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Discharge

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## PERIPHYTIC COMMUNITY RESPONSE TO CHRONIC NUTRIENT ENRICHMENT BY A RESERVOIR DISCHARGE<sup>1</sup>

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**Abstract.** Periphytic communities were investigated using glass slide substrates at four sites downstream from the montane Hyalite Reservoir, Montana, USA. Comparison of the most upstream site with the three lower sites revealed that the discharges to Hyalite Creek stimulated periphytic productivity, increased periphytic proportions of chlorophyll *a* in the organic accumulations, and increased diatom species diversity and evenness. As nitrogen concentration was the only stream physiochemical parameter which correlated with periphytic variations, it is probable that ammonia nitrogen discharged from the reservoir was the primary factor influencing periphytic growth. *Cocconeis placentula* var. *lineata* dominated generally  $\approx 70$ –80% of the diatom communities at the three downstream sites whereas only three individuals of this species were observed at the upper site. Data from two successional series following colonization of the slides suggested that species other than *Cocconeis* had higher initial growth rates. It appears the *Cocconeis* become dominant at the three downstream sites because of higher efficiencies for obtaining or incorporating limiting nitrogen resources; species other than *Cocconeis* dominated the diatom communities in which nitrogen concentrations were enriched, apparently because of higher potential growth rates which could be realized with the elevated nutrient conditions. A brief review of the literature and new data presented indicate that species diversity first increases and then decreases as a function of resource abundance.

**Key words:** chlorophyll; diatoms; diversity; eutrophication; Montana; nitrogen limitation; periphyton; primary productivity; reservoir impact.

### INTRODUCTION

Much recent effort in stimulus-response ecology (Regier and Rapport 1978) has been directed toward defining the paradigm of community response to nutrient enrichment. Kirchner (1977) criticized various previous enrichment experiments, which employed only single fertilizer applications, as providing "acute" stresses and therefore affecting only organisms capable of rapid responses; to evaluate the effects of "chronic" stresses, repeated or continual fertilization must be investigated.

Nutrient concentrations of effluent waters from reservoirs having deep-water discharges are frequently elevated over levels found in waters influent to the reservoirs (Wright 1967, Hynes 1970, Smith 1973, Soltero et al. 1973, Rada 1974, Knight et al. 1976, Martin and Arneson 1978). This enrichment of the immediate downstream environment produces a chronic perturbation on the resident populations; but, as pointed out by both Wright (1967) and Soltero et al. (1973), intensive studies of community responses to this form of eutrophication are lacking. Various qualitative observations of plant growth stimulation immediately below reservoirs have been presented (e.g., Finnell 1953, Pfitzer 1954, Neel 1963, Stober 1963 and Ward 1974, 1976). In addition, McConnell and Sigler (1959) noted that the minimum periphytic chlorophyll production

below a reservoir on the Logan River, Utah, exceeded the maximum production for sampling sites above that reservoir.

In studying stream response to perturbation, periphyton, the entire attached aquatic community, has several distinct attributes: it remains in a fixed location, integrating the environmental parameters which impact on it (Patrick 1973). It permits relatively easy sampling, has a relatively short response time, and reflects changes in the aquatic system through changes in diatom diversity (Stoneburner et al. 1976). Therefore, periphyton and its resident diatom populations provide an ideal system for investigating the effects of nutrient enrichment on community function and structure.

This report describes periphytic development and growth in a stream below a montane reservoir with a deep-water release. The results of two studies are presented: the first characterizes temporal and spatial periphytic growths and diatom populations on microscope slides at four stream sites below the reservoir; the second examines increasing periphytic accumulations and diatom succession on two series of slides at a single site.

### STUDY AREA

Hyalite Creek originates in a high-mountain, steep-slope drainage between Yellowstone National Park and Bozeman, Montana. The creek is impounded near its headwaters to form the 84-ha Hyalite Reservoir, having a maximum depth of 27 m. Discharges descend

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TABLE 1. Sampling season means ( $\pm 1$  SD) or ranges of physical and chemical parameters at the study sites during 16 June to 18 October 1976 (\*indicates parameters where significant differences,  $P < .05$ , occurred among data; sites not significantly heterogeneous are indicated by connective underlining).

Parameter	H1	H1A	H1B	H2
Temperature ( $^{\circ}\text{C}$ )	$8.5 \pm 2.5$	$8.4 \pm 2.5$	$8.2 \pm 2.5$	$8.8 \pm 2.2$
Turbidity (JTU) <sup>†</sup>	$2.4 \pm 1.3$	$2.7 \pm 1.6$	$2.2 \pm 0.9$	$2.6 \pm 1.0$
Conductivity ( $\mu\text{S}/\text{cm}$ )*	$63 \pm 7$	$65 \pm 6$	$97 \pm 20$	$102 \pm 18$
pH (ranges)	<u>7.2–8.3</u>	<u>7.4–8.8</u>	<u>7.1–8.5</u>	<u>7.6–9.0</u>
Alkalinity ( $\text{CaCO}_3$ mg/l)*	$30 \pm 3$	$31 \pm 3$	$46 \pm 10$	$49 \pm 9$
Hardness ( $\text{CaCO}_3$ mg/l)	$29 \pm 3$	...	...	...
Ortho $\text{PO}_4\text{-P}$ ( $\mu\text{g}/\text{l}$ )	$50 \pm 6$	$50 \pm 6$	$47 \pm 4$	$46 \pm 6$
Total $\text{PO}_4\text{-P}$ ( $\mu\text{g}/\text{l}$ )	$63 \pm 8$	$63 \pm 9$	$60 \pm 8$	$62 \pm 11$
$\text{NO}_3\text{-N}$ ( $\mu\text{g}/\text{l}$ )	$6 \pm 6$	$8 \pm 9$	$8 \pm 9$	$5 \pm 6$
$\text{NO}_2\text{-N}$ ( $\mu\text{g}/\text{l}$ )	$1 \pm 1$	$1 \pm 1$	$1 \pm 1$	$1 \pm 1$
$\text{NH}_3\text{-N}$ ( $\mu\text{g}/\text{l}$ )*	$26 \pm 11$	$9 \pm 5$	$13 \pm 9$	$10 \pm 7$
Total inorganic N ( $\mu\text{g}/\text{l}$ )*	$33 \pm 13$	$19 \pm 11$	$22 \pm 9$	$16 \pm 8$

<sup>†</sup> Jackson Turbidity Units.

from an outlet 23 m below the spillway through a montane valley, alternating between unshaded flood plains and dense forests of lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas fir (*Pseudotsuga menziesii*). Aquatic bacterial populations and water chemistry in the drainage have been investigated for over a decade (e.g., Stuart et al. 1971, Schillinger and Stuart 1978).

Below the reservoir four sites, ranging in elevation from 2012 m to 1865 m, were selected in Hyalite Creek for periphyton studies. Sites H1, H1A, H1B and H2 were 10 m, 1.9 km, 4.0 km and 7.3 km downstream of the reservoir outlet, respectively. A map of the study area is presented in Stuart et al. (1971).

Light conditions at all stations were ostensibly similar, being unshaded throughout the majority of each day. Bottom materials had similar compositions at all sites, ranging from sand and gravel to polished cobble and boulders; stream bed gradients were 81, 55 and 42 m/km at the three successive downstream sites. Water depths ranged from 0.6–1.2 m, early in the study, to 0.3–0.6 m. During the study mean daily discharge from Hyalite Reservoir, the major water source to the sites, ranged between 4.8 and 5.8 m<sup>3</sup>/s, until 30 July. Subsequently, discharges were progressively reduced in steps at approximately 2-wk intervals to 1.4 m<sup>3</sup>/s on 14 September; this level was maintained through the end of this study (Marcus et al. 1978).

Volcanic igneous rocks dominate the watershed above Hyalite Reservoir; due to the chemical and weathering resistance of the igneous materials, such drainages tend to be relatively low in most dissolved minerals except phosphorus (Dillon and Kirchner 1975). Drainages below the reservoir contain areas of Mesozoic sedimentary rock, a belt of Precambrian sedimentary rock and patches of Precambrian metamorphic rock (Chadwick 1969).

Samples for water quality analyses were collected

at approximately weekly intervals (15 dates) during this study (Schillinger and Stuart 1978). All samples were collected between 0700 and 1200, with the earliest collections occurring upstream. Table 1 presents a summary of the physical and chemical data. Temperature, turbidity, pH and concentrations of orthophosphate, total phosphate, nitrate-nitrogen and nitrite-nitrogen were relatively uniform among the sites. Conductivity and alkalinity increased downstream, reflecting the increasing influence of sedimentary rock in the drainage. Ammonia nitrogen dominated the total inorganic nitrogen; the highest concentrations of both occurred at the Site H1. Algal-assay bottle tests conducted on water from the sites repeatedly indicated that nitrogen concentrations were limiting to algal growth at all sites throughout this study (Schillinger and Stuart 1978). Hardness and related salinity factors were determined only at Site H1 on five dates during the study; mean concentrations in milligrams per litre  $\pm 1$  SD were calcium  $7.8 \pm 1.0$ , magnesium  $2.3 \pm 0.3$ , sodium  $1.7 \pm 0.3$ , potassium  $1.9 \pm 0.1$ , chlorine  $0.2 \pm 0.2$  and sulfate  $2.4 \pm 0.4$ . More complete presentations of physical and chemical data at the study sites and the standard analytical methods used are presented in Schillinger and Stuart (1978).

#### METHODS AND MATERIALS

Studies began in June 1976 when spring runoff into Hyalite Creek decreased sufficiently to allow placement of artificial substrates for periphyton colonization; sampling concluded with the fall freezes in October. Periphyton samples were collected by incubating  $25 \times 75$  mm glass microscope slides at each site. Plexiglass diatometers, modified from Patrick and Reimer (1966), mounted on concrete blocks (ca. 40 cm square by 10 cm thick) held eight slides, long edge down, at 1-cm intervals near the stream bottom. Diatometers were placed in similar microhabitats to min-

imize variations in physical conditions (e.g., stream depths); additionally, the leading wedge-shaped deflector on the diatometers helped to standardize water flow to the slides.

Prior to incubation in the stream, new slides were soaked in concentrated  $H_2SO_4$ , thoroughly rinsed with water, dried, and heated to  $500^\circ C$  for at least 0.5 h. Subsequently, all slides were handled with forceps to reduce organic contamination. Slides destined for total mass (dry mass) and organic mass (ash-free dry mass) determination were weighed to the nearest 0.5 mg before placement in a slide box for transport to the sites.

To investigate temporal and spatial periphytic patterns at the four sampling sites, microscope slides were submerged with overlapping exposure periods. On 18 June 1976 the first slides were introduced to all sites. Plans to introduce slides at 14-d intervals were upset by the heavy spring rains which caused exposure periods to vary. The high water also destroyed diatometers at Sites H1A and H1B, temporarily delaying sample collection at these sites. An exposure period of about 1 mo was completed for most samples; data from the colonization and succession studies suggested that such an exposure period provided maximum estimates of periphytic productivity.

On each sampling date for a site, a set of four glass slides was inserted into the diatometer: two slides were used for mass and pigment analyses; one slide was used for quantitative diatom population studies; and one slide provided a sample for bacterial analyses.

A separate study to investigate periphytic colonization and diatom succession was conducted at Site H2 by incubating two overlapping series of slides. The site was selected to represent the low nutrient condition existing in the study area. Each series had four pairs of slides: one slide of each pair provided a sample for total-accumulation, organic standing crop and chlorophyll *a* analyses; and the second slide provided a sample for diatom population study.

The four pairs of slides comprising the first series were immersed in the stream 18 June 1976. High stream flow from the recurring spring rains prevented access to the diatometer until 16 July 1976; at that time the first slide pair of the first series was removed. Additional slide pairs from the first series were subsequently removed following progressively longer exposure periods. As each pair of slides was removed for the first series, a new slide pair for the second series was installed in the emptied slots of the diatometer. Following exposure of all slides comprising the second series, these slides were simultaneously removed. Slide pairs of the first series were exposed for 28, 35, 42 and 54 d; exposures in the second series were for 35, 28, 21 and 9 d, respectively.

Slides recovered from all studies were placed in individual wide-mouth amber bottles after any macroinvertebrates were removed. Slides for accumulated

mass and pigment analyses were broken to ensure complete immersion in bottles containing 25 ml of acetone. These bottles were wrapped with aluminum foil and kept on ice to help prevent pigment degradation during transport to the laboratory. Bottles containing slides for periphytic population analyses held an algal preservative.

In the lab, bottles containing pigment-analysis samples were stored at  $<0^\circ C$  for 1–4 d (Weber 1973). To clear the pigment extracts following storage, extract aliquots were spun for 5 min at high speed in a clinical centrifuge before analyses on a Beckman Model DU-2 spectrophotometer. Chlorophyll *a* concentrations ( $mg/m^2$ ), an indicator of algal or phycoperiphytic biomass, were calculated using tricolorimetric formulas of the American Public Health Association (1971) and Strickland and Parsons (1972). Following spectrophotometric analyses, the extracts were returned to their respective bottles. Dry and organic accumulations were determined by depositing the contents of each bottle (periphyton, preweighed slide and acetone) in a tared evaporating dish, evaporating the acetone, and then following the procedures of Weber (1973). To permit comparison with the literature, 50% of the organic mass is assumed to be carbon (Stockner and Armstrong 1971, Wetzel 1975).

Net periphytic productivity ( $mg\ C \cdot m^{-2} \cdot d^{-1}$ ) was estimated by dividing the total carbon accumulation per slide by the number of days submerged to give an average daily productivity for the exposure period. In the accumulation and succession studies the method of Kevern et al. (1966) was additionally used to estimate potential maximum periphytic productivity for each series. Briefly, their method determines the ascending linear slope from a plot of organic accumulations on slides vs. exposure times; they equated the value of this slope to the daily net productivity of a well-established algal growth existing on a natural stream bottom.

Slides used for enumerating algal populations were scraped in the laboratory and rinsed with measured amounts of the preservative solution. A subsample of each mixture was cleaned for diatom analysis (Patrick and Reimer 1966, Hasle and Fryxell 1970). Permanent mounts of diatoms were made with Hyrax (Weber 1973). To determine the percent composition of each taxon, diatoms were counted at  $1000\times$  on a Nikon Model S-ke Microscope with an interference-phase attachment. Random fields were counted until  $>300$  diatom valves or 200 microscopic fields were counted. Cooper and Wilhm (1975) found that counts of 100 individuals from periphytic populations provided species diversity values which were not significantly different from diversity values obtained in counts two to four times larger for the same population.

Diatom diversity ( $D_s$ ) was calculated by  $D_s = (\sum p_i^2)^{-1}$ , where  $p_i$  is the portion of all individuals be-

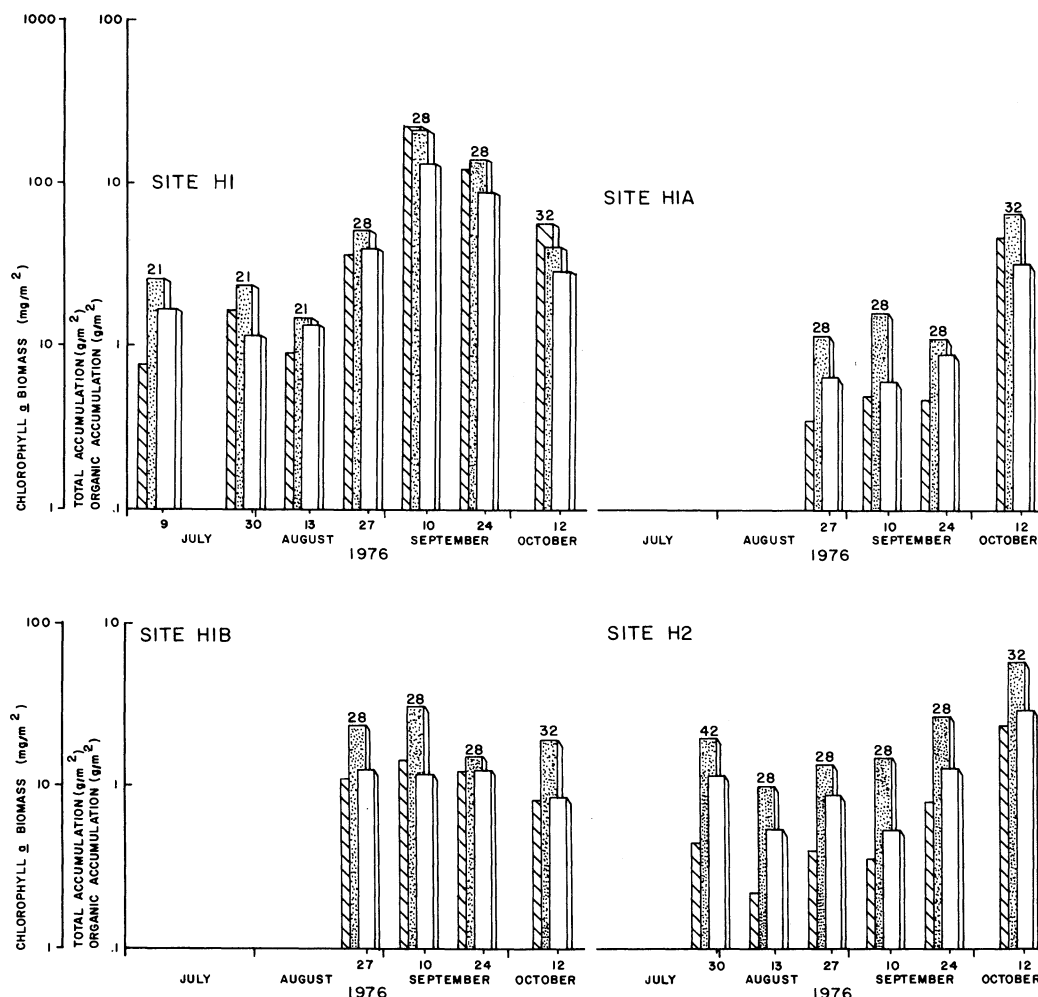


FIG. 1. Means of periphytic organic standing crop accumulation (clear bars), total periphytic accumulation (stippled bars) and chlorophyll *a* biomass (hatched bars) on the collection dates shown by the abscissas for the four Hyalite Creek sites. The length of the incubation period in days for each collection is given at the top of each column set.

longing to the  $i^{\text{th}}$  species. MacArthur (1972) suggested this index as a useful measure in competitive communities. Diatom evenness ( $J$ ) was evaluated through  $J = H'/\log N_s$ , where  $H'$  is Shannon-Wiener's diversity and  $N_s$  is the number of species (Pielou 1966).

Slides for bacterial analyses were placed in sterile, wide-mouth bottles which were kept on ice during transport. In the lab slides were scraped using aseptic techniques and washed into sterile 0.1% peptone phosphate buffer. Dilutions of the suspension were surface plated onto Difco tryptone glucose extract agar, the plates incubated at 20° for five days and the number of organisms per centimetre of slide surface determined (Schillinger and Stuart 1978).

To evaluate site differences within parameters, 1-way ANOVA with Studentized-Newman-Kuel (SNK) statistics or chi-square tests for goodness of fit were computed (Sokal and Rohlf 1969). Product-moment

correlation coefficients were calculated to determine the degree of association between selected parameters measured during the study (Sokal and Rohlf 1969).

## RESULTS

### *Temporal and spatial periphytic patterns*

Mean chlorophyll *a*, organic and total accumulations on the slides at the four sites for each date are presented in Fig. 1. To aid in interpreting the data, the ordinates are scaled such that when the two parameters plot at equal heights, chlorophyll *a* biomass is 1% of the organic accumulation. At Site H1 periphytic accumulations tended to decrease initially (Fig. 1). This trend reversed in mid-August and continued to mid-September when the mean accumulations peaked at 21.3 g/m<sup>2</sup> total dry mass, 13.6 g/m<sup>2</sup> organic mass and 176 mg/m<sup>2</sup> chlorophyll *a*. Following this peak, ac-

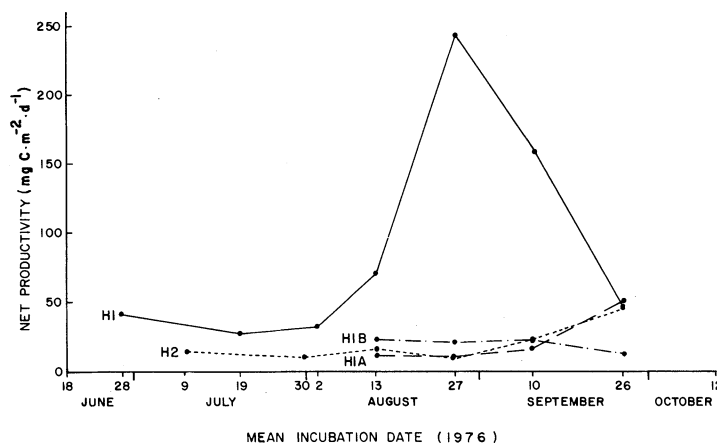


FIG. 2. Patterns of net periphytic productivity at the four Hyalite Creek sites during the study.

cumulations progressively decreased through the end of the study. Chlorophyll *a* comprises markedly less than 1% of the organic accumulation in two of the seven sampling collections. The highest mean was 1.9% on 12 October 1976.

Periphytic accumulations on slides collected from sites downstream of Site H1 were generally less than those found at the upper site and the patterns of accumulation differed as well (Fig. 1). Accumulation patterns also differed somewhat among the three downstream sites. Chlorophyll *a* at both Sites H1A and H2 generally averaged less than 1% of the mean organic accumulation. The only exception occurred in the final collections from Site H1A on 12 October 1976 when chlorophyll *a* averaged 1.3% of the organic matter. At Site H1B chlorophyll *a* generally averaged near the 1% level.

Greatest periphytic productivity occurred at Site H1 throughout most of the study (Fig. 2). Productivity peaked during the period 13 August to 10 September 1976 with the highest mean daily periphytic value observed during this study ( $242 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ). Productivity then decreased through the end of the study; the mean daily productivity estimated for the final expo-

sure period, 10 September to 12 October 1976, was only  $47 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ .

Mean daily periphytic productivity downstream from Site H1 generally remained low during the study, ranging from about 10 to  $23 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  (Fig. 2). Only during the final exposure period did productivity at Sites H1A and H2 closely approximate that found at Site H1. In this final period, productivity at Site H1B fell to nearly one-half the value which it had maintained previously.

The large differences in periphytic productivities on the slides between the upper and three lower sites were reflected by the visible differences in standing crops of epilithic algae. At Site H1 the stream bed was carpeted with dense growths of the chlorophyte *Prasiola* sp., with intermingled growths of the chrysophyte *Hydrurus* sp. Only occasional tufts of these algae colonized scattered rocks at the lower sites. Of these two species, only *Hydrurus* sp. was occasionally found on the slides and then predominantly at Site H1.

Greatest average total mass and organic accumulation occurred at Site H1 (Table 2). Organic accumulations comprised an average 70% of the periphytic total accumulation at Site H1; organic accumulations

TABLE 2. Sampling season means ( $\pm 1$  SD) of periphytic accumulations from the study sites for total dry mass (T.M.) and total dry mass accumulation rate, organic mass (O.M.) and organic mass accumulation rate, proportion organic matter (O.M.:T.M.), chlorophyll *a* accumulation, chlorophyll *a* to organic mass ratio (Chl *a*:O.M.), and net periphytic productivity (N.P.).

Site	T.M.		O.M.		O.M.:T.M. ( $\times 100$ )	Chl <i>a</i> mg/m <sup>2</sup>	Chl <i>a</i> :O.M. ( $\times 100$ )	N.P. mg C $\cdot \text{m}^{-2} \cdot \text{d}^{-1}$
	g/m <sup>2</sup>	mg $\cdot \text{m}^{-2} \cdot \text{d}^{-1}$	g/m <sup>2</sup>	mg $\cdot \text{m}^{-2} \cdot \text{d}^{-1}$				
H1	$7.9 \pm 7.5^*$	$289 \pm 258^*$	$4.8 \pm 4.6^*$	$177 \pm 161^*$	$70 \pm 19^*$	$62 \pm 40^*$	$1.2 \pm 0.6^\dagger$	$83 \pm 80^*$
H1A	$2.9 \pm 3.2$	$94 \pm 105$	$1.4 \pm 1.5$	$44 \pm 45$	$52 \pm 15$	$15 \pm 25$	$0.8 \pm 0.4$	$22 \pm 22$
H1B	$2.3 \pm 0.8$	$81 \pm 30$	$1.1 \pm 0.2$	$40 \pm 10$	$47 \pm 12$	$12 \pm 3$	$1.0 \pm 0.1$	$20 \pm 5$
H2	$2.5 \pm 1.8$	$81 \pm 57$	$1.2 \pm 0.9$	$40 \pm 27$	$52 \pm 12$	$8 \pm 8$	$0.6 \pm 0.2$	$20 \pm 14$

\* Significantly different ( $P < .05$ ) from H1A, H1B and H2.

† Significantly different ( $P < .05$ ) from H2.

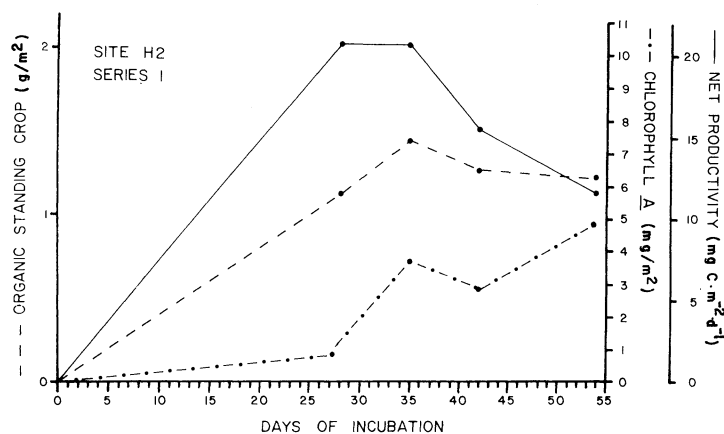


FIG. 3. Patterns of organic standing crop accumulation, chlorophyll *a* biomass and net periphytic productivity during the first series of slides at Site H2.

at the lower sites averaged about 50% of the total periphytic accumulations.

Chlorophyll *a* accumulations at Site H1 averaged four to eight times greater than occurred at the downstream sites, indicating a larger biomass of phycoperiphyton at the upper site. Only at Sites H1 and H1B did chlorophyll *a* constitute an average of 1% or more of the total organic dry mass in the periphyton samples.

The ranking observed for mean seasonal periphytic productivity was the same as that for mean chlorophyll *a* accumulations (Table 2); these 2 parameters were significantly correlated ( $r = .995$ ,  $P < .01$ ). Greatest mean seasonal productivity occurred at Site H1 and was about four times higher than found for any of the lower three sites. Correlation coefficients calculated among mean productivities during the study at the

sites and the respective means for each physiochemical parameter analyzed indicated only ammonia nitrogen as significantly correlated with periphytic productivity ( $r = .972$ ,  $P < .05$ ).

Sixty-one diatom taxa were identified. *Hannaea arcus* dominated the early diatom populations at Site H1. It was replaced by *Synedra cyclopus* var. *robustum*, which persisted as dominant until middle to late August. Subsequently and through the remainder of the study, dominance was shared by several species, most notably *Fragilaria vaucheriae*, *Gomphonema herculeana*, *Navicula pelliculosa*, *Melosira varians* and *S. cyclopus* var. *robustum*.

*Cocconeis placentula* var. *lineata* was the dominant diatom ( $\approx 70$ – $80\%$ ) at the three lower Hyalite Creek sites during the entire study. *Melosira varians* was important at Sites H1A and H1B, while at Site H2 it was present only in minor populations ( $< 10\%$ ). Other species which comprised at least 10% of the total diatom population in at least one sample from three lower study sites included *C. placentula* var. *euglypta*, *Achnanthes lanceolata* and *A. lanceolata* var. *dubia*. Proportions of *C. placentula* var. *lineata* declined from nearly 80% to below 40% of the diatom community on the slides at Site H1A during the final incubation period. A chi-square test for goodness of fit indicated no significant differences in the mean proportions of the five dominant diatom species among the three downstream sites during this study.

Sampling season means at the four sites revealed that Site H1 averaged the greatest number of diatom taxa as well as the highest diatom diversity and evenness (Table 3). ANOVA indicated highly significant ( $P < .01$ ) differences among the respective means of diatom diversity and evenness. Analysis of the diversities at the sites with the SNK multiple comparisons test indicated that Site H1 was significantly ( $P < .05$ ) different from the three lower sites which did not differ among themselves. Using all data, the multiple

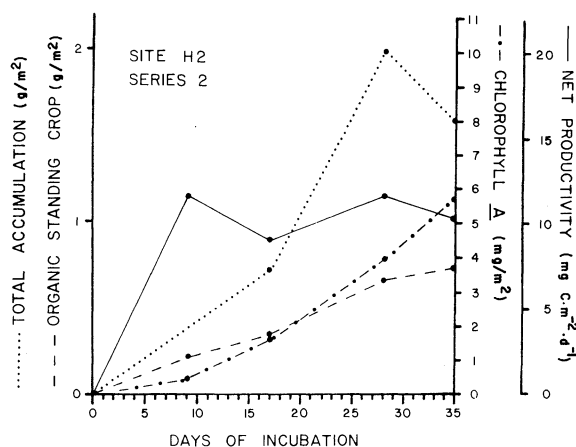


FIG. 4. Patterns of organic standing crop accumulation, total periphytic accumulation, chlorophyll *a* biomass and net periphytic productivity during the second series of slides at Site H2.

TABLE 3. Mean number of periphytic diatom taxa ( $N_s$ ), diversity ( $D_s$ ) and evenness ( $J$ ) at each study site (see text for significant differences).

Site	$N_s$	$D_s$	$J$
H1	15.7	4.57	0.66
H1A	12.8	2.86	0.56
H1B	13.0	2.08	0.49
H2	14.2	1.88	0.44

comparisons analysis of diatom evenness indicated that Site H1 was similar to Site H1A while significantly ( $P < .05$ ) different from the two lower sites; the lower three sites were similar among themselves. During the final incubation period, diatom diversity at Site H1A was greater than twice that obtained for any other incubation period at that site. If the species evenness values for the last collection period are excluded, multiple comparisons analysis indicated a significant ( $P < .05$ ) difference between Site H1 and all three downstream sites; these three sites were similar among themselves. Of the physiochemical parameters, only ammonia nitrogen ( $r = .469$ ,  $P < .05$ ) and total inorganic nitrogen ( $r = .719$ ,  $P < .01$ ) concentrations were found to be significantly correlated to diatom diversity.

Bacterial densities on the slides at the sites generally increased during the study (Marcus et al. 1978). Also, there was a trend of increasing densities with increasing distance below the reservoir: mean numbers of bacteria found on the slides were: Site H1 20 000/cm<sup>2</sup>. Site H1A 20 000/cm<sup>2</sup>, Site H1B 30 000/cm<sup>2</sup> and Site H2 61 500/cm<sup>2</sup>. However, mean bacterial populations were not significantly different among the sites during this study.

The only benthic macroinvertebrates observed on the slides or diatometers were the filter-feeding larvae of *Simulium* sp. These black fly larvae occurred predominantly at the three downstream sites.

#### Colonization and succession on glass slides

In the first of the two series of slides at Site H2, the high water accompanying the recurring spring rains caused glass to erode from the submerged slides. This loss of mass from the preweighed slides prevented determination of the total periphytic accumulation on the slides. However, data for chlorophyll *a*, organic accumulations, net periphytic productivity and diatom populations were obtained because these data did not depend on knowing the initial mass of the slides.

Organic standing crops peaked on slides exposed for 35 d, then decreased with longer exposure; chlorophyll *a* concentration continued to increase through completion of this series (Fig. 3). Net periphytic productivity reached maximum values of 21 mg C·m<sup>-2</sup>·d<sup>-1</sup> between 28 to 35 d of incubation, then decreased. The method of Kevern et al. (1966), based on the prepeak

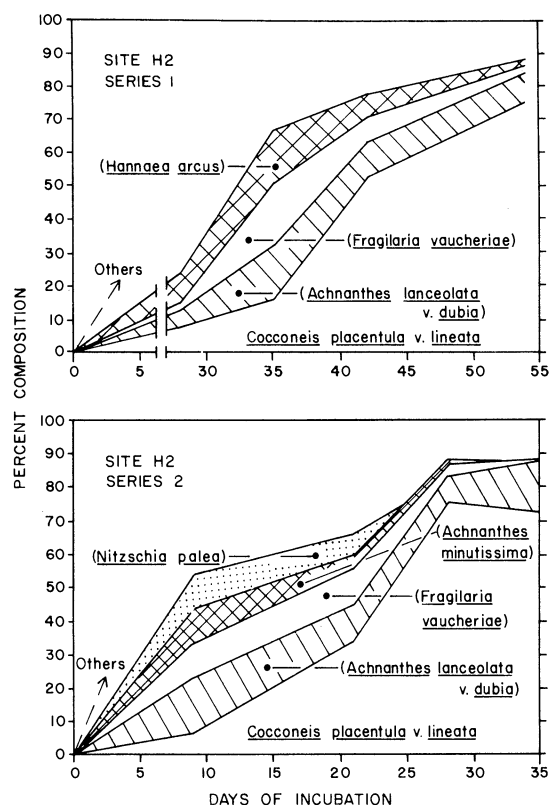


FIG. 5. Diatom succession during both periphytic colonization series at Site H2.

slope of the organic accumulation (Fig. 3), estimated periphytic productivity to be 20 mg C·m<sup>-2</sup>·d<sup>-1</sup>.

Total periphytic accumulations in the second series of slides at Site H2 increased until day 28 of the study, then decreased; both organic masses and chlorophyll *a* biomasses continued to increase throughout this series (Fig. 4). Productivity peaked by day 10 and remained relatively constant during the remainder of the series. Net daily productivities for samples collected both on the 10th and 28th days of exposure were estimated as 12 mg C·m<sup>-2</sup>·d<sup>-1</sup>; a value of 11 mg C·m<sup>-2</sup>·d<sup>-1</sup> was obtained using the method of Kevern et al. (1966).

During both series the abundance of *Cocconeis placentula* var. *lineata* increased from a relatively minor early proportion to dominance of the final diatom community (Fig. 5). Other diatom species concurrently declined in importance.

In both succession series, species numbers and diversities first increased, then decreased with increasing incubation time and biomass accumulation (Fig. 6). Near the end of both incubation series species numbers and diversity appeared to be stabilizing.

Product-moment correlation coefficients were calculated among the individual values for the various parameters measured during these colonization and



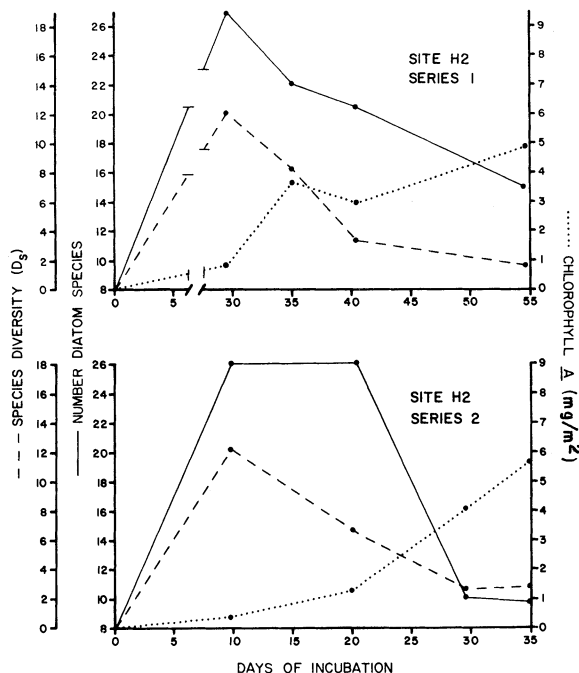


FIG. 6. Changes in diatom species numbers and species diversity in relation to increasing chlorophyll *a* biomass during both periphytic colonization series at Site H2.

succession studies. Coefficients were determined both for each individual series and for both series combined. The only highly significant correlations ( $P < .01$ ) were between diatom numbers and chlorophyll *a* biomasses both in Series 2 and in the combination of both series. Organic weights and periphytic productivity were significantly correlated ( $P < .05$ ) for the combined series.

## DISCUSSION

### *Effects of the reservoir effluent*

The periphytic communities studied downstream of Hyalite Reservoir appear to have been responding primarily to variations in stream nitrogen concentrations. Previous investigations of below-reservoir streams have suggested that the downstream biotic gradients found were primarily attributable to (1) discharges having artificially regulated diurnal and seasonal patterns for water temperatures and flow rates, and (2) differences in channel morphologies and substrates (e.g., Ward 1974, 1976; Ward and Stanford 1979). But in Hyalite Creek these factors apparently were only secondary influences for the periphytic variations observed during this study: water temperatures, flow rates and streambed characteristics were similar at all sites. Mean stream temperatures at the four sites were not significantly different (Table 1). The importance of this statistical homogeneity is emphasized by the fact that temperature data from Site H1 were collected at the mean time 0735, when the stream should have been

relatively cooler, and data from Site H2 were collected at the mean time 1055, when the stream should have been relatively warmer from solar heating. This suggests that only moderate diurnal thermal fluxes may have occurred at the sites during this study and that diurnal temperatures at all sites were similar.

Of the physiochemical parameters investigated concurrently with the periphyton in Hyalite Creek, only ammonia-nitrogen and total-nitrogen concentrations correlated with periphytic parameters. Both the algal-assay bottle tests (Schillinger and Stuart 1978) and the low ( $<1$ ) nitrogen-to-phosphorus ratios at the sites (Table 1) indicate chronic nitrogen limitations in the stream below Hyalite Reservoir. In cases of algal limitations by low nitrogen concentrations, Keeney (1973) suggested that, while algae may utilize either organic or inorganic nitrogen, ammonia nitrogen appears to be preferentially used. Data suggest that nitrogen fixed by algae in Hyalite Reservoir eventually becomes available for downstream discharge primarily in the form of ammonia (Marcus et al. 1978). It is this discharge, then, that provides the major influence producing the differences in periphytic growths and diatom species observed among the Hyalite Creek sites.

The most obvious effect of the nutrient enrichment was increasing periphytic productivity; net productivity at the site immediately below the reservoir averaged about four times greater than estimated for the three downstream sites (Table 2). Average periphytic productivity at the downstream sites are among the lowest published values (cf. Stockner and Shortreed 1976).

In addition to increased productivity, Site H1 was the only site to average greater than 1% chlorophyll in the organic portion of the periphyton (Table 2). Weber and McFarland (1969) observed that in any relatively pure, healthy algal community chlorophyll *a* comprises 1 to 2% of the total organic accumulation. Of course, this proportion depends on such factors as genetics, light intensity and nutrition. When chlorophyll *a* constitutes less than 1% of a natural periphytic organic accumulation, they suggest that heterotrophic organisms (e.g., bacteria) comprise a large portion of the periphyton or that algal chlorophyll production is limited by environmental factors. Since mean bacterial densities on the slides were not significantly different among the Hyalite Creek sites, it is doubtful that the differences in chlorophyll *a* proportions can be attributed to heterotrophic populations. There is also no reason to suspect that divergent evolution has lead to phenotypic variations in periphytic chlorophyll *a* proportions among the sites. Finally, physical conditions at the sites were apparently similar. Therefore, varying proportions of periphytic chlorophyll *a* at the sites appear most directly due to nutrient, i.e. nitrogen, availability. Reduction of chlorophyll concentration per unit biomass by nutrient limitation has previously been observed (e.g., Wright 1960). The chlorophyll/

organic-mass ratios at Site H1 indicate an adequate nutrient supply. It is probable that nitrogen was rapidly depleted by benthic algae as the waters flowed downstream; when reaching the lower sites, the depressed stream nitrogen concentrations limited periphytic growth and depressed proportions of chlorophyll *a* in the algae. This pattern is typical below effluent outfalls where large algal communities rapidly utilize discharged nutrients and depress productivity in downstream communities (Cooper and Wilhm 1975). The confluence with Hyalite Creek of a small tributary draining a logging area may have influenced the chlorophyll *a* proportions at Site H1B.

Differences in periphytic organic proportions at the sites may be related to the sporadic presence of the non-diatom *Hydrurus* sp. on the slides at the upper site. Periphytic assemblages in which diatoms predominate contain lower percentages of organic matter than do assemblages where non-diatoms occur in the communities (McIntire 1975). Thus, while the numerical occurrence of *Hydrurus* on the slides of Site H1 was minor, the biomass contributed by the gelatinous thalli of this alga may have been sufficient to increase organic proportions over the low percentages associated with the diatom communities on slides at the three downstream sites.

At sites below the enriching influence of the reservoir discharge, there existed a relatively stable composition of dominant diatoms; the discharges shifted diatom dominance at Site H1 and most downstream dominants were rarely observed in the samples. Unfortunately, differences in the ecological requirements of the dominant species cannot be used to document environmental differences between the sites; the dominant taxa at all sites are adapted to wide ranges of environments (Patrick and Reimer 1966, Lowe 1974).

With the altered diatom dominance, there was a significant increase in the diversity ( $D_s$ ) and evenness of diatoms at Site H1 over the downstream sites (Table 3). Patrick and Strawbridge (1963) suggested a positive relationship between environmental favorableness and both species diversity and evenness. Thus, the nutritive conditions produced by the reservoir discharge appeared to create a more favorable environment for diatoms.

The effects of nitrogen enrichment on the periphyton of Hyalite Creek are further emphasized by the seasonal periphyton dynamics at Site H1A (Figs. 1 and 2, Table 3). During the final incubation period (10 September to 12 October), three events unique to this site occurred: (1) productivity for the period was at least three times greater than occurred during any other incubation period; (2) it was the only period when the proportion of chlorophyll *a* in the periphyton exceeded 1% of the organic matter; and (3) diatom diversity was 2.6 times greater and evenness was 1.8 times greater than the respective average values for the previous periods. The stimulus for these phenomena like-

ly was related to the declining autumnal periphytic production at Site H1, probably due to decreasing autumnal temperatures. Water temperatures recorded after 10 September displayed a continual pattern of decrease; decreasing temperatures would tend to reduce physiological abilities of algae to maintain previously high productivities. The resulting attrition of the algal carpet at Site H1 released nutrients and enriched the downstream environment. During the last half of this final incubation period a trend of decreasing ammonia concentration at Site H1 was accompanied by increasing ammonia at Site H1A (Schillinger and Stuart 1978).

In summary, the addition of nitrogen from Hyalite Reservoir to the relatively unproductive Hyalite Creek stimulated periphytic productivity, improved the physiological condition of the algae as indicated by increased chlorophyll *a* proportions, and created a more favorable environment as indicated by increased diatom species diversity and evenness. While such alterations may only exist in Hyalite Creek during the summer to early fall period, these alterations would likely increase populations of aquatic macroinvertebrates, strengthen the food base for resident fish populations and, in turn, increase the available harvest of this resource.

#### *Response of species diversity to eutrophication*

The pattern typically associated with eutrophication of water bodies is one of increasing productivity and decreasing species diversity (e.g., Williams 1964, Wilhm and Dorris 1968). Much less typical of eutrophication is the pattern observed in Hyalite Creek of increasing productivity and increasing diversity. In fact, the relationship between aquatic eutrophication and algal diversity has been viewed as obscure (Kalff and Knoechel 1978). Empirical studies in terrestrial environments similarly indicate that communities variously respond to nutrient enrichment by increasing, decreasing or maintaining diversity with increasing productivity (Hurd et al. 1971, Hurd and Wolf 1974, Mellinger and McNaughton 1975, Kirchner 1977).

Odum (1975) suggested that if a system with a high diversity is perturbed, the stress can decrease diversity, but if the system starts with a low diversity, the perturbation may increase diversity. While no mechanism was suggested through which these responses occur, he did theorize that low diversity systems tend to be subsidized by high levels of allochthonous energy or nutrient inputs, whereas highly diverse systems are not similarly subsidized. Yount (1956:292) proposed the existence of a "general optimum . . . defined as the environmental conditions under which the majority of species on earth live." Conditions which depart from the optimal for any environmental gradient cause a decrease in diversity. Employing a similar reasoning, Huston (1979) hypothesized that

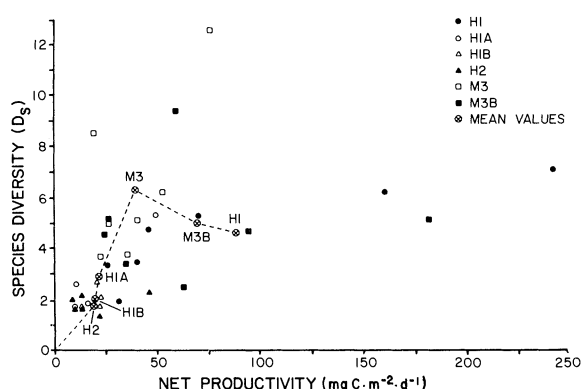


FIG. 7. Relationship of diatom species diversity to periphytic productivity at four sites in Hyalite Creek and two sites in Bozeman Creek. Mean values for the sites are connected.

diversity first increases and then decreases as a function of environmental parameters. This hypothesis is intuitive when one considers an extreme example. In the absence of environmental nutrients there will be neither productivity nor species. As nutrients become present and continue to increase concentrations, both productivities and species numbers are likely to increase. Then, with continually increasing fertility, the conditions begin to inhibit species, diversity decreases, and, eventually, productivity again becomes zero, e.g., an overfertilized lawn. Whittaker and Niering (1975) present several plots showing such a relationship of vegetation diversity to moisture and elevation gradients.

The occurrence in nature of the pattern hypothesized by Huston (1979) is given additional support by the data in Fig. 7. This figure shows diversity to first increase, then to level or decrease with increasing productivity; while diversity appears to decrease on the plot with increasing productivity, mean diversities at the sites with the three highest mean periphytic productivities are not significantly different. The productivity plots reflect primarily the nutritive conditions at the six sites because, of the physiochemical parameters measured, only ammonia-nitrogen and total-nitrogen concentrations correlated with productivity (Marcus et al. 1978). Accompanying the Hyalite Creek data in Fig. 7 are data from samples I collected in a concurrent study using the same techniques at two Bozeman Creek sites (Sites M3 and M3B). While these studies will be detailed in a subsequent paper, it is informative to briefly note a few characteristics of Bozeman Creek. Below the montane Site M3, Bozeman Creek is extensively impacted by cattle grazing. Like Hyalite Creek, Bozeman Creek is nitrogen limited (Schillinger and Stuart 1978). Both creeks share many of the same diatom species; all of those found

to comprise >10% in any sample were common to both creeks (Marcus et al. 1978).

Data on diatom populations both from the lower three Hyalite Creek sites and from the succession studies at Site H2 suggest that *Cocconeis placentula* var. *lineata* was the dominant diatom during this study in the "climax" community on the slides in undisturbed Hyalite Creek. Accompanying the ascent of *Cocconeis* to dominance during the succession studies, there was first an increase and then a decrease of diatom diversity (Fig. 5). This pattern is typical of both laboratory and natural systems during the successional approach to climax (Odum 1969).

Patrick (1970) noted that grazing on periphyton by *Physa* caused diatom diversity to decrease as *Cocconeis placentula* became dominant. This response may have related to the fact that *Cocconeis* secrete a jelly-like substance which cements the individual's entire valve face to the substrate; other taxa generally incorporate into the periphyton in a less secure manner (Patrick 1948). It is doubtful that invertebrate grazing pressure was very important to the periphytic diatoms studies in Hyalite Creek because the only benthic macroinvertebrates observed on the slides and diatometers were filter-feeding larvae.

Decreasing periphytic diversities with lengthening exposure times have also been recorded by Yount (1956) and Patrick (1967). Patrick et al. (1954) theorized that decreasing numbers of diatom species accompanying longer exposures are related to (1) detrital accumulations on the substrates creating undesirable environments for increasingly more species and/or (2) continual decreases in substrate space through increased population densities causing slower reproducing diatoms to be replaced by taxa with greater reproductive rates. Competition for space was suggested by Brown and Austin (1973) as the primary factor regulating dominance between two diatom species: the first species to become established on their study slides became the eventual dominant. While emphasizing the importance of the initial inocula in determining algal community composition, Talling (1962) also stressed that differences in intrinsic growth rates are of major importance in determining community dominants.

In the clear waters of Hyalite Creek during this study, diatom dominance appeared regulated by competition for space between taxa having different intrinsic growth characteristics. Early in both successional series at Site H2 (Fig. 5), individuals other than *Cocconeis placentula* var. *lineata* comprised greater proportions of the diatom community. For example in Series 2 after 9 d of incubation, five diatom species had higher percent compositions on the slides than did *Cocconeis*; this suggests that species other than *Cocconeis* have higher reproductive rates. Later in the successional series, *Cocconeis*' domination of ≈70–80% of the diatom community indicates this diatom

possessed superior competitive abilities on the slides at the downstream sites. The superior abilities may have partly related to the substrate-adhering properties of *Cocconeis* (Patrick 1948); diatoms less securely attached were more likely to be displaced by stream scour and/or movement of black fly larvae across the slides. Such events could eventually increase the probability that securely attached *Cocconeis* would replace other displaced taxa. It is likely, however, that the mechanism of substrate adhesion was incidental in determining dominance because (1) similar scouring of the slides occurred at Site H1 and *Cocconeis* was rarely observed in collections from this site, and (2) *Cocconeis* proportions were found to decrease in the final collections from Site H1A when larvae were present on the slides. It is more likely that increasing *Cocconeis* proportions related to interspecific competition for limited nitrogen resources.

Smith (1976) suggested that earlier successional dominants tend to have relatively higher reproductive rates and that later dominants tend to be relatively more efficient in resource acquisition and use. As colonization progressed on the slides at the three downstream Hyalite Creek sites, it is likely the competition increased for the already limiting nitrogen. Competition for limiting resources can enhance differences in resource utilization efficiencies among species; those species most efficient at capturing and incorporating limiting resources into their own biomass are likely to become the successful competitors (Neill 1975). This suggests that *Cocconeis* on the slides at the downstream sites had relatively higher nutrient utilization efficiencies and that competition for limiting nitrogen in the microenvironments surrounding the periphyton may have enhanced interspecific differences in these efficiencies which led to the high *Cocconeis* proportions observed.

When additional nitrogen subsidized the periphytic environment, diatom species diversity increased as *Cocconeis* proportions declined in the diatom community. Only three individuals of *C. placentula* var. *lineata* were recorded from all of the diatom counts of Site H1 samples. This near exclusion of *Cocconeis* from the periphytic diatom community may be associated with the familiar concept of differing relationships between growth rates and nutrient concentrations among the competing species (e.g., Jannasch 1967, Mickelson et al. 1979). Under this hypothesis, *Cocconeis* would have had higher growth rates than other competing diatoms at lower microenvironmental nitrogen concentrations. Additions of nitrogen to the system would then increase the growth rates of other diatom species more rapidly than for *Cocconeis*. As nitrogen concentrations increased from levels of the downstream sites to those found at Site H1, the growth rates of other species would begin to exceed that of *Cocconeis* and the plot of *Cocconeis* growth rate as

a function of nutrient concentration would cross under the functional plots of other species. At nitrogen concentrations exceeding the crossover points, diatoms other than *Cocconeis* would have competitively higher growth rates and *Cocconeis* proportions would be depressed. For two-species competitions the model of Bierman et al. (1973) predicts that in limiting nutrient systems the algal species with the low reproductive rate and high nutrient uptake efficiency will dominate, but in nonlimiting systems the species with the opposite characteristics will dominate. Therefore, while the downstream nitrogen concentrations appear to favor *Cocconeis*, increasing nitrogen concentrations would likely favor other species. This relationship is supported by the data.

In conclusion, conflicting results of previous studies of species diversity responding to eutrophication suggest that these studies dealt with responses to environmental changes occurring on either side of those conditions optimal for maximum diversity. When enrichment produced conditions which approached the optimum, diversity increased; when the resulting conditions exceeded the optimum, diversity decreased. Domination of periphytic diatoms at the unenriched Hyalite Creek sites appears to have been primarily a function of competition among taxa with differing efficiencies for acquiring and incorporating limiting nitrogen concentrations; the diatom species which appeared most efficient became dominant and species diversity was depressed. With nitrogen enrichment, domination of the periphytic diatoms appeared to shift to a competition among species with differing maximum potential reproductive rates; those diatoms which appeared to possess the higher rates shared dominance and species diversity increased.

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