TECHNICAL REPORT STANDARD TITLE PAGE

1. Report No. WA-RD-39.2	2. Government Accession No.	3. Recipient's Catalog No.
4. Title and Subtitle EFFECTS OF VELOCITY AND NUTRIENT ALTERATIONS ON STREAM PRIMARY PRODUCERS AND ASSOCIATED ORGANISMS		5. Report Date November 1978 6. Performing Organization Code
7. Author(s) Richard R. Horner and Eugene B. Welch		8. Performing Organization Report No. WA-RD-39.2
9. Performing Organization Name and Address Environmental Engineering and Science Program Department of Civil Engineering, FX-10 University of Washington Seattle, Washington 98195		10. Work Unit No. 11. Contract or Grant No. Y-1804
12. Sponsoring Agency Name and Address Washington State Department of Transportation Highway Administration Building Olympia, WA 98504		13. Type of Report and Period Covered Interim 6/77 - 8/78 14. Sponsoring Agency Code

15. Supplementary Notes

The study was conducted in cooperation with the U.S. Department of Transportation, Federal Highway Administration, under the title Runoff Water Quality.

16. Abstract

Velocity and nutrient studies at 12 sites in Western Washington streams indicated that 50 cm/sec is the critical average current velocity where the productive base of the food web is impacted. Swiftly flowing streams rich in nutrients should not be slowed to this value, and slowly flowing streams should not be altered to have velocities greater than this value.

17. Key Words Velocity, Nutrients, Streams, Washington State, Aquatic Ecosystem, Periphyton	18. Distribution Statement

19. Security Classif. (of this report) Unclassified	20. Security Classif. (of this page) Unclassified	21. No. of Pages 72	22. Price

Form DOT F 1700.7 (8-69)
HWY F-RM341-004
6/72

TABLE OF CONTENTS

ABSTRACT

An intensive series of experiments designed to investigate development of the periphytic community at the base of stream food webs was conducted at twelve field sites during the summer season. Periphyton was sampled quantitatively from natural substrates (flattened natural stream rocks) and was analyzed for chlorophyll a and adenosine triphosphate (ATP) as biomass measurements. Site selection and scheduling largely eliminated light and temperature as variables, permitting concentration on the factors velocity, inorganic nutrients and organic carbon. The study was intended to increase understanding of the biological roles of these variables for application to the analysis of highway construction and operational impacts on streams. Of particular interest were stream channel reconstruction activities and drainage of storm runoff, the latter possibly increasing nutrient concentrations and both potentially affecting velocities. Analyzing attached algal growth developing under broad ranges of velocity and concentration of phosphorus, the limiting nutrient, revealed that velocity increase up to approximately 50 cm sec^{-1} enhanced the rate of biomass accumulation when phosphorus concentration was greater than a minimum level. This level depended on the magnitudes of the velocities and other factors. Otherwise, greater biomass developed in slow currents. It was hypothesized that the erosive effect of the current retarded accumulation, unless nutrient availability was such that the positive influence of turbulent diffusion of dissolved substances to the cells overcame frictional shear. Velocities above 50 cm sec^{-1} eroded an increasingly greater portion of periphyton production because of the prominence of the negative scour effect. The definition and use of a heterotrophic index, as the ratio of ATP to chlorophyll a, demonstrated that high ordinary velocities and elevated peaks following storms favored the attached consumers relative to the primary producers.

On the basis of these results it is recommended that highway construction and operations prevent harmful impacts on stream ecosystems by the following measures:

1) To protect the productive base of the food web, avoid increase in average current velocity from less than to much more than 50 cm sec^{-1}; that is particularly important for streams of low fertility like most in the Cascades.

2) Avoid frequent velocity peaks well above 50 cm sec^{-1} in reaches of streams where velocity averages less than 50 cm sec^{-1}.

3) To reduce the risk of a nuisance condition resulting from a substantial increase in algal or bacterial accrual, avoid substantial velocity increases within the range of 0-50 cm sec^{-1} where limiting nutrient concentration or organic carbon is relatively high.

4) For the same reason avoid substantial nutrient or organic carbon concentration increases where average velocity approaches 50 cm sec^{-1}.

5) Again for this reason, avoid decreasing velocity in a very swiftly flowing stream rich in nutrients to less than 60 cm sec^{-1} unless it can be shown that other ecological benefits are greater than nuisance created by increased periphyton accrual.

PREFACE

This report summarizes the research work performed under Task D of the Highway Runoff Water Quality Research Project. It presents and discusses the most important facets of the literature review, experimental methods and experimental results and highlights the implications of the results for highway construction and operations. Additional detail on all aspects of program is available in the dissertation prepared under this task by Horner (1978).

Readers interested only in findings and recommendations may find that the Abstract and the last section on Consequences of special interest.

INTRODUCTION

The Problem in Perspective

Physical changes to natural channels have accompanied construction in the vicinity of streams and rivers for many years. An activity frequently instigating channel reconstruction projects has been highway building. The objective in these instances is usually to remove the natural meandering pattern from the highway's path and thus involves entirely rebuilding a portion of the channel. In other situations somewhat less extensive modifications may be undertaken, such as stream bank reconstruction or reinforcement or dredging. Alterations such as these have the potential to change the whole character of the stream from visual, hydraulic and biological standpoints. Effects are numerous and complex and may extend from the affected reach downstream, to the adjacent flood plain and even, as fish migrations are impacted, to upstream spawning areas.

In the past, rebuilt channels often were characterized by uniformly elevated current velocities, replacement of the natural alternating pool and riffle pattern with a more constant channel profile, largely fine and shifting substrate materials and bare stream banks. Replacement of varied natural habitats with more uniform conditions of human design has led to loss of species diversity, an ecologically destabilizing effect (Patrick, 1973).

It is now not uncommon for channel modifications to be designed to maintain the original channel pattern, geometric characteristics and substrates and to reduce vegetation removal (Washington State Highway Department, 1977). The objectives of these measures are to provide habitats, velocities and water temperatures in the reconstructed channel similar to the original and to minimize erosion. Still, a lengthy stabilization period must be expected, and the success of these techniques has not been widely evaluated.

A second potential stream impact associated with a neighboring highway arises during regular operation and maintenance of the roadway. Storm runoff draining to the stream transports a variety of contaminants, including biodegradable organic wastes, mineral nutrients, silt, grease and oil, heavy metals and organic toxicants. In the case of small streams, where the highway runoff may substantially elevate the stream's discharge, the presence of the highway can also significantly modify current velocity and other aspects of the flow regime during and after storms.

All components of the aquatic ecosystem are subject to the widespread and varied effects of altered flow conditions or water quality due to either channel reconstruction or storm drainage. Including resident and anadromous fish, benthic macroinvertebrates and various autotrophic and heterotrophic microorganisms attached to surfaces within the stream, the natural ecosystem is too diverse to permit a thorough general treatment of impacts and their effects. Researching this problem requires matching specific members of the biological community and specific environmental conditions for study.

Research under Task D of the Highway Runoff Water Quality project to date has been concerned with the periphyton, the attached community occupying the base of stream food webs. This segment of the ecosystem is a natural point to begin the inquiry into the effects on stream biota of certain highway construction and operational practices because of its direct or indirect role in nourishing higher organisms. The algal component of the periphyton usually represents the most significant source of food production through photosynthesis in relatively shallow and rapidly flowing streams. Herbivores among the periphytic animal life and the free-living macroinvertebrates feed on this material and transfer its energy along the food chain to the fish.

Impacts on the periphyton selected for study were alterations of current velocity, plant nutrients and the biodegradable organic matter which feeds the attached heterotrophic organisms. Modification of the current is a possible result of both channel reconstruction and draining large amounts of storm runoff into fairly small water courses. Containing substantial concentrations of both inorganic and organic nutrients (Horner _et al_, 1977), highway runoff is capable of increasing periphytic algal, consumer and decomposer growth.

Stream Morphology

In approaching a study involving the physical nature of a stream or the possible effects of physically altering the water course, both subjects of interest in this work, it is very important to understand the processes operating to initially establish and subsequently modify the natural channel. Knowledge of these processes is the best guide to designing channel modifications producing the least possible overall damage to the integrity of the biological and supporting systems and to assessing the probable impacts of human intrusion.

The course assumed by a stream in transporting water from higher to lower elevations is determined by general physical principles and local geological conditions. The explanations of the processes involved were largely developed and reported at length by Leopold and Wolman (1960) and Leopold _et al_.(1964) and reviewed by Leopold and Langbien (1966). A summary of the extensive work of the Leopold team follows.

The key to the form of a stream course laterally, longitudinally and in cross-section is the natural effort to equalize and minimize the physical work done. The most probable path is that coming closest to achieving that ideal.

Typifying river courses is a meandering pattern, which is most prominently in evidence where the river traverses a gentle slope in a medium consisting of fine-grained material that is easily eroded and transported but has sufficient cohesiveness to provide firm banks. The research team demonstrated close correspondence between typical actual stream meanders and the "sine-generated" curve arising from the solution of mathematical equations. Such a curve is preferred to a straight path because it produces more uniform energy dissipation over an extended reach. This particular curve also tends to form in preference to other geometric curves because it minimizes directional change through the reach and thus the work performed. As a consequence, bank erosion is both minimized and distributed, rather than concentrated locally.

The mechanism for developing and continuously changing a stream's course is the ability of the water to erode, transport and deposit solid materials. This mechanism, coupled with the variations in velocity vectors laterally, longitudinally and with depth, produces the bed profile and cross-sectional shape of the channel. The circulatory system resulting from this dynamic action erodes material from the concave stream bank and tends to deposit it at the convex bank, forming a point bar there. Repetition of this pattern over time shifts the stream across its valley, resulting eventually in the channel occupying every possible position between the valley walls in forming the floodplain.

In addition to explaining the determination of a stream's course, the researchers documented the regularity of the familiar alternating riffle/pool pattern. They found that shallow zones giving rise to riffles tend to be located alternately on each side of the stream at intervals roughly twice the meander wavelength. These zones are interspersed with deeper pools.

On the broader scale, the Leopold team discovered that the longitudinal profile of the entire river system is concave. Concavity concentrates the steepest slopes near the headwaters, where discharges are smallest, and minimize work in the system as a whole. There is thus a unity in the physics of naturally flowing river systems surrounding the tendency toward minimum but uniform energy expenditure.

Characteristics of Stream Periphyton

The periphyton includes all the organisms that are attached to a submerged substrate but which do not penetrate into it. It is composed, typically, of unicelluar and filamentous algae and attached protozoa, bryozoa and rotifers. Convention frequently extends the periphyton community boundary to embrace bacterial and fungal growth forming on substrates in an analogous manner. Such growths are often documented to be successional forms thriving in highly organically enriched waters (Curtis and Harrington, 1971). Given the interest in the development of the entire attached community, the present study has employed methods of measurement which reflect the growth of all of the above-mentioned sessile organisms.

Generic representation in the periphytic community varies considerably geographically and environmentally, but common forms include those listed in Table I.

The periphyton is characterized by considerable heterogeneity stemming partially from the various surfaces available for attachment. It is thus appropriate to broadly classify periphyton according to substrate as: (1) epiphytic, attached to macrophytic plants; (2) epilithic, growing on submerged rocks; (3) epipelic, associated with the sediments; (4) episammic, growing on sand; and (5) epizooic, growing on surfaces of animals (Wetzel, 1975).

Table I. Genera Most Commonly Represented Among the Periphyton (Compiled from many references in the periphyton literature)

Diatoms -- *Navicula*, *Diatoma*, *Cymbella*, *Cocconeis*, *Synedra*, *Ceratoneis*, *Melosira*, *Gomphonema*, *Nitzchia*, *Fragillaria*, *Achnanthes*, *Cyclotella*

Filamentous green algae -- *Cladophora*, *Tetraspora*, *Stigeoclonium*, *Oedogonium*, *Tribonema*, *Ulothrix*, *Spirogyra*

Filamentous blue-green algae -- *Oscillatoria*, *Lyngbya*, *Phormidium*

Protozoa -- *Stentor*, *Carchesium*, *Vorticella*, *Tetrahymena*, *Colpidium*, *Glaucoma*, *Paramecium*

Bacteria -- *Sphaerotilus*, *Zooglea*, *Beggiatoa*

Fungi -- *Fusarium*

The field component of this research should thus be specified as encompassing the development of the epilithic periphyton.

Periphyton growth observes a general pattern of colonization followed by a sigmoid growth curve (Kevern *et al*., 1966). Although mobile heterotrophs may colonize more rapidly, early stages are largely autotrophic. Heterotrophs gain importance as time proceeds and the community ages. Colonization accounts for a substantial portion of the initial lag phase of growth and is a major factor to be considered in periphyton sampling programs. Properly, experiments designed to estimate growth characteristics should be conducted between the end of the colonization period and the onset of losses caused by the death of subsurface material. Castenholz (1961), Neal *et al*. (1967), Slack *et al*. (1973) and American Public Health Association (1975) were in general agreement that the colonization period normally extends for approximately two weeks.

While sufficient exposure of sample substrates is required where the objective is to monitor mature communities, sampling must proceed before the sigmoid growth curve reaches an asymptote, designated as approximately two months by Kevern _et_ _al_. (1966). At this time production falls to a minimal amount, and peeling and sloughing soon begin as underlying cells die and lose attachment.

Rather than presenting a case for a fairly predictable sigmoid growth, stream periphyton is actually likely to follow a highly irregular and rapidly changing development pattern dictated by species composition and environmental conditions. Short-lived natural occurrences frequently destabilize the system and greatly affect the periphyton positively or negatively. High flow rates from storm runoff generally reduce the standing crop by the scouring action of suspended particles and the friction of elevated current velocities. A sudden influx of nutrients contributed by urban or agricultural runoff may, on the other hand, spur the growth of a nutrient-limited community. All of these phenomena, arising between the conclusion of colonization and the onset of the equilibrium phase and natural sloughing, are additional elements for consideration in the planning and final analysis of any study of the stream periphyton.

Ecological Relationships Involving the Periphyton

The ecological significance of any organism or community lies in its relationships with such units in the larger system. Being a diverse assemblage of organisms, the periphyton interacts with other groups within stream ecosystems in various ways. In trophic terms the periphyton include algal primary producers and microscopic primary consumers and decomposers. Each form is a potential food source for higher organisms. Attached algae are particularly dominant in primary production over other plant forms in shallow, rapidly flowing, well-lighted streams.

Many investigators have been concerned with quantifying the productivity of periphytic autotrophs. Lack of standardized procedures and the considerable variability of stream habitats has created such wide dispersion in results that little can be generalized from these data. The only possible generalization is that the level of primary production is a strong function of environmental conditions. In some situations it is so substantial as to be the dominant factor at the base of the food web. In other cases, especially in wooded streams where light is low, algal production is so meager that consumers must rely on organic materials produced in the terrestrial portion of the watershed. In these cases Hynes (1963) concluded that, without imported matter, the stream would be virtually barren.

Turning from production to transfer of food through the ecosystem, several studies are relevant to the role of periphytic algae in nourishing consumers. Cummins _et_ _al_. (1966) found that herbivores in Linesville Creek, Pennsylvania, amounted to about 30 per cent of total macroconsumer biomass. Consumers of dead organic material (detritus) represented approximately an equal share, with secondary macroconsumers, which feed on both groups, making up the remainder. If primary and detrital consumers are assumed to contribute equally to the secondary group, it may be estimated that periphytic primary production was ultimately responsible for about half of the animal biomass in this stream.

Southworth and Hooper (1974) measured primary production in artificially defined channels set in a natural stream enriched by inorganic and organic materials. Benthic consumers were 30 per cent more abundant in the inorganically enriched case, where primary production was double that in control and organically enriched channels. Elimination of primary production by restricting light reduced grazers by 29 per cent, even though detritus was still available.

Elwood and Nelson (1972) measured periphyton production and grazing rates in a small woodland stream by a ^{32}P balance method. In experiments conducted at three different times of the year, they estimated periphyton net production rates as 22, 24 and 16 mg ash-free dry weight m^{-2} day^{-1} and grazing rates on periphyton for the respective periods as 23, 15 and 14 mg ash-free dry weight m^{-2} day^{-1}. Their results demonstrate that autotrophic production is heavily used in the system; in fact, grazers control periphyton standing crop. Eichenberger (1975) documented a similar effect in artificial channels. Here the density of filamentous algae decreased almost directly with increase of midge larvae density.

The expected connection between periphyton production at the bottom of the food chain and fish at the top has not been thoroughly explored. It has been reported (Lyford and Gregory, 1975) that a reach of an Oregon mountain stream experiencing increased periphyton production following removal of the shading canopy by clearcutting had approximately twice the trout standing crop of a neighboring control reach. Insect emergence was also considerably greater in the more productive zone. Warren *et al*. (1964) observed increased trout production in a previously unproductive stream which had been experimentally fertilized with sucrose that increased the production of *Sphaerotilus* (bacteria). The important subject of food utilization and energy transfer is a primary need in aquatic ecological research.

Periphyton Development in Response to Nutrients

Sládecková (1964) discussed the factors influencing the occurrence and abundance of periphyton and concluded that the supply of dissolved nutrients is the most important among them. With the diverse representation of organisms in the periphyton, a discussion of major growth nutrients must consider mineral elements, required by algal forms, and preformed organic compounds nourishing the heterotrophs. With reference to the autotrophs, of fundamental interest is the nutrient most limiting to growth and thus having the greatest degree of control over production. The most limiting nutrient has generally been found to be either phosphorus or nitrogen in studies of flowing water, with carbon (Wright and Mills, 1967; Dickman, 1973) or trace metals (Wuhrmann and Eichenberger, 1975) occasionally identified.

The apparent paradox of strong algal growth coincident with a low concentration of one of the essential macronutrients is not infrequently observed in streams and lakes. Goldman (1968) and Brehmer _et_ _al_. (1969) found a negative association between algal production and nitrogen content. Cushing (1967), Ball _et_ _al_. (1969) and Brown (1973) all showed a decrease of phosphorus concentration to accompany elevated growth, while Flemer (1970) recorded his lowest nitrogen and phosphorus concentrations during the greatest periphyton bloom. Evidence offered by Caperon (1968), Fitzgerald (1969), Lin (1971) and Droop (1973) suggests algae possess an ability to absorb and store quantities of both nutrients far in excess of present needs. These stores serve as a supply source for further growth.

Of particular interest in stream ecology is the relationship between nutrient concentrations and the propagation of nuisance algal forms such as the filamentous green alga _Cladophora_. Such organisms out-compete former community members which are preferred as food by consumers. Species diversity and system stability decline, although community biomass and productivity may remain the same or increase. The research of Neil and Owen (1964) in Lake Huron and Pitcairn and Hawkes (1973) in English rivers found an elevated phosphorus concentration to be the leading factor in spurring growths of Cladophora.

The heterotrophic portion of the periphyton community is nourished by organic compounds passing with the water or trapped in the attached mat. This mat possesses a certain ability to trap particles from the water. Particulate matter can be directly ingested by the animals, while the bacteria and fungi require dissolved materials, which may be excreted by the consumers. Ormerod et al. (1966) experimented with artificial channels fertilized by organic and inorganic nutrients under conditions of controlled velocity and temperature. Their results illustrated the mechanisms controlling the development of bacterial and fungal growth, which frequently achieves nuisance proportions. The general conclusion of their research was that the heterotrophic species ultimately established depended on the types of inorganic and organic nutrients provided. Fertilization with specialized wastes, such as spent sulfite waste liquor and sucrose, led to dominance by the nuisance bacteria Sphaerotilus. Unspecialized sewage produced increases of the less objectionable fungus Fusarium. Ehrlich and Slack (1969) and Cummins et al. (1972) conclusively demonstrated the role of specialized wastes in creating a Sphaerotilus-dominated periphyton community with more specific experiments.

Various observers, beginning with Kolkwitz and Marsson (1908), have contributed to formulating a systematic portrait of the response of periphyton to the discharge of wastewaters including inorganic and organic nutrients. This "saprobien system" comprises descriptions of overall associations among algae, protozoa, rotifers, bacteria, fungi and larger organisms typical of certain water quality states. Its theoretical basis is that the periphyton, being stationary, is subjected to all water quality conditions existing at a

Table II: Saprobien System for Organic Waste Addition to a Stream (generalized by Welch, 1976, from Fjerdingstad, 1964)

Zone	Chemical	Biological
Oligosaprobity (Clean)	BOD < 3 mg l^{-1} O_2 high Complete mineralization of organic matter	Diatoms diverse Filamentous green algae present Filamentous bacteria and ciliated protozoa scarce
Polysaprobity (Septic)	H_2S high O_2 low NH_3 high	Algae not abundant Protozoa absent Fecal and saprobic bacteria (not filamentous) abundant
α Mesosaprobity (Polluted)	Amino acids high H_2S low $O_2 < 50\%$ saturation BOD > 10 mg l^{-1}	Some tolerant algae (1) Filamentous bacteria abundant (2) Ciliated protozoa abundant (3) Great biomass, low diversity
β Mesosaprobity (Recovery)	$NO_3 > NO_2 > NH_3$ $O_2 > 50\%$ saturation BOD < 10 mg l^{-1}	Great diatom biomass, low diversity (4) Ciliated protozoa (5) Blue-green algae abundant (6) Filamentous green algae abundant (7)

Notes:
(1) Gomphonema, Nitzchia, Oscillatoria, Phormidium, Stigeoclonium typically

(2) Sphaerotilus, Zooglea, Beggiatoa

(3) Colpidium, Glaucoma, Paramecium, Carchesium, Vorticella

(4) Melosira, Gomphonema, Nitzchia, Cocconeis

(5) Stentor

(6) Phormidium, Oscillatoria

(7) Cladophora, Stigeoclonium, Ulothrix

particular spot and integrates their effects. Table II summarizes one expression of the saprobien system, organized according to the usual progression from waste discharge, through self-purification to recovery. The full system description presented includes the chemical changes affecting the biota.

As illustrated by the saprobien system descriptions, a leading result of stream enrichment is succession to species with nuisance tendencies. The most fundamental effects of succession at the base of the food web are species shifts throughout the system, generally to organisms less efficient in transferring energy from level-to-level, and reduced diversity at all levels. The ultimate result is usually reduced fish production or at least decreases in fish of interest to human consumers. Other potential effects of filamentous algae or slime growths are their ability to reduce dissolved oxygen through respiration and the oxygen demand produced by their decay,as well as interference with water supplies by creating taste and odor problems and clogging intakes.

Periphyton Development in Response to Current Velocity

The velocity and pattern of current flow is a dominant characteristic in the environment of any organism inhabiting a stream. Of greatest importance are conditions in the immediate vicinity of the organism, in what might be termed the "microzone". Research on the role of the current in the ecology of attached stream communities has centered primarily on the effects of variable velocity on biomass accumulation, species composition, certain physiological processes and the uptake of various dissolved substances. Most of this work has been conducted in artificial channels because of the greater control that could be exerted over experiments. Confirmation of results in natural streams is rare and not coordinated with laboratory findings.

Early studies by Butcher (1946) and Amberg and Cormack (1960) revealed that smaller nutrient concentrations were required to attain algal growth levels or accrual rates in flowing waters equal to those in still or more slowly moving water. Odum and Hoskin (1957) noted increased metabolism of periphyton communities with increased velocity. Whitford and Schumaker (1961) measured higher rates of phosphorus uptake and respiration by several algal species at elevated velocity in experiments conducted in the range 0-40 cm sec^{-1}. Others, including Whitford (1960) and Reisen and Spencer (1970), found species differences in the response to velocity variation, with the growth of certain organisms advanced by an increase in the current and the development of others retarded.

McIntire has performed a considerable amount of artificial channel research on various aspects of lotic periphyton. His comparison of growth in 9 and 38 cm sec^{-1} currents (McIntire, 1966) revealed filamentous green algae dominance in the former case and diatom dominance in the latter. Colonization was initially retarded in the faster current but growth eventually accumulated more rapidly in that case. Export rates were about four times as great at 38 than at 9 cm sec^{-1}, with the result that biomasses were approximately equal at the end of the experiment. Chlorophyll *a* level was, however, higher in the faster current. McIntire (1968) reported on the response of various algal species to current and light variation. Among the diatoms, some species were indifferent to current, some were positively affected and the diatom *Melosira varians* was retarded by velocity increase to 35 cm sec^{-1}. Algae other than diatoms were actually more abundant in still water. Total biomass increased with current at high illumination but not at low light level.

As with McIntire's work, most artificial channel research has measured growth at velocities less than 50 cm sec^{-1}. Phaup and Gannon (1967) found that Sphaerotilus biomass increased in proportion to velocity increase from 18 to 45 cm sec^{-1}. The experiments of both Sperling and Hale (1973) and Rodgers and Harvey (1976) demonstrated that substantially faster uptake of radioactive carbon-14 occurs in a moderate current than in still or very slowly flowing water. Pertinent to the periphytic heterotrophs, Wuhrmann (1972) and Wuhrmann et al. (1975) reported a rate of sugar uptake by decomposing organisms twelve times as high at 24 cm sec^{-1} than at 4 cm sec^{-1}.

Field studies confirming the laboratory findings reported above are few. Ball et al. (1969) observed the following behavior in the Red Cedar River, Michigan:

Velocity:	0-30.5 cm sec^{-1}	Rapid colonization, slow growth, low standing crop
	30.5-61 cm sec^{-1}	Greatest standing crop
	61-91.5 cm sec^{-1}	Slow colonization but substantial standing crop at end of experiment
	91.5-137 cm sec^{-1}	Lowest standing crop

Reisen and Spencer (1970) demonstrated a negative relationship between overall diatom density and current velocity up to 66.3 cm sec^{-1} over the short term but a strongly positive relationship over the full six-week term of the experiment. These results provide field confirmation of McIntire's observation that current retards initial colonization and biomass accumulation but assists productivity ultimately.

A rather extensive body of literature thus maintains that general periphytic biological activity and growth increases with current velocity increase up to at least 50 cm sec^{-1}. The apparent reason for this behavior, most clearly stated by Whitford (1960), is that turbulence increases the diffusion of nutrients to all surfaces through a concentration gradient extending out from the surfaces.

The rather sparse data collected at very high velocities supports the belief that biomass accumulation is hindered by currents approaching 1 m sec^{-1} and higher. In this situation attachment is prevented in the case of many species, and those managing to gain a tenuous foothold are easily removed by the frictional force developed. The base for reproduction is thus minimal, and the community grows slowly and is limited in diversity. Rapids and riffle areas normally have fast currents, but storm runoff can elevate velocities considerably in any section. Following storms the great increase in suspended particles also acts to raise the frictional force. Brehmer _et_ _al_. (1969) gave most of the blame to particulates carried by runoff for nearly destroying the periphyton standing crop after a heavy summer storm.

Taken together, results of artificial channel and field experiments still leave certain important questions unanswered regarding the periphytic autotrophs and heterotrophs of streams and the environmental forces acting upon them. These matters include the relative importance of the many variables operating in natural streams, the interplay between current velocity and the most important of the other variables,and reasonable means to predict the effects at the base of the food web of altering the principal controlling factors. The work reported here considered these and other subjects in the interest of advancing understanding of the processes operating in the natural system. The work had a further interest in applying the knowledge thus gained to practical problems, such as the evaluation of stream channel reconstruction projects and storm drainage proposals.

EXPERIMENTAL METHODS

Organization of the Study

Experimental work was centered around amassing data on the accrual rate of periphytic biomass, and the autotrophic component of the community specifically, in several natural streams during the prime summer growing season. At the same time, measurements were taken of current velocity, concentrations of certain nutrients, the level of organic carbon carried by the streams and certain quantities governing the light, temperature and general water quality conditions that affect the communities studied. Streams and sites within streams were selected to provide a range of velocities and phosphorus, nitrogen and organic carbon concentrations, while offering a reasonably high degree of uniformity in light, water temperature and other important water quality variables. The study could thus concentrate primarily on response to differing velocities and levels of nourishment.

Sampling site locations are listed in Table III and located on the map (Figure 1). Sites are numbered from downstream to upstream locations. Sampling spots were selected where light intensity would be high throughout the day, although some periods of shading inevitably occurred. Further, the selection included only locations where periphyton collectors could be placed at fairly shallow depths and in water generally low in turbidity to permit efficient light penetration and enhance working conditions. U. S. Geological Survey flow monitoring stations existed near all sampling sites except those on the Pilchuck and Cedar Rivers.

Table III: Stream Sampling Site Locations

Stream	Site Number	Location
Pilchuck River	PR-1	Immediately north of present highway SR 2 at Snohomish
	PR-2	Same
	PR-3	Same
Swamp Creek	SC-1	Immediately south of highway SR 522 at Kenmore
	SC-2	Same
Juanita Creek	JC-1	Immediately south of Juanita Drive in Juanita Beach County Park
	JC-2	Immediately west of 100th Avenue N.E. at Juanita
Issaquah Creek	IC-1	Immediately north of S.E. 56th Street north of Issaquah
	IC-2	Off S.E. Sycamore Drive south of Issaquah
Cedar River	CR-1	Immediately north of highway SR 169 at Maple Valley
Big Soos Creek	BSC-1	Off Auburn-Black Diamond Road at state fish hatchery
	BSC-2	Same

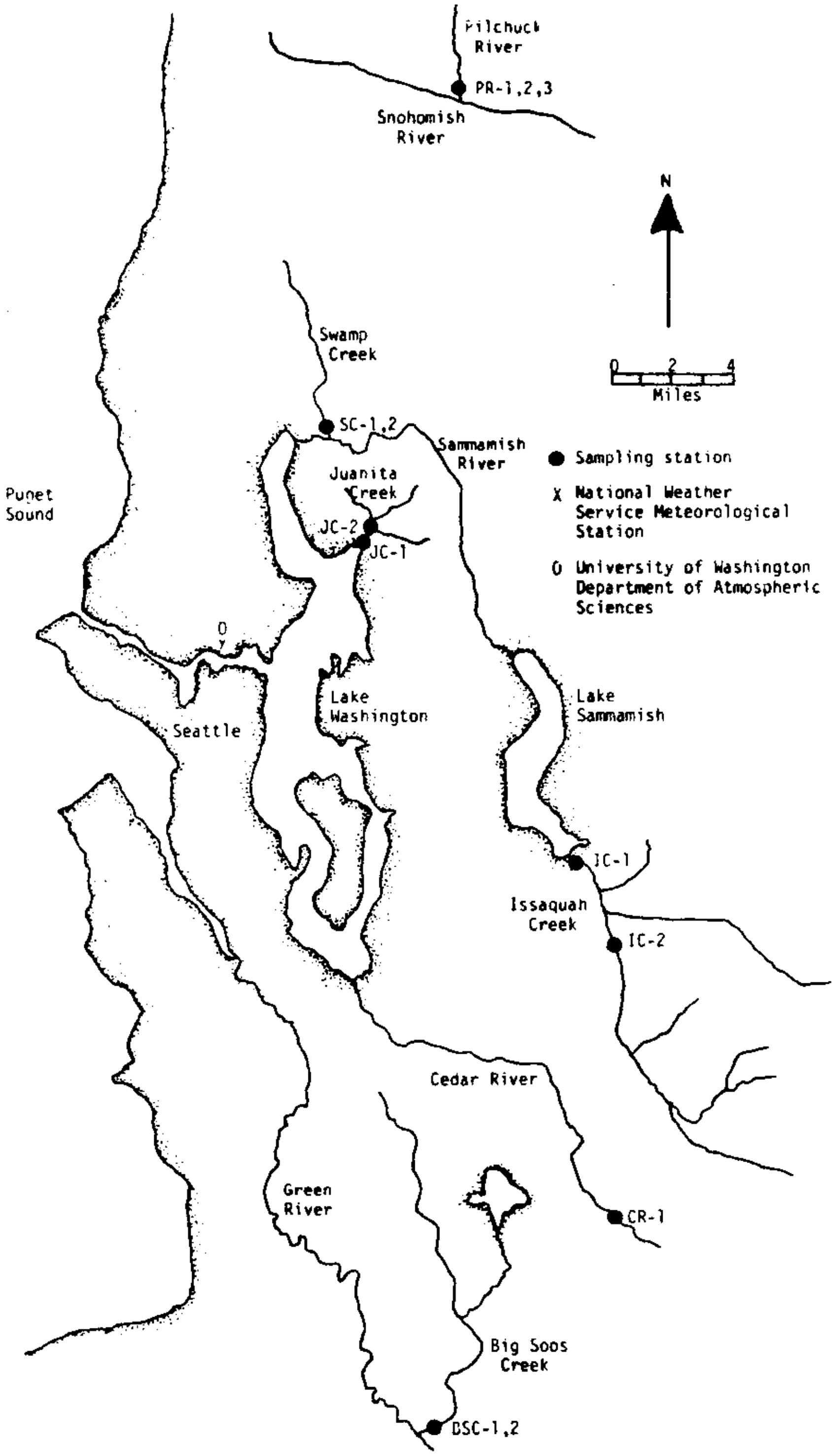

Figure 1: Stream Sampling Site Vicinity Map

Monitoring of Periphyton Community Development

The selection of methods for collecting and analyzing stream periphyton in the present work was guided by the objectives established and the experience reported with alternative procedures (reviewed by Horner, 1978). To permit sampling periphyton under varying environmental conditions, an artificial substrate had to be selected and collection technique devised to permit experimentation in streams of varying morphometry and discharge and fully exposed to public access. Analysis of the collected periphyton had to be concentrated on procedures which would best elucidate the development of the autotrophic and heterotrophic communities. To permit the processing of the large number of samples gathered in the intensive program, methods also had to be efficient and conserving of time. Measurements of chlorophyll a and adenosine triphosphate (ATP) were selected from among the available techniques as best filling these needs. Found only in living organisms (Weber, 1973), the latter quantity represents the total living biomass, and conversion to non-detrital organic carbon can be made with a relatively high degree of confidence (Holm-Hansen, 1970; 1973). As the major photosynthetic pigment, chlorophyll a is a conveniently measured quantity with which to assess the development of the autotrophs.

Flattened rocks gathered from streams were adopted as the means of quantitatively collecting periphyton. This selection was made on the basis of the success reported by Brenner (personal communication) in recovering samplers from streams situated in heavily populated areas. An additional consideration was the potential offered by the natural material for establishing communities similar to indigenous growth. A flat, smooth surface was formed by cutting medium-sized rocks in half on a diamond saw. Three such collectors were placed in approximately 50 cm of water or less at each sampling site. The flat face was oriented vertically and parallel to the flow.

During the initial mid-summer phase of collection (July-August, 1977), only communities expected to have completed colonization were sampled. As advised in the literature, colonization during this summer period was estimated to require one to two weeks. Thus, communities were sampled at the ages of approximately two, three and four weeks. In the interest of investigating colonization and the development of specific communities over time, the late summer phase of collection (September, 1977) comprised weekly sampling intervals from single substrates over a four-week period. The total sampling effort yielded approximately 110 separate samples, each of which was analyzed for chlorophyll a and ATP.

Periphyton was collected by carefully scraping growth from a portion of the flat surface was a razor blade into a wide-mouth jar containing distilled water. The scraping was followed by brushing additional material into the jar with a tooth brush. Both processes were repeated until no visible periphyton removal occurred. The area scraped was traced on grid paper for later measurement by planimeter. Sample jars were transported to the laboratory in an ice chest. Substrates involved in the continuing late summer weekly sampling program were marked with fast-drying paint where material had been removed to insure that no newly-colonizing growth would be gathered in subsequent weeks. The rocks were then returned to the spots in the stream from which they had been removed.

In the laboratory the periphyton was prepared for analysis of chlorophyll a and ATP the day of collection. Following dispersion of clumps by vigorous shaking, measured subsamples were drawn for the chlorophyll a and ATP analyses. Chlorophyll a concentration was determined fluorometrically in 90 per cent acetone extracts as outlined in Strickland and Parsons (1972) using a Turner fluorometer and expressed in mg m^{-2} on the basis of the area sampled.

Subsamples intended for ATP analysis were extracted in boiling TRIS buffer according to the procedure of Holm-Hansen and Booth (1966). The extract was analyzed in a JRB, Inc., ATP photometer, following the same procedure, and expressed in mg ATP m^{-2} of surface sampled.

Measurement of Water Quality Variables

The primary water quality variables of concern in the research were orthophosphate and total soluble phosphorus, nitrate-plus-nitrite- and ammonia-nitrogen and dissolved and particulate organic carbon. Also of interest for generally characterizing water quality and judging possible effects on results extraneous to the primary variables were water temperature, pH, specific conductivity, total alkalinity and turbidity. All variables were measured on a biweekly schedule corresponding with periphyton sampling throughout the program.

Water temperature was measured with a mercury thermometer immersed in the stream. A water sample was collected at the same time for analyses of pH, specific conductivity and total alkalinity onsite, and turbidity, dissolved nutrients and organic carbon in the laboratory. The pH was measured with a Porto-matic model 175 pH meter and specific conductivity with a Lab-line model MC-1, Mark IV instrument. Total alkalinity was determined by titration with 0.02 N sulfuric acid to an end point defined by mixed indicator according to the procedure in Standard Methods (American Public Health Association, 1975). The remainder of each sample was transported to the laboratory in an ice chest.

Total soluble and orthophosphate-phosphorus were analyzed according to the molybdenum blue colorimetric methods of Murphy and Riley (1962), with absorbance read at 885 nm on a Beckman model DK-2A spectrophotometer. Nitrate-plus-nitrite- and ammonia-nitrogen were determined on a Technicon AutoAnalyzer II, the former by a cadmium reduction procedure and the latter using a phenolhypochlorite technique.

The total organic carbon (TOC) is a sum of the dissolved (DOC) and particulate organic carbon (POC). TOC is generally comprised of biodegradable matter of mostly terrestrial origin, but aquatic production and point or non-point sources of synthetic organic chemicals also contribute. Total organic carbon was measured in the water sample to form a record of the relative degree of autotrophy or heterotrophy represented by the streams studied. These data were considered particularly in analyzing ATP results. DOC and POC were determined by combusting organics in a LECO model 507-200 induction furnace and measuring the resulting carbon dioxide gas on a Beckman model 865 infrared analyzer.

Turbidity is a function of all materials suspended in water, with i
suspended solids being of most concern here. The particulates that crea
turbidity interfere with light transmission by scattering incident radia
aid scour of attached growth and cause other adverse effects less releva
this work. Turbidity was measured on a relative Formazin Turbidity Unit
scale using a Hach Chemical Company model 2100A nephalometric turbidimet

Data analyses were conducted with reference to average water quality conditions existing over the respective growth periods. Averages were estimated by computing the means of readings taken over the various periods.

The nutrient most limiting to algal biomass and growth rate was determined experimentally by algal growth potential (AGP) experiments according to the procedure outlined by the National Eutrophication Research Program, U.S. Environmental Protection Agency (1971). According to this procedure, filtered stream samples were fertilized with measured quantities of nitrogen, phosphorus and the two minerals in combination and inoculated with cells of the green alga

Selenastrum capricornutum. Experimental vessels were incubated at 24C in a light incubator. Growth was monitored at set intervals by reading light transmittance in a Coleman 130 spectrophotometer at 675 nm. Transmittance was converted to optical density, which was in turn converted to an index. Successive changes in this index were plotted with respect to time to produce the growth curves. The relative maxima and slopes of the curves indicated the nutrient most limiting to biomass and growth rate, respectively. Results of the AGP experiments were considered in light of other observations during the data analysis to firmly establish the most limiting nutrient.

Measurement of Physical Variables

To measure current velocity in the vicinity of the periphyton collectors, a propeller-type current meter was designed and built at the Harris Laboratory of the University of Washington for use in the research project. The meter was equipped with a range selector switch and was calibrated to give a direct needle reading in either ft sec^{-1} or ft min^{-1}. Measurements were taken as close as possible to the flat face of the periphyton collector. Velocity was measured at every substrate at least biweekly. Where samples were taken more frequently, velocity was measured on every sampling occasion. Depth was also measured biweekly at every collector with a meter stick.

Data analyses were conducted with reference to average current velocities over the respective growth periods. For sampling stations on Swamp Creek, Juanita Creek, Issaquah Creek and Big Soos Creek, daily discharge records at nearby USGS gaging stations (U.S. Geological Survey, 1977) were available to aid in estimating averages. For these stations velocities measured at each collector over the entire study were graphed with respect to discharge.

In many cases, particularly those where collectors rested on uniform gravel stream beds, relationships were nearly linear. Linear regression equations with high coefficients of determination (r^2) were derived for use in estimating velocities on each day during growth periods. Means of daily estimates were then computed. When a linear relationship did not result, the graph was used in making daily estimates. Sampling sites on the Pilchuck and Cedar Rivers had no nearby USGS gaging stations to provide discharge records. Here it was necessary to use less accurate mean velocity estimates prepared by averaging whatever readings were taken over growth periods.

Previous research reviewed by Horner (1978), established the role of light in periphyton growth. It was desired to eliminate light as a variable among sampling sites in order to concentrate on current velocity, nutrients and organic carbon. To gage the success in reaching this goal and to permit the evaluation of the effects of any light variation on periphyton growth, a survey was conducted during the summer experimental period at each sampling station. Intensity was measured with a Photo Research Corporation Spectra Lumicon light meter held immediately above the collectors in the stream. The survey was conducted by taking a series of measurements at each site throughout the photoperiod. Readings were taken only during periods of full sun, and the survey at all stations was completed within the first week of September, 1977. Spot readings were also taken earlier to gage the differences in mid-day intensities over the summer. Light intensities were then graphed with respect to time, and the plots were integrated by planimeter to permit a comparison of the total light received by each site in a day's time. The graphs were also useful in estimating the length of time during which light was below saturation level at each site and the approximate intensity during that period.

It was also desired to conduct field experiments over a period expected to be fairly uniform in solar radiation. To gage the success in achieving this goal and to provide a basis for correcting if necessary, solar radiation records were obtained from the University of Washington Department of Atmospheric Sciences. These measurements were made at a point, shown on the map in Figure 1, roughly equidistant between the northernmost and southernmost stream sites. Solar radiation was measured with an Eppley 180° pyranometer and recorded by a Lintronic integrating recorder.

Data Analysis

The success of a research program in extending knowledge ultimately depends on the uses to which the data are put. Data analysis was a distinct challenge in this work because of the large number of variables potentially affecting periphyton development and the rather numerous stream habitats used to achieve wide ranges in the variables of interest. Here the principal objective of data analysis was to characterize development of the periphytic community as a whole, and its algal component in particular, with respect to current velocity and the limiting nutrient. The goal was to increase understanding of these interactions for forecasting the probable effects on the base of stream food webs created by construction which modifies velocity or storm drainage that intermittently increases the current and the concentration of nutrients and organic materials.

For this purpose measured areal ATP and chlorophyll *a* concentrations represented total and autotrophic periphyton community development (or biomass accrual) respectively. In addition, a relative measure expressing the development of algal food producers with respect to the total community was defined and termed the heterotrophic index (HI):

$$HI = \frac{(\text{mg ATP m}^{-2})\ (250\text{ mg carbon/mg ATP})}{\text{mg chlorophyll } \underline{a}\text{ m}^{-2}}$$

The conversion factor transforming ATP to total living carbon biomass was based on the recommendation of Holm-Hansen (1973). The index is a convenient method of judging the relative dominance of heterotrophs and autotrophs in the periphyton community.

The data analysis was aimed at discovering relationships among periphyton development and the various measured independent variables: time; current velocity; concentrations of orthophosphate and total soluble phosphorus; nitrate-plus-nitrite- and ammonia-nitrogen and total organic carbon. In addition, the supply rates of phosphorus, nitrogen and carbon were defined as the multiple of concentration and velocity and included in the analysis. The importance of light variations in affecting results was also considered.

Several strategies were formulated to serve the objectives of the program. First, graphs were produced to illustrate variations in chlorophyll a, ATP and the heterotrophic index over time at each monitoring station for each experimental period. Variations in average velocities over the same periods were also shown. A second useful technique employed at an early stage in the analysis was ranking of dependent periphyton accrual and independent environmental variables in a side-by-side arrangement. Ranking aided in identifying general associations which could be explored later with more powerful analytical methods.

Preliminary analyses demonstrated that attempts to generalize results across streams and over wide ranges of the principal independent variables would require a multivariate approach to account for a substantial part of the variation in dependent variables. Correlation and multiple linear regression techniques are effective multivariate analysis tools. The former procedure provides information on positive and negative associations between variable pairs and the statistical significance of these associations. Multiple linear regression was previously employed in algal research by Goldman et al. (1968), Brown (1973) and Dunn (1976). It is a least-squares computation of the best fit between one dependent and a host of independent variables. The equation form is:

$$Y = a_o + a_1X_1 + a_2X_2 + \ldots + a_nX_n$$

The general purpose of multiple regression analyses was to formulate descriptive models of community behavior which might be interpreted to discern trends in the relationships. Such models represent activity without necessarily depicting the specific mechanisms thought to be operating. Rather they are constructed of a linear combination of all variables considered to have a part in the activity.

Correlations and multiple regressions were performed by the STEPWISE digital computer program developed by Rao (1977), available at the University of Washington Academic Computer Center. It was run on the CDC Model 6400 computer at the Center. For these statistical analyses a logarithmic transformation was applied to the dependent chlorophyll a and ATP variables. Transformation generally normalizes distributions, producing compliance with the assumptions of statistical procedures. This practice follows the precedents of Barnes (1952), Cassie (1963), Goldman et al. (1968) and Brown (1973) in previous aquatic primary production studies.

EXPERIMENTAL RESULTS

General Summary

The experimental program yielded a wide range of velocity, phosphorus, nitrogen and organic carbon values, as desired, while confining temperature, pH, specific conductivity, total alkalinity and light variations within much narrower limits, also according to plan. Water samples from various monitoring stations were generally comparable in turbidity, but the two major rainstorms during the experimental period produced moderately to highly elevated readings. Table IV shows the measured ranges of the physical and chemical variables, and Table V lists means over the entire experimental period for each station.

Weather conditions during the study were of interest because of the effects of solar radiation and temperature on primary production and of storm runoff on the attached community as a whole. A U.S. Weather Service station located in Seattle at a point about equidistant from the northernmost and southernmost stream sampling stations (see Figure 1) served as the primary reference for meteorological data (U.S. Department of Commerce, 1977). Field notes kept during the sampling program included the observed effects of weather on stream conditions and the periphyton.

Significant meteorological events during the period included the extended drought from July 12 to August 23 and the rainstorms of August 23-26 and September 18-20. Clear conditions prevailed during most of the drought period, maximizing light intensity and total light received by the autotrophic periphyton. The only rains substantially increasing stream discharges, depths, current velocities and turbidities were the late August storm and the smaller event of September 18-20. The earlier storm most likely affected mature periphyton communities sampled during the period and colonization of bare substrates planted before the cessation of elevated discharge.

Table IV: Overall Ranges of Experimental Variables

Variable	Unit	Minimum	Maximum
Current Velocity	cm sec^{-1}	0.3	137.2
pH	-	6.6	7.6
Specific conductivity	μmho cm^{-1}	66.0	198.0
Total alkalinity	mg l^{-1} as $CaCO_3$	24.0	66.0
Turbidity	FTU	0.4	64.0
Temperature	C	11.5	18.0
Orthophosphate phosphorus	μg l^{-1}	2.6	78.9
Total soluble phosphorus	μg l^{-1}	8.9	118.0
Nitrate-plus-nitrite-nitrogen	μg l^{-1}	Trace	1029.0
Ammonia-nitrogen	μg l^{-1}	9.0	100.0
Dissolved organic carbon	μg l^{-1}	0.8	12.3
Particulate organic carbon	μg l^{-1}	28.7	1003.0

TABLE V: Mean Values of Experimental Measurements at Each Sampling Station.

Variable	Unit	Station PR	SC	JC-1	JC-2	IC-1	IC-2	CR	BSC
pH	-	7.0	7.1	7.0	7.1	7.2	7.4	7.4	7.1
specific conductivity	μmho cm^{-1}	70	154	156	155	115	99	72	111
Total alkalinity	mg l^{-1} as $CaCO_3$	26.1	53.4	55.1	54.1	46.4	41.3	30.1	40.1
Turbidity	FTU	3.2	4.6	15.4	13.4	18.0	11.3	0.6	3.8
Temperature	C	14.3	14.5	15.9	14.7	15.0	14.3	13.5	14.1
Orthophosphate-phosphorus	μgl^{-1}	7.5	56.2	46.5	32.3	24.4	17.8	8.3	28.0
Total soluble phosphorus	μgl^{-1}	15.5	83.0	65.4	46.6	36.2	27.9	12.0	40.5
Nitrate-plus-nitrite-nitrogen	μgl^{-1}	73.0	496.9	324.7	316.1	320.3	254.3	77.8	469.3
Ammonia-nitrogen	μgl^{-1}	32.2	21.2	14.5	36.1	34.5	37.9	22.8	46.2
Dissolved organic carbon	μgl^{-1}	3.0	6.4	6.1	6.3	3.6	3.3	1.6	4.3
Particulate organic carbon	μgl^{-1}	250.5	254.3	236.8	221.1	327.0	352.6	149.6	281.5

Weekly sampling documented considerable substrate scouring during the September storm.

As described previously, a plot of measured velocity versus discharge on the same day was found to be a feasible means of estimating velocity on any day. Fourteen of the twenty-four plots prepared assumed a nearly linear form, suggesting the use of linear regressions of velocity on discharge to express the relationship. These regression equations explained 82.3 - 99.6 per cent of the variation in velocity due to variation of discharge, and thus served as an excellent means of estimating velocity each day of the experimental period. Nonlinear curves were less satisfactory but represented an improvement over relying on infrequent field measurements where USGS stream gauging stations existed.

Light variations among monitoring stations proved to be minor in the context of the general uniformity and to not have an important influence over results. With regard to variation over time, however, the total daily solar radiation recorded at the central station indicated two periods of distinctly different weather (July 7 - August 25 and August 25 - September 21), producing daily mean values of 450.7 and 310.0 g cal cm^{-2}, respectively. These means represent a highly statistically significant difference ($P < 0.001$). Moreover, they correspond to very different average intensities: 28.2 and 20.7 g cal cm^{-2} hr^{-1} with approximately 16 and 15 hr photoperiods, respectively. Additionally, the spot readings on July 7 showed a maximum mid-day intensity approximately 33 percent higher than in the first week of September.

Reference to the light inhibition literature reviewed by Horner (1978) demonstrates that elevated mid-day intensities existing for an extended period during the summer drought exceeded the level generally known to inhibit algal photosynthesis. Measured chlorophyll _a_ and ATP accumulations were overall substantially smaller in the mid-summer compared to the late summer period, probably as a result of light inhibition. Accordingly, data were analyzed by treating the two periods separately.

Algal growth potential experiments conducted on a sample of each stream monitored were unanimous in demonstrating that phosphorus fertilization increased both the rate of growth and the ultimate biomass of the test alga much more effectively than nitrogen. This indication of phosphorus limitation is confirmed by examining the relative amounts of nitrogen and phosphorus present in the water samples. The ratios of nitrate-plus-nitrite nitrogen to orthophosphate-phosphorus and of total inorganic nitrogen (nitrate, nitrite and ammonia) to total soluble phosphorus in the assayed water samples exceed the average ratio in algal cells of 7.2:1(Sverdrup et al., 1942), thus indicating phosphorus limitation. The ratios in samples drawn for assaying are higher than the averages in some streams over the full experimental period because of the occurrence of nitrogen depletion during periods of heavy algal growth. On these occasions the inescapable conclusion is that nitrogen is momentarily most limiting or that N and P limit simultaneously.

Elementary Data Analysis

The overall strategy of data analysis was to initially search for trends in the results collected at each stream and then to analyze a combined data set to discern general tendencies. Of particular interest was the establishment of trends appearing to fit data from both specific streams and combined streams. As the major step in the first direction, plots of chlorophyll a and ATP biomass, as well as heterotrophic index, versus time were prepared to compare periphyton development between stations on each stream for each experimental period. The same graphs contained plots of average velocities versus time over the same periods. The purpose of the graphs was to investigate the role of velocity in influencing periphyton growth under uniform, or at least very similar, environmental conditions other than velocity. This exercise was most satisfying when applied to the experiment of August 25 - September 21, when four weekly measurements of periphyton accrual were available, except where collectors could not be recovered due to the storm which concluded the experiment.

Figures 2-4 present representative plots, selected from those prepared for the late-summer experiment, which illustrate important tendencies in the results. Figures 2 and 3 contain time series plots of chlorophyll a and ATP, respectively. Figure 4 illustrates representative data on heterotrophic index versus time. In each graph the curves representing periphyton development were smoothed to represent the pattern expected between sampling dates. The storm beginning on September 18 was represented by a slope change on that date. Where the exeistence of USGS gauging stations provided daily records, weekly means were used to plot velocity versus time curves. Otherwise, the plots were based on measurements taken on weekly sampling occasions.

The curves of Figure 2 demonstrate several key points concerning the assistance velocity provides periphytic algae under certain conditions and, conversely, the results of frictional scouring in other circumstances. The most basic point demonstrated by the graphs is that current velocity is a critical determinant of attached autotrophic growth in streams. Two sites on Juanita Creek with very similar nutrient content have chlorophyll a accrual which differs by thirty-fold after 20 days of growth. Other stations also demonstrate considerable divergence among sites. Velocity should, indeed, be recognized in efforts to characterize stream primary production.

More specifically, the graphs for the Pilchuck River, Juanita Creek and Big Soos Creek indicate that chlorophyll a accrual is inversely related to velocity. On the other hand, the Swamp Creek plot shows that higher biomass develops in faster flowing water. It is notable that PO_4-P concentration in Swamp Creek averaged 51.5 μ g l^{-1} for the period and is substantially higher than the other streams considered in Figure 2. Moreover, the velocity at site SC-2 averaged 50-60 cm sec $^{-1}$, lower than at sites PR-1, PR-2 and JC-2. The same trends were apparent in the experiments performed earlier in the program: growth at the site with faster current generally exceeded that at the site with slower flow in the relatively rich Swamp Creek, in contrast to that in the streams having lower phosphorus concentrations. This evidence that velocity assists algal growth to a greater degree in richer than in poorer waters was noted for other phases of data analysis. Whereas velocity increase up to a point does appear to advance the level of ultimate biomass accrual, at least where the limiting nutrient concentration is sufficient, all plots in Figure 2 demonstrate that initial colonization is favored by lower velocities.

Runoff associated with the storm of September 18-20 accounts for scouring of periphyton growth exhibited by the curves in Figure 2. Results for Swamp, Juanita and Big Soos Creeks also demonstrate that communities adapted to higher average velocities decline to a smaller degree than do those inhabiting sites having slower currents ordinarily. The considerable loss of chlorophyll a at site JC-1 in connection with a peak velocity not substantially higher than average suggests that erosion may be due more to elevated turbidity than current.

Two selected time-series plots for ATP. presented in Figure 3, represent development of both autotrophic and heterotrophic segments of the periphyton. Excepting a frequently-noted tendency for ATP to decline earlier than chl a, these curves show trends similar to the chl a results, which represent the algal component alone. Again, moderately high velocity favored growth in the rich Swamp Creek more obviously than in streams having lower nutrient concen-

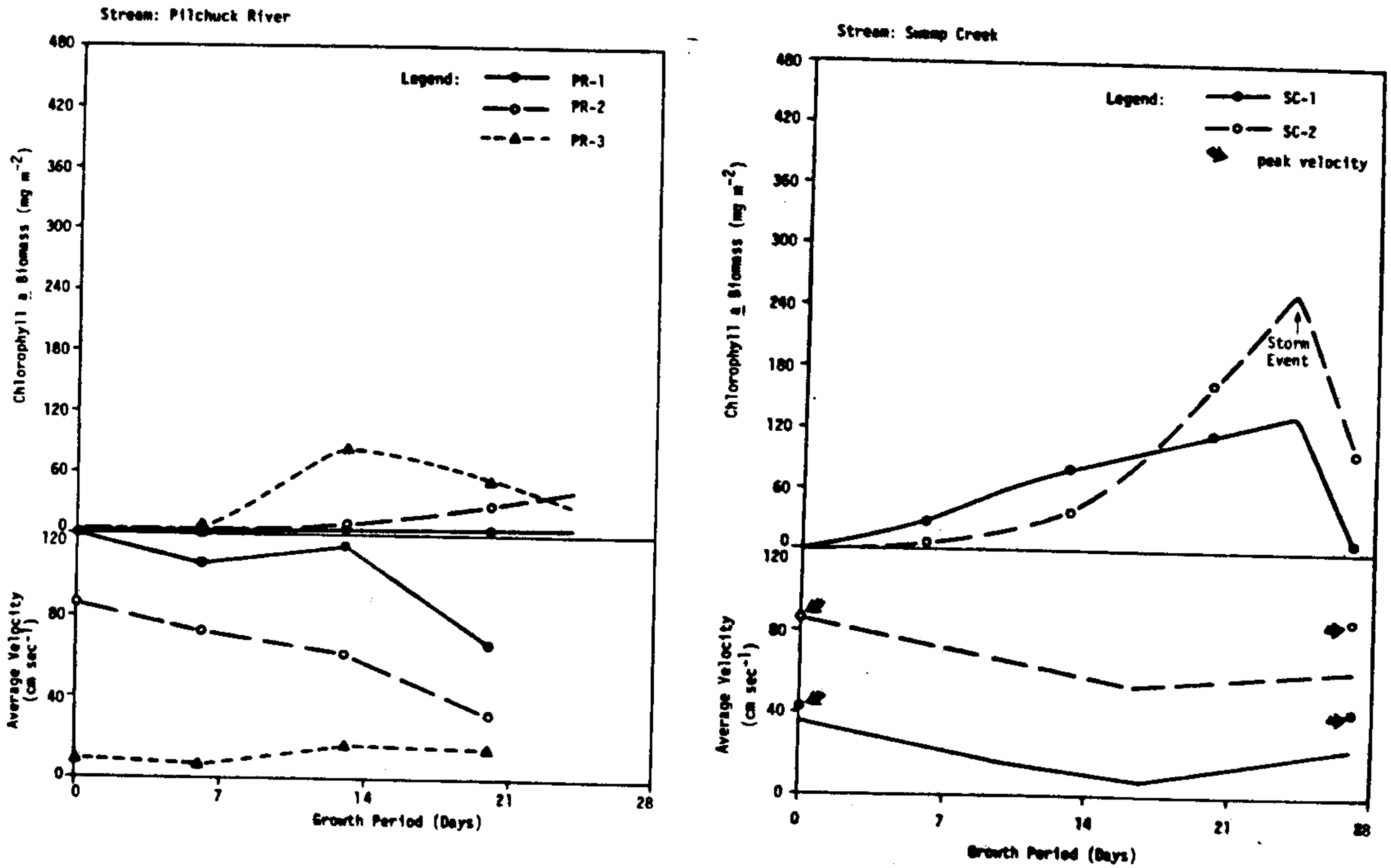

Figure 2: Plots of Chlorophyll a versus Time and Average Velocity versus Time for Four Streams (August 25-September 21, 1977)

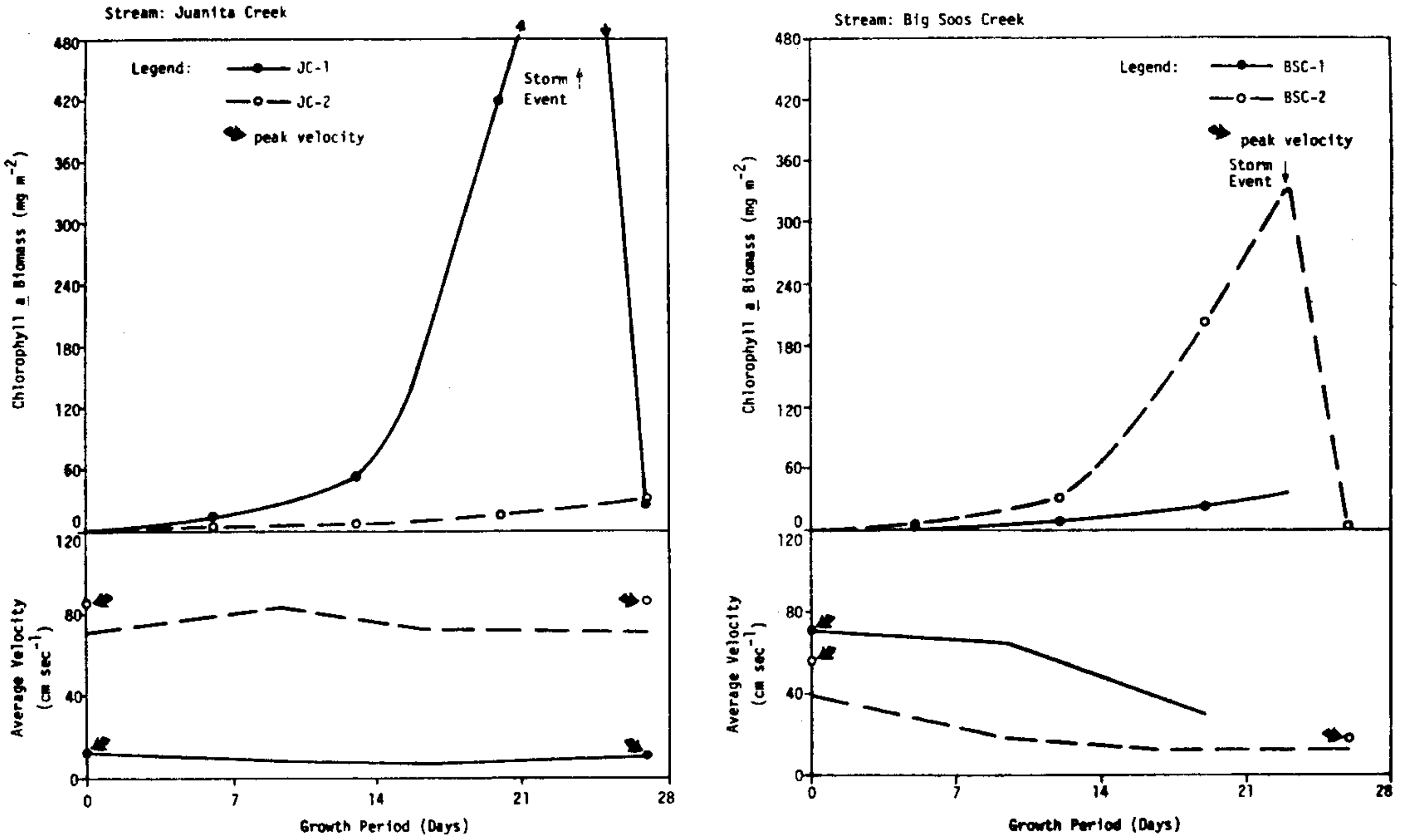

Figure 2 (Continued)

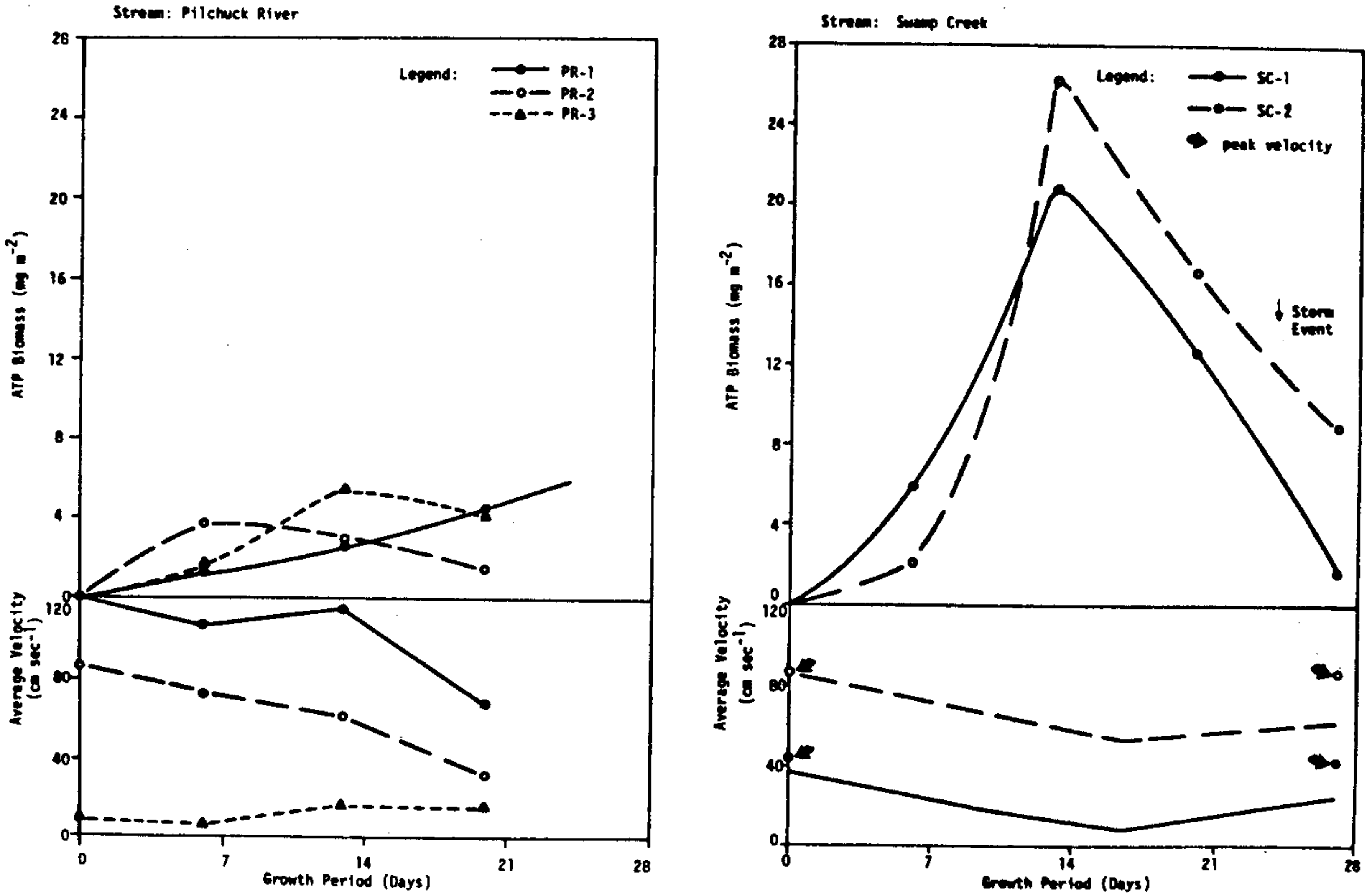

Figure 3: Plots of ATP Versus Time and Average Velocity Versus Time for Two Streams (August 25-September 21, 1977).

trations. This tendency of the faster flowing Swamp Creek site to build higher ATP biomass was also evident in experiments performed in July and August. Initial colonization was favored by lower velocity, however, consistent with chlorophyll a results. Where scour of the ATP biomass occurs as a result of elevated runoff, another parallel with the chlorophyll a results was apparent. Communities adapted to higher pre-storm velocities again suffered less during the high discharge period than those normally existing at low velocities.

The heterotrophic index was defined and employed to permit a direct comparison of the behavior of autotrophic periphyton with the community as a whole. Representative plots of heterotrophic index with time are illustrated in Figure 4. These curves express two important points concerning the effect of velocity on the periphyton. In every case the collectors having higher average velocities had higher indices than the lower velocity station. Graphs of the results of earlier experiments generally confirm this tendency. Thus, velocity assisted the heterotrophs to a greater extent than the algae. Secondly, erosion resulting from the storm of September 18-20 usually increased the heterotrophic index, with the greatest increase in each stream occurring at the site experiencing the greater amount of scour. Quite clearly, the heterotrophs withstand the friction of rapid and turbid storm flows better than do algal forms.

The most elementary step in analyzing a combined data set involved ranking the magnitudes of dependent and independent variables side-by-side, from largest-to-smallest, for comparative purposes. This exercise was performed for five separate experiments spread through the entire period of study and representing periphyton communities of different ages.

The ranking tables prepared as described were investigated to discover associations between specific dependent and independent variables. High and

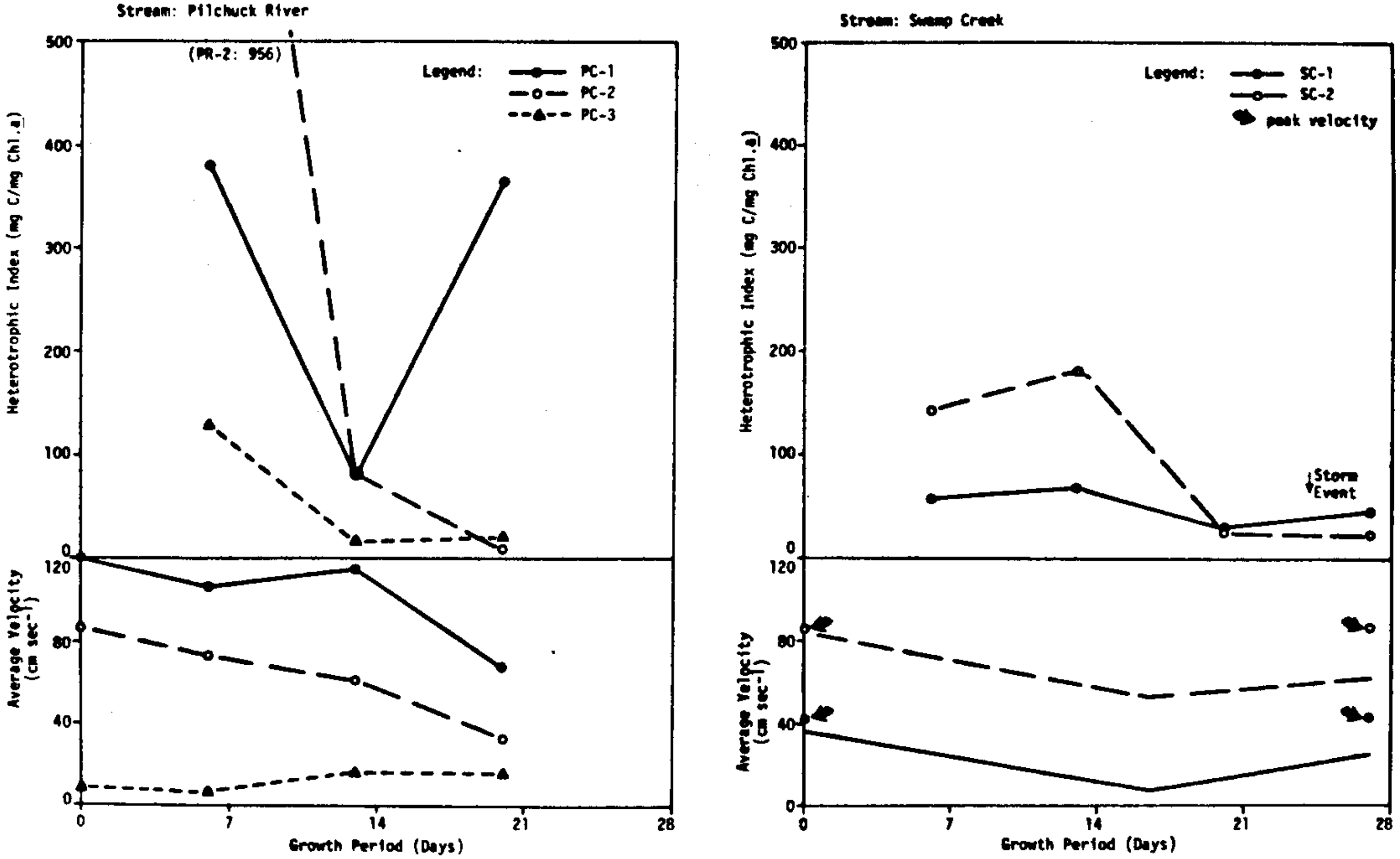

Figure 4: Plots of Heterotrophic Index Versus Time and Average Velocity Versus Time for Four Streams (August 25-September 21, 1977).

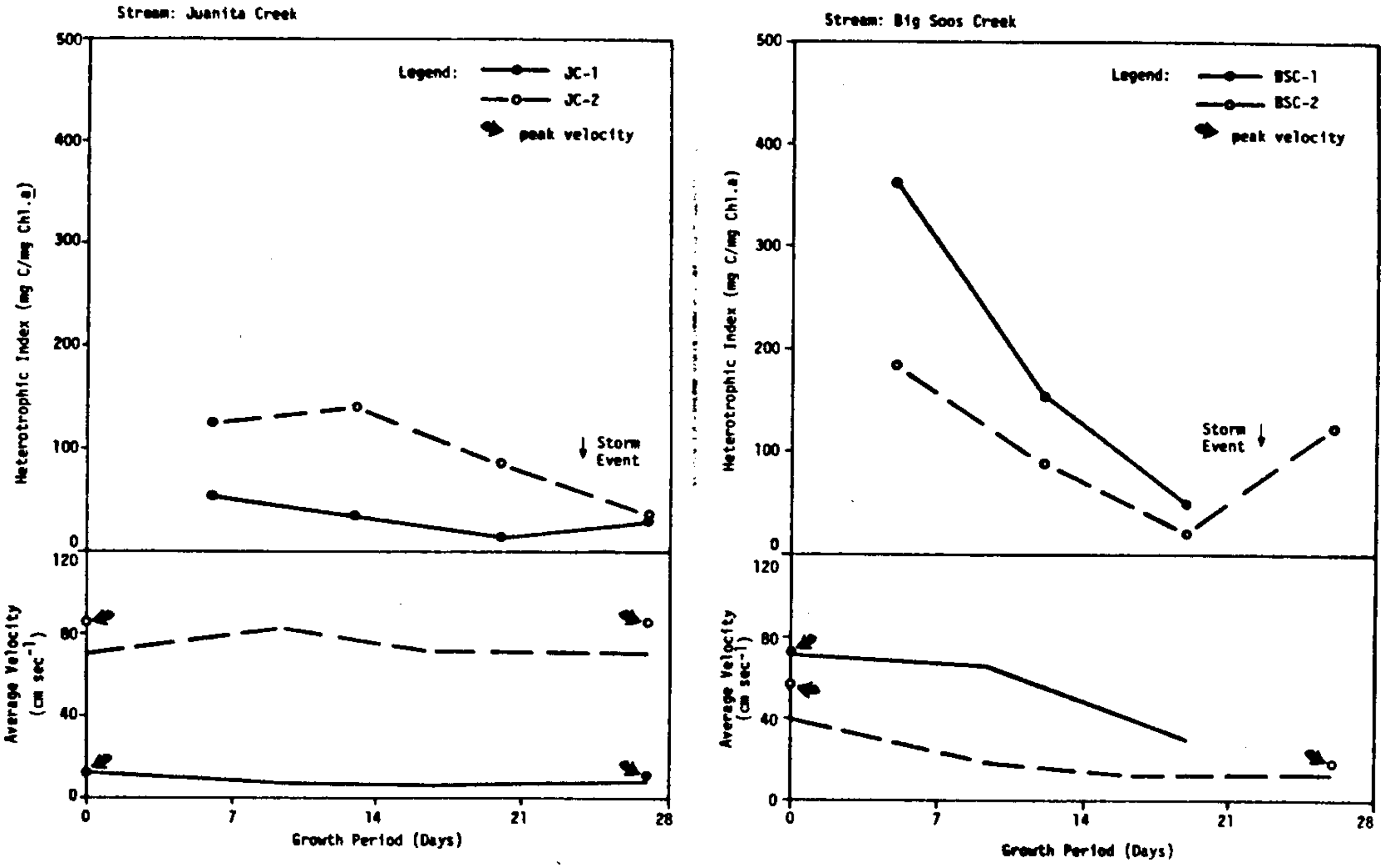

Figure 4 (Continued)

low values for periphyton accrual were thus associated with high, moderate or low measures of environmental variable where possible. At this point it was discovered that very similar associations appeared whether young or mature communities were considered. The numbers of times each association occurred in the five exercises were then totaled. Those associations arising most frequently were finally tabulated and are presented in Table VI.

Table VI: The Most Conclusive Associations Resulting from the Ranking Exercise

Dependent Variable	Independent Variable Association
High chl. a	Moderate average velocity Moderate peak velocity Moderate-high PO_4-P concentration Moderate-high total soluble phosphorus concentration
Low chl. a	High velocity High peak velocity Low PO_4-P concentration Low total soluble phosphorus concentration Low NO_3+NO_2-N concentration
High ATP	Moderate average velocity Moderate peak velocity
Low ATP	None
High heterotrophic index	Moderate-high average velocity Moderate-high peak velocity
Low heterotrophic index	Moderate-low velocity Moderate-low peak velocity

The summary of the ranking exercise reveals several interesting and potentially important points, which may be regarded as preliminary conclusions subject to further verification by other data analyses. Quite clearly, building a large biomass requires moderate average and peak velocities. High-ranking chlorophyll a and ATP almost never occurred at the highest (near 100 cm sec^{-1}) or lowest (near zero) velocities. Conversely, the lowest biomass was usually associated with very high velocities. While these trends appear in both chlorophyll a and ATP data, they are better established in the former case.

The association of high chlorophyll a with moderately high PO_4-P and total soluble phosphorus concentrations and low chlorophyll a with low phosphorus levels adds evidence to the conclusion from algal growth potential experiments that P is the limiting nutrient at most times in the streams studied. Nitrate-plus-nitrite nitrogen is less important, but low levels apparently are involved along with low phosphorus in retarding growth. This analysis did not show ammonia-nitrogen concentration to have a major role in determining periphyton accrual. Likewise, dissolved and particulate organic carbon concentrations were not obviously instrumental in building ATP biomass. The supply rates of nutrients demonstrated much less association with biomass than did concentrations, although moderately high PO_4-P and total soluble phosphorus supply rates did seem to increase chlorophyll a accrual.

A final point expressed by Table VI is that, other factors being equal, velocity increase almost always favored the decomposing organisms over the algae, yielding a high heterotrophic index. In addition, high indices were usually associated with sites less endowed with mineral nutrients. This association is quite natural, since many heterotrophs can subsist on organic materials produced on land and dropped or washed into the stream.

Correlation and Regression Analyses

Following graphing of individual stream results and ranking of variables in a combined data set, selected statistical procedures were applied to the combined data to further develop general trends. These methods possess the advantage over the elementary techniques of expressing quantitatively the association between one dependent and any number of independent variables simultaneously in a computationally efficient manner. On the other hand, the linear form of the correlation and regression analyses employed may not correspond to the character of natural processes. Thus, the methods are best applied in biological work to determine the direction and strength of tendencies, rather than to model behavior for predictive purposes and understanding of processes.

Correlation expresses positive or negative associations among variables by means of the correlation coefficient, R. Simple correlation considers pairs of variables in isolation from others. The statistical significance of correlation coefficients computed here was evaluated by means of a t-test (Rohif and Sokal, 1969).

Results of correlating measures of periphyton community development with environmental variables are presented in Table VII. Among the nutrients, orthophosphate and total soluble phosphorus concentrations demonstrated a highly significant positive association with chlorophyll a. Nitrate-plus nitrite-nitrogen was also positively correlated at a lower significance level, again demonstrating the primary role of phosphorus in limiting algal growth in the streams studied. No significant correlations with nutrient supply rates occurred.

The highly significant negative correlation with current velocity should not be regarded seriously in a functional sense, given that ranking exercises showed moderate, rather than the lowest or highest, velocities to best promote chlorophyll a accrual. The relationship between periphyton development and velocity or any multiple of velocity is thus nonlinear and not amenable to correlation analysis. Time-series plots in Figure 2 also suggested an interaction between velocity and limiting nutrient which introduces a complexity not manageable by simple correlation techniques. The best strategy for further work thus appeared to be multivariate analyses of periphyton growth in limited velocity ranges.

Correlations involving ATP demonstrated the dual control exerted over that quantity by both inorganic and organic nutrients. Orthophosphate-phosphorus concentration and supply rate and dissolved organic carbon concentration and supply rate all correlated positively and significantly with ATP.

The heterotrophic index had strong negative correlations with total soluble phosphorus and nitrate-plus-nitrite nitrogen concentrations and a highly significant positive association with velocity. These tendencies are all consistent with those resulting from ranking and graphing exercises. Dissolved and total organic carbon supply rates showed significant positive associations with the index.

The results of the previously reported ranking, graphing and simple correlation exercises all strongly implied that full representation of periphyton growth must be approached with reference to several independent variables. The creation of a multivariate expression describing how a system behaved may be conveniently accomplished with multiple linear regression techniques. The result of applying the method is a mathematical relationship linking one dependent with several independent variables, with each term in linear form.

With the guidance provided by all the methods of data analysis reported heretofore, the work proceeded to investigate subsets of the data by means of multiple regression techniques. The key observations guiding the design of this phase were the apparent ability of moderate velocities to enhance

Table VII: Correlations Among Periphyton Development Measures and Environmental Variables

	Log Chlorophyll *a*	Log ATP	Heterotrophic Index
Current velocity	-***	-	+***
Orthophosphate-phosphorus concentration	+***	+**	-
Total soluble phosphorus concentration	+***	+	-**
Nitrate-plus-nitrite-nitrogen concentration	+*	-	-***
Ammonia-nitrogen concentration	-	-	-
Orthophosphate-phosphorus supply rate	+	+**	+
Total soluble phosphorus supply rate	+	+	+
Nitrate-plus-nitrite supply rate	+	-	-
Ammonia-nitrogen supply rate	-**	-	+*
Dissolved organic carbon concentration	N.A.	+***	+
Total organic carbon concentration	N.A.	-	-*
Dissolved organic carbon supply rate	N.A.	+***	+**
Total organic carbon supply rate	N.A.	-	+*

Notes: (1) Positive correlation: +. Negative correlation: -.

(2) Number of samples = 94. * indicates statistical significance ($P < 0.05$).
** indicates high statistical significance (($P < 0.01$)
*** indicates very high statistical significance ($P < 0.001$). Otherwise, the reported correlation is not statistically significant.

(3) N.A. -- not applicable

periphyton growth relative to very low and very high currents and the suggestion of an interaction between velocity and limiting nutrient. The full data set was thus subdivided into three velocity ranges: less than 20 cm sec^{-1}; 20-50 cm sec^{-1}; 50-80 cm sec^{-1}. The > 80 cm sec^{-1} range was not included in this analysis because of its representation of a very narrow range of phosphorus concentrations. Because of the considerably higher level of growth noted during the late-summer (August 25 - September 21) compared to the earlier experiments, separate analyses were conducted for the two periods. For each data subset, regression equations were developed for the heterotrophic index and logarithmic transformations of chlorophyll _a_ and ATP.

Several strategies exist for selecting independent variables in multiple regression equations (Draper and Smith, 1966). The most commonly applied techniques are to preselect all of the variables on theoretical grounds or to employ the stepwise procedure, which applies statistical criteria to evaluate the acceptance of variables into the equation (Draper and Smith, 1966; Rao and Miller, 1971). A combination of the two strategies proved to be the most workable procedure in this analysis. Thus, variables of greatest interest were preselected, while selection of those of secondary concern was left to the stepwise option.

The usefulness of a multiple regression equation developed as described depends on its fit to trends hypothesized on sound theoretical grounds and the proportion of variance which it explains. The latter criterion is expressed by the square of the multiple correlation coefficient (R^2) representing the association among variables.

The most satisfactory multiple regression equations developed from the combined data set, those largely fitting expected trends and explaining an acceptable proportion of the variance, involved chlorophyll _a_ (logarithmically-transformed). Table VIII presents this set of equations. Independent variables in these equations were time, current velocity and orthophosphate-phosphorus concentration, all preselected. Nitrate-nitrogen and light intensity were also tested for optional selection on the stepwise basis. The fact that the former variable was rejected points out the primary effect of phosphorus over nitrogen as a determinant of algal growth. Rejection of the second demonstrates the experimental control achieved over light differences among sampling stations.

Investigation of the multiple regression equations shows several trends of interest and importance. Algal (chl a) accrual in both experimental periods responded positively to velocity in the range 20-50 cm sec^{-1}. On the other hand, response was negative in both periods in the 50-80 cm sec^{-1} range. At the lowest velocities the relationship of accrual to velocity was inconclusive, being negative in one case and positive in the other. Thus, the equations predict that velocity increase beyond 50 cm sec^{-1} will decrease the accumulation of periphytic algae, while increases in the range terminating at 50 cm sec^{-1} are likely to aid algal growth.

It may also be noted in Table VIII that both equations developed for the 20-50 cm sec^{-1} velocity range have negative initial coefficients (a_o), although these coefficients are positive in every other case. This occurrence is coupled with sharp increases in the phosphorus coefficients in both cases compared to the respective equations for the < 20 cm sec^{-1} range. These tendencies together express mathematically the prediction that a velocity increase from the low to the medium range would hinder chlorophyll a accumulation where phosphorus concentration is relatively low but advance growth at higher concentrations. This behavior is illustrated more clearly by Figure 5, a generalized plot portraying trends in algal accrual predicted by the equations for both experimental periods.

Table VIII: Multiple Regression Equations for Log Chlorophyll a Within Various Current Velocity Ranges fro Two Experimental Periods

Equation	R^2	n	Experimental Period (2)	Velocity Range (cm sec^{-1})
Log Chl. a $= .638 + .0161T + .1051V + .0226P$	.374	24	1	< 20
$= -1.473 - .0712T + .0725V + .0627P$	.459	13	1	20 - 50
$= 1.736 + .0231T - .0341V + .0556P$	.546	8	1	50 - 80
$= 1.107 + .1918T - .0902V + .0349P$	.779	7	2	< 20
$= -6.871 + .3576T + 0806V + .0997P$	.531	7	2	20 - 50
$= .804 + .1636T - .0270V + .0362P$	.699	15	2	50 - 80

Notes: (1) Symbols: Chl. a = chlorophyll a (mg m^{-2})
T = Time (days)
V = Current velocity (cm sec^{-1})
P = Orthophosphate-phosphorus concentration (μg l^{-1})
n = Number of datapoints

(2) Period 1 -- July 7 - August 25, 1977. Period 2 -- August 25 - September 21, 1977.

A consistent pattern thus appeared in the analysis of results for the individual stream cases and in the statistical treatment of the combined data set. Graphing results for the respective streams generally showed chlorophyll a accumulation to be inversely related to velocity, except when orthophosphate-phosphorus concentration continuously surpassed 45 $\mu g\ l^{-1}$. In these instances, which occurred mostly on Swamp Creek, growth at the station having a velocity of approximately 50 cm sec^{-1} exceeded that at 10-20 cm sec^{-1} after about two weeks of growth. The results for ATP, which exhibited behavior parallel to chlorophyll a in most cases, confirmed these observations. Multiple regression equations derived from the full data set for both the earlier and later experimental periods demonstrated the same trend: chlorophyll a accumulation is predicted to be favored by velocity increase as long as orthophosphate-phosphorus exceeds a minimum value, which depends on the two velocities being compared. Otherwise, accrual is more rapid at relatively low velocity. Graphs of individual stream results and multiple regression predictions also agree where high velocities are concerned: the lowest standing crops are both observed and predicted in that region. It should be noted that these results are in general agreement with the consensus of the literature. Specific confirmation of the interaction between velocity and nutrients noted here does not appear because previous studies did not encompass the wide range of both velocity and limiting nutrient concentration investigated in this work.

In explanation of the tendencies described, it is hypothesized that offsetting mechanisms, both functions of velocity, are involved. Velocity increase apparently assists the uptake of dissolved nutrients by improving turbulent diffusion. In contrast, any increase adds to the shear stress tending to tear material from the attachment surface. The latter effect must predominate unless nutrient abundance is sufficient to establish an

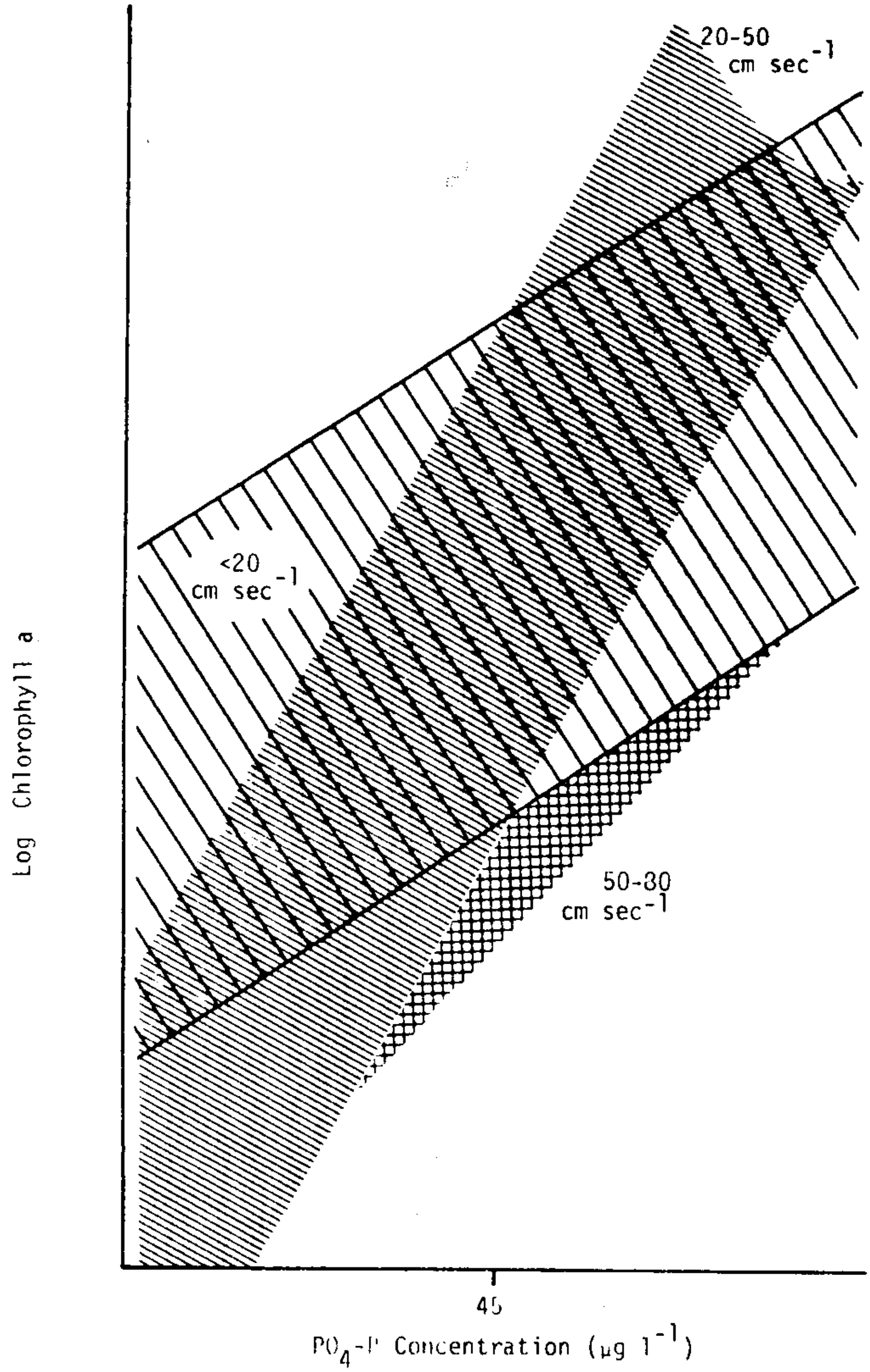

Figure 5: Generalized Plot of Multiple Regression Results Illustrating Predicted Dependence of Chlorophyll a on PO$_4$-P Concentration and Velocity (14 Days' Growth).

efficient delivery system. Velocity increase to a level well above 50 cm sec^{-1} increases friction to the point that improved nutrient delivery is of little practical value.

CONSEQUENCES OF THE RESEARCH FOR HIGHWAY CONSTRUCTION AND OPERATIONS

General Considerations

The practical objective of the research effort was to gain sufficient understanding of biological activity at the base of stream food webs to better analyze impacts on the ecosystem created by flow and runoff modification. It was hypothesized that channel reconstruction activities and highway runoff discharges which substantially alter current velocity have a significant influence on the periphyton. Another effect was expected as a result of elevated concentrations of nutrient materials in storm drainage. Sufficient understanding of the associations among periphyton development, velocity and nutrients resulted from the experiments to make several statements concerning the management of highway construction and operational practices which impinge on streams.

A point which should be made prior to this discussion is that managing a complex, initially balanced natural system must proceed very cautiously and with reference to specific conditions existing in the case at hand. With the periphyton serving as a basic food source of great importance in most small and medium-sized streams, the level and type of growth at the first food web position has consequences throughout the ecosystem. In addition to the effect on food supply, it must also be recognized that modification of environmental conditions may directly impact higher organisms among the macroinvertebrates and fish through habitat disruption. These particular impacts were not considered in the research reported here, which represents only one phase of the problem. Efforts are underway to expand the knowledge of channel reconstruction impacts at all ec levels by studying a section of the Pilchuck River being rechannele highway construction. This study will document pre-construction background physical, chemical and biological conditions for comparison with measurements to be taken during the post-construction recovery period.

Implications of the Research Concerning the Attached Algae

Results of the experiments confirmed the truth of the hypothesis that the current velocity has considerable, even overriding, influence over the development of attached algal communities in streams. Speaking generally, chl a readings at two sites in the same stream, only meters apart and experiencing identical light, temperature and water quality conditions, frequently differed widely. Only average velocity varied in these cases; thus, the role of the current cannot be dismissed in any investigation of periphytic algae.

The influence of velocity is most dramatically seen when storm flows increase it to a highly erosive level. Experiments embracing the two storms during the program documented losses of a substantial majority of the prestorm chl a in such situations. Monitoring before and after the storm of August 23-26, 1977, revealed greatly increased levels of algal biomass in the period after the storm compared to that before where normal and storm flows differed greatly. In addition to apparently more favorable light in the later period, likely causes of this pattern were the existence of much bare area suitable for colonization and little competition for nutrients. Where velocity variation is considerable, then, periphytic biomass alternates between very low and relatively high levels. Accordingly, food supply for herbivores fluctuates over a wide range. It is reasonable to expect that frequent storms accompanied by heavy runoff would prevent the growth of a periphyton crop adequate to support a stable herbivore community, probably to the detriment of its predators.

Weekly sampling during the late summer and the storm of September 18-20, which concluded the experiment, provided an opportunity to study behavior during a highly erosive flow more closely. It was noted that the greatest percentage loss of chl a occurred where ordinary velocities were low. Apparently, species adapted to rapid flow suffered relatively less than those accustomed to a slow current. This observation indicates that the destruction of the attached community is relatively more severe the greater the range between ordinary and elevated velocities.

These results offer some guidance to fulfill a planning or management objective aimed at protecting the integrity of the productive base of the food web where highway construction or operations impinge on a stream. Any reconstructed channel should, accordingly, avoid an increase in average velocity that would exceed 50 cm sec^{-1}. Where the concern is drainage of storm runoff to a stream, frequent velocity peaks well above 50 cm sec^{-1} should be prevented by avoiding direct drainage of volumes of stormwater which would be a significant factor in creating elevated peaks in the stream.

Another major result of the research program is that a velocity increase up to approximately 50 cm sec^{-1} will increase algal accrual if the limiting nutrient concentration surpasses a minimum value. Such a velocity increase created by channel reconstruction for example, could conceivably benefit the ecosystem as a whole if the former production level was low. For example, a velocity increase from 10 to 35 cm sec^{-1} at 40 μg PO_4-P 1^{-1} could increase diatom production and biomass to the benefit of higher organisms. Another possibility, however, is that a substantial increase in algal production could involve primarily nuisance species (Fjerdingstad, 1964). To decrease the chance of this occurrence, results of the research would recommend the avoidance of a substantial velocity increase within the 0 - 50 cm sec^{-1} range where limiting nutrient concentration is relatively high (> 40-50 g l^{-1} for orthophosphate-phosphorus limitation). Likewise, a possible nuisance may be avoided by prohibiting a substantial nutrient concentration increase through storm drainage where average velocity already approaches 50 cm sec^{-1}. Small increases of velocity at low nutrient concentration or of nutrients at low velocity would pose little threat of a nuisance condition, however.

One other possible construction modification that might be injurious to the periphyton and its consumers is rechanneling a very swiftly flowing stream rich in nutrients into a broader and perhaps deeper water course. That change would act to reduce velocity and the loss rate of biomass that is rather rapidly produced because of the richness. Providing a greater productive base and decreased loss rate in this manner would create the potential for a periphyton explosion and succession to nuisance species. Thus, any alteration to the natural system carries a risk demanding careful consideration of the background condition and the proposed changes.

Implications of the Research Concerning the Attached Heterotrophs

Sharing stream bed habitats with the periphytic algae are attached consumers and decomposers such as protozoa, bacteria and fungi. These organisms exist on the algae or particulate and dissolved organics carried by the stream. Their presence was registered in this research by the heterotrophic index, and their food supply was represented by particulate and dissolved organic carbon measurements. Primarily because the range of dissolved organic carbon was restricted to low concentrations, large amount of heterotrophic growth were not evident and the investigation did not yield results as clear-cut as those for attached algae. Nevertheless, the data analysis did produce several insights regarding this component of the periphyton.

The major concerns relative to the heterotrophs are that they not achieve a dominant position over the primary producing algae nor be composed of nuisance type bacteria. Graphs of heterotrophic index versus time for the various streams partially clarified the factors which might contribute to these problems. The higher index (more heterotrophs) was generally observed at the site with faster current. Further, the occurrence of periphyton losses due to scour was nearly always accompanied by an increase in the index, even where it had been decreasing over the previous two weeks. As one explanation for these very consistent observations, the animal members of the periphyton may have a greater ability to cling to the substrate than the algae and thus exist in relatively greater abundance in fast currents. If this is true, they would also better survive erosive stresses. A second conceivable reason is that sudden velocity increases detach much of the algae, making more food available to the decomposers residing downstream. A related effect may be the entrainment and transport of organic materials formerly sequestered in the stream bed.

As a consequence of the observed associations between velocity and heterotrophic development, it can be recommended that highway construction and drainage plans avoid substantial average and peak velocity increases particularly where the load of dissolved organic compounds carried by the stream is relatively high. Also to reduce the risk of heterotrophic nuisances, storm runoff entering streams should not significantly increase the level of dissolved organic carbon. The measurement of only low values of this quantity in this research prevents the establishment of critical dissolved organic carbon concentrations at this time.

A Deterministic Model of Periphyton Development

Results of the research program demonstrated in several ways that the accumulation of attached algae in streams is enhanced by improved turbulent diffusion of nutrients but retarded by the frictional shear force of the current velocity. A mathematical model based on these opposing mechanisms would be useful in designing and evaluating highway construction and drainage projects affecting the flow or limiting nutrient concentration. Analysis of the data concluded with the proposal of a first approximation to such a model. Sufficient data did not exist to firmly establish and evaluate the model, and several special studies are required to further develop or confirm the applicability of its various parameters. This discussion will be confined to the general form of the model. Horner (1978) discusses the proposal in all the detail available at this time.

In its present state the model is confined to the development of periphytic algae limited by orthophosphate-phosphorus. It hypothesizes that the net growth of chlorophyll _a_ is a function of the growth rate potential in the absence of any frictional scour less the rate of erosion. The growth rate potential is considered to be composed of facters representing limiting nutrient uptake rate, the existing community density, light, molecular diffusion of the dissolved nutrient in a quiescent case and the growth-assisting effect of the current based on mass transfer by turbulent diffusion. The rate of erosion of attached biomass is taken to be a function of the current velocity. The basic form of the proposed model is thus:

net growth rate of chlorophyll _a_ = Growth rate potential − rate of erosion

$$\frac{db}{dt} = f_1(\mu, L, k_f, k_{fo}, B_{max}, B) - f_z(V)$$

where : B = algal biomass, represented by chlorophyll a (mg m^{-2})

t = time (days)

f_1, f_2 = mathematical functions

μ = uptake rate of limiting nutrient, a function of concentration and temperature (day $^{-1}$)

L = light factor (dimensionless)

k_f = mass transfer coefficient with turbulent diffusion, a function of velocity (cm sec^{-1})

k_{fo} = mass transfer coefficient in a quiescent or laminar flow system as a function of temperature (cm sec^{-1})

B_{max} = maximum sustainable chlorophyll a

V = current velocity (cm sec^{-1})

This formulation is intended to apply only to the lag and exponential phases of algal growth, prior to the occurrence of widespread cell death, and a constant-velocity condition. Hence, it omits the effects of extraordinary erosion due to the elevated velocities and sediment transport accompanying storm runoff.

The function f_1 was conceived as a multiple of the various factors affecting the delivery and uptake of the limiting nutrient. This approach follows the general pattern set by Watt (1968) for the general case of population growth, Chen (1970) for phytoplankton and McIntire (1973,1975) for periphyton. Forms for the parameters μ, L, k_f and k_{fo} were tentatively selected from the literature. The second function was modeled as V^{Θ}, where Θ is an exponent established with the use of experimental data. Proportionality constants associated with each function and B_{max} were also evaluated on the basis of data. The growth rate differential equation is linear and may be integrated with an initial condition $B = 0$ at $t = 0$.

Although the model is not yet sufficiently developed and verified for use in water quality management, it has promise for future application in that area and is a notable consequence of the research project. It is capable of representing the rather complex nonlinear association between algal growth and the current and limiting nutrient concentration discovered in the research. At the same time the proposed form permits an exact analytical differential equation solution and consists of a manageable number of parameters which can be individually investigated in future work. Based on the mechanisms demonstrated or hypothesized to operate in the natural system, the general forms of these parameters have been applied successfully in past modeling efforts. With an existing field-derived data base, model development can proceed with specialized laboratory experiments designed to strengthen and further verify it.

BIBLIOGRAPHY

Amberg, H.R., and J.F. Cormack, 1960. Factors affecting slime growth in the lower Columbia River and evaluation of some possible control measures. Pulp and Paper Magazine of Canada, Technical Section, February, 1960, pp. 70-80.

American Public Health Association. 1975. Standard Methods for the Analysis of Water and Wastewater, 14th edition. Washington, American Public Health Association, Inc., 1193 pp.

Ball, R.C., N.R. Kevern and K.J. Linton. 1969. The Red Cedar River Report. II. Bioecology. Pulb. Mus. Michigan State University, Biology Series, 4: 107-157.

Barnes, H. 1952. The use of transformations in marine biological statistics. J. Cons. perm. int. Explor. Mer., 18: 61-71.

Brehmer, M.L., R.C. Ball and N.R. Kevern. 1969. Nutrients and primary production in a warm-water stream. Technical Report No. 4, Red Cedar River Series, Institute of Water Research, Michigan State University, 87 pp.

Brenner, R.N. Municipality of Metropolitan Seattle, Seattle. Personal communication.

Brown, S.D. 1973. Site variation in littoral periphyton populations: Correlation and regression with environmental factors. Int. Revue ges. Hydrobiol., 58: 437-461.

__________. 1946. Studies in the ecology of rivers. VI. The algal growth in certain highly calcareous streams. J. Ecol., 33: 268-283.

Caperon, J. 1968. Population growth response of Isochrysis galbana to nitrate variation at limiting concentrations. Ecol., 49: 866-972.

Cassie, R.M. 1963. Macrodistribution of plankton. Oceanogr. Mar. Biol. Ann. Rev., 1: 223-252.

Castenholz, R.W. 1961. An evaluation of a submerged glass method of estimating production of attached algae. Verh. Internal. Verein. Limnol., 14: 155-159.

Chen, C.W. 1970. Concepts and utilities of ecological models. J.San. Eng. Div. ASCE, 96: 1085-1097.

Cummins, K.W., W.P. Coffman, P.A. Roff. 1966. Trophic relationships in a small woodland stream. Verh. Internat. Verein. Limnol., 16: 627-638.

__________, M.J. Klug, R.G. Wetzel, R.C. Petersen, K.F. Suberkropp, B.A. Manney, J.C. Wuycheck and F.O. Howard. 1972. Organic enrichment with leaf leachate in experimental lotic systems. Bioscience, 22: 719-722.

Curtis, E.J., and D.W. Harrington. 1971. The occurrence of sewage fungus in rivers of the United Kingdom. Water Res., 5: 281-290.

Cushing, C.E. 1967. Periphyton productivity and radionuclide accumulation in the Columbia River, Washington, U.S.A. Hydrobiol., 29: 125-139.

Dickman, M. 1973. Changes in periphytic algae following bicarbonate additions to a small stream. J. Fish. Res. Board of Canada, 30: 1882-1884.

Draper, N.R., and H. Smith. 1966. Applied Regression Analysis. New York, John Wiley and Sons, Inc., 407 pp.

Droop, M.R. 1973. Some thoughts on nutrient limitation in algae. J. Phycol., 9: 264-272.

Dunn, R.W. 1976. Seasonal variations in periphyton, chlorophyll a algal biomass and primary production in a desert stream. M.S. Thesis, Department of Biology, Idaho State University, Pocatello, 312 pp.

Ehrlich, G.G., and K.V. Slack. 1969. Uptake and assimilation of nitrogen in micro-ecological systems. In: Spec. Tech. Publs. Am. Soc. Test. Mater., 448, Microorganic Matter in Water. Philadelphia, A.S.T.M. pp. 11-23.

Eichenberger, E. 1975. On the quantitative assessment of the effects of chemical factors on running water ecosystems. Schweiz. Z. Hydrol., 37: 27-34.

Elwood, J.W., and D.J. Nelson. 1972. Periphyton production and grazing rates in a stream measured with a ^{32}P material balance method. Oikos, 22: 295-303.

Fitzgerald, G.P. 1969. Field and laboratory evaluations of bioassays for nitrogen and phosphorus with algae and aquatic weeds. Limnol. Oceanogr., 14: 206-212.

Fjerdingstad, E. 1964. Pollution of streams estimated by benthal phyto-microorganisms. I. A saprobic system base on communities of organisms and ecological factors. Int. Rev. Ges. Hydrobiol., 49: 63-131.

Flemer, D.A. 1970. Primary productivity of the North Branch of the Raritan River, New Jersey. Hydrobiol., 35: 273-296.

Goldman, C.R., M. Gerletti, P. Javornicky, U. Melchiovri-Santolini and E. De Amezaga. 1968. Primary productivity, bacteria, phytoplankton and zooplankton in Lake Maggiore: Correlations and relationships with ecological factors. Mem. Ist. Ital. Idrobiol., 23: 49-127.

Holm-Hansen, O. 1970. ATP levels in algal cells as influenced by environmental conditions. Plant Cell Physiol., 11: 689-700.

__________. 1973. Determination of total microbial biomass by measuring adenosine triphosphate. In H.L. Stevenson and R.R. Colwell, Estuarine Microbial Ecology. Columbia, University of South Carolina Press, pp. 73-89.

__________, and C.R. Booth. 1966. The measurement of adenosine triphosphate in the ocean and its ecological significance. Limnol. Oceanogr., 11: 510-519.

Horner, R.R. 1978. Stream periphyton development in relation to current velocity and nutrients. Ph.D. Dissertation, Department of Civil Engineering, University of Washington, Seattle, 273 pp.

__________, T.J. Waddle and S.J. Burges. 1977. Review of the literature on water quality impacts of highway operations and maintenance. A report prepared for the Washington State Highway Department by the Department of Civil Engineering, University of Washington, Seattle, 53 pp.

Hynes, H.B.N. 1963. Imported organic matter and secondary productivity in streams. Proc. XVI Internat. Congr. Zool., 4: 324-329.

Kevern, N.R., J.L. Wilhm and G.M. Van Dyne. 1966. Use of artificial substrata to estimate the productivity of periphyton. Limnol. Oceanogr. 11: 499-502.

Kolkwitz, R., and M. Marsson. 1908. Okologie der pflanzlichen Saprobien. Ber. Deutsch. Bot. Ges., 26a: 505-519.

Leopold, L.B., and W.B. Langbein. 1966. River Meanders. Sci. Amer., 214: 60-70.

__________, and M.G. Wolman. 1960. River Meanders. Bull. Geol. Soc. Am., 71: 769-794.

__________, __________, and J.P. Miller. 1964. Fluvial Processes in Geomorphology. San Francisco, W.H. Freeman, 522 pp.

Lin, C.K. 1971. Availability of phosphorus for Cladophora growth in Lake Michigan. Proc. 14th Great Lakes Res. Conf., pp. 39-43.

Lyford, J.H., Jr., and S.V. Gregory. 1975. The dynamics and structure of periphyton communities in three Cascade Mountain streams. Verh. Internat. Verein. Limnol., 19: 1610-1616.

McIntire, C.D. 1966. Some effects of current velocity on periphyton communities in laboratory streams. Hydrobiol., 27: 559-570.

__________. 1968. Structural characteristics of benthic algal communities in laboratory streams. Ecol., 49: 520-537.

__________. 1973. Periphyton dynamics in laboratory streams: a simulation model and its implications. Ecol. Monogr., 43: 399-419.

__________. 1975. Periphyton assemblages in laboratory streams. In B.A. Whitton, River Ecology. Berkeley, University of California Press, pp. 403-430.

Murphy, J., and J.P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta, 27: 31-36.

National Eutrophication Research Program, U.S. Environmental Protection Agency. 1971. Algal Assay procedure bottle test. Washington, U.S. Environmental Protection Agency.

Neal, E.C., B.C. Patten and C.E. DePoe. 1967. Periphyton growth on artificial substrates in a radioactively contaminated lake. Ecol., 48: 918-924.

Neil, J.H., and G.E. Owen. 1964. Distribution, environmental requirements and significance of Cladophora in the Great Lakes. Great Lakes Research Division, University of Chicago Publ., 11: 113-121.

Odum., H.T., and C.M. Hoskin. 1958. Comparative studies on the metabolism of marine waters. Publs. Inst. Mar. Sci. Univ. Texas, 5: 15-46.

Ormerod, J.G., B. Grynne and K.S. Ormerod. 1966. Chemical and physical factors involved in heterotrophic growth response to organic pollution. Verh. Internat. Verein. Limnol., 16: 906-910.

Patrick, R. 1973. Effects of channelization on the aquatic life of streams. Highway Research Board Special Report 138.

Phaup, J.D., and J. Gannon. 1967. Ecology of Sphaerotilus in an experimental outdoor channel. Water Res., 1: 523-541.

Pitcairn, C.E.R., and H.A. Hawkes. 1973. The role of phosphorus in the growth of Cladophora. Water Res., 7: 159-171.

Rao, P. 1977. STEPWISE and REGRESS, multiple regression programs. Center for Quantitative Studies, University of Washington, Seattle, 11 pp.

__________, and R.L. Miller. 1971. Applied Econometrics. Belmont, California, Wadsworth Publishing Company, 235 pp.

Reisen, W.K., and D.J. Spencer. 1970. Succession and current demand relationships of diatoms on artificial substrates in Prater's Creek, South Carolina. J. Phycol., 6: 117-121.

Rodgers, J.H., Jr., and R.S. Harvey. 1976. The effect of current on periphytic productivity as determined using carbon-14. Water Resour. Bull., 12: 1109-1118.

Rohlf, F.J., and R.R. Sokal. 1969. Statistical Tables. San Francisco, W.H. Freeman, 253 pp.

Slack, K.V., R.C. Averett, P.E. Greeson and R.G. Lipscomb. 1973. Methods for collection and analysis of aquatic biological and microbiological samples. Washington, U.S. Gov. Printing Office, 165 pp.

Sladeckova, A. 1964. Factors affecting the occurrence and stratification of sessile protozoans in artificial reservoirs. Tech. Water, 8: 483-490.

Southworth, G.R., and F.F. Hooper. 1974. Prediction of Environmental quality in de-enriched stream systems. Report to Office of Water Resour. Res. by Inst. of Water Res., Michigan State University, East Lansing, (NTIS No. PB-235 924), 67pp.

Sperling, J.A., and G.M. Hale. 1973. Patterns of radiocarbon uptake by a thermophilic blue-green alga under varying conditions of incubation. Limnol. Oceanogr., 18: 658-662.

Strickland, J.D.H., and T.R. Parsons. 1972. A Practical Handbook on Seawater Analysis. Bull. 167. Fish. Res. Bd. Canada.

Sverdrup, H.U., M.W. Johnson and R.H. Fleming. 1942. The Oceans, Their Physics, Chemistry and General Biology. Englewood Cliffs, New Jersey, Prentice-Hall, Inc., 1087 pp.

U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, Environmental Data Service. 1977. Climatological data. Annual summary, 1977. State of Washington.

U.S. Geological Survey. 1977. Discharge, in cubic feet per second, water year October 1976 to September 1977. (for Swamp Creek, Juanita Creek, Issaquah Creek and Big Soos Creek). Tacoma, Washington, Office, U.S. Geological Survey.

Warren, C.E., J.H. Wales, G.E. Davis and P. Doudoroff. 1964. Trout production in an experimental stream enriched with sucrose. J. Wildl. Mgt., 28: 617-660.

Washington State Highway Department. 1977. Draft Environmental Impact Statement, SR 2, Fobes Hill to North Monroe Interchange.

Watt, K.E.F. 1968. Ecology and Resource Management. New York, McGraw-Hill Book Company, 450 pp.

Weber, C.I. 1973. Recent developments in the measurement of the response of plankton and periphyton to changes in their environment. In G.E. Glass, Bioassay Techniques and Environmental Chemistry. Ann Arbor, Michigan, Ann Arbor Science Publishers, Inc., pp. 119-138.

Welch, E.B. 1976. Ecological Effects of Waste Water. ASUW Lecture Notes, University of Washington, Seattle, 226 pp.

Wetzel, R.G. 1975. Limnology. Philadelphia, W.B. Saunders Company, 743 pp.

Whitford, L.A. 1960. The current effect and growth of freshwater algae. Trans. Am. Microscop. Soc., 79: 209-302.

______________, and G.L. Schumacher. 1964. Effect of a current on respiration and mineral uptake in Spirogyra and Oedogonium. Ecol., 45: 168-170.

Wright, J.C., and I.K. Mills. 1967. Productivity studies on the Madison River, Yellowstone National Park. Limnol. Oceanogr., 12: 568-577.

Wuhrmann, K. 1972. Stream purification. In R. Mitchell, Water Pollution Microbiology. New York, Wiley-Interscience, pp. 119-151.

______________ and E. Eichenberger. 1975. Experiments on the effects of inorganic enrichment of rivers on periphyton primary production. Verh. Internat. Verein. Limnol., **19**: 2028-2034.

______________, ____________, H.A. Leidner and D. Wuest. 1975. Uber den Einfluss der Stromungsgeschwindigkeit auf die Selh-streinigung in Fliessgewassern. Schweiz. Z. Hydrol., **37**: 253-272.