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Aquatic Biological Investigations of the Muskeg River Watershed

> Project WS 1.3.2 August 1979

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A list of research reports published to date is included at the end of this report.

Enquiries pertaining to the Canada-Alberta Agreement or other reports in the series should be directed to:

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Aquatic Biological Investigations of the Muskeg River Watershed

Project WS 1.3.2

AOSERP Report 67

This report may be cited as:

Lock, M.A., and R.R. Wallace. 1979. Aquatic biological investigations of the Muskeg River watershed. Prep. for Alberta Oil Sands Environmental Research Program by Freshwater Institute, Environment Canada. AOSERP Report 67. 29 pp. The Hon. John W. (Jack) Cookson Minister of the Environment 222 Legislative Building Edmonton, Alberta

and

The Hon. John Fraser Minister of the Environment Environment Canada Ottawa, Ontario

Sirs:

Enclosed is the report "Aquatic Biological Investigations of the Muskeg River Watershed".

This report was prepared for the Alberta Oil Sands Environmental Research Program, through the Water System, under the Canada-Alberta Agreement of February 1975 (amended September 1977).

Respectfully,

andre W. Solodzuk, P. Eng.

Chairman, Steering Committee, AOSERP Deputy Minister, Alberta Environment

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AQUATIC BIOLOGICAL INVESTIGATIONS OF THE MUSKEG RIVER WATERSHED

DESCRIPTIVE SUMMARY

BACKGROUND

AOSERP biological investigations have been conducted in the Muskeg River watershed since 1976 (see, for example, AOSERP Reports 49 and 58). The present project intended to provide a definitive report on the Muskeg River watershed by addressing the following objectives:

- To complete the description of the baseline states of the fish, aquatic macro-invertebrates, and algal and bacterial components of the aquatic ecosystem in the Muskeg River watershed;
- To complete a detailed description of the aquatic habitat in the Muskeg River watershed;
- To provide an estimate of the significance of the Muskeg River watershed to the Athabasca River system;
- 4. To develop a qualitative biological "box" model of the Muskeg River watershed that includes energy flow, nutrient cycling, and predator-prey relationships; and
- To describe the effects on the aquatic ecosystem of any development-related activities in the Muskeg River basin.

ASSESSMENT

A draft of the report was reviewed by university scientists in Alberta and British Columbia and the authors took opportunity to use their input which assures the scientific basis of the report. The reader should be alerted to the fact that not one of the project team stayed with the project for a full year. Thus, many of the objects set forth in the project design were left unfulfilled. However, it is our impression that much useful data were gathered by the project and we therefore recommend distribution of the report. It should be noted though that the report doesn't necessarily reflect the views of either Alberta Environment or Environment Canada.

The Alberta Oil Sands Environmental Research Program accepts this report "Aquatic Biological Investigations of the Muskeg River Watershed" and thanks the authors for their efforts.

S.B. Smith, Ph.D Program Director Alberta Oil Sands Environmental Research Program

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AQUATIC BIOLOGICAL INVESTIGATIONS OF THE MUSKEG RIVER WATERSHED

bу

M.A. LOCK and R.R. WALLACE Environment Canada Freshwater Institute

for

Alberta Oil Sands Environmental Research Program

Project WS 1.3.2

August 1979

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ABSTRACT

The epilithic microbial and micro-invertebrate communities under conditions of light and shade were studied from April to November 1978. During a period of increasing light intensity from May to June, the level of chlorophyll α (an algal biomass indicator) and numbers of Bacillariophyta in the shade were considerably higher than the level and numbers in the light. This was considered to be evidence supporting the hypothesis that the midsummer decline in algal populations was due to light inhibition. Numbers of bacteria and carbohydrate, total organic carbon (TOC) and total organic nitrogen (TON) concentrations were significantly correlated with algal biomass in the light whereas only numbers of bacteria and carbohydrate were correlated with algal biomass in the shade. The potential causal relationships between these parameters are discussed. The population dynamics of the micro-invertebrate populations are discussed in relation to the quantity and quality (C:N ratio of epilithon) of their food supply. Lastly, the relevance of these findings to oil sands development is discussed, where the alteration of the river's light regime by the removal of riparian vegetation could result in decreased production while silt additions during the months of May to July could result in increased productivity.

ACKNOWLEDGEMENTS

Special thanks go to Judy Buchanan for her outstanding technical support in the field and in the laboratory and also for assistance in data analysis and drafting of the figures.

Sincere thanks go to Gary Jenkerson for algal sorting and counting and to Brenda Brown, Dale Williams, Nancy Provencal, and Susan Cumming for sorting and counting of the micro- and macroinvertebrates and for their preliminary data analysis.

Sincere thanks are also due to our pilots and their engineers who transported us efficiently, safely, and cheerfully in the field, especially Fred Wiskar, Rick Churcott, Mike Jeffery, and Dave Percintile, and Jack Leroux. Thanks also go to Dirk Hadler and Carl Closs for field operations and to Nargis Champsi for office services.

This research project WS 1.3.2 was funded by the Alberta Oil Sands Environmental Research Program, a joint Alberta-Canada research program established to fund, direct, and co-ordinate environmental research in the Athabasca Oil Sands area of northeastern Alberta.

1. INTRODUCTION

An examination of the baseline states of the microbial communities of rivers draining through muskeg in the Alberta Oil Sands Environmental Research Program (AOSERP) study area was begun by Lock and Wallace (in prep. a) using a variety of techniques on natural and artificial substrates. The present study is one of two projects continuing that line of investigation. One of these, by Hickman et al. (in prep.), examined the detailed community biomass changes of the benthic algae and determined their ability to fix carbon and nitrogen in five muskeg rivers. This study set out to obtain a more detailed understanding of some of the epilithon components at one study site in one of those rivers, the Muskeq River, and to examine the role of shade in the community dynamics of the river. Determinations over time were made of bacterial numbers, algal biomass (chlorophyll α) and algal numbers, carbohydrate concentration, total organic carbon concentration (TOC), total organic nitrogen concentration (TON), and the numbers and biomass of microinvertebrates living within the epolithon. Epilithic samples were collected from standardized granite (Lock and Wallace in prep.a) established in the river in April 1977 which had been colonized by epilithon under conditions of full light and artificial shade. This was an experiment to test the hypothesis previously proposed (Lock and Wallace in prep. a), that during the months of maximum light intensity (June, July, and August), the levels of illumination reaching the epilithon are sufficient to inhibit photosynthesis and result in the observed decline in epilithic biomass over those months. If this hypothesis was correct, then a reduction of illumination by an artificial shade would be expected to retard or even prevent the midsummer epilithon decline.

An understanding of the midsummer decline of epilithon is of importance when considering the overall productivity of muskeg rivers and how this productivity might be affected by oil sands extraction activities. For example, if riparian vegetation is removed from existing rivers or not returned to reclaimed rivers, the absence of natural shading during the months of June,

July, and August may result in a reduction of carbon fixed in those rivers. This would be expected to produce concomitant reductions in productivity throughout the river's trophic structure. 2. MATERIALS AND METHODS

The study site was located in a riffle area in the Muskeg River in the AOSERP study area (Figure 1), 10 km above its confluence with the Athabasca River $(47^{\circ}08'N, 111^{\circ}35'W)$. Discharge over the study period was monitored by Water Survey of Canada, and levels of conductivity, ammonium-nitrogen $(NH_4 - N)$, nitrate and nitrite-nitrogen $(NO_3 + NO_2 - N)$, phosphate-phosphorus $(PO_4 - P)$, and dissolved organic carbon (DOC) were determined by Chemex Laboratories Ltd. according to the methods of Traversy (1977). The extent of shading beneath the shade was measured with a Licor LI-185 quantum light meter using an LI-1925 quantum sensor sensitive to light of 400 to 700 nm (photosynthetically active radiation, PAR).

To enable standardized comparisons of the epilithic communities to be made between conditions of light and shade, discs of granite (15 cm diameter and 1 cm thick), which had been in the river for 12 months, were used for the study. Three were placed beneath the shade and three were placed at the light site 10 m downstream. In addition to the already colonized discs, a further nine uncolonized discs were installed at each site for subsequent sampling after a three-month colonization period. It was considered that discs colonized for 15 months were equivalent to discs colonized for three months. The shade, which consisted of a wooden frame 3 x 3 m covered with four layers of black fiberglass 1 mm mesh screening, was placed on top of four stakes in the middle of the river. A 'skirt' of four layers of mesh was attached around the frame such that it just reached the water level. The height of the skirt was adjusted at 14-day intervals as the water level changed. The distance from the top of the shade to the river bed was 140 cm. The shade was installed in the river on 16 May 1978. The study period was from April to November 1978.

The population density of bacteria and algae and the concentrations per unit area of chlorophyll α carbohydrate, TOC, and TON were determined as in Lock and Wallace (in prep. b). The invertebrates living within the microbial films were operationally defined as micro-invertebrates as they never exceeded 5 mm in



Figure 1. The AOSERP study area.

length. They were preserved in 10% formalin and sorted from the microbial film matrix under x12 magnification and stored in 70% ethanol.

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3. RESULTS

The physical and chemical parameters are presented in During the open-water period extending from April to Table 1. November 1978, the temperature ranged from 0 to 16° C, conductivity from 120 to 340 S·m⁻¹, NH₄ - N from 20 to 50 μ g·L⁻¹, NO₃ + NO₂ - N from <3 to 8 μ g·L⁻¹, PO₄ - P from <3 to 14 μ g·L⁻¹, DOC was usually in the range of 21 to 26 mg·L⁻¹, and pH from 7.8 to 8.1. During winter ice-cover (March) and ice break-up (April), high conductivities (\sim 450 S·m⁻¹), NH₄ - N concentrations (\sim 550 µg·L⁻¹), and $NO_3 + NO_2 - N$ concentrations ($\sqrt{70} \mu g \cdot L^{-1}$) were measured. Mean daily discharge (Figure 2) for each month varied considerably throughout the study period from a winter minimum of 0.3 $m^3 \cdot s^{-1}$ (March) increasing to the spring melt water peak of 12.0 $m^3 \cdot s^{-1}$ in May. Discharge declined after this to a second minimum in July $(1.2 \text{ m}^3 \cdot \text{s}^{-1})$ but then rose steadily throughout August and September reaching a peak of $32.5 \text{ m}^3 \cdot \text{s}^{-1}$ which was 2.7 times the normal maximum spring melt peak. These extremely high water levels prevented sampling during the months of September and October as the experimental site was located in mid-stream, the deepest part of the riffle.

The widely fluctuating flow conditions throughout the summer (Figure 2) also prevented the maintenance of constant shade conditions. Due to falling water levels throughout June and early July, an increasingly wide gap developed between the bottom of the skirt and the water. This had the effect of reducing the original 50% shading to 10% or less under direct sunlight by the middle of July; however, under cloudy conditions the shading effect remained around the 50% level. On 10 July and again on 17 July the skirt of the shade was lowered to the new water level. No further adjustments could be made after this date because the extremely rapid flooding of the river (Figure 2) at the end of August raised the water level such that it was impossible to reach the shade until the last sampling date on 8 November. The lowering of the skirt produced shade in the range of 80 to 90% of full light.

	March	April	Мау	June	July	August	Septembe
Mean daily discharge (m³•s ⁻¹)	9.0	113	324	174	43	125	210
Temperature (°C)	0	0	6.5	16.0	16.0	14.2	0.1
Conductivity (S•m ⁻¹)	465	430	120	170	340	272	187
$NH_4 - N (\mu g \cdot L^{-1})$	530	580	50	40	20	31	215
$NO_3 + NO_2 - N (\mu g \cdot L^{-1})$	58	82	5	8	3	3	<3
PO₄ - P (µg•L ⁻¹)	6	8	13	<3	10	14	9
DOC (mg·L ⁻¹)	13	18	22	53	24	21	26
рН	7.6	7.5	7.8	7.8	7.8	7.8	8.1

Table 1. Physical and chemical parameters of the Muskeg River in 1978.

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Figure 2. River discharge in $m^3 \cdot s^{-1}$ in 1978.

Algal biomass (chlorophyll α) in the light increased from April to May, decreased through June and July, and then rose again through August (Table 2 and Figure 3). A similar response was observed in the algal biomass in the shade, except in May when the concentration of chlorophyll α was 2.4±0.3 µg·cm⁻² and in June 1.9±0.3 μ g·cm⁻²; these were 1.4 and 6.3 fold significant increases over the equivalent concentrations in the light (p<0.05). However, by the end of July there was no significant difference between them (~0.25 μ g·cm⁻²) and at the end of August there was only 0.7 μ g·cm⁻² in the shade but 1.8 μ g·cm⁻² (2.6 times as much) in the light. The decreases in chlorophyll α in May coincided with radiation levels rising above 300 kW·m⁻² (Figure 4). Increases in chlorophyll α from July to August coincided with a fall in the radiation level below 315 kW·m⁻². Inspection of the data on the major algal groups (Table 3 and Figure 5) did not reveal any major differences in size between the populations of the Cyanophyta and Chlorophyta in the light and shade. However, a general depression in numbers of Cyanophyta cm⁻² was noted during the months of June, July, and August (Table 3 and Figure 5). A much more varied picture was presented by the Bacillariophyta. In May there were considerably more cells in the light, but by June this situation was reversed with 11.3 times as many Bacillariophyta occurring beneath the shade. In July, similar amounts were found, but by August there were nearly six times as many Bacillariophyta in the light which increased to a 25 fold difference by November, although an absolute reduction had occurred under both light conditions between August and November.

Chlorophyll α concentrations in the light exhibited significant positive correlations (p<0.05 to <0.001) between bacteria, carbohydrate, TOC, and TON (Table 4). This pattern was also observed when algal numbers were tested for a correlation with carbohydrate TOC and TON with the exception of the Cyanophyta, where no association was detected. However, bacteria were only positively correlated with the Bacillariophyta in the light. Bacterial numbers in the light also showed significant positive correlations (p<0.001) with TOC and TON but not with

Sampling	Light	Sessile	Suspended	Chlorophyll $lpha$	Carbohydrate	TOC	TON	C:N
Time	Regime	Bacteria (cm ⁻²)	Bacteria (ml ⁻¹)	$(\mu g \cdot cm^{-2})$	(µg•cm ⁻²)	$(\mu g \cdot cm^{-2})$	(µg•¢m ⁻²)	
24 April	Light	7.3±0.9x10 ⁷	1.9±0.2×10 ⁶	0.9±0.2	20.9±4.0	-	-	-
24 May	Light	7.7±0.7×10 ⁷	1.3±0.1x10 ⁶	1.7±0.2	23.1±2.6	-	-	-
	Shade	4.8±0.5×10 ⁷	1.3±0.1×10 ⁶	2.4±0.3	12.7±2.3	-	-	-
27 June	Light	5.5±0.4×10 ⁷	1.1±0.1×10 ⁶	0.3±0.1	3.5±0.5	72±28	12±2	6.0
	Shade	7.8±1.0×10 ⁷	1.1±0.1×10 ⁶	1.9±0.3	2.7±0.5	48±12	16±4	3.0
25 July	Light	6.3±0.8×10 ⁷	1.8±0.1×10 ⁶	0.3±0.1	6.2±1.2	72±11	10±0	7.2
	Shade	1.1±0.9×10 ⁷	1.8±0.1×10 ⁶	0.2±0.1	3.2±0.3	44±4	10±0	4.4
22 August	Light	2.3±0.3×10 ⁸	1.5±0.1x10 ⁶	1.8±0.4	21.6±1.6	4380±802	406±60	10.8
	Shade	4.1±0.5×10 ⁷	1.5±0.1x10 ⁶	0.7±0.1	6.7±1.5	1174±90	174±7	6.7
8 November	Light	2.2±0.5×10 ⁷	4.6±4.5×10 ⁵	1.1±0.2	18.5±6.6	20±10	10±0	2.0
	Shade	1.0±0.2×10 ⁷	4.6±4.5×10 ⁵	0.2±0.2	3.1±0.7	280±90	/ 10±0	28.0

Table 2. Epilithic biomass determinations on granite discs under light and shade conditions in the Muskeg River in 1978.



Figure 3. Epilithic biomass determinations on granite discs under light (0) and shade (0) conditions in the Muskeg River in 1978.





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Date	, , , , , , , , , , , , , , , , ,	Cyanophyta	Bacillariophyta	Chlorophyta
25 April	Light	3.0 × 10 ⁵	1.2 x 10 ⁵	4.4 × 10 ⁵
22 May	Light	7.0 x 10 ⁵	5.6 × 10^4	2.4 × 10^5
	Shade	3.5 x 10 ⁵	1.6×10^4	7.6 x 10^4
27 June	Light	1.5 × 10 ⁵	4.7×10^{3}	2.6 x 10^4
	Shade	8.0×10^4	5.3 × 10 ⁴	3.0×10^4
25 July	Light	1.6 x 10 ⁵	1.6×10^4	6.2×10^4
	Shade	2.6 x 10 ⁵	1.7×10^{4}	5.2 × 10^4
22 August	Light	3.5×10^5	2.3 × 10^5	1.7 x 10 ⁵
	Shade	2.5 × 10^5	4.0×10^{4}	5.3 × 10^4
8 November	Light	7.1 × 10 ⁵	8.0×10^4	5.0 × 10^4
	Shade	5.4 × 10^5	3.2×10^3	5.9 × 10^4

Table 3. Numbers of algal cells cm^{-2} on granite discs in the light and shade over time in 1978.



Figure 5. Number of algal cells cm^{-2} in the light (----) and shade (_____) over time in 1978.

	Light		Shade	
	r	df	r	df
Chlorophyll α /Sessile bacteria	+0.59 ^a	10	+0.81 ^b	8
Chlorophyll a /Carbohydrate	+0.89 ^b	10	+0.63 ^a	8
Chlorophyll a/TOC	+0.85 ^b	6	-0.25 ^c	6
Chlorophyll a/TON	+0.85 ^b	6	-0.23 ^c	6
Sessile bacteria/Carbohydrate	+0.36 ^c	10	+0.19 ^C	8
Sessile bacteria/TOC	+0.98 ^b	6	+0.02 ^c	6
Sessile bacteria/TON	+0.98 ^b	6	+0.16 ^C	6
Bacteria/Cyanophyta	-0.16 ^C	10	-0.74 ^b	8
Bacteria/Bacillariophyta	+0.83 ^a	10	+0.83 ^a	8
Bacteria/Chlorophyta	+0.18 ^C	10	-0.44 ^C	8
Carbohydrate/Cyanophyta	+0.71 ^a	10	-0.15 ^c	8
Carbohydrate/Bacillariophyta	+0.69 ^b	10	-0.16 ^C	8
Carbohydrate/Chlorophyta	+0.65 ^b	10	+0.77 ^a	8
TOC/Cyanophyta	+0.01 ^C	6	+0.08 ^c	6
TOC/Bacillariophyta	+0.94 ^a	6	+0.21 ^c	6
TOC/Chlorophyta	+0.97 ^a	6	+0.37 ^c	(
fON/Cyanophyta	+0.02 ^c	6	-0.80 ^a	6
TON/Bacillariophyta	+0.95 ^a	6	+0.10 ^C	6
[ON/Chlorophyta	+0.97 ^a	6	+0.20 ^C	(

Table 4. Correlation coefficient values (r) between the epilithon components in the light and shade.

a p<0.05

^b p<0.01

^c not significant

carbohydrate. In the shade, chlorophyll α concentrations were positively correlated with bacterial numbers and carbohydrate, but neither was correlated with any of the other parameters. In general, this same pattern held for the correlation of algal numbers with the other parameters under shade conditions.

In the light, the C:N ratios ranged from 6.0 to 10.8 while in the shade the C:N ratios ranged from 3.0 to 6.7. However, this situation was dramatically reversed in November when the ratios became 2.0 in the light and 28 in the shade. The differences between the mean numbers of micro-invertebrates (Table 5 and Figure 2) per 100 cm² in the light or shade were not significant, presumably because of the high variability exhibited by the data. However, data on the biomass of micro-invertebrates suggest that biomass was greater in the shade for the months of May through July with the trend reversing during August and November.

Date	Light		Chironomidae		Total		Chironomidae As % of Total	
	Regime		Numbers	Weight (mg)	Numbers	Weight (mg)	Numbers (%)	Weight (%)
24 April	Light	Mean Upper Lower	24.3 108.8 0	0.12	24.3 108.8 0	0.17 - -	100 - -	100 - -
22 May	Light	Mean Upper Lower	6.3 37.8 0	0.09 _ _	18.5 103.3 0	0.06 _ _	34	83
	Shade	Mean Upper Lower	8.0 31.5 0	0.1 _ _	49.8 109.0 16.8	0.44 _ _	16	22
27 June	Light	Mean Upper Lower	0 0 0	0 _ _	0 0 0	0 _ _	-	-
	Shade	Mean Upper Lower	14.5 83.5 0	0.55 - -	35.0 204.5 0	1.98 - -	À1	28
	• .	_ 51101	0		0		continued	

Table 5. Numbers and weights of micro-invertebrates per 100 cm² on granite discs under light and shade conditions in the Muskeg River in 1978 (numbers with 95% confidence).

Date	Light		Chironomidae		Total		Chironomidae As % of Total	
	Regime		Numbers	Weight (mg)	Numbers	Weight (mg)	Numbers (%)	Weight (%)
25 July	Light	Mean Upper Lower	22.3 90.8 0	0.03	29.3 89.0 0.8	0.03	76	99
	Shade	Mean Upper Lower	31.8 106.8 0	0.04 _ _	41.0 178.0 0	2.44 _ _	78	2
22 August	Light	Mean Upper Lower	118.5 536.0 11.8	0.41 _ _	136.5 579.8 18.3	0.57 - -	87	73
	Shade	Mean Upper Lower	10.8 49.0 0	0.13	10.8 49.0 0	0.15 - -	100	100
8 November	Light	Mean Upper Lower	26.2 126.7 0	0.07 - -	33.8 124.5 0	0.85 - -	77	8
	Shade	Mean Upper Lower	3.7 19.6 0	0.01 - -	3.7 19.6 0	0.01 - -	`100 /	100

Table 5. Concluded.

4. DISCUSSION

Although the data are limited, the increased growth of algae (as evidenced by chlorophyll α concentration and numbers of Bacillariophyta) beneath the shade during the months of May and June, when the ambient light levels were high, is in agreement with the hypothesis that high light levels may be at least partially responsible for the midsummer algal decline noted in this study and others (Lock and Wallace in prep. a; Hickman et al. in prep.). However, the detailed interpretation of this study was complicated by problems associated with the effectiveness of the shade. From its initial installation in May to the middle of July, the shading capacity changed from an initial level of 50%to less than 10% under direct sunlight. This was due to an increasing amount of light entering below the skirt as a consequence of a falling water level. The decrease in water level itself also permitted more light to reach the epilithic algae. Thus, through the combination of these two factors, the levels of illumination underneath the shade may well have reached a level which was too high for even the algae beneath the shade to accommodate and resulted in their observed delayed decline (Figure 6).

In the middle of July, the shade skirts were lowered to once again reach the water and this resulted in a shade effect ranging from 75% at the end of July to 98% at the last reading taken in August. However, even with a declining light level and a rising water level, a small increase in algal biomass beneath the shade was noted towards the end of August. A concomitant but larger biomass increase was noted in the algae in full light where the combination of water depth and light level presumably facilitated the algal growth to reach a level comparable to the peak in May (Figure 6). Similar light levels were recorded at the limit of these two algal biomass peaks in the light, 308 kW·m⁻² in May and 238 kW·m⁻² in August. However, the water level in May was twice that in August; thus, the available light energy at the river bed may have been even more similar. It is also now obvious that, for



Figure 6. Summary figure showing smoothed chlorophyll α concentrations compared with smoothed discharge and radiation plots in 1978.

future studies, a continuous record of underwater photosynthetically active radiation would be extremely desirable, particularly if a series of rivers were to be compared (Wong et al. 1976).

The possibility that temperature might have been responsible for the algal decline would now seem unlikely, since in June, a substantial decline had taken place in the chlorophyll α concentration and numbers of Bacillariophyta in the light while there was no significant difference in the chlorophyll α concentration and numbers of Bacillariophyta beneath shade in May and June. Since the water temperature at the two sites was always identical the only major difference was in the level of illumination.

Interpretation of the algal responses has so far been restricted mainly to biomass as indicated by chlorophyll α . Consideration of the major taxonomic groups suggests that the prime responders to light intensity were the Bacillariophyta, since the Cyanophyta and Chlorophyta did not undergo any substantial population changes. Also, by inference, the Bacillariophyta must also contribute the greatest amount of chlorophyll α and, presumably, biomass to the algal community.

It is appropriate now to consider the responses of the other components of the epilithon. Bacterial numbers were similar in the light and shade and showed significant, positive correlation with chlorophyll α and the Bacillariophyta. The simplest hypothesis to explain this phenomenon, assumes these parameters to be causally related, where the bacteria are growing in response to the increased extracellular and lytic products of the algal cells. Carbohydrate in the epilithon will come from living microbial material and also the ubiquitous polysaccharide matrix (PSM) within which the micro-organisms live and with which a significant positive correlation is noted with chlorophyll α concentration and numbers of Chlorophyta. However, carbohydrate concentrations are generally lower in the shade than in the light. This leads to the speculation that this may represent a reduction of the amount of PSM material in the shade which in turn suggests that under normal

light conditions the PSM may have a shading function. Testing of this hypothesis would require a specific analysis for PSM material.

Correlations of chlorophyll α and bacteria with TOC and TON were highly significant in the light, but not significant in the shade. The former relationships in the light would be amenable to a partial explanation on the basis of carbon fixation (algae) and organic carbon uptake (bacteria) causing a rise in the carbon content of the epilithon. However, a calculated value of the unexpected amounts of living carbon (Winberg 1971) amounts to only about 10% of the total organic carbon present; thus, it appears that a major proportion of the epilithic organic carbon is nonliving. This of course is not an unusual observation for aquatic systems (Wetzel 1975) yet it is intriguing to note that the TOC and the living biomass increase concurrently. A possible explanation for this would be the ability of the PSM to attract particulate and dissolved organic matter from the water (Marshall 1976) with greater amounts being removed with the greater development of the PSM through increased microbial activity. No obvious explanation can be offered for the variable TOC and TON fluctuations beneath the shade.

McMahon et al. (1974) recently examined the possibility of using the carbon:nitrogen ratio as an index of the nutritional quality of epilithon for aquatic snails where they found a low C:N ratio (3 to 6) to support greatest growth and fecundity. Russel-Hunter (1970) suggested, on theoretical nutritional grounds, that the upper limit of C:N for invertebrate food materials for satisfactory growth would be 17:1. In this study, a C:N ratio of 3 to 7:1 was observed beneath the shade and 6 to 10 8:1 in the light during the months of June to August. On the basis of the studies of McMahon et al. (1974) and Russel-Hunter (1970) and the observed C:N ratio, a larger micro-invertebrate community would be expected beneath the shade. In terms of biomass, this was true for the first two months, and in numbers, for only the month of June. It is possible that the advantage of a "high quality food source" quality food which perhaps had other advantages connected with the food material also acting as its physical environment. At the end of the study, in November, the much higher biomass and numbers of micro-invertebrates in the light were explicable on the basis of food quality where the C:N ratio was 2:1 in the light and a very high 23:1 in the shade. It must, however, be borne in mind that monthly changes in numbers and biomass-will also be influenced by the life cycles of the insects comprising the micro-invertebrates, which in this study were primarily Chironomidae.

In conclusion, it is important to stress that the even suppression of light over a large area of river bed by the shade in this study was a very simple model of the anticipated effect of shade. Eber (1971) was able to show that throughout the day in a forest, patches of light of varying intensity migrate around the floor as the angle of the sun changes. It seems reasonable to expect that similar effects will take place within rivers. Thus, there will be patches of river bed which experience perhaps full sunlight throughout the day while another area close by may be in perpetual shade. This would seem to offer the beginnings of an explanation for the heterogeneity exhibited by running water ecosystems, where an initial patchiness in the growth of algae due to a heterogenous light regime is transmitted throughout the trophic structure of the river.

Finally, these findings are of direct relevance to the industrial development of the area. Firstly, the riparian vegetation, as well as providing shade to the river, also supplies allochthonous matter and thus is probably critical in maintaining its productivity. Removal of the riparian trees could result in a decline in river production. Secondly, increased silt loads and their associated attenuation of light (Wong et al. 1976) could result in increased or decreased productivity depending upon the time of year the silt enters the river. If it entered during the months of June, July, and August, the productivity might be expected to rise, but outside of those months, overall productivity of the river would be expected to decline. These effects of silt upon

the light regime are, of course, ancillary to any of its more direct effects and possible synergistic or antagonistic effects should be considered when developing strategies to minimize ecosystem disruption.

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