SHORT COMMUNICATIONS

RESPONSE OF EPIPHYTIC DIATOM COMMUNITIES FROM THE TAILWATERS OF GLEN CANYON DAM, ARIZONA, TO ELEVATED WATER TEMPERATURE

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ABSTRACT

The composition of epiphytic diatom communities from the cold tailwaters (12°C) of Glen Canyon Dam, Arizona, was analysed after a 2 wk incubation period at 12°C, 18°C and 21°C. There was a significant change in diatom composition between 12°C and 18°C, while no significant changes occurred between 18°C and 21°C. This suggests that a temperature threshold exists between 12°C and 18°C for the diatom flora in the tailwaters of Glen Canyon Dam. At the two higher water temperatures, smaller and closely adnate taxa became more important numerically than larger, upright, cold water stenotherms. The potential importance of this compositional shift in epiphytic diatoms on macroinvertebrate grazers has management implications regarding different release programs from reservoirs.

KEY WORDS Epiphytic diatoms Elevated water temperature Rivers Tailwaters

INTRODUCTION

Hypolimnetic discharges from reservoirs are quite common and can modify the composition and quantity of downstream algal communities in lotic systems as a result of changes in nutrient loading, flow regulation, light penetration, and water temperature (Lawson and Rushforth, 1975; Ward, 1976a; Lowe, 1979). Epiphytic diatoms are frequently important primary producers in the tailwaters of these deep-release dams (Lawson and Rushforth, 1975; Lowe, 1979; Dufford *et al.*, 1987) and cold-water stenotherms usually dominate in the cool, nutrient-rich downstream sites (Dufford *et al.*, 1987).

Surface release reservoirs (Ward and Stanford, 1987) or selective depth withdrawal systems (Cassidy and Dunn, 1987; Cowx *et al.*, 1987) can potentially discharge water with constant, elevated temperatures to downstream sites. Increases in downstream water temperature may produce major qualitative and quantitative changes in the fauna also (Fraley, 1979; Ward, 1976b; Cowx *et al.*, 1987; Saltveit and Brabrand, 1987).

The U.S. Fish and Wildlife Service has suggested a modification in the water release program at Glen Canyon Dam in order to improve the habitat for the humpback chub (*Gila cypha*), a species endemic to the Colorado River (Stanford and Ward, 1986a). Presently, cool water (ca. 12°C ± 2°C) from the hypolimnion of Lake Powell is released into what was formerly a warm, turbid segment of the Colorado River (Stanford and Ward. 1986b). The new plan proposes to release warmer subsurface water from the epilimnion of Lake Powell into the tailwaters of the Colorado River which would elevate the present water temperature of downstream sites to 18–21°C during the summer. The plan to modify the release program at Glen Canyon Dam was postponed because too little information was available on the

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potential impacts of elevated water temperatures on downstream biota, and no information was available on the placement of exotic fish into the Colorado River below the dam.

The objective of this study was to provide information on the effects of elevated water temperature on important algal primary producers below Glen Canyon Dam. The composition of epiphytic diatom communities from the tailwaters of Glen Canyon Dam was compared after a 2 wk incubation period in laboratory circulation chambers at 12°C, 18°C and 21°C.

STUDY SITE AND METHODS

The headwaters of the Colorado River originate in the Rocky Mountains of northern Colorado and its tributaries drain the mountains of Colorado, Utah, Wyoming, and New Mexico, U.S.A. The Colorado flows southwesterly for 2320 km until it empties into the Gulf of California in Mexico (Stanford and Ward, 1986b) The highly erodible sediments of the arid Southwest produce high sediment loads and turbidity during certain seasons in the lower reaches of the Colorado River. Certain impoundments along the Colorado, however, have made profound effects on flow, temperature, and sedimentation. For instance, the 24 km reach between Glen Canyon Dam and Lee Ferry, Arizona, was once part of a warm, turbid desert river. Following impoundment this reach was converted into a section with cool (12°C), clear, nutrient-rich waters. These modified conditions along with stable rock substrata support a dense stand of the filamentous green alga. *Cladophora glomerata* (L.) Kütz. with associated epiphytes, and one of the finest trout fisheries in the western U.S.A. (Stanford and Ward, 1986a).

Stones (<50 cm^2 in surface area) with the attached filamentous green alga, *Cladophora glomerata*, the filaments of which were colonized by epiphytes, were randomly collected in the Colorado River at Lee Ferry, Arizona, on September 9 and 25, 1986. The composition of the epiphytic diatom assemblage in the thermally constant tailwaters of Glen Canyon Dam is similar throughout the year (Usher *et al.*, 1987). The stones were transported in ice chests filled with Colorado River water to a Frigid Unit 'Living Stream' (Model #LSW–700) holding tank at Northern Arizona University. The stream tank was maintained at 12°C ± 1°C with 200 μEin m^{-2} s^{-1} light energy on a 16:8 h (L:D) photoperiod.

Two separate two-week experiments (collections from September 9 and 25) were conducted to determine the importance of water temperature on the composition of epiphytic diatoms. In each experiment, six stones were randomly selected from the 'Living Stream tank and placed into a cylindrical plexiglass circulating system (16 cm diameter and 12 cm high) containing water from the Colorado River. The circulating chambers were designed after the systems used by Walde and Davies (1984). Each circulating chamber held 1·5 L of water which flowed at a rate of 20–25 cm s^{-1} through a holding tank with 35 L of water. Three circulating systems, each containing six stones colonized by *Cladophora* and epiphytes, were placed in environmental incubators set at 12°C ± 1°C, 18°C ± 1°C, and 21°C ± 1°C, respectively. Each incubator was set at 150–200 μEin m^{-2} s^{-1} on a 16:8 h (L:D) photoperiod. Three additional stones were randomly selected from the 'Living Stream' tank to be used as initial controls.

The epiphytic assemblages were allowed to incubate at the respective temperatures for 2 wk. Water was replaced at the end of the first week with water collected at Lee Ferry. At the end of each experiment, three stones were randomly selected from each of the three circulating chambers at each temperature treatment and all *Cladophora* and epiphytes were removed from the stones. The epiphytes were cleaned with 30 per cent hydrogen peroxide and potassium dichromate. Prepared slide mounts of cleaned material were examined and diatom cells were enumerated and species relative abundances determined. Two-way ANOVA computations between species and temperature were performed on pooled values from the two experiments, because no significant differences were noted between the two experimental trials.

RESULTS AND DISCUSSION

The abundant standing crop of *Cladophora glomerata* in the tailwaters of Glen Canyon Dam supported a luxuriant growth of epiphytic diatoms (Usher *et al.*, 1987). Five taxa, including *Rhoicosphenia curvata*

(Kütz.) Grun. ex Rabh., *Diatoma vulgare* Bory, *Cocconeis pediculus* Ehr., *Achnanthes minutissima* Kütz., and *Cymbella affinis* Kütz. comprised over 85% of the diatom epiphyte assemblage on *C. glomerata* throughout the year in the cool tailwaters at Lee Ferry (Usher *et al.*, 1987). These five diatom species are important epiphytes on *Cladophora* in the Colorado River from Glen Canyon Dam, Arizona, to Diamond Creek, 394 km downstream (Czarnecki and Blinn, 1978; Usher *et al.*, 1987). All taxa, including *Cladophora,* are common in the cool tailwaters of other major dams (Lowe, 1979; Dufford *et al.*, 1987). Water temperatures in the Colorado River remain below 14°C throughout Glen and Grand Canyons because of the hypolimnion release at Glen Canyon Dam.

After the two week period, diatom assemblages (i.e. five dominants) incubated at the three water temperatures differed significantly ($F_{2\ 75} = 4{\cdot}98$; $p < 0{\cdot}01$). The population of a large chain forming species (*Diatoma vulgare*) decreased most dramatically with elevated water temperature, and the upright taxon (*Rhoicosphenia curvata*) showed the next greatest decrease (Figure 1). The combined relative abundance of these two species decreased from 58 per cent (s.e. ± 2·9) in the initial field controls to 30 per cent (s.e. ± 1·6) and 18 per cent (s.e. ± 1·1) at 18°C and 21°C, respectively. In contrast, the adnate taxon, *Cocconeis pediculus*, and two smaller taxa, *Achnanthes minutissima* and *Cymbella affinis*, increased from 33 per cent (s.e. ± 1·8) to 59 per cent (s.e. ± 2·3) of the assemblage at 21°C, with *A. minutissima* and *C. pediculus* showing the greatest increase (Figure 1).

The remaining taxa ('other') comprised 7 per cent (s.e. ± 0·5) of the diatom assemblage at 12°C and increased to 17 per cent (s.e. ± 1·3) and 23 per cent (s.e. ± 1·5) at 18°C and 21°C, respectively (Figure 1). This category included 14 taxa with *Achnanthes lanceolata* (Breb.) Grun, *Gomphonema olivaceum* (Lyngb.) Kütz, *Gomphonema parvulum* Kütz. *Navicula cryptocephala* Kütz., and *Nitzschia dissipata* (Kütz.) Grun. being the most abundant. All of these taxa increased in trials with elevated water temperature.

Diatoma vulgare has been referred to as a cold water taxon by a number of investigators, while *C. pediculus. A. minutissima, R. curvata* and *C. affinis* are known to exist in a wide range of temperatures (Patrick and Reimer, 1966; Lowe, 1974; Bahls *et al.*, 1984). This concurs with our findings on temperature tolerance for each of these species except for *R. curvata*. The subtle interactions within the epiphyton assemblage undergoing change may be responsible for the loss of *Rhoicosphenia* cells at elevated temperatures. Alternatively, the population of *R. curvata* in the constant, cool waters of Lee Ferry may have become less resilient to temperature change. The fact that there was no significant difference ($F_{1\ 60} = 0{\cdot}50, p > 0{\cdot}05$) in taxonomic composition of the diatom assemblage between the initial field controls and trials at 12°C suggests that flow rate and nutrients were similar within the experimental circulating chambers during the two week incubation period.

Stevenson and Stoermer (1982) noted that *C. pediculus* was the dominant epiphyte on *Cladophora* along the wave-swept shores of Lake Huron during the summer when water temperatures reached 23°C. *C. pediculus* was replaced by *R. curvata* during November at temperatures of 8°C. Perhaps these seasonal changes in species dominance reflect, in part, the thermal requirements of these two taxa in addition to competition with the *Cladophora* substratum as proposed by Stevenson and Stoermer (1982).

The greatest change in diatom assemblage from Lee Ferry occurred between trials at 12°C and 18°C ($F_{1\ 60} = 11{\cdot}41, p<0{\cdot}01$), however there was no significant difference ($F_{1\ 60} = 0{\cdot}66, p > 0{\cdot}05$) between experimental trials at 18°C and 21°C. This suggests that a threshold in temperature exists between 12 to 18°C for the diatom flora in the tailwaters of Glen Canyon Dam. Hustedt (1939) classified diatoms according to their ability to tolerate various temperature regimes. His scheme indicates that the upper limits for the cold-water stenotherms is 15°C and that temperate stenotherms range from 15–25°C. Patrick (1971, 1977) and Tuchman and Blinn (1979) also discussed the dramatic effect of small changes in water temperature on community structure at temperatures near the upper tolerance limits of diatom taxa.

In summary, our findings suggest that increases in water temperature, due to different release programs from reservoirs, could modify downstream epiphytic diatom assemblages within a two week period. At elevated water temperatures, the closely adnate forms like *C. pediculus* and smaller taxa like *A. minutissima* and *C. affinis* replace the larger, upright, light-shielding overstory species (i.e. *Diatoma vulgare* and *Rhoicosphenia curvata*) that dominate in cool tailwater systems (Lowe, 1979). This may have

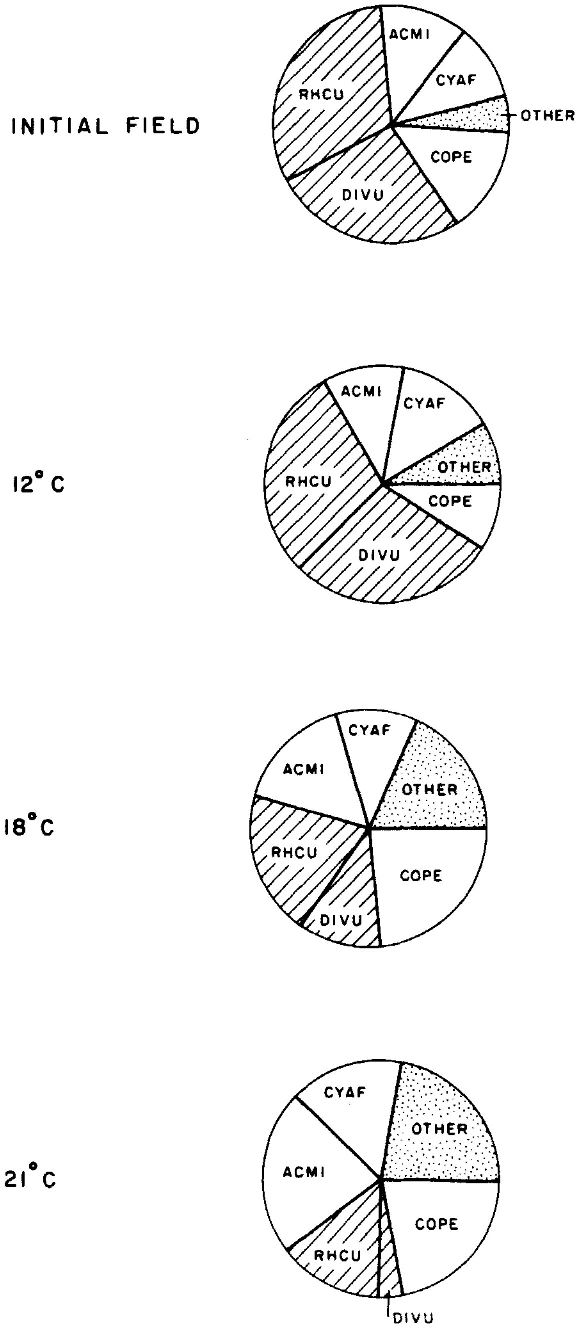

Figure 1. Pie diagrams illustrating relative proportions of selected diatom species and remaining diatom taxa ('other'; stipled section) for initial field assemblages and at 12°C, 18°C, and 21°C in laboratory circulation chambers. Hatched sections represent diatoms that are large and upright. Acmi = *Achnanthes minutissima*, Cyaf = *Cymbella affinis*, Cope = *Cocconeis pediculus*, Divu = *Diatoma vulgare*, Rhcu = *Rhoicosphenia curvata*.

an important long term effect on the composition of primary consumers in tailwater systems because recent studies have demonstrated that larger, upright diatom species are consumed over smaller adnate taxa by macroinvertebrate grazers (Sumner and McIntire, 1982; Steinman *et al.*, 1987; Colletti *et al.*, 1987). Increases in water temperature may also affect the composition of invertebrate grazers (Ward and Stanford, 1982) and elevated temperature may reduce the standing crop of *Cladophora* substratum available for epiphytes (Bellis and McLarty, 1967; Whitton, 1970), both of which emphasize the close interactions within and between trophic levels and physico-chemical parameters.

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