866-870.
- Wood, K.G. 1968. Photosynthesis of Cladophora under unnatural conditions. pp 121-133. In: D.F. Jackson (ed), *Algae, Man and Environment*. Syracuse Univ. Press, Syracuse, N.Y. 554 pp.
- Woodbury, A.M., S. Flowers, D.W. Lindsay, S.D. Durrant, N.K. Dean, A.W. Grundman, J.R. Crook, W.H. Behle, H.G. Higgins, G.R. Smith, G.G. Musser and D.B. McDonald. 1959. Ecological studies of the flora and fauna in Glen Canyon. *University of Utah Anthropological Papers* 40(7):1-229.