8013523

**Gislason, Jeffrey Charles**

EFFECTS OF FLOW FLUCTUATION DUE TO HYDROELECTRIC PEAKING ON BENTHIC INSECTS AND PERIPHYTON OF THE SKAGIT RIVER, WASHINGTON

*University of Washington* PH.D. 1980

University
Microfilms
International 300 N. Zeeb Road, Ann Arbor, MI 48106

PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark __√__.

1. Glossy photographs or pages _____
2. Colored illustrations, paper or print _____
3. Photographs with dark background _____
4. Illustrations are poor copy _____
5. Pages with black marks, not original copy _____
6. Print shows through as there is text on both sides of page _____
7. Indistinct, broken or small print on several pages __√__
8. Print exceeds margin requirements _____
9. Tightly bound copy with print lost in spine _____
10. Computer printout pages with indistinct print _____
11. Page(s) __48__ lacking when material received, and not available from school or author.
12. Page(s) _____ seem to be missing in numbering only as text follows.
13. Two pages numbered _____. Text follows.
14. Curling and wrinkled pages _____
15. Other _____

Effects of Flow Fluctuation Due to Hydroelectric Peaking

on Benthic Insects and Periphyton of the Skagit River, Washington

by

Jeffrey Charles Gislason

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1980

Approved by Quentin J. Stober
(Chairperson of the Supervisory Committee)

Program Authorized
to Offer Degree College of Fisheries

Date 12/20/79

Doctoral Dissertation

In presenting this dissertation in partial fulfillment of the requirements for the Doctoral degree at the University of Washington, I agree that the library shall make its copies freely available for inspection. I further agree that extensive copying of this dissertation is allowable only for scholarly purposes. Requests for copying or reproduction of this dissertation may be referred to University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, to whom the author has granted "the right to reproduce and sell (a) copies of the manuscript in microform and/or (b) printed copies of the manuscript made from microform".

Signature Jeffrey C. Gisleason

Date 12/20/79

TABLE OF CONTENTS


Page

LIST OF FIGURES . . . . . . . . . . . . . . . . . . . . . . . . . iv

LIST OF TABLES . . . . . . . . . . . . . . . . . . . . . . . . . viii

ACKNOWLEDGMENTS . . . . . . . . . . . . . . . . . . . . . . . . x

INTRODUCTION . . . . . . . . . . . . . . . . . . . . . . . . . . 1

STUDY AREA . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

MATERIALS AND METHODS . . . . . . . . . . . . . . . . . . . . . 16

PHYSICAL PARAMETERS . . . . . . . . . . . . . . . . . . . . . 16
PERIPHYTON . . . . . . . . . . . . . . . . . . . . . . . . . . 19
BENTHIC INSECTS . . . . . . . . . . . . . . . . . . . . . . . 21
EXPERIMENTAL STUDIES . . . . . . . . . . . . . . . . . . . . 26

RESULTS . . . . . . . . . . . . . . . . . . . . . . . . . . . . 31

PHYSICAL AND CHEMICAL PARAMETERS . . . . . . . . . . . . . . 31

Streamflow Pattern . . . . . . . . . . . . . . . . . . . . 31
Exposure Level . . . . . . . . . . . . . . . . . . . . . . 43
Water Quality . . . . . . . . . . . . . . . . . . . . . . 53
Temperature . . . . . . . . . . . . . . . . . . . . . . . 60
Substrate Analysis . . . . . . . . . . . . . . . . . . . . 62
Current Velocity . . . . . . . . . . . . . . . . . . . . . 64

PERIPHYTON . . . . . . . . . . . . . . . . . . . . . . . . . . 64

Effects of Exposure . . . . . . . . . . . . . . . . . . . . 64
Comparison of the Three Rivers . . . . . . . . . . . . . . 70

BENTHIC INSECTS . . . . . . . . . . . . . . . . . . . . . . . 78

Microdistribution . . . . . . . . . . . . . . . . . . . . . 79
Effects of Exposure . . . . . . . . . . . . . . . . . . . . 83
Experimental Studies . . . . . . . . . . . . . . . . . . . 92

Flow Fluctuation Experiments . . . . . . . . . . . . . . 92
Stranding Avoidance . . . . . . . . . . . . . . . . . . . 101
Desiccation Survival . . . . . . . . . . . . . . . . . . 103

Effects of Peaking Fluctuation in the Unexposed Zone. . 105

Page

Standing Crop . . . . . . . . . . . . . . . . . . . . 105
Taxomonic Composition . . . . . . . . . . . . . . . 119
Diversity . . . . . . . . . . . . . . . . . . . . . 124
Trophic Structure . . . . . . . . . . . . . . . . . 127

DISCUSSION . . . . . . . . . . . . . . . . . . . . . . . . 132

PHYSICAL PARAMETERS . . . . . . . . . . . . . . . . . 132
PERIPHYTON . . . . . . . . . . . . . . . . . . . . . . 133
BENTHIC INSECTS . . . . . . . . . . . . . . . . . . . 137
IMPLICATIONS FOR FISH FEEDING . . . . . . . . . . . . 147
RECOMMENDATIONS . . . . . . . . . . . . . . . . . . . 149

REFERENCES CITED . . . . . . . . . . . . . . . . . . . . . 150

APPENDIX I: Benthic insect taxa collected in the Skagit, Sauk and Cascade rivers . . . . . . . . . . . . . 158

APPENDIX II: Mean chlorophyll a ($mg/m^2$) at unexposed or minimally exposed sample locations at sampling stations with 96 percent confidence interval . . . 161

APPENDIX III: Mean number of insects per $m^2$ in the unexposed zone at each sampling station with the 95 percent confidence interval. Since the confidence interval was calculated with log transformed data, it is asymmetrical around the mean . . . . . . . . . . . . . . . . . . . . 162

APPENDIX IV: Mean weight of preserved insects ($g/m^2$) in the unexposed zone at each sampling station with the 95 percent confidence interval. Since the confidence interval was calculated with log transformed data, it is asymmetrical around the mean . . . . . . . . . . . . . . . . . . . . . 163

## LIST OF FIGURES


| Number | | Page |
|---|---|---|
| 1. | Skagit Basin study area with periphyton and benthic insect sampling stations . . . . . . . . . . . . . . . . . . | 10 |
| 2. | Diagram of a single artificial stream channel and a cross-sectional view showing initial and final water levels during the stranding experiments . . . . . . . . . . . . . | 27 |
| 3. | Hydrographs of mean daily discharges at gaging sites on the Sauk, Cascade and Skagit rivers for 1976 . . . . . . . . . | 32 |
| 4. | Hydrographs of mean daily discharges at gaging sites on the Sauk, Cascade and Skagit rivers for 1977 . . . . . . . . . | 33 |
| 5. | Long-term natural and regulated streamflow patterns for the Skagit River at Newhalem (1954-1975) . . . . . . . . . . . | 34 |
| 6. | Natural and regulated streamflow for the Skagit River at Newhalem for 1976 and 1977 . . . . . . . . . . . . . . . . | 35 |
| 7. | Daily range of flow fluctuations for the Skagit River at Newhalem (USGS) for 1976 . . . . . . . . . . . . . . . . . . | 37 |
| 8. | Daily range of flow fluctuations for the Skagit River at Newhalem (USGS) for 1977 . . . . . . . . . . . . . . . . . . | 38 |
| 9. | Daily range of flow fluctuations for the Skagit River at Marblemount (USGS) for June through December 1976 . . . . . | 39 |
| 10. | Daily range of flow fluctuations for the Skagit River at Marblemount (USGS) for 1977 . . . . . . . . . . . . . . . . | 40 |
| 11. | Daily range of flow fluctuations for the Sauk River (USGS) for 1976 . . . . . . . . . . . . . . . . . . . . . . . . | 44 |
| 12. | Daily range of flow fluctuations for the Sauk River (USGS) for 1977 . . . . . . . . . . . . . . . . . . . . . . . . | 45 |
| 13. | Daily range of flow fluctuations for the Cascade River (USGS) for August through December 1976 . . . . . . . . . . | 46 |
| 14. | Daily range of flow fluctuations for the Cascade River (USGS) for 1977 . . . . . . . . . . . . . . . . . . . . . . | 47 |
| 15. | Location of benthic insects and periphyton sampling sites along the upper and lower Skagit River sampling transects . | 54 |

| Number | | Page |
|---|---|---|


16. Location of benthic insect and periphyton sampling sites along the upper and lower Sauk River sampling transects . . 55

17. Location of benthic insect and periphyton sampling sites along the Cascade River transects . . . . . . . . . . . . . 56

18. Semi-monthly water temperature (°F and °C) for the Skagit (above Alma Creek), Sauk and Cascade rivers during 1976 and 1977 . . . . . . . . . . . . . . . . . . . . . . . 61

19. Stream profiles at the lower Skagit sampling transect showing maximum and minimum water levels during the six-week colonization periods for periphyton samples collected in October and November 1976 . . . . . . . . . . . . . . . . 66

20. Stream profiles at the lower Skagit sampling transect showing maximum and minimum water levels during the six-week colonization periods for periphyton samples collected in January and February 1977 . . . . . . . . . . . . . . . . 67

21. Chlorophyll _a_ content and exposure level of periphyton samples collected at the lower Skagit, lower Sauk and Cascade stations from October 1976 through February 1977. . 69

22. Periphyton standing crop as indicated by chlorophyll _a_ content of samples collected at the lower Skagit and lower Sauk stations . . . . . . . . . . . . . . . . . . . . 71

23. Periphyton standing crop as indicated by chlorophyll _a_ content of samples collected at the upper Skagit and Cascade stations . . . . . . . . . . . . . . . . . . . . . 72

24. Density of benthic insects at sampling locations along the lower Skagit transect from May 1976 to February 1977 . . . 80

25. Density of benthic insects at sampling locations along the lower Skagit transects from May 1977 to November 1977 . . . 82

26. Relationship between insect density and water depth at the upper and lower Skagit stations during May, July and September 1977 . . . . . . . . . . . . . . . . . . . . . . 84

27. Stream profiles at the lower Skagit station showing maximum and minimum water levels during the two weeks prior to benthic insect sampling in May and July 1976 . . . . . . . 86

| Number | | Page |
|---|---|---|
| 28. | Stream profiles at the lower Skagit station showing maximum and minimum water levels during the two weeks prior to benthic insect sampling in September and November 1976 . . . . . . . . . . . . . . . . . . . . . . | 87 |
| 29. | Density and biomass of benthic insects and exposure levels at sampling locations on the lower Skagit sampling transect during 1976 . . . . . . . . . . . . . . . . . . . . . | 88 |
| 30. | Relationship between benthic insect density and hours of exposure during the two weeks prior to sampling at the lower Skagit station under fluctuating flow conditions . . | 89 |
| 31. | Benthic insect density at the lower Skagit and lower Sauk sampling stations . . . . . . . . . . . . . . . . . . . . . | 106 |
| 32. | Benthic insect density at the upper Skagit, upper Sauk and Cascade sampling stations . . . . . . . . . . . . . . . . . | 107 |
| 33. | Benthic insect biomass (wet weight) at the lower Skagit and lower Sauk sampling stations . . . . . . . . . . . . . | 108 |
| 34. | Benthic insect biomass (wet weight) at the upper Skagit. upper Sauk and Cascade sampling stations . . . . . . . . . . | 109 |
| 35. | Seasonal variation in benthic macroinvertebrate density in the Skagit, Sauk and two other rivers in western North America . . . . . . . . . . . . . . . . . . . . . . . | 111 |
| 36. | Density of Ephemeroptera and Plecoptera in the unexposed zone of the Skagit and Sauk rivers . . . . . . . . . . . . | 116 |
| 37. | Density of Diptera and Trichoptera in the unexposed zone of the Skagit and Sauk rivers . . . . . . . . . . . . . . . . | 117 |
| 38. | Density of _Ephemerella inermis_, _Rithrogena_ and _Baetis_ in the unexposed zone at the lower Skagit station . . . . . . | 118 |
| 39. | Density of _Alloperla_, _Acroneuria_ and _Ephemerella tibialis_ in the unexposed zone at the lower Skagit station . . . . . | 120 |
| 40. | Density of _Arctopsyche_ and _Brachycentrus_ in the unexposed zone at the lower Skagit station . . . . . . . . . . . . . | 121 |
| 41. | Percent composition of each benthic insect order at the upper and lower Skagit and upper and lower Sauk stations. . | 122 |

Number Page

42. Diversity at the upper and lower Skagit and upper and lower Sauk stations . . . . . . . . . . . . . . . . . . . . 125

43. Percent composition of each benthic insect trophic category at the upper and lower Skagit and upper and lower Sauk stations . . . . . . . . . . . . . . . . . . . . 130

44. Width of the periphyton zone during a water level fluctuation of 0.5 m and during stable median flow . . . . . . . 136

LIST OF TABLES


| Number | | Page |
|---|---|---|
| 1. | Physical characteristics at sampling stations . . . . . . . | 12 |
| 2. | Mean daily range in water level (m) during each month in 1976 at the Skagit at Newhalem and Marblemount, the Sauk and the Cascade USGS gaging stations . . . . . . . . . . . | 41 |
| 3. | Mean daily range in water level (m) during each month in 1977 at the Skagit at Newhalem and Marblemount, the Sauk and the Cascade USGS gaging stations . . . . . . . . . . . | 42 |
| 4. | Percentage of time that the artificial substrate periphyton samplers were exposed to desiccation during the six-week period prior to sampling . . . . . . . . . . . . . . . . . . | 49 |
| 5. | Percentage of time that the streambed at periphyton sampling locations was exposed to desiccation during the six-week period prior to sampling . . . . . . . . . . . . . . . . . . | 51 |
| 6. | Percentage of time that the streambed at benthic insect sampling locations was exposed to desiccation during the two-week period prior to sampling . . . . . . . . . . . . . . | 52 |
| 7. | Mean annual chemical water quality parameters in the Skagit River at Newhalem and in the Sauk River at the lower sampling station from October 1976 through September 1977 . . . . . | 57 |
| 8. | Mean monthly turbidity (JTU) at stations on the Skagit, Cascade and Sauk rivers during 1976 . . . . . . . . . . . . . | 58 |
| 9. | Mean monthly turbidity (JTU) at stations on the Skagit, Cascade and Sauk rivers during 1977 . . . . . . . . . . . . . | 59 |
| 10. | Substrate composition at the Skagit and Sauk River benthic insect sampling stations expressed as percent of substrate material retained on each sieve, with 95% confidence limits | 63 |
| 11. | Mean bottom current velocity (cm/sec) at sampling stations | 65 |
| 12. | Results of analysis of variance (ANOVA) and multiple comparison tests comparing mean chlorophyll a at sampling stations during the stable flow period . . . . . . . . . . | 74 |
| 13. | Range of chlorophyll a values in the Skagit, Sauk and several other North American streams . . . . . . . . . . . | 77 |

Number | Page


| Number | | Page |
|---|---|---|
| 14. | Number, density and percent composition of insects collected with the Coleman-Hynes basket sampler . . . . . . | 91 |
| 15. | Percent composition of benthic insects at sampling stations during May and July 1976 . . . . . . . . . . . . . . . . . | 93 |
| 16. | Percent composition of benthic insects at sampling stations during September and November 1976 . . . . . . . . . . . . | 94 |
| 17. | Mean number of insects per substrate tray in experimental and control artificial stream channels before and after experimental flow fluctuation . . . . . . . . . . . . . . . . | 95 |
| 18. | Percent composition of benthic insects in experimental and control artificial stream channels before and after one week of periodic exposure . . . . . . . . . . . . . . . . . . | 99 |
| 19. | Percent composition of benthic insects in experimental and control artificial stream channels before and after 48 hours of continuous exposure . . . . . . . . . . . . . . . . . | 99 |
| 20. | Percent composition of drifting aquatic insects in the experimental artificial stream channel during dewatering and rising water and in the control channel during the same time period . . . . . . . . . . . . . . . . . . . . . . . | 100 |
| 21. | Percentage of aquatic insect larvae stranded and not stranded during experimental flow reductions . . . . . . . | 102 |
| 22. | Percent mortality of aquatic insect larvae exposed to desiccation for 24 hours on dry and damp substrates . . . . | 104 |
| 23. | Results of analysis of variance (ANOVA) and multiple comparison tests comparing mean benthic insect density at sampling stations . . . . . . . . . . . . . . . . . . . . | 113 |
| 24. | Trophic classification of aquatic insects (excluding Chironomidae) collected in the Skagit and Sauk rivers . . . | 128 |

## ACKNOWLEDGMENTS

I would like to express my appreciation to the members of my Supervisory Committee, Dr. Quentin J. Stober, Chairman, and Drs. Robert L. Burgner, Ernest O. Salo, Frieda B. Taub and Eugene B. Welch, for their guidance throughout the study and for their review of the manuscript. Thanks also to Mr. Ron Bates, Seattle City Light Engineering Department, for his help in designing the artificial stream and locating a suitable site and to the City Light personnel at Newhalem, Washington, who constructed and installed the artificial stream channels.

# INTRODUCTION

The streamflow pattern below the Seattle City Light hydroelectric project on the Skagit River is influenced primarily by the demand for electrical power. During the day, when demand is at its peak, more water is released through turbines to generate power than at night, when demand is usually lower. This pattern of power generation is known as hydroelectric peaking. As a result of peaking, streamflow downstream of the project can fluctuate widely during a 24-hour period.

Several investigators (Powell 1958, Radford and Hartland-Rowe 1971, Fisher and LaVoy 1972, MacPhee and Brusven 1973, Trotzky and Gregory 1974) have reported reductions in the standing crop of bottom fauna under similar conditions of fluctuating flow below hydroelectric dams. Standing crop below the dam was lower than standing crop in the same stream above the dam, further downstream, or in nearby control streams. The reduction has been attributed to a number of flow-related causes.

Periodic exposure of the stream margins to desiccation during diel flow fluctuation was a major cause of the reduction. Powell (1958) noted that a "zone of fluctuation" and a "permanent-flow zone" were present in the Blue River, Colorado, below a hydroelectric dam. The zone of fluctuation was covered by water during part of the day and exposed to desiccation and freezing during the rest of the day, while the permanent-flow zone remained continuously submerged. Insect biomass per unit area above the reservoir was as much as 32 times greater and never less than 2.5 times greater than biomass in the zone of fluctuation below the dam. Kroger (1973) and Brusven et al. (1974) reported substantial insect mortality in the exposed margins of the Snake River following reductions in flow below irrigation and hydroelectric reservoirs. Neel (1963), Radford and Hartland-Rowe (1971) and Kroger (1973) have stated that epilithic algae within stream margins is affected by exposure during flow reductions, but the effects have not been measured.

Fisher and LaVoy (1972) examined the effects of the level of exposure on benthic macroinvertebrate standing crop and community structure. They sampled benthic macroinvertebrates along a cross-stream transect over a two-and-a-half-month period at a single site on the Connecticut River. The part of the transect near the edge of the stream was exposed for a greater percentage of time than the deeper sections near midstream. Density, biomass and diversity increased along the transect as depth increased and the percent exposure time decreased, and were highest in the unexposed zone. Although MacPhee and Brusven (1973) did not measure the level of exposure, they also found that abundance and diversity of benthic insects increased from shallow to deeper water in the Clearwater River, Idaho, following a period of fluctuating streamflow. Prior to the onset of flow fluctuation, abundance and diversity had decreased from shallow to deeper water.

Several other researchers have cited high or low current velocity during maximum and minimum daily flows as the cause of reduced bottom fauna. Radford and Hartland-Rowe (1971) found that the standing crop of benthic organisms below a hydroelectric dam on the Kananaskis River, Alberta, was reduced, when compared with a control stream. The insect community was dominated by torrential species, and the low standing crop was attributed to the flushing action of high flows during reservoir releases. In contrast, Trotzky and Gregory (1974) reported that slow current velocity during daily minimum flows appeared to limit abundance and diversity of swift-water insects on the Kennebec River, Maine. Insect abundance was greater above the dam than immediately below it, and generally increased downstream. The range of flow fluctuation in this river was extreme, with a mean daily minimum flow of 8.5 $m^3$/sec and a daily maximum of about 170 $m^3$/sec.

However, other researchers have observed enhanced benthic standing crop below hydroelectric dams despite daily flow fluctuation. Pfitzer (1954) indicated that the benthos was enhanced by the cooler temperature regime below a hypolimnial release dam in Tennessee, although great daily fluctuations in discharge and current velocity occurred. Pearson et al. (1968) found that standing crop was much greater at a site 12 km below a dam on the Green River, Utah, than at sites further downstream (69 to 126 km below the dam), in spite of large daily fluctuations in water level. Due to reduced seasonal flooding, the import of sand and silt from upstream was reduced, resulting in a more stable substrate at the site 12 km below the dam. Apparently the beneficial effects of seasonal flow stability offset the detrimental effects of diel flow fluctuation.

In addition to affecting benthic standing crop directly, flow fluctuations may also increase the drift rate of benthic organisms.

Rapid flow reductions have frequently been observed to increase the drift rate of aquatic insects (Minshall and Winger 1968, Pearson and Franklin 1968, Radford and Hartland-Rowe 1971, MacPhee and Brusven 1973). The increase may be substantial, as it was in the Clearwater River, Idaho, where the drift rate was 95 times greater at a site affected by a flow reduction than at an unaffected site (MacPhee and Brusven 1973). Sudden increases in flow, both artificial and natural, have also been shown to increase invertebrate drift (Anderson and Lehmkuhl 1968, Pearson and Franklin 1968).

If benthic insect standing crop in the Skagit River has been reduced by flow fluctuation due to hydroelectric peaking, as it has in other streams, the reduction could have detrimental effects on the economically important fish species. Several species of Pacific salmon, as well as steelhead, spawn in the Skagit or its tributaries, and aquatic insects are the major source of food for the juvenile salmonids during their residence in the mainstem Skagit (Graybill _et al_. 1979). A severe reduction in the food supply of these fish would affect their freshwater growth and survival.

Reduced periphyton standing crop due to flow fluctuation may also affect insect standing crop, and, ultimately, the fish populations. Although detrital input from terrestrial sources provides most of the energy in small, shaded, headwater streams (Fisher and Likens 1973, Cummins 1974), instream autotrophic production assumes a much greater role in stream metabolism as streams increase in size (Cummins 1975, Fisher 1977). In large rivers without forest canopies, like the Skagit, autotrophic production is probably a significant source of energy, and reductions may lead to lower insect standing crop and altered composition.

The present study was initiated in 1976 to investigate the effects of peaking flow fluctuation on the benthic insects and periphyton of the Skagit River and Pacific Northwest coastal streams in general. No previous studies of the effects of peaking flow fluctuation have been conducted in coastal streams of the Pacific Northwest, and it is difficult to predict the effects in these streams from the results of studies done in other geographical areas of North America. The effects of a given streamflow pattern, including daily peaking fluctuation, in a particular river depend on the environmental conditions in the river, and the same streamflow patterns may have different effects in different rivers (Ward 1976).

Environmental conditions in Pacific Northwest coastal streams differ considerably from conditions in other streams that have been studied. Extreme seasonal fluctuations in discharge occur in coastal streams due to heavy rainfall during fall and winter and to the melting of the mountain snowpack during spring and early summer. Rapid daily increases in streamflow typically occur during periods of heavy rainfall. Selection may favor those species of aquatic insects that are behaviorally or morphologically adapted to avoid stranding during flow reductions, resist desiccation on exposed substrate, or withstand current velocity changes during natural flow fluctuations. The substrate of coastal streams is usually composed of coarse particles (cobbles) which can reduce the effects of high discharge (Hynes 1970) and stranding (Brusven et al. 1974). The additional fluctuation due to hydroelectric peaking may not affect the benthic fauna as severely as it has in other streams, due to a possible faunal adaptation to flow fluctuation and the mitigating effect of large substrate particles.

The results of a Skagit River study should have broad applicability in interpreting and predicting the effects of flow fluctuation below existing and future hydroelectric dams on coastal streams and other large streams of the Pacific Northwest where environmental conditions are similar to conditions in the Skagit.

Previous investigators have largely ignored the effects of flow fluctuation on the benthos in the area of the streambed that is not exposed during diel flow fluctuation. Powell (1958) stated that the permanent-flow, or unexposed zone was responsible for most of the bottom fauna production below a hydroelectric dam, since standing crop was reduced in the fluctuating-flow, or exposed zone. However, Powell did not measure production or standing crop in the unexposed zone. Fisher and LaVoy (1972) sampled benthos within the unexposed zone, but did not compare standing crop in the unexposed zone with standing crop at other unaffected sites to determine if standing crop had been reduced. Other researchers investigating the effects of flow fluctuation did not measure exposure time in the areas of the streambed where they sampled.

The overall objective of the present study was to determine if benthic insect standing crop and community structure in the section of the Skagit River between Gorge Powerhouse and the confluence of the

Sauk River had been altered by peaking flow fluctuation and to determine the probable causes of any changes. Since no pre-important data relating to benthic insect standing crop were available, and the Skagit above the reservoirs was relatively inaccessible, it was necessary to compare the benthic community in the Skagit with the community in an unregulated control stream to detect any changes caused by regulation.

The specific objectives were twofold. One was to determine the effects of periodic exposure on the benthic insects within the zone of exposure at the river margins. Due to the relative importance of epilithic algae as an energy source in large streams, the effect of exposure on periphyton standing crop was also investigated. Experimental studies were also conducted in an artificial stream to observe the effects of exposure under controlled laboratory conditions and to determine the ability of selected species of aquatic insects to avoid stranding during flow reduction and to withstand desiccation on exposed substrate. The other objective was to determine the effect of peaking flow fluctuation on benthic insects within the unexposed area at midstream. It was originally intended to sample the benthic insect community at bimonthly intervals over at least a one-year period encompassing a complete annual cycle of the insect community and streamflow.

Due to unusual flow conditions in the Skagit during 1977, the scope of the investigation was expanded. Because of drought conditions during the winter of 1976-77, water levels in the reservoirs were low during the spring and summer of 1977. Power was not generated on a peaking basis from mid-April 1977 to mid-November 1977, resulting in a relatively stable daily flow pattern. These unusual circumstances provided a rare opportunity to document the effect of seven months of stable flow in a river previously subject to daily peaking flow fluctuation. It was also possible to discern the effects of flow fluctuation on the benthic insect community in the Skagit by comparing community structure and standing crop under fluctuating flow in 1976 and stable flow in 1977, in addition to comparing separate river ecosystems as was originally planned.

## STUDY AREA

The benthic insect and periphyton communities in three western Washington streams, the Skagit, Sauk and Cascade rivers, were examined during the study. The Skagit River, above the mouth of the Sauk, is a 5th order stream, according to Strahler's (1957) stream classification method. The Sauk is also a 5th order stream, while the Cascade is a 4th order stream. The location of the rivers and sampling stations is shown in Fig. 1.

The Skagit is a regulated stream for most of its length. It originates in British Columbia, Canada, and flows 204 km through Washington to Puget Sound. The first 49 km of the American Skagit are impounded behind a series of three hydroelectric dams, forming three contiguous reservoirs. These hydroelectric facilities are operated by Seattle City Light (SCL) and provide electrical power to the city of Seattle. Water stored in Gorge Lake, the last reservoir in the series, is transported through a tunnel to Gorge Powerhouse at Newhalem. After passing through the turbines at the powerhouse, the water re-enters the river channel. The 4 km section of river channel between Gorge Dam and the powerhouse at Newhalem is dry except when water is released through the spillway of the dam. The Skagit is free-flowing from Newhalem to its mouth.

The Sauk and Cascade rivers are unregulated tributaries of the Skagit. The Sauk meets the Skagit near the town of Rockport, 44 km below Newhalem, while the Cascade enters the Skagit near Marblemount,

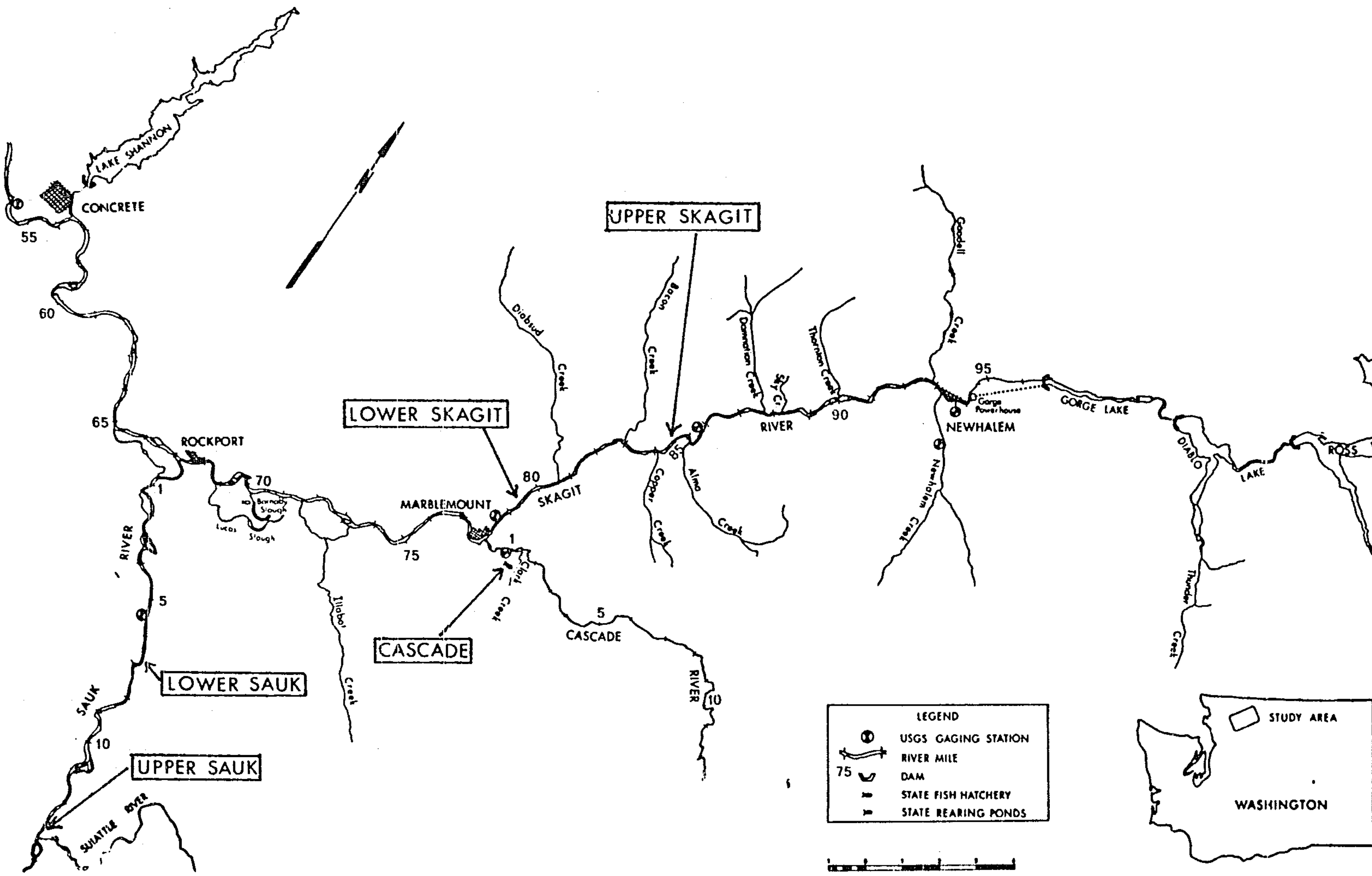


Fig. 1. Skagit Basin study area with periphyton and benthic insect sampling stations.

25 km below Newhalem. The drainage area and mean annual discharge at the Sauk River stations were slightly lower than at the Skagit stations (Table 1), but stream order was the same. However, the Cascade River was considerably smaller than either the Skagit or Sauk rivers.

The Sauk River served as the primary control stream, since it was more physically similar to the Skagit between Newhalem and Rockport than the smaller Cascade River. However, the Sauk River, unlike the upper Skagit, was subject to frequent periods of high turbidity during the summer months. It was not known if the level of suspended sediment was high enough or if the duration of the turbid periods was long enough to have a significant effect on the periphyton or benthic insect communities. If Sauk River standing crop were reduced by siltation during the turbid periods, it would have confounded the comparison between standing crop under unregulated flow in the Sauk with standing crop under regulated flow in the Skagit.

The Cascade River was not as turbid as the Sauk and served as a secondary unregulated control stream. If standing crop was similar in the Sauk and Cascade when both rivers were clear, but lower in the Sauk during the period of high turbidity, it would indicate that the Sauk River standing crop has been affected by turbidity. The Cascade benthic insect and periphyton communities would then be compared with the Skagit River communities to determine the effects of the regulated flow regime.

All three rivers drained portions of the western slope of the North Cascade mountains. This area receives a high amount of precipi-

Table 1. Physical characteristics at sampling stations. Discharge values for the upper Sauk station are estimates based on drainage area. Bottom velocities pertain to shoreline areas only.

| Station | Discharge ($m^3$/sec) | | | Drainage Area ($km^2$) | Mean Bottom Velocity (cm/sec) |
|---|---|---|---|---|---|
| | Mean Annual | Range | | | |
| | | 10/75 - 9/76 | 10/76 - 9/77 | | |
| Skagit (upper) | 159 | 36 - 895 | 33 - 660 | 3300 | 49 |
| Skagit (lower) | 176 | 53 - 878* | 43 - 753 | 3577 | 43 |
| Sauk (upper) | 120 | — | — | 1782 | 55 |
| Sauk (lower) | 125 | 36 - 1850 | 28 - 804 | 1849 | 61 |
| Cascade | 29 | 8 - 326 | 6 - 240 | 445 | 43 |

* The USGS gaging station near the lower Skagit station was inoperative at the time when the 895 $m^3$/sec flow occurred at the upper Skagit station.

tation, particularly during the late fall and winter months, and much of this precipitation falls as snow at the higher elevations. The large amounts of rainfall and melting snow result in a wide range between annual maximum and minimum streamflow (Table 1).

Other than the impoundment of the Skagit, there was no obvious difference in the amount of human perturbation within upper Skagit, Sauk and Cascade River watersheds that could adversely affect water quality. Cultural and agricultural development within all three watersheds (excluding the lower Skagit area) is minimal. Although there is some logging activity in the drainage areas of all three rivers, most of the watershed below the timberline remains heavily forested.

Two sampling stations were established on the Skagit and Sauk rivers. Only one was located on the Cascade River. The upper Skagit and lower Skagit stations were 16.1 and 24.1 km below Newhalem, respectively. The upper Sauk and lower Sauk stations were 30.5 and 20.9 km, respectively, above the confluence of the Sauk and Skagit. The Cascade station was 1.4 km above the confluence of the Cascade and Skagit rivers. The terms "upper" and "lower" indicate the proximity of the station to the hydroelectric facilities on the Skagit and distinguish one station from the other, and do not necessarily indicate that a station is located in the upper or lower section of the river. Both Skagit stations were located in the upper half of the American Skagit, while both Sauk stations were in the lower section of that river.

These stations were selected on the basis of similar substrate particle sizes, gradient and slope of the shoreline. Accessibility was also a consideration in selecting stations on the Sauk and Cascade rivers. The surface of the streambed was armored with cobbles, approximately 8 to 30 cm in diameter, over compacted cobbles, gravel and sand at all stations. Mean bottom current velocity ranged from 43 to 61 cm/sec in the areas where bottom samples were collected (Table 1). Samples were collected in areas where the streambed sloped gradually from the bank of the river channel to midstream to ensure that the sample sites at a series of depths would be separated by several meters.

The banks of the river channel at all stations were heavily forested. Riparian vegetation was generally similar at all stations and was composed primarily of red alder (Alnus rubra) with bigleaf maple (Acer macrophyllum), Douglas fir (Pseudotsuga menziesii), western hemlock (Tsuga heterophylla) and western red cedar (Thuja plicata). Due to the width of the river channel at all stations, only small portions of the river were shaded during early morning and late afternoon.

The section of the Skagit under investigation in this study was utilized as a rearing area by the juveniles of Pacific salmon and steelhead trout (Salmo gairdneri). Chinook (Oncorhynchus tshawytscha) and coho (O. kisutch) juveniles utilized the study area extensively, while chum (O. keta) and pink salmon (O. nerka) juveniles utilizes it to a minor extent. Resident rainbow trout, Dolly Varden (Salvelinus malma), mountain whitefish (Prosopium williamsoni), largescale sucker (Catastomus macrocheilus), brook trout (Salvelinus fontinalis), threespine stickleback (Gasterosteus aculeatus), sculpins (Cottus spp.), longnose dace (Rhinichthys cataractae) and brook lamprey (Lampetra richardsoni) are also found in the upper Skagit. Cutthroat trout (Salmo clarki) were notably absent from the study area (Graybill et al. 1979).

Chinook, coho, chum and pink salmon also spawn in the Sauk and Cascade rivers (Williams et al. 1975). These rivers probably contain most of the other fish species recorded in the Skagit River.

The artificial stream channels were located outdoors, adjacent to Ladder Creek at the town of Newhalem. A head tank and pipe system, formerly part of the town's water supply system, were already available at this site and were capable of supplying a large volume of Ladder Creek water to the experimental stream channels. The site was accessible only through a locked gate, making it an ideal location for the experimental stream. However, the area was heavily shaded, allowing little direct sunlight to penetrate. As a result, air temperatures were up to 9°C cooler at the experimental stream site than on the exposed shoreline of the Skagit River. Insect mortality rates on the dewatered substrate in the experimental stream, subject to cool air temperatures, were probably lower than would have been the case under the warmer temperture regime typical of the open shoreline of the Skagit during the summer.

# MATERIALS AND METHODS

## PHYSICAL PARAMETERS

Hourly gage height records from the U. S. Geological Survey (USGS) streamflow gaging station nearest to each sampling station were used to determine flow patterns. The USGS gage at Marblemount was located 1.3 km below the lower Skagit station, while the USGS gage near Alma Creek was 2.4 km above the upper Skagit station. The USGS gage on the lower Sauk River was used to determine the discharge pattern at both the upper and lower Sauk River sampling stations. This gage was 2.6 km below the lower station and 12.2 km below the upper station. The Cascade River sampling station was within 100 m of the gaging station on the Cascade. No major tributary streams entered the rivers between a gaging station and a sampling station, and the flow pattern at the gage was considered to the actual flow pattern at the sampling site.

In order to determine the effects of exposure to desiccation on periphyton and benthic insect standing crop and community structure, it was necessary to calculate the pre-sampling exposure level for each individual sampling site at the sampling stations. To facilitate this calculation, samples were collected along the submerged part of a permanent transect that was perpendicular to streamflow. The transects extended from what appeared to be the high water line at maximum annual flow to a point near midstream and crossed the part of the stream channel that was usually dry during much of the year. Since the transect sloped toward midstream, the position of the edge of the stream on the transect varied with water level. Exposure time was determined by calculating the number of hours that the stream edge had been below a particular sampling location on the transect, thus leaving it exposed to desiccation.

The relationship between the position of the stream edge on the transect and gage height was determined for each transect. The distance between a permanent stake at the annual high water line and the stream edge was measured periodically over a wide range of water levels, including levels near the annual maximum and minimum. A plot was constructed with distance from the stake to stream edge on one axis and gage height (at the time when the distance was measured) on the other axis. A curve was drawn through the points which described the inverse relationship between gage height, or water level, and distance from the stake to the stream edge.

These plots were analogous to the rating tables used by the USGS to determine discharge at any gage height. By using the distance and gage height curves, one could estimate the location of the stream edge, in terms of distance from the stake at the high water line, at any gage height. Conversely, it was possible to estimate the gage height at the time when the stream edge was at a particular distance from the stake.

With the aid of these distance and gage height curves, the exposure time was estimated for each sample site on the transect. After samples had been collected at the desired depths along the submerged portion of the transect, the distance from the stake at the high water line to each sample site was measured. A sample site would have been submerged whenever this measured stake-to-sample site distance had been equal to the stake-to-stream edge distance prior to sampling. For example, a sampling site 20 m from the stake at the high water line would have been barely submerged whenever the stream edge had also been 20 m from the stake. Using the distance and gage height curves, the "critical" gage height, or gage height at the time when the stake-to-sample site distance would have been equal to the stake-to-stream edge distance, was determined for each sample site. In the case of the above example, the critical gage height would be the gage height when the stream edge was 20 m from the stake. Whenever the actual gage had been less than the critical gage height value during any specified period prior to sampling, the site would have been exposed to desiccation; whenever it had been equal to or greater than the critical value, the site would have been submerged.

The critical gage height value was compared with hourly USGS gage height records for the two or six week period prior to sampling. The number of hours that the actual gage height was below this critical value was equal to the number of hours that the sample site had been exposed.

The method of exposure calculation was modified slightly due to occasional malfunctioning of the streamflow gages during exposure calculation periods. If data were not available from one of the Skagit River gages, the complete discharge records from the other functional gage were used to determine exposure time. When either the Sauk or Cascade gage was inoperative, it was necessary to assume that the flow pattern prior to sampling, as indicated by the operative gage, was the same in both unregulated rivers. This was a reasonable assumption, since flow patterns were almost identical over a two-year period in both rivers, differing only in the volume.

Fortunately, whenever the Sauk or Cascade gage was inoperative during an exposure calculation period, records from the other operative gage always indicated that the water level at sampling time was lower than it had been during the preceding two or six weeks. Thus, only unexposed sites were sampled on these occasions. It was assumed that the water level had declined in a similar manner in the other river, and that samples were also collected in only unexposed areas.

Turbidity was measured at or above benthic sampling stations from June 1976 through the first week of November 1977. Three to five measurements were made at each station per month, using a Hach portable engineer's laboratory. All stations were sampled on the same day whenever measurements were made.

The size composition of the substrate particles at the upper and lower Skagit and upper and lower Sauk stations was determined using the method described by McNeil and Ahnell (1964). Four replicate streambed substrate samples were collected near the sampling transect at each station on October 17-18, 1978.

PERIPHYTON

Artificial substrates were used to collect samples of periphyton from October 1976 through March 1977. The artificial substrate sampler was constructed of two 0.6 x 15 x 5 cm plexiglass plates attached in a horizontal position to a small wood block. The wooden block was bolted to the upper surface of a 15 x 40 x 60 cm concrete block. Four samplers, each with two replicate plexiglass plates, were placed at different depths along the sampling transects at the lower Skagit, lower Sauk and Cascade stations. During river flow fluctuations, the plexiglass plates on the samplers were periodically exposed and submerged. Those samplers in shallow water were exposed more frequently than those in deeper areas. The colonized plexiglass plates were removed every six weeks and replaced with clean plates. Six weeks were required for complete colonization of artificial substrates in Oregon streams in the Cascade Mountains (Lyford and Gregory 1975). The colonized plates were frozen and transported to the laboratory, where the periphyton was scraped from the upper surface.

Despite the heavy concrete base, the artificial substrate samplers were susceptible to washout during high flows and had to be replaced several times. A technique for direct removal of periphyton from streambed rocks was devised which avoided the problems associated with the artificial substrate samplers. This new method was used to collect samples in May 1977 and on all subsequent sample dates.

The technique involved the removal of all periphyton from a 16 $cm^2$ area on the upper surface of natural streambed rocks. A rubber template with a 4 x 4 cm square cut in the center was held against the upper surface of the rock after it had been removed from the streambed, and the area inside the square was thoroughly scrubbed with a small nylon brush. The detached algae was then washed into a collecting bottle. Samples were concentrated on a 0.45 μ membrane filter and frozen for transportation to the laboratory.

Samples were collected in May, June, July, September and November 1977. On each sampling date, two replicate samples of five rocks each were collected at four different depths (15, 25, 35 and 45 cm) along the sampling transects at the upper and lower Skagit, lower Sauk and Cascade stations.

Samples collected from both artificial and natural substrates were dried in a desiccator under refrigeration. Chlorophyll a content was determined using the method for the determination of chlorophyll a in the presence of phaeophytin a (American Public Health Association 1975). The percentage of time that each artificial substrate sampler or sample site was exposed to desiccation during the six weeks prior to sampling was also calculated.

BENTHIC INSECTS

Benthic insects were sampled only at the lower Skagit, lower Sauk and Cascade stations during 1976. During 1977, samples were collected at the upper and lower stations on both the Skagit and Sauk rivers. The additional stations were established on the Skagit and Sauk rivers because it was desirable to have a site on the Skagit closer to Newhalem and subject to a greater degree of flow fluctuation, and to have a station on the Sauk subject to lower turbidity levels. The addition of two more stations greatly increased the number of bottom samples to be sorted. In order to limit the samples to a reasonable number, benthic insect sampling was discontinued at the Cascade station.

A 0.25 $m^2$ quadrat sampler (351 μ mesh), designed by Malick (1977) was used to sample benthic insects. This sampler was a larger, heavier version of the standard Surber sampler (Surber 1937). A large quadrat size was needed to sample in the Skagit, Sauk and Cascade rivers due to the large stones in the surface of the streambed. The quadrat sampler could be used in water up to 45 cm deep.

Usually the sub-surface, or hyporheic fauna is not sampled when using this type of sampler. Large numbers of benthic organisms may be present below the surface of the streambed in the hyporheic zone (Coleman and Hynes 1970, Stanford and Gaufin 1974, Williams and Hynes 1974). In order to sample as many hyporheic insects as possible, the large surface stones within the quadrat were first removed from the substrate and washed in the sampler net. The remaining substrate was then stirred three times with a rake to a substrate depth of 15 cm, allowing the insects within the substrate to be washed into the net. The extensive use of fixed location sub-surface sampling devices of the type described by Coleman and Hynes (1970) or O'Conner (1974) would have been impractical due to the difficulties of installation and retrieval under the severely fluctuating flow regime in the Skagit and due to the prohibitive number of samplers that would have to be placed along a transect to ensure that several different water depths were sampled regardless of seasonal flow level.

The number of replicates collected and the depths at which samples were collected along the transects were different in 1976 and 1977. During 1976, two replicates were collected at locations 15, 30 and 45 cm below the surface of the water at the lower Sauk and Cascade sampling stations and at the lower Skagit station in May only. From July through November 1976, two replicates were collected at depths of 15, 25, 35 and 45 cm at the lower Skagit station. During 1977, four replicate samples were collected at each of four locations (15, 25, 35 and 45 cm deep) along the transects at all stations.

Samples were preserved in the field with 70% ethanol containing rose bengal dye (100 mg/l). Current velocity was measured as close to the bottom as possible at each sample site with a Gurley No. 625 Pygmy-type current meter.

A single Coleman-Hynes basket-type sampler was used to sample benthic insects at the lower Skagit station to compare this method of sampling with the quadrat sampling method. The basket sampler was identical to the sampler used by Malick (1977) in the Cedar River, Washington. It was a double cylinder of perforated metal, 30 cm long and had a top surface area of 0.036 $m^2$. A hole 30 cm deep was dug in the streambed, and the sampler was placed in the hole in a vertical position. The sampler and the area around the sampler were filled with the material removed from the hole, leaving the top of the cylinder flush with the surface of the streambed. It was implanted on May 20, 1976 and removed four months later on September 2. Material contained in the inner cylinder was collected and preserved.

All benthic insects were hand-picked from detritus and inorganic material under a variable-power dissecting microscope, identified to order and counted. Each order was subsampled separately, and subsampled insects were identified to the lowest practicable level, usually genus, using keys contained in Usinger (1956), Allen and Edmunds (1959, 1961a, 1961b, 1962, 1963, 1965, 1976), Smith (1968), Edmunds et al. (1976) and Wiggins (1977).

Insect biomass was estimated by multiplying the volume of preserved insects by 1.05, the value for specific gravity of stream insects used by Hynes (1961). To measure volume, insects were first removed from the preservative and placed on absorbent paper for approximately one minute, allowing excess preservative on the surface of the insects to drain and evaporate. A 3 ml graduated cylinder, constructed from a section of a 10 ml pipette, was filled with preservative to the 1 ml mark, and insects were dropped into the liquid. The volume of preservative displaced by the insects was measured to the nearest 0.02 ml. Volume measurements of Trichoptera do not include the volume of larval or pupal cases. Although the weight of preserved insects is less than live weight, due to shrinkage and weight loss in 70% ethanol (Stanford 1973), biomass comparisons among stations would not be affected since the same preservation method was used consistently.

Due to the contagious, or clumped, spatial distribution of benthic insects on the stream bottom, the frequency distribution of insect counts is usually non-normal (Elliott 1977). In the present study, the variances and means of insect counts were not independent, and the variance was usually larger than the mean, indicating a probable negative binomial frequency distribution. Therefore, a logarithmic transformation was applied prior to all parametric statistical calculations to normalize the data, as recommended by Elliott (1977).

The percentage of time that the substrate was exposed during the two weeks prior to sampling was calculated for each sample location. The selection of a two-week exposure calculation period was based on the time necessary for complete recolonization of the stream bottom by benthos. Recolonization rates for barren substrates varied from two weeks (Waters 1964) to four weeks (Mason et al. 1967) and over four weeks (Coleman and Hynes 1970). Potential problems were foreseen under particular flow patterns using an exposure calculation time greater than the recolonization time. For example, if it takes only two weeks to recolonize the stream bottom, and a four-week exposure calculation time were used, misleading results would be obtained if the streambed were exposed continuously or frequently during the first two weeks, severely reducing insect abundance, and then submerged continuously for the next two weeks. In this situation, the benthos would have time to recolonize the affected areas before sampling, resulting in a normal seasonal standing crop but a high exposure level. These results would give the false impression that high exposure had no effect on insect abundance.

Using an exposure calculation period less than the recolonization time could also be misleading — for example, a two-week exposure calculation period when the recolonization time is four weeks. High exposure of the streambed for two weeks followed by a two-week period of no exposure would probably result in a standing crop much lower than the normal seasonal value, since the insects have had only two weeks to recolonize the streambed and need four weeks for complete recolonization. In this case, standing crop at sampling time would be lower than normal, while exposure calculated over the last two weeks would also be low. The investigator would probably assume that some factor other than exposure reduced insect abundance.

It was concluded that the period of exposure calculation should be as long as the time necessary for complete recolonization to avoid the problems mentioned above. Since the precise time for recolonization of denuded areas in the Skagit was not known, it was necessary to use a value from the literature. Actual determination of the recolonization time by removal of insects from an area of the streambed and sampling at intervals until insect abundance returned to the original level would have been impractical. Frequent flow fluctuations during 1976 would have periodically removed insects from the area, preventing complete recolonization. Two weeks appeared to be a reasonable estimate of recolonization time, and an equally long two-week exposure calculation period was used.

EXPERIMENTAL STUDIES

Four artificial stream channels were constructed at the Ladder Creek site in 1976. A diagram of a single channel is shown in Fig. 2. Each of the channels was 2.4 m long, 45 cm wide and 28 cm deep. Up to four 36 x 41 cm trays containing gravel substrate were placed in the bottom of each channel. The trays were filled with a sand and gravel mixture almost to the top. A layer of 5 cm gravel was added to the surface of the trays used in the stranding avoidance experiments, while 5-15 cm rocks were used in the trays in the flow fluctuation experiments.

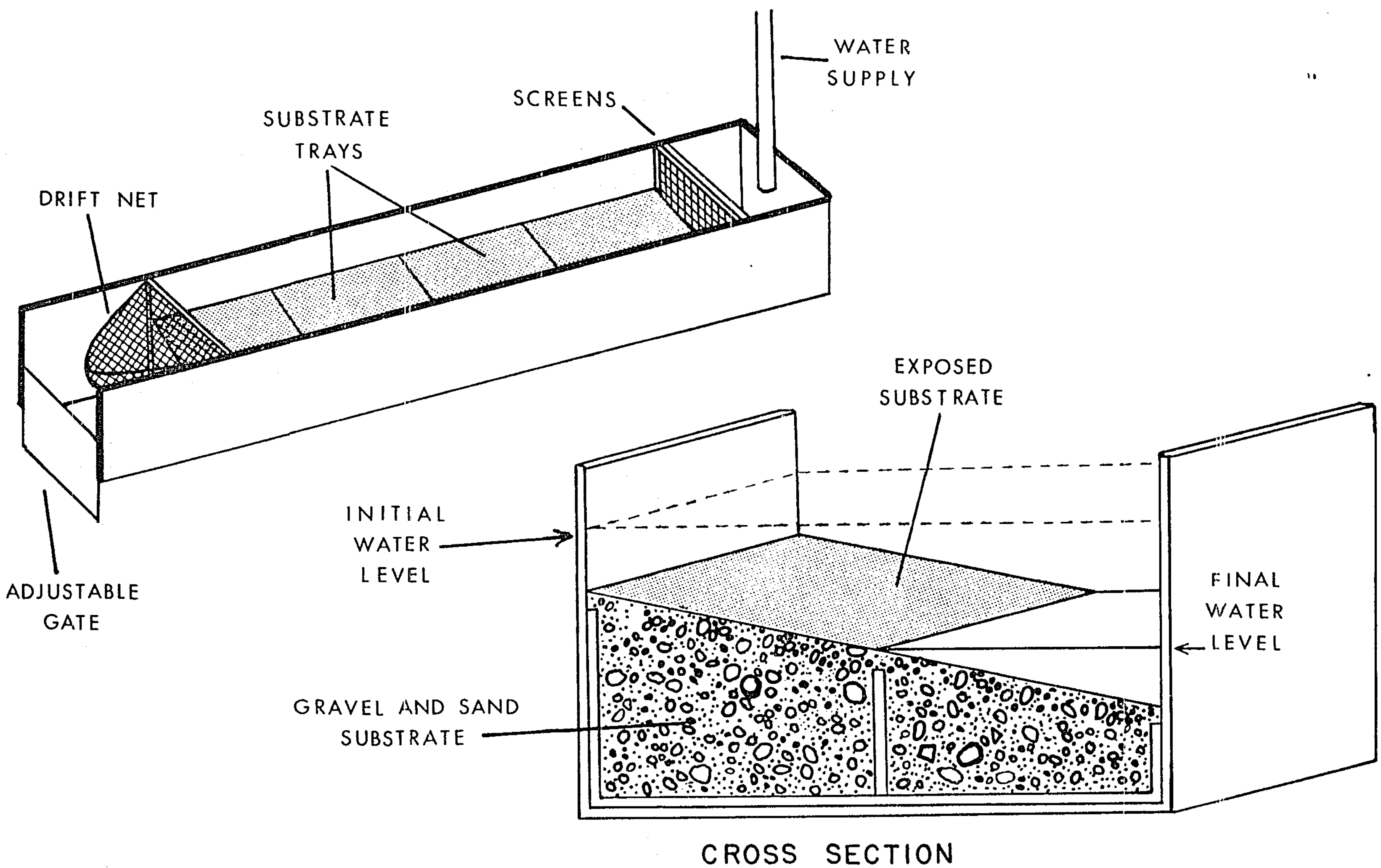


Fig. 2. Diagram of a single artificial stream channel and a cross-sectional view showing initial and final water levels during the stranding experiments.

The trays sloped from one side of the channel to the other (24 percent slope), simulating a sloping river shoreline. A screen (333 μ mesh) at the upstream end of the channel prevented insects and debris larger than 333 μ from entering, a drift net (333 μ mesh) at the downstream end collected drifting insects and a screen on the top trapped emerging adults.

Water depth and velocity in each channel were controlled by manipulation of an inflow valve and a sluice gate at the end of the channel. Average velocity in the channels remained relatively constant as the depth was changed, and ranged from 12 to 16 cm/sec at the valve and gate settings used.

The effects of two different types of flow pattern on density and composition of benthic insects in an artificial stream channel were examined during 1977. Preparation of channels was similar for all experiments. Rocks colonized by algae were collected in the Skagit and placed in the substrate trays in the two channels. Six bottom samples were collected with a 0.25 $m^2$ quadrat sampler at the lower Skagit River benthic sampling site, and the uncounted insects and detritus from three samples were distributed as evenly as possible over the four substrate trays in each channel. Water was maintained at a constant level in both channels for one week to allow the insect community to stabilize. Prior to initating experimental flows, the substrate tray from the downstream end of each channel was removed, and the aquatic insects were collected to determine if equal numbers were present in both channels. The trays with substrate material were then returned to their original location in the channel.

After the one week stabilization period, the experimental channel was either (1) dewatered for 18 hours a day for seven days, or (2) dewatered for 48 continuous hours. Two replicate experiments were conducted using the first flow pattern, while only one experiment was conducted with the second pattern. The water level was always raised and lowered at a rate of 21 cm per hour. Organisms drifting out of the experimental channel during increasing or decreasing flow were collected in a drift net. During the flow manipulations in the experimental channel, drift was also collected in the control channel for comparison. At the conclusion of the experiments, the three undisturbed trays in each channel were removed and the insects were collected for analysis.

Three species of aquatic insects were tested to determine their ability to avoid becoming stranded during flow reductions in an artificial stream channel. At the start of an experiment, water level was adjusted so that the entire substrate surface was submerged. After 50 insects of a single species were released in the upper half of the upstream tray, the water level was lowered at a rate of 21 cm per hour. The upper half of the sloping substrate tray was completely exposed and only the lower half was submerged after 30 minutes of dewatering. Insect movement during dewatering was observed visually, and the number of insects that remained in or on the exposed substrate after 24 hours was compared with the number that moved to the lower, submerged half of the substrate trays. The number of insects that avoided stranding by drifting was also recorded.

Three species of insects commonly found in the Skagit and Sauk rivers were tested during 1977: Ephemerella tibialis (Ephemeroptera), Acroneuria pacifica (Plecoptera) and Dicosmoecus sp. (Trichoptera). Insects were collected in the Skagit River and transported in a cooler to the artificial stream site where they were allowed to acclimate for 24 hours in screened cages in the channels. The range in body length of insect larvae tested was 6-8 mm for E. tibialis and 10-15 mm for A. pacifica. The case lengths of the Dicosmoecus larvae ranged from 17 to 26 mm. Two replicate stranding avoidance tests were conducted with each of the three species, using 50 individuals in each test.

The three species of aquatic insects tested for ability to avoid stranding were also examined to determine ability to survive desiccation on dewatered substrates in the event of stranding. Insect larvae were placed in petri dishes or plastic containers with a one-cm layer of either dry or damp sand on the bottom. A control was also used to estimate mortality caused by handling. Control insects were subjected to the same handling procedure as the experimental insects but were placed in a screened cage in flowing water rather than on sand substrates. Percent mortality of experimental and control insects was determined after 24 hours. Equal numbers of a single species, ranging from 40 to 50 insects, were placed on the dry and damp sand substrates and in the control cage.

# RESULTS

## PHYSICAL AND CHEMICAL PARAMETERS

### Streamflow Pattern

There was a noticeable difference between the 1976 and 1977 seasonal flow patterns. During 1976, when precipitation was at or near normal levels, the seasonal flow pattern in the Skagit at Marblemount and in the Sauk and Cascade rivers (Fig. 3) was characterized by periods of higher discharge during late fall and winter months, due to increased precipitation, and in late spring and early summer, due to snowmelt. As a result of drought conditions during the winter of 1976-77, the high flows due to spring snowmelt were of lower magnitude in 1977, and the spring runoff period was shorter (Fig. 4).

A comparison of the long-term natural flow pattern in the Skagit River at Newhalem with the regulated pattern (Fig. 5) revealed that regulation reduced streamflow during the spring runoff period (May-July) while it augmented streamflow during the other months of the year. Natural flow is the amount of water that flowed into the reservoirs above Newhalem, and therefore is the volume of water that would have flowed past Newhalem without regulation. When the annual regulated flow pattern and annual natural flow pattern were compared, it was apparent that this type of flow modification occurred during 1976 and most of 1977 (Fig. 6). However, in 1977, regulated streamflow continued to be less than natural flow during most of August, September, November and December.

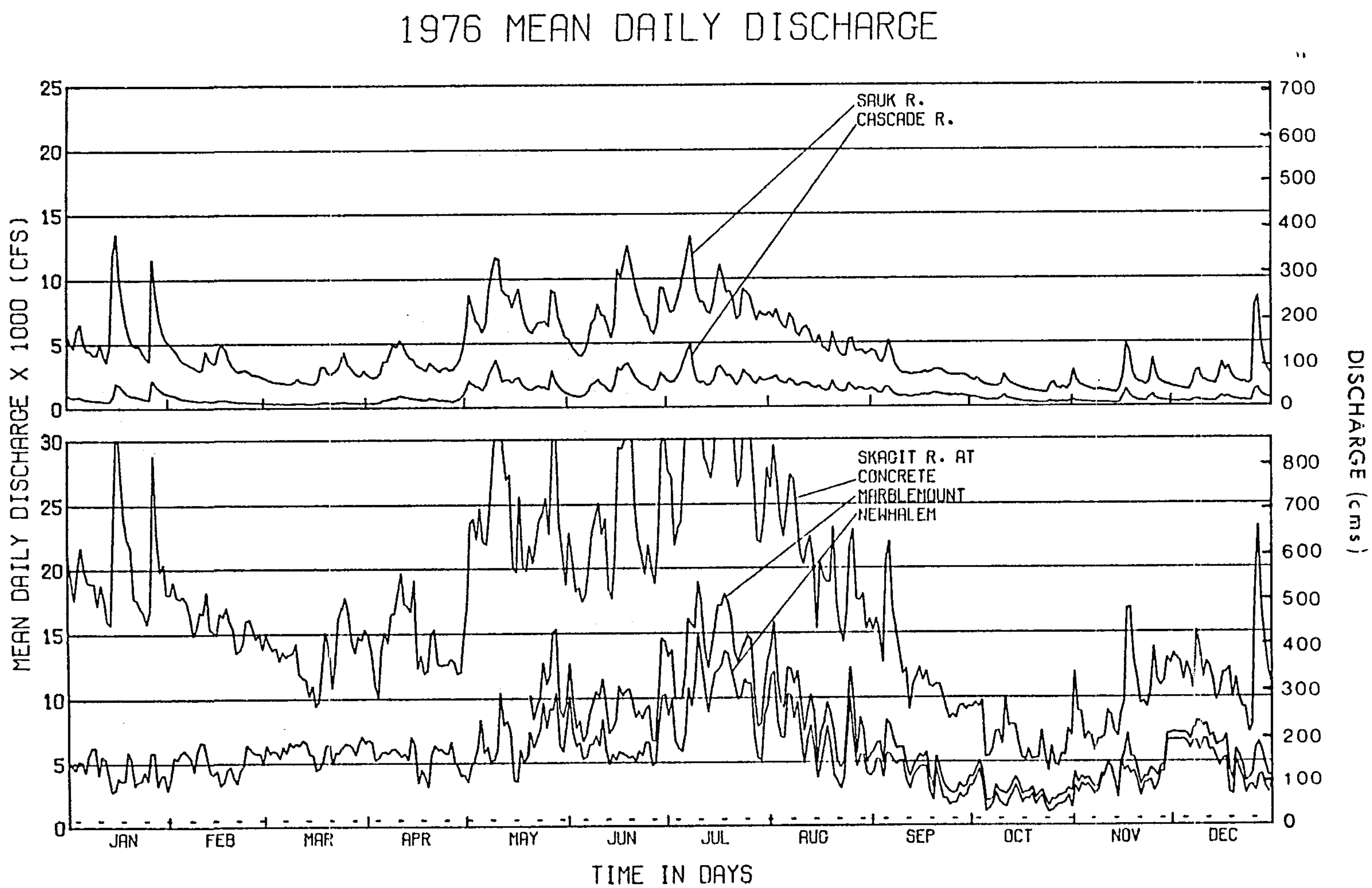


Fig. 3. Hydrographs of mean daily discharges at gaging sites on the Sauk, Cascade, and Skagit rivers for 1976 (USGS).

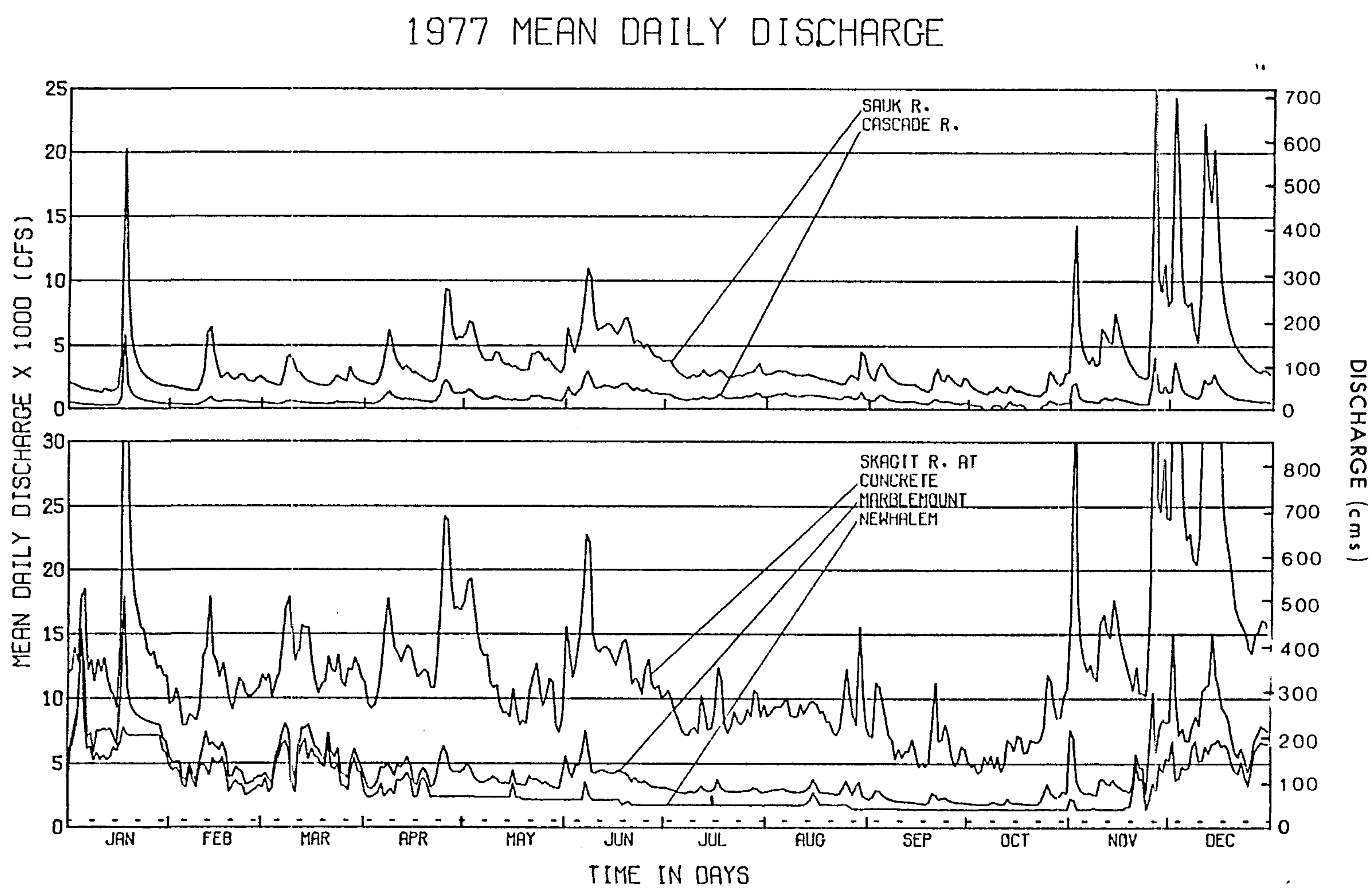


Fig. 4. Hydrographs of mean daily discharges at gaging sites on the Sauk, Cascade, and Skagit rivers for 1977 (USGS).

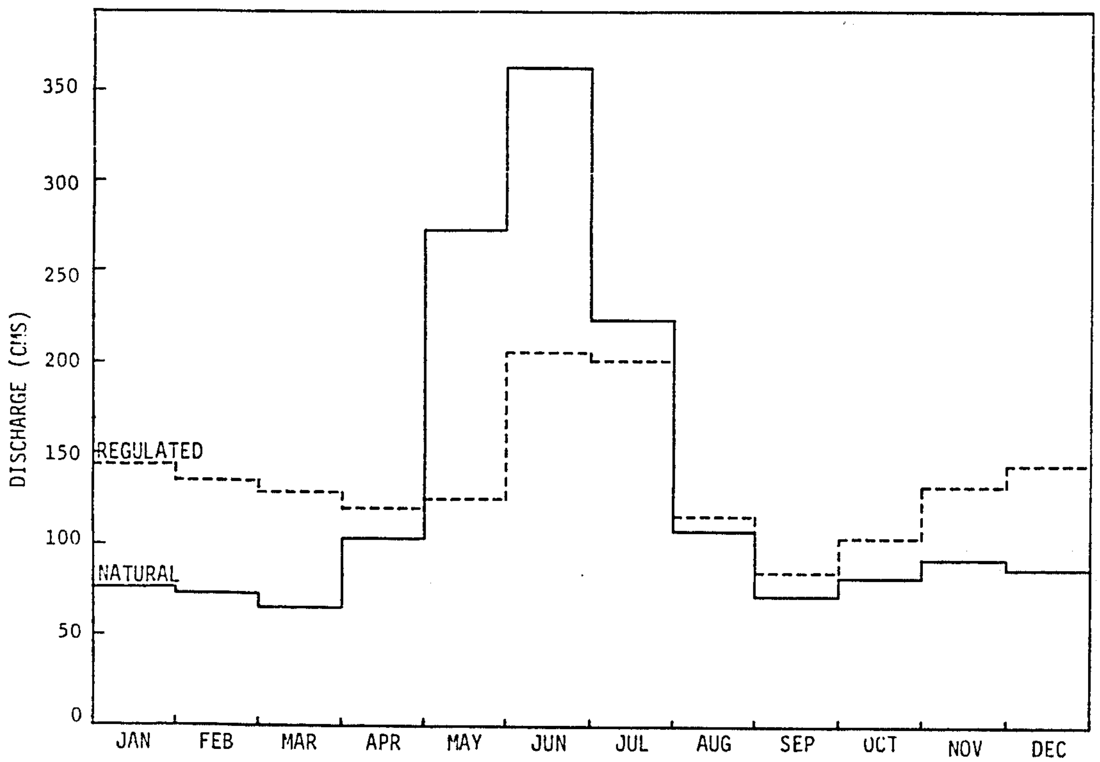


Fig. 5. Long-term natural and regulated streamflow patterns for the Skagit River at Newhalem (1954-1975) (SCL and USGS).

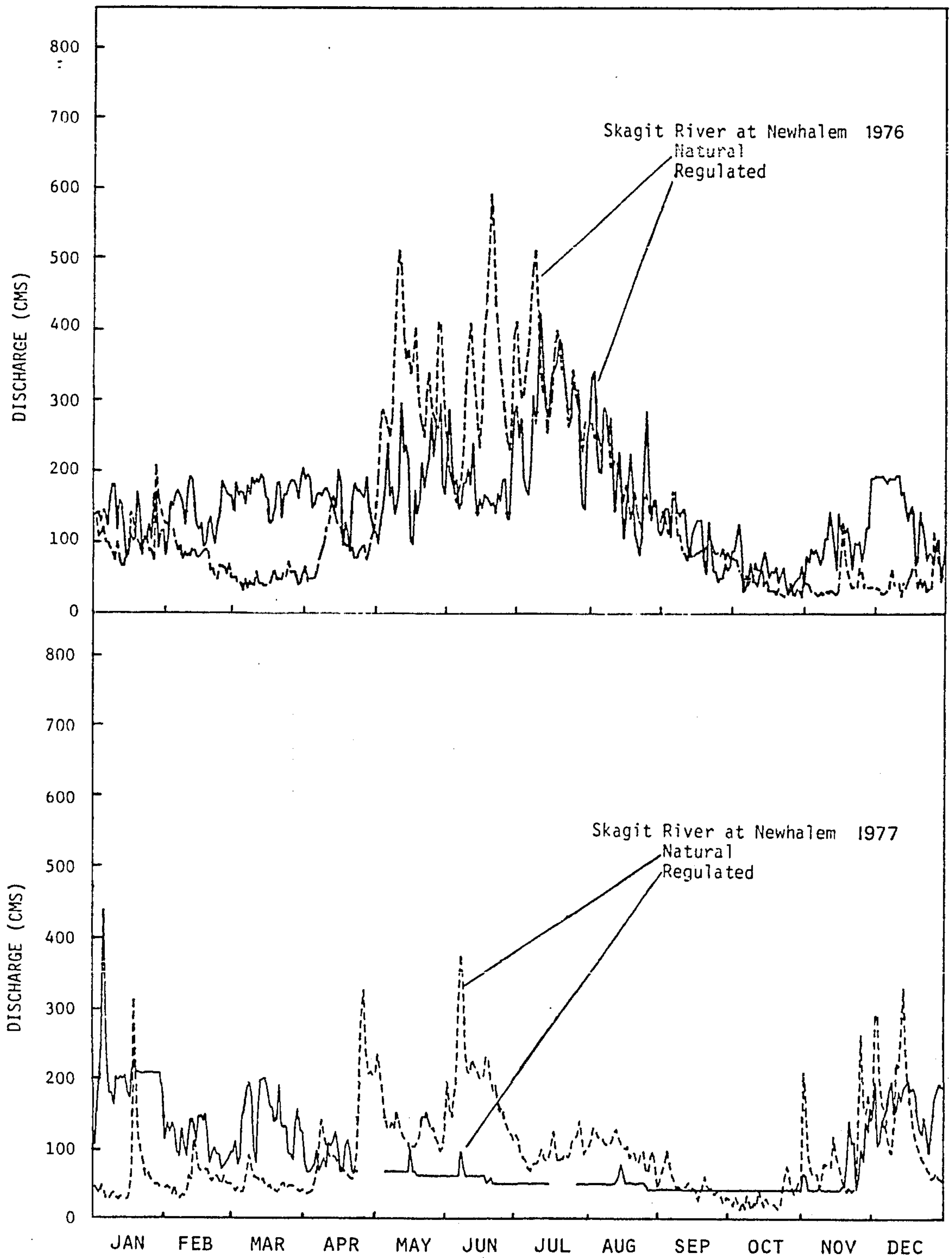


Fig. 6. Natural and regulated streamflow for the Skagit River at Newhalem for 1976 and 1977 (SCL and USGS).

The short-term, daily streamflow pattern in the Skagit River was also influenced by regulation. The hydroelectric facilities on the Skagit were operated to produce peaking power from January 1976 to mid-April 1977. As a result, diel flow fluctuations occurred at Newhalem (Fig. 7 and 8) and at Marblemount (Fig. 9 and 10) during this time period. Due to low water levels in the reservoirs, no daily hydroelectric peaking occurred from mid-April to mid-November 1977. During this time, flow was nearly stable at Newhalem and fluctuated little at Marblemount. Peaking was resumed in mid-November as water levels in the reservoirs returned to normal.

While peaking was occurring, there was a pronounced difference between the degree of daily water level fluctuation in the Skagit and the unregulated Sauk and Cascade rivers. The mean daily range in water level for the months June 1976 to March 1977 ranged from 0.21 m to 0.43 m at the Marblemount USGS gaging station, near the lower Skagit sampling station (Table 2 and 3). At the same time, the mean daily range per month never exceeded 0.12 m in the Sauk and 0.09 m in the Cascade. Mean daily fluctuation between high and low water levels was always greater in the Skagit at Marblemount than in the Sauk or Cascade rivers.

The severity of the daily flow fluctuations downstream of Newhalem was usually dampened by tributary inflow. The mean daily range in water level was always less at Marblemount than at Newhalem from June 1976 through April 1977 (Table 2 and 3). High tributary inflow due to heavy rainfall occasionally increased the degree of daily flow fluctua-

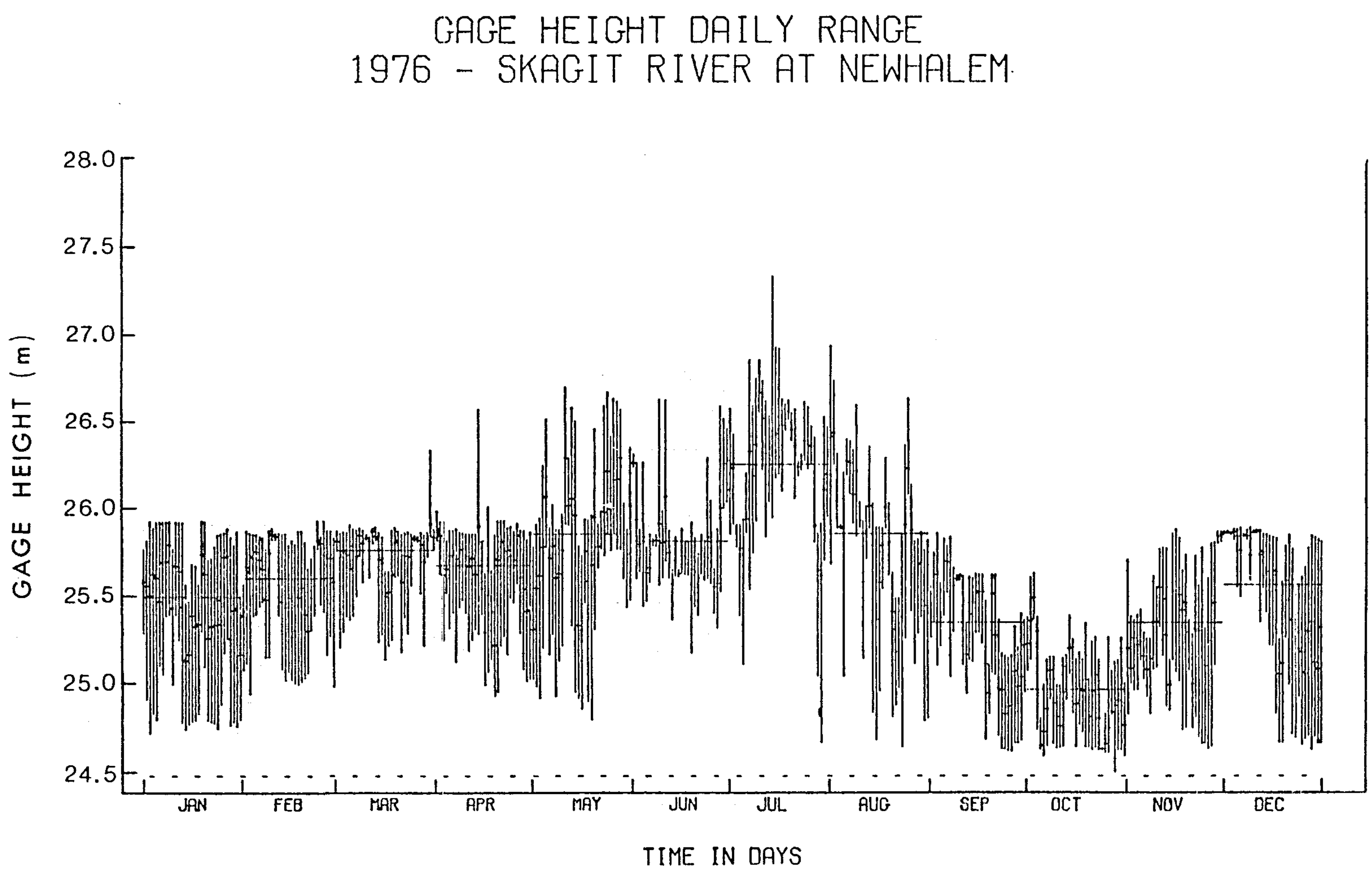


Fig. 7. Daily range of flow fluctuations for the Skagit River at Newhalem (USGS) for 1976.

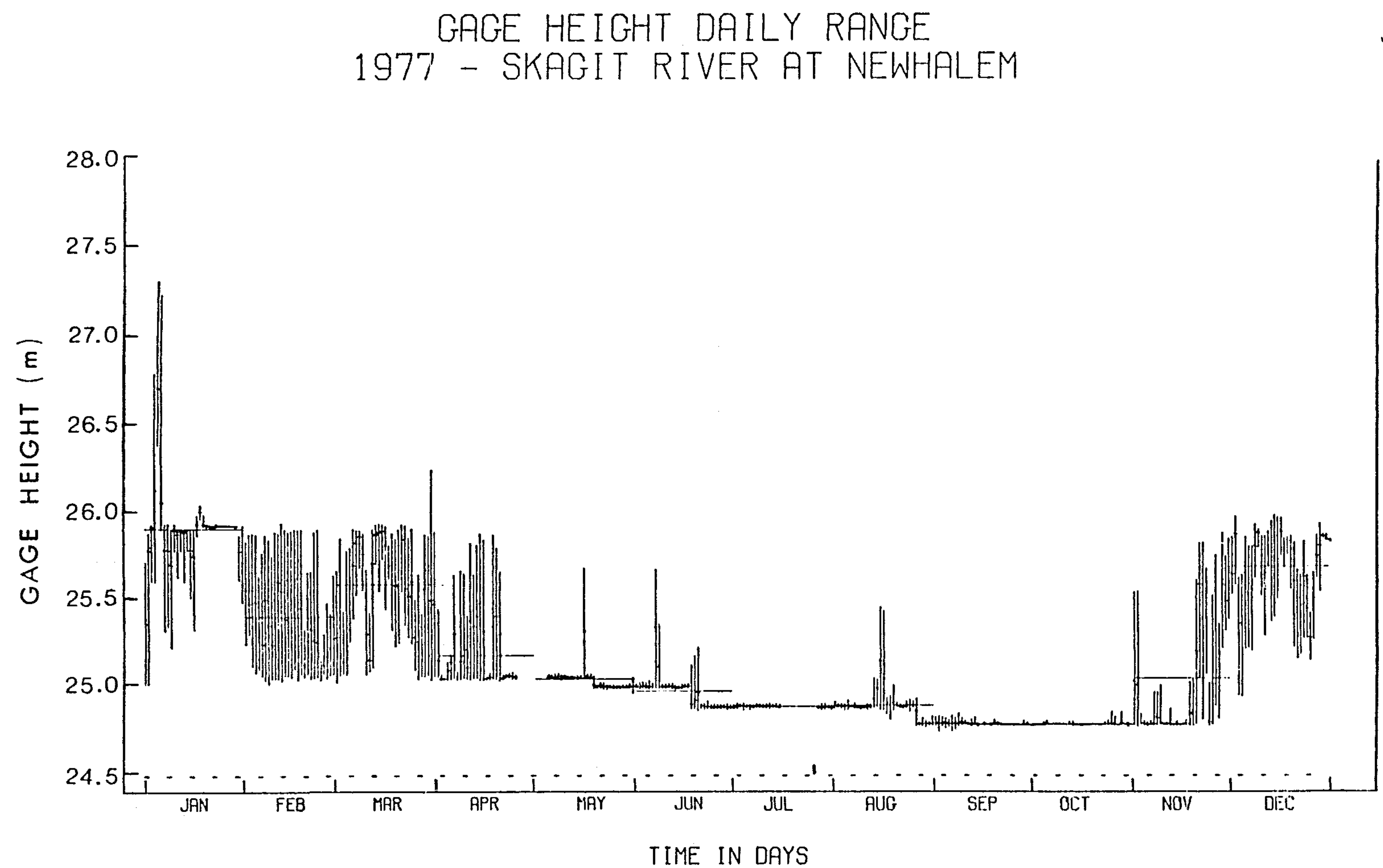


Fig. 8. Daily range of flow fluctuations for the Skagit River at Newhalem (USGS) for 1977.

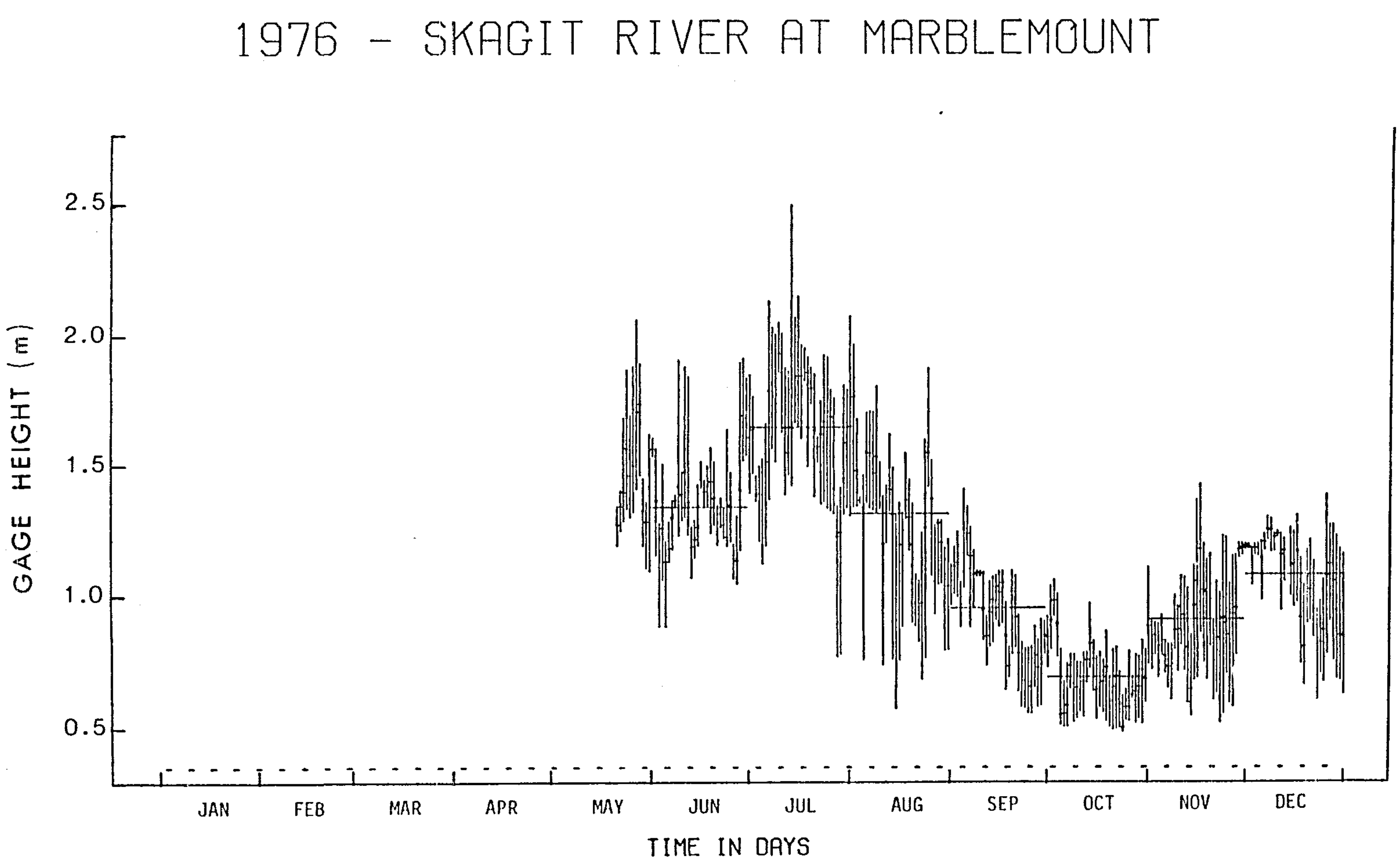


Fig. 9. Daily range of flow fluctuations for the Skagit River at Marblemount (USGS) for June through December 1976.

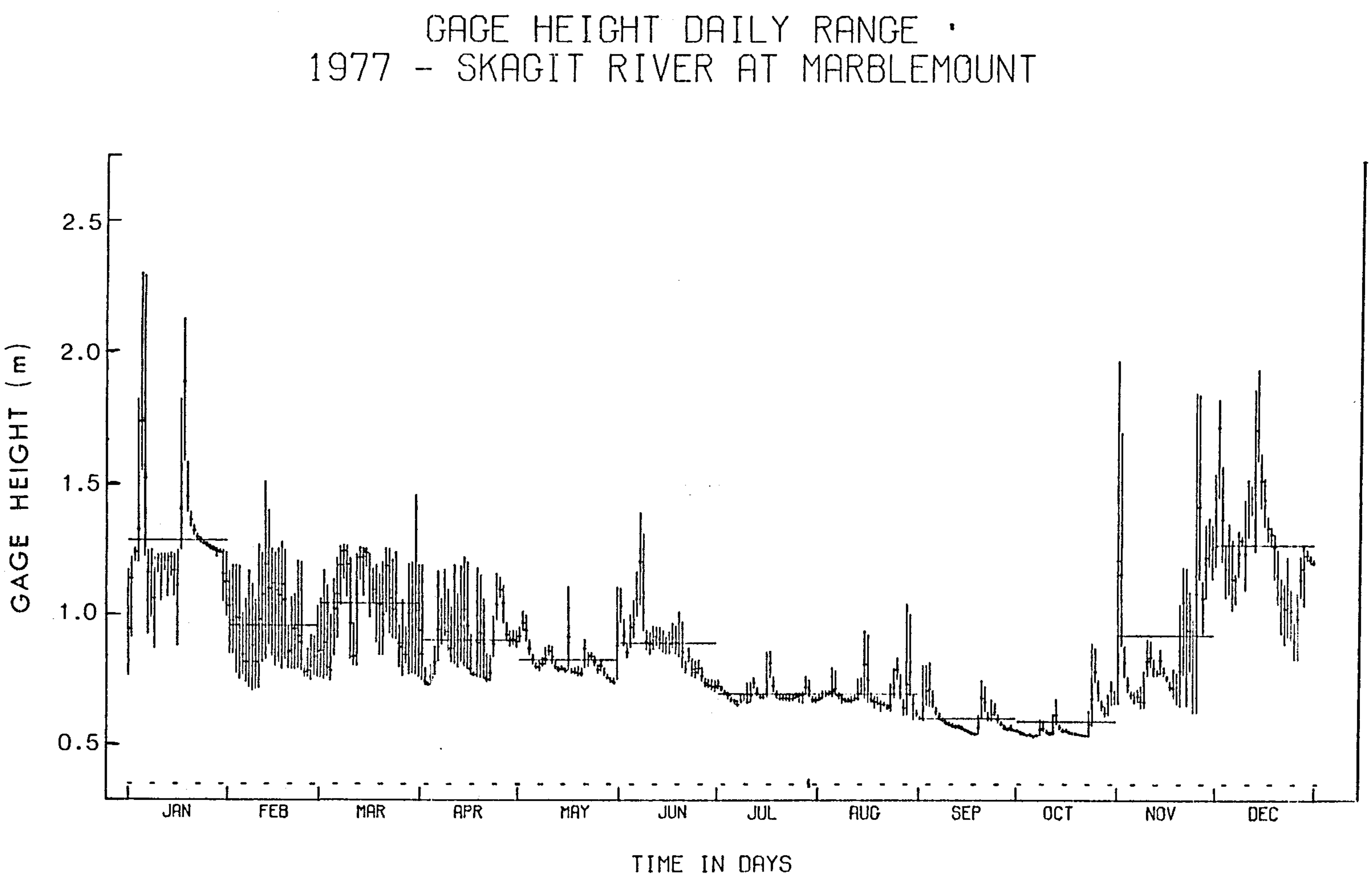


Fig. 10. Daily range of flow fluctuations for the Skagit River at Marblemount (USGS) for 1977.

Table 2. Mean daily range in water level (m) during each month in 1976 at the Skagit at Newhalem and Marblemount, the Sauk, and the Cascade USGS gaging stations.

| | STATION | | | |
|---|---|---|---|---|
| Month | Skagit at Newhalem | Skagit at Marblemount | Sauk | Cascade |
| January | 0.87 | -- | 0.16 | -- |
| February | 0.59 | -- | 0.05 | -- |
| March | 0.36 | -- | 0.06 | -- |
| April | 0.55 | -- | 0.05 | -- |
| May | 0.81 | -- | 0.11 | -- |
| June | 0.41 | 0.28 | 0.09 | -- |
| July | 0.57 | 0.43 | 0.12 | -- |
| August | 0.68 | 0.43 | 0.09 | 0.09 |
| September | 0.47 | 0.22 | 0.05 | 0.03 |
| October | 0.43 | 0.21 | 0.05 | 0.04 |
| November | 0.61 | 0.33 | 0.11 | 0.07 |
| December | 0.58 | 0.26 | 0.10 | 0.06 |
| Annual mean | 0.58 | -- | 0.09 | -- |
| May-October mean | 0.56 | -- | 0.09 | -- |

Table 3. Mean daily range in water level (m) during each month in 1977 at the Skagit at Newhalem and Marblemount, the Sauk, and the Cascade USGS gaging stations.

| | STATION | | | |
|---|---|---|---|---|
| Month | Skagit at Newhalem | Skagit at Marblemount | Sauk | Cascade |
| January | 0.33 | 0.23 | 0.12 | 0.07 |
| February | 0.68 | 0.35 | 0.04 | 0.05 |
| March | 0.55 | 0.28 | 0.05 | 0.02 |
| April | 0.37 | 0.20 | 0.09 | 0.07 |
| May | 0.04 | 0.05 | 0.07 | 0.05 |
| June | 0.09 | 0.10 | 0.14 | 0.12 |
| July | 0.01 | 0.04 | 0.05 | 0.05 |
| August | 0.09 | 0.08 | 0.05 | 0.09 |
| September | 0.03 | 0.04 | 0.08 | 0.07 |
| October | 0.01 | 0.04 | 0.06 | 0.05 |
| November | 0.34 | 0.27 | 0.28 | 0.16 |
| December | 0.37 | 0.21 | 0.23 | 0.09 |
| Annual Mean | 0.24 | 0.15 | 0.11 | 0.07 |
| May-October Mean | 0.05 | 0.06 | 0.08 | 0.07 |

tion downstream from Newhalem instead of dampening fluctuation during periods of peaking. This effect was evident in mid-January 1977 and in November and December 1977.

Precipitation or snowmelt also produced occasional daily increases in water level in the Sauk River of a meter or more (Fig. 11 and 12). These large daily flow fluctuations were confined to the months of November, December and January and did not occur on a daily basis as in the Skagit. Although water level rose rapidly on these occasions, it usually subsided gradually, requiring several days to return to its previous level. The pattern of daily flow fluctuation in the Cascade River (Fig. 13 and 14) was nearly identical to the pattern in the Sauk and differed only in magnitude of the fluctuations.

During the period of relatively stable flow, mid-April 1977 to mid-November 1977, the degree of flow fluctuation was similarly low in all three rivers. The mean daily fluctuation in water level in the Skagit River at Marblemount from May through October 1977 was only 0.06 m, while it was 0.08 and 0.07 m in the Sauk and Cascade rivers, respectively. The variation in water level during this time period was caused by the same natural factors, precipitation and snowmelt, in all three rivers, resulting in similar patterns of daily flow fluctuation.

Exposure Level

Calculation of exposure time during a specified period prior to sampling is a useful method for summarizing the exposure history of a particular area of the river bottom. Its primary use is in comparing standing crops in zones of the same stream that were subjected to

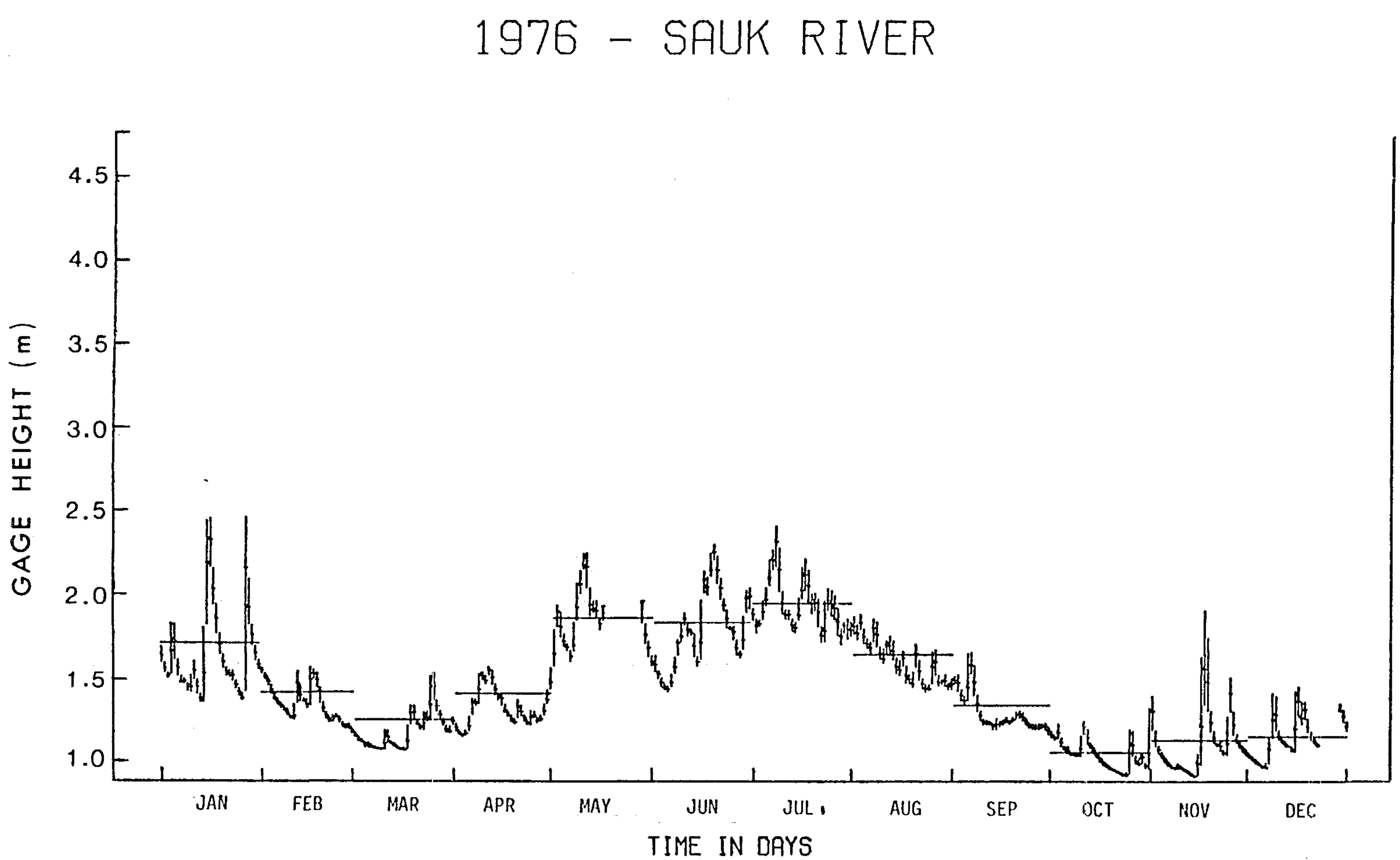


Fig. 11. Daily range of flow fluctuations for the Sauk River (USGS) for 1976.

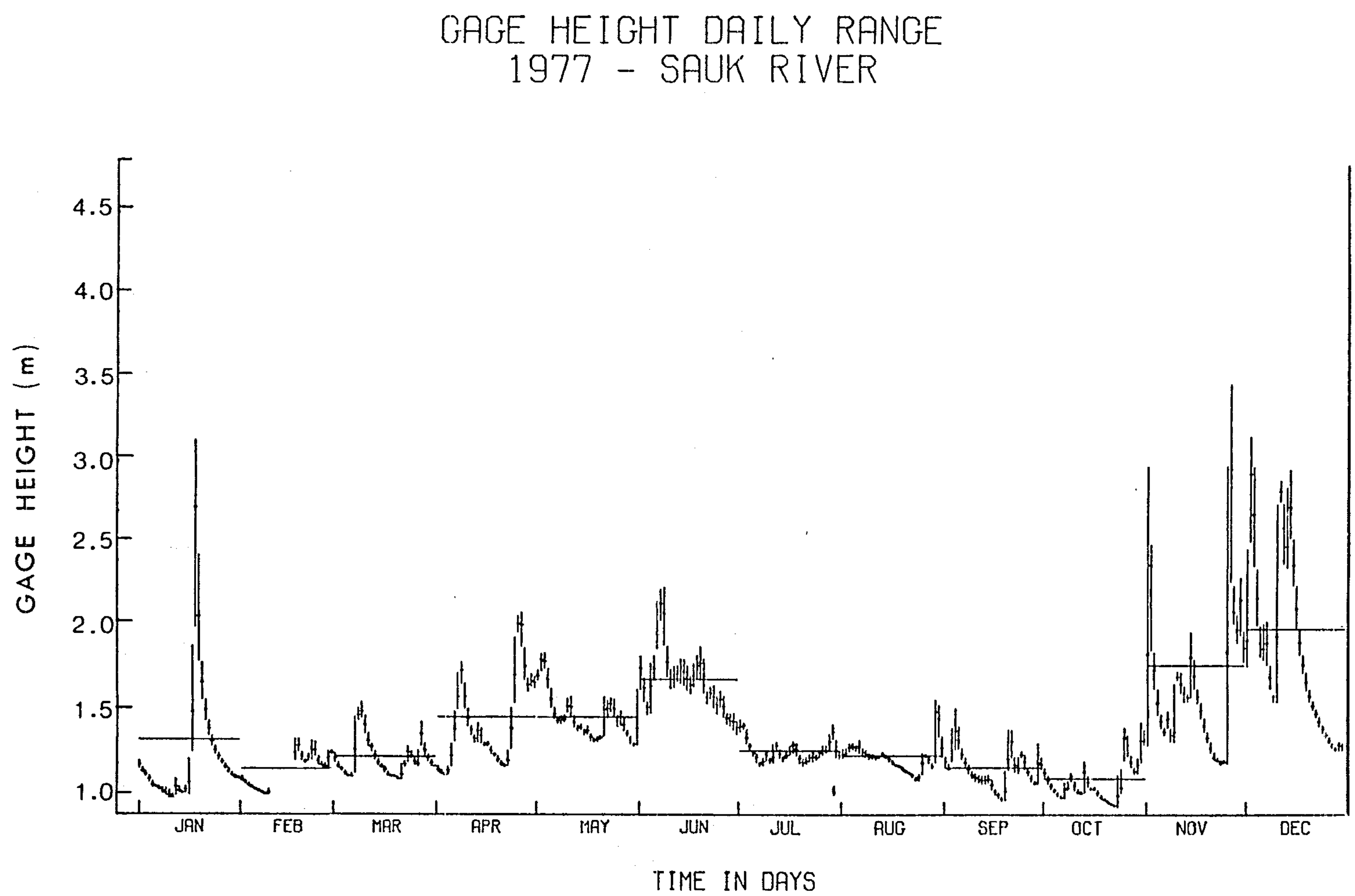


Fig. 12. Daily range of flow fluctuations for the Sauk River (USGS) for 1977.

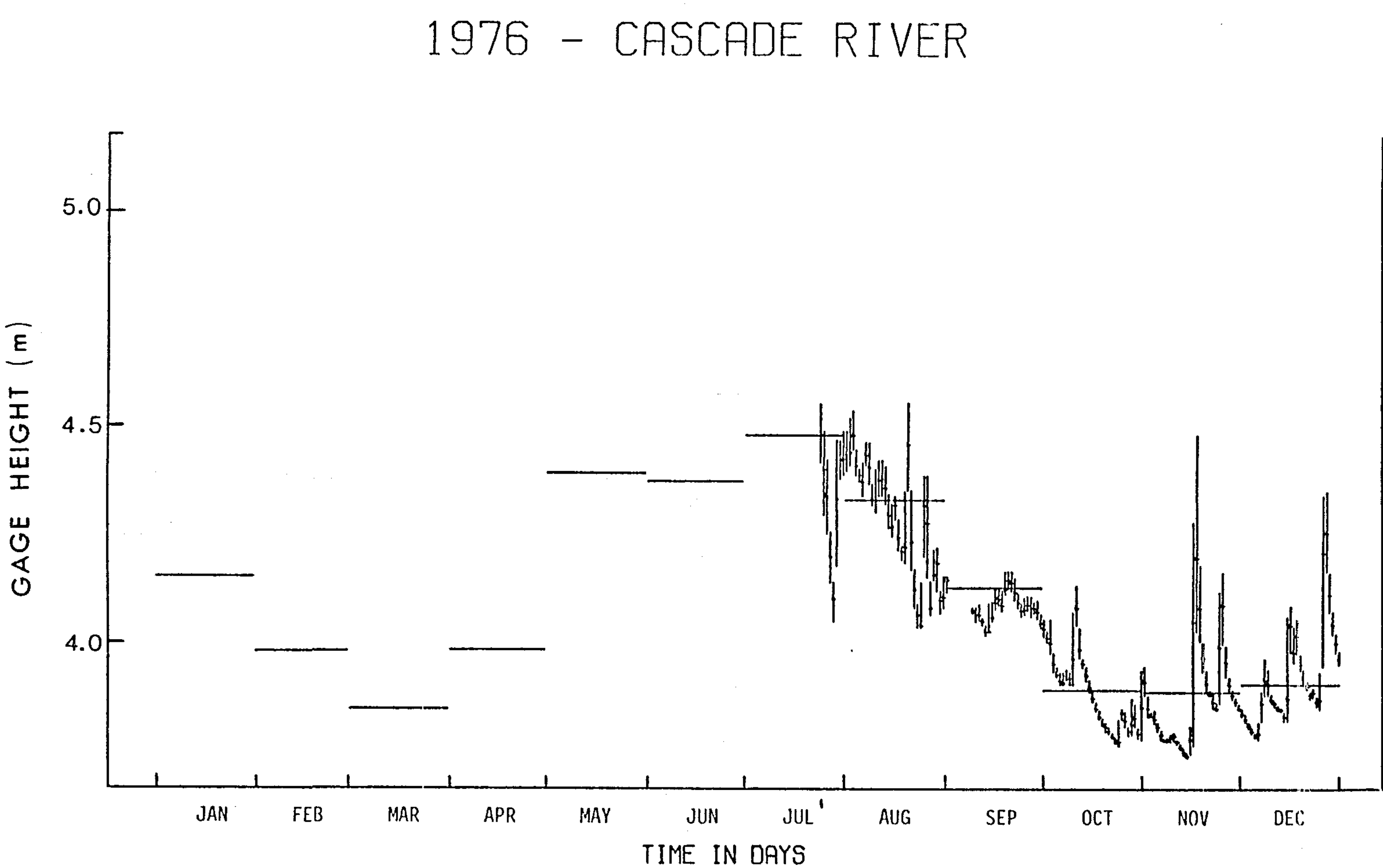


Fig. 13. Daily range of flow fluctuations for the Cascade River (USGS) for August through December 1976.

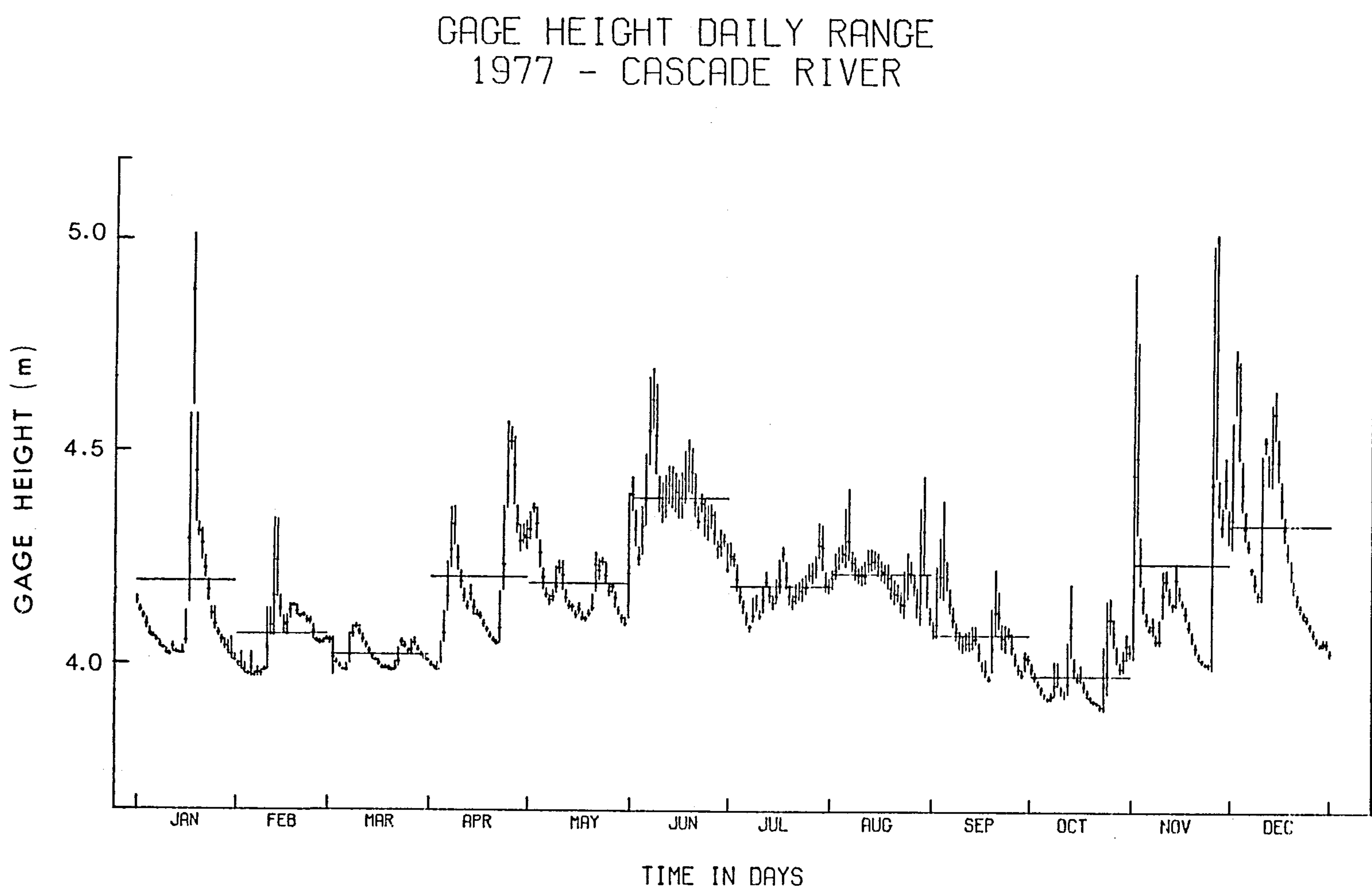


Fig. 14. Daily range of flow fluctuations for the Cascade River (USGS) for 1977.

Tablé 4. Percentage of time that the artificial substrate periphyton samplers were exposed to desiccation during the six-week period prior to sampling. Samplers were located on a cross river transect, and depth increased with the sampler number.

| Station | Date | Sampler Number | | | |
|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 |
| Skagit (Lower) | 10/14/76 | 72 | 41 | 40 | 20* |
| | 11/29/76 | 100 | 87 | 81 | 56* |
| | 1/12/77 | 24 | 13 | 5* | 2* |
| | 2/24/77 | 44 | 25 | 9 | 0 |
| Sauk (Lower) | 10/15/76 | 81 | 9 | 0 | 0 |
| | 11/30/76 | 91 | 72 | 0 | 0 |
| | 1/12/76 | 92 | 54 | 0 | 0 |
| | 3/21/77 | 87 | 7* | 0 | 0 |
| Cascade | 10/15/76 | 40 | 22 | 0 | 0 |
| | 11/30/76 | 95 | 90 | 80 | 39* |
| | 1/12/77 | 93 | 83 | 61 | 14* |
| | 3/21/77 | 100 | 100 | 81 | 38* |

* Results from these exposed samplers were used in calculating the mean for the sampling station.

the lower Skagit and Cascade stations made it difficult to compare rivers in 1976.

The flows were relatively stable during the period when the periphyton was removed directly from streambed rocks. As a result, there was relatively little exposure of the sampling sites (Table 5). None of the upper Skagit sites were exposed prior to sampling from May to November 1977. The 15-cm sites in May and June 1977 were exposed early in the six-week exposure calculation period, and the periphyton apparently had enough time to return to a high level before sampling. The other sites at the lower Sauk and Cascade stations marked with an asterisk (*) were also exposed early in the six-week period, allowing the periphyton to recolonize before sampling.

There was no exposure of benthic insect sampling locations during the two-week exposure calculations period at the lower Sauk and Cascade stations in 1976 (Table 6). The amount of exposure at sites at the lower Skagit station was high during May, September and November 1976, and no samples were collected in unexposed areas in May or November. During 1977, there was little exposure at any of the stations other than at the upper Skagit station in February. All 16 replicate samples were used to calculate the station means during 1977, with the exception of the upper Skagit station in February. Since periphyton and benthos were always sampled at the same depths and usually on the same dates in 1977, the six-week exposure figures in Table 5 also represent the amount of exposure for benthic insect sample locations during the six weeks prior to sampling.

Table 5. Percentage of time that the streambed at periphyton sampling locations was exposed to desiccation during the six-week period prior to sampling.

| Station | Sampling Date | Depth of Water at Sample Site (cm) 15 | 25 | 35 | 45 |
|---|---|---|---|---|---|
| Skagit (Upper) | 5/11/77 | 0 | 0 | 0 | 0 |
| | 6/16/77 | 0 | 0 | 0 | 0 |
| | 7/26/77 | 0 | 0 | 0 | 0 |
| | 9/14/77 | 0 | 0 | 0 | 0 |
| | 11/ 9/77 | 0 | 0 | 0 | 0 |
| Skagit (Lower) | 5/ 6/77 | 8* | 0 | 0 | 0 |
| | 6/16/77 | 10* | 0 | 0 | 0 |
| | 7/26/77 | 0 | 0 | 0 | 0 |
| | 9/14/77 | 0 | 0 | 0 | 0 |
| | 11/ 9/77 | 0 | 0 | 0 | 0 |
| Sauk (Lower) | 5/ 5/77 | 38 | 0 | 0 | 0 |
| | 6/17/77 | 63* | 0 | 0 | 0 |
| | 7/27/77 | 0 | 0 | 0 | 0 |
| | 9/13/77 | 0 | 0 | 0 | 0 |
| | 11/ 8/77 | 43* | 0 | 0 | 0 |
| Cascade | 5/10/77 | 63 | 25 | 9* | 0 |
| | 6/17/77 | 52 | 36 | 0 | 0 |
| | 7/25/77 | 0 | 0 | 0 | 0 |
| | 9/14/77 | 0 | 0 | 0 | 0 |
| | 11/10/77 | 74* | 62* | 44* | 8* |

*Results from these exposed sample locations were used in calculating the mean for the sampling station.

Table 6. Percentage of time that the streambed at benthic sampling locations was exposed to desiccation during the two-week period prior to sampling.

| Station | Sampling Date | Depth of Water at Sample Site (cm) | | | | |
|---|---|---|---|---|---|---|
| | | 15 | 25 | 30 | 35 | 45 |
| Skagit (Upper) | 2/24/77 | 72 | 64 | -- | 50 | 16* |
| | 5/11/77 | 0 | 0 | -- | 0 | 0 |
| | 7/26/77 | 0 | 0 | -- | 0 | 0 |
| | 9/14/77 | 0 | 0 | -- | 0 | 0 |
| | 11/9/77 | 0 | 0 | -- | 0 | 0 |
| Skagit (Lower) | 5/20/76 | 35 | | 21 | | 16* |
| | 7/28/76 | 1* | 1* | -- | 0 | 0 |
| | 9/14/76 | 40 | 33 | -- | 6 | 0 |
| | 11/12/76 | 96 | 86 | -- | 69 | 22 |
| | 2/24/77 | 0 | 0 | -- | 0 | 0 |
| | 5/6/77 | 0 | 0 | -- | 0 | 0 |
| | 7/26/77 | 0 | 0 | -- | 0 | 0 |
| | 9/14/77 | 0 | 0 | -- | 0 | 0 |
| | 11/9/77 | 0 | 0 | -- | 0 | 0 |
| Sauk (Upper) | 2/17/77 | 0 | 0 | -- | 0 | 0 |
| | 5/ 5/77 | 17* | 12* | -- | 11* | 10* |
| | 7/27/77 | 0 | 0 | -- | 0 | 0 |
| | 9/13/77 | 0 | 0 | -- | 0 | 0 |
| | 11/8/77 | 0 | 0 | -- | 0 | 0 |
| Sauk (Lower) | 5/21/76 | 0 | -- | 0 | -- | 0 |
| | 7/14/76 | 0 | -- | 0 | -- | 0 |
| | 9/15/76 | 0 | -- | 0 | -- | 0 |
| | 11/12/76 | 0 | -- | 0 | -- | 0 |
| | 2/17/77 | 16* | 0 | -- | 0 | 0 |
| | 5/ 5/77 | 10* | 0 | -- | 0 | 0 |
| | 7/27/77 | 0 | 0 | -- | 0 | 0 |
| | 9/13/77 | 0 | 0 | -- | 0 | 0 |
| | 11/ 8/77 | 0 | 0 | -- | 0 | 0 |
| Cascade | 5/21/76 | 0 | -- | 0 | -- | 0 |
| | 7/14/76 | 0 | -- | 0 | -- | 0 |
| | 9/15/76 | 0 | -- | 0 | -- | 0 |
| | 11/12/76 | 0 | -- | 0 | -- | 0 |

*Results from these exposed sample locations were used in calculating the mean for the sampling station.

The distances from the permanent marker near the high water line to each periphyton and benthic sample location are shown in Figs. 15-17.

Water Quality

Water quality data provided by the USGS indicate that the Skagit and Sauk rivers are both low pH, highly oxygenated, low nutrient streams (Table 7). Mean annual specific conductance, pH and dissolved oxygen levels were nearly identical in both rivers. The amount of total nitrate, ammonia nitrogen and total phosphorus were slightly higher in the Sauk River. The Skagit River water samples were collected at a point less than one km below Gorge Powerhouse and reflect the low nutrient content of the reservoir water being released at the powerhouse.

Turbidity levels were much lower at all stations during August and September 1976 (Table 8) than during the same months in 1977 (Table 9). The Skagit and Cascade were considerably less turbid than the Sauk during July and August 1977. The drainage basins of the three rivers contain numerous glaciers, and the increased turbidity in 1977 was caused primarily by glacial flour in the water. Glacial melting was more extensive in 1977 than in 1976 because of low precipitation during the winter and generally warmer air temperature during the summer. Several streams contributed suspended sediment of glacial origin to the Skagit above Gorge Dam, and it appears that the amount of sediment in the river below Newhalem was reduced by settling in the reser-

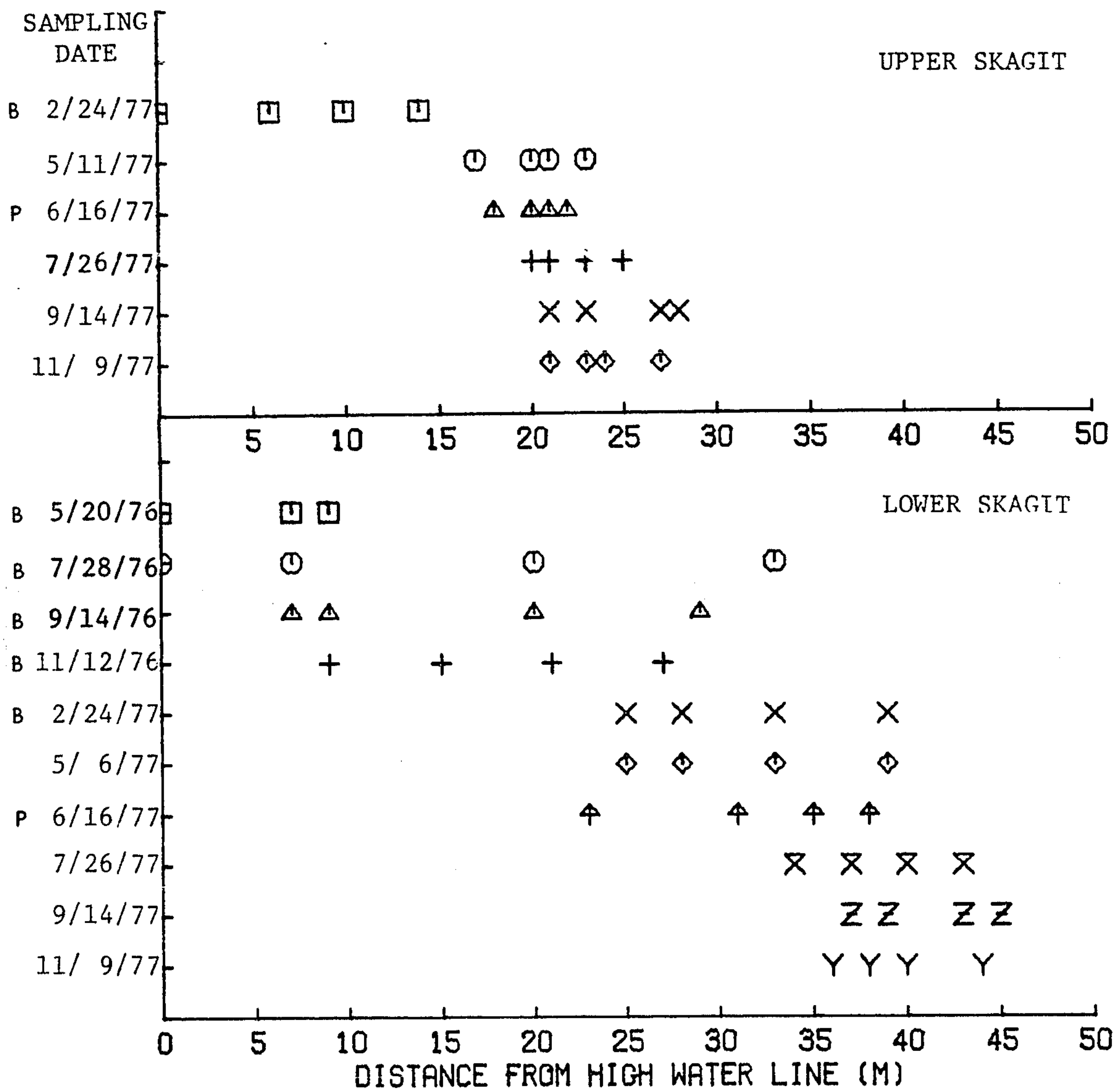


Fig. 15. Location of benthic insect and periphyton sampling sites along the upper and lower Skagit River sampling transects. A ( B ) denotes dates on which only benthic insects were sampled, while ( P ) denotes dates on which only periphyton was sampled.

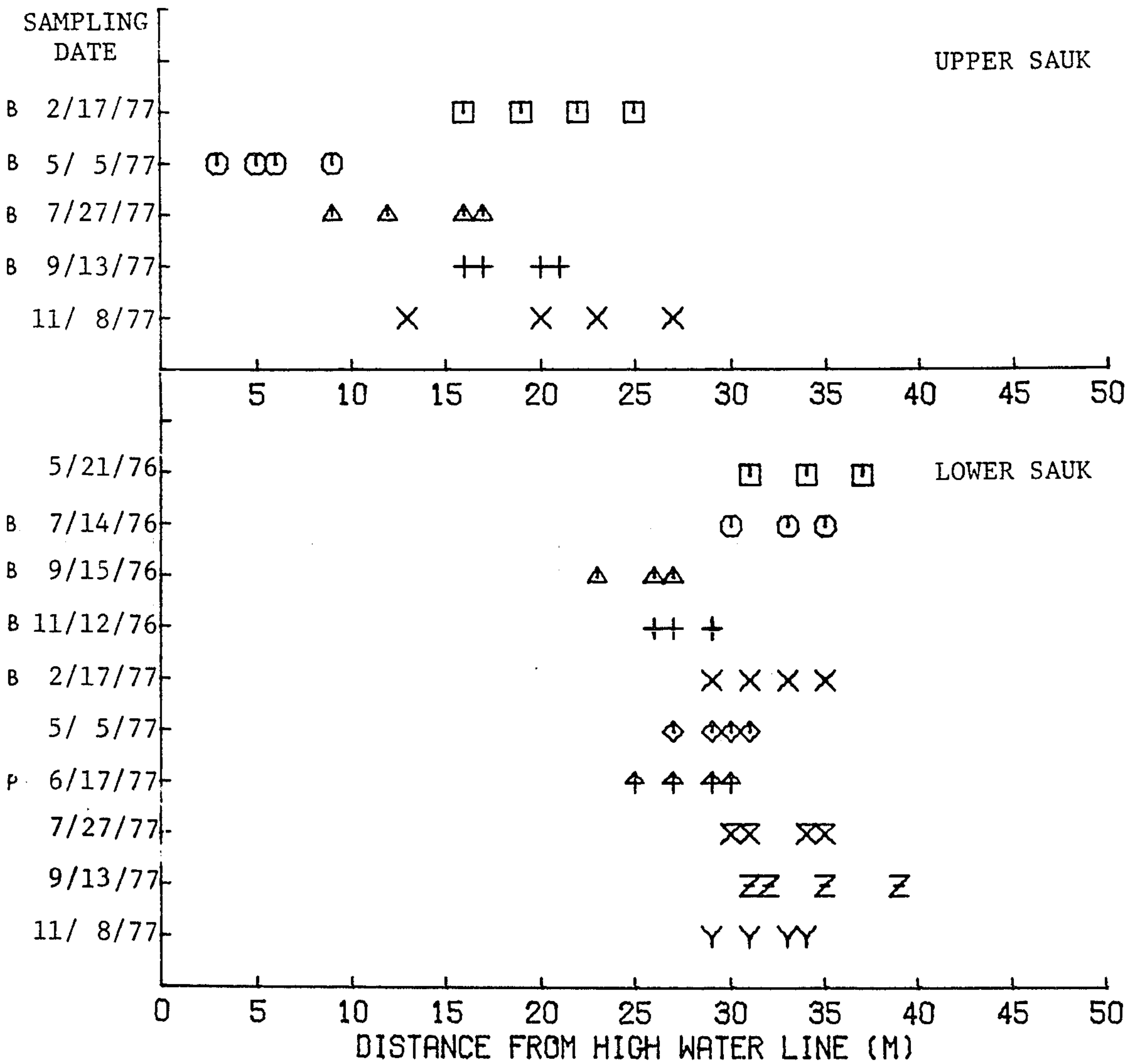


Fig. 16. Location of benthic insect and periphyton sampling sites along the upper and lower Sauk River sampling transects. A ( B ) denotes dates on which only benthic insects were sampled, while ( P ) denotes dates on which only periphyton was sampled.

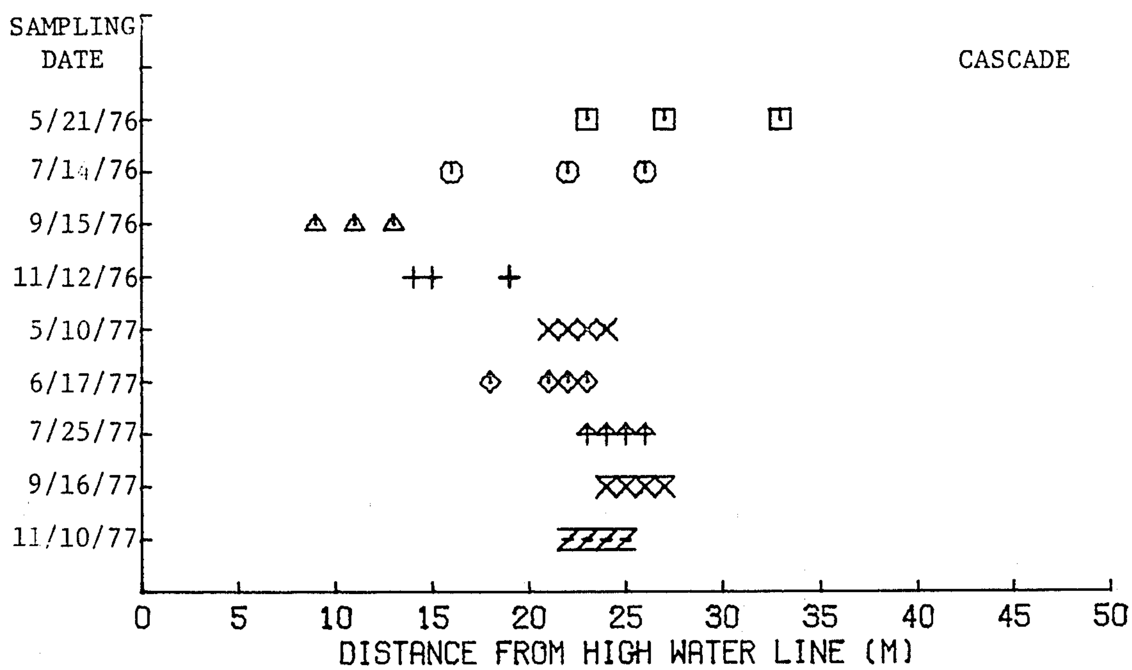


Fig. 17. Location of benthic insect and periphyton sampling sites along the Cascade River transects. Only benthic insects were sampled during 1976, while only periphyton was sampled in 1977.

Table 7. Mean annual chemical water quality parameters in the Skagit River at Newhalem and in the Sauk River at the lower sampling station from October 1976 through September 1977 (after USGS).

| Parameter | River | |
|---|---|---|
| | Skagit | Sauk |
| Specific conductance (micromhos/$cm^2$) | 58 | 57 |
| pH | 7.3 | 7.4 |
| Dissolved oxygen (mg/1) | 12.2 | 12.0 |
| Total nitrite plus nitrate (mg/1 N) | 0.06 | 0.12 |
| Total ammonia nitrogen | 0.04 | 0.07 |
| Total phosphorus (mg/1 P) | 0.01 | 0.05 |
| Dissolved orthophosphorus (mg/1 P) | < 0.00 | < 0.00 |

Table 8. Mean monthly turbidity (J.T.U.) at stations on the Skagit, Cascade, and Sauk rivers during 1976.

| | Station | | | |
|---|---|---|---|---|
| Month | Skagit at Newhalem | Skagit at Marblemount | Cascade | Sauk Lower |
| June | 1.7 | 3.3 | 8.3 | 7.7 |
| July | 4.0 | 5.6 | 13.0 | 31.0 |
| August | 4.7 | 4.3 | 3.7 | 13.0 |
| September | 0.3 | 0 | 0.5 | 15.0 |
| October | 0 | 0 | 1.0 | 5.0 |
| November | 2.6 | 2.8 | 2.0 | 8.4 |
| December | 6.3 | 9.3 | 11.3 | 11.5 |
| Mean | 2.8 | 3.6 | 5.4 | 12.7 |
| June-November mean | 2.1 | 2.5 | 4.4 | 14.1 |

Table 9. Mean monthly turbidity (J.T.U.) at stations on the Skagit, Cascade, and Sauk rivers during 1977.

| MONTH | STATION | | | | |
|---|---|---|---|---|---|
| | Skagit at Newhalem | Skagit at Marblemount | Cascade | Sauk Upper | Sauk Lower |
| January | 4.2 | 4.4 | 6.4 | -- | 5.8 |
| February | 5.0 | 6.7 | 10.0 | -- | 6.7 |
| March | 3.8 | 3.7 | 4.3 | -- | 4.3 |
| April | 5.3 | 6.3 | 7.6 | -- | 15.0 |
| May | 3.3 | 3.4 | 3.2 | -- | 5.2 |
| June | 6.3 | 5.3 | 6.7 | -- | 19.3 |
| July | 2.0 | 4.7 | 2.8 | 20.0 | 43.8 |
| August | 10.0 | 7.3 | 9.0 | 39.5 | 197.5 |
| September | 5.3 | 5.3 | 30.0 | 8.3 | 30.5 |
| October | 4.8 | 4.2 | 4.6 | 8.8 | 24.0 |
| November | 5.0 | 2.0 | 3.0 | 6.0 | 9.0 |
| Mean | 4.9 | 4.8 | 8.1 | 18.1 | 34.4 |
| June-November Mean | 5.6 | 4.9 | 10.1 | -- | 60.7 |

voirs.

The difference in turbidity levels between the upper and lower Sauk stations was caused by suspended sediment of glacial origin contributed by the Suiattle River. Water from the Suiattle River entered the Sauk immediately above the upper sampling station on the opposite side of the Sauk and did not become mixed with Sauk River water until it had flowed past the sampling transect. As a result, comparatively clear upper Sauk River water flowed over the shoreline area of the transect where samples were collected, while the turbid Suiattle River water flowed over the unsampled portion of the transect.

Temperature

The annual thermal patterns in the three rivers during 1976 and 1977 are shown in Fig. 18. During 1976, water temperatures ranged from 3.5 to 10.7°C in the Skagit and from 3.9 to 11.8°C in the Sauk. The minimum water temperature was not recorded in the Cascade in 1976, but the maximum was 9.6°C. Maximum annual temperatures were several degrees higher in 1977, when water temperatures varied between 4.2 and 12.4°C in the Skagit, between 2.4 and 14.3°C in the Sauk, and between 1.9 and 14.1°C in the Cascade. Maximum temperatures also occurred one month earlier, in July 1977. Due to the release of water stored in the reservoirs, Skagit River water temperatures were higher than Sauk River temperatures from October through December and usually lower from February to September. Water temperatures in the Cascade River were generally lower than in either the Skagit or Sauk rivers.

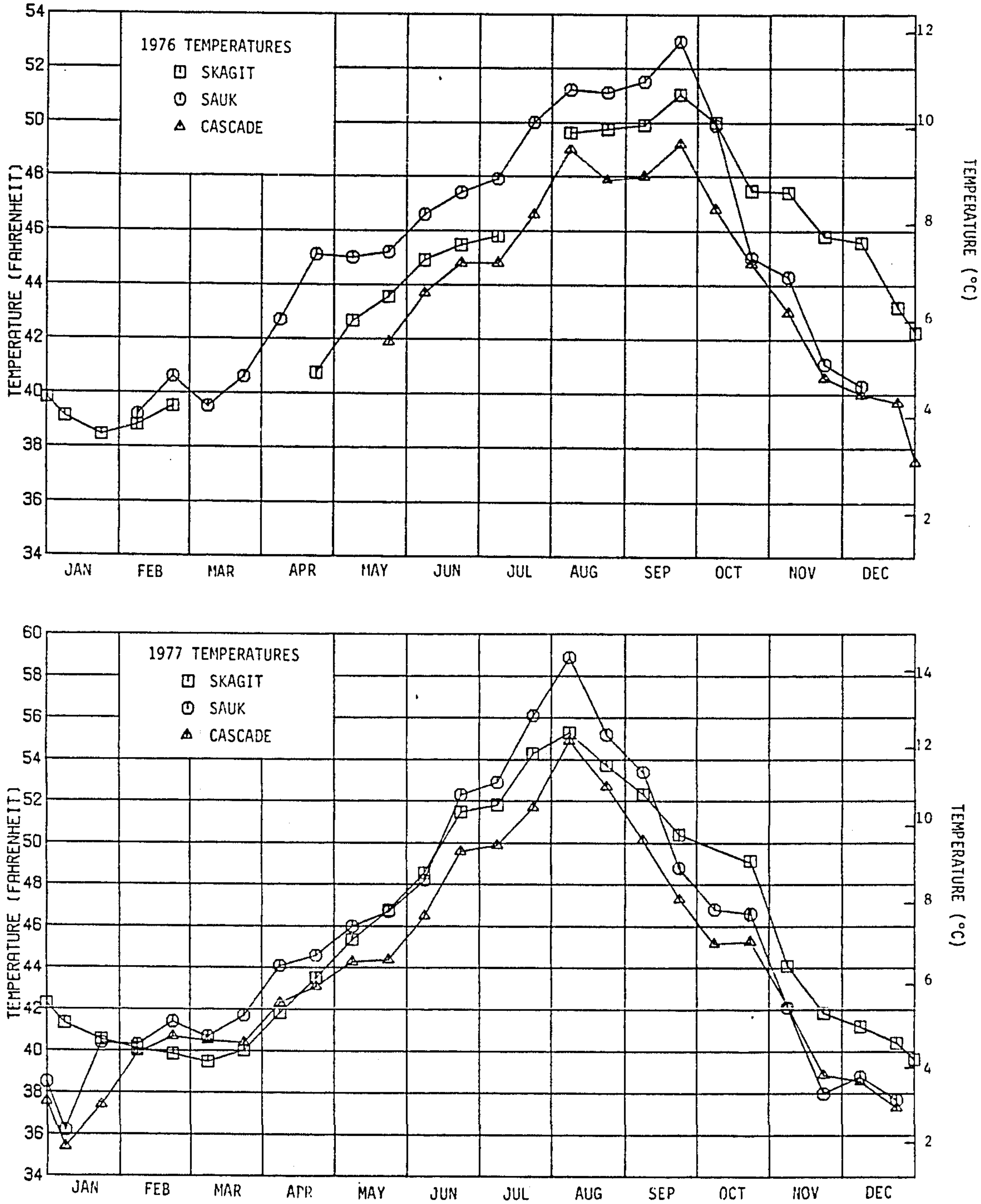


Fig. 18. Semi-monthly water temperature (°F and °C) for the Skagit (above Alma Creek), Sauk, and Cascade rivers during 1976 and 1977 (SCL).

Substrate Analysis

The size composition of the substrate particles differed only slightly among the Skagit and Sauk River stations (Table 10). The substrate was composed mainly of large particles at all stations, and over 50% of the volume of the substrate samples consisted of particles larger than 6.7 mm. When a Kruskall-Wallis test was used to compare percentages of each size category at the four stations, no significant differences were found among stations in seven of the ten size classes. There were significant differences ($p = .05$) only in the 0.85, 0.425 < 0.106 mm size categories. The lower Sauk had the highest percentage of 0.85 mm particles, the upper Skagit had the highest percentage of 0.425 mm particles, and the two Skagit stations both had higher percentages of particles < 0.106 mm.

Although this method of substrate analysis indicated the general size distribution of substrate particles, and perhaps porosity of the substrate, it cannot detect sedimentation of the streambed surface. Sedimentation, or the deposition of sand and silt in the interstices between stones on the surface of the streambed, reduces the habitat available for surface-dwelling insects and may reduce benthic standing crop (Cordone and Kelley 1961, Nuttal 1973, Brusven and Prather 1974).

There was an obvious difference in the amount of interstitial sand and silt in the regulated Skagit and the unregulated Sauk and Cascade rivers. The channels of all three streams were well-armored with cobbles. A large amount of inorganic sediment was visible between the bottom cobbles of Sauk and Cascade rivers during the summer of 1977.

Table 10. Substrate composition at the Skagit and Sauk River benthic insect sampling stations expressed as percent of substrate material retained on each sieve, with the 95% confidence limits.

| Sieve Size (mm) | STATION | | | |
|---|---|---|---|---|
| | Skagit (Upper) | Skagit (Lower) | Sauk (Upper) | Sauk (Lower) |
| 26.9 | 33.4 ± 11.3 | 35.7 ± 19.3 | 38.3 ± 6.9 | 37.3 ± 4.9 |
| 13.2 | 11.3 ± 3.6 | 15.6 ± 5.0 | 12.5 ± 1.5 | 12.5 ± 3.5 |
| 6.7 | 8.6 ± 1.8 | 11.4 ± 2.2 | 11.7 ± 7.0 | 7.6 ± 1.9 |
| 3.35 | 7.0 ± 3.3 | 10.3 ± 4.2 | 8.6 ± 1.1 | 4.9 ± 4.3 |
| 1.70 | 10.4 ± 3.4 | 10.9 ± 4.1 | 8.3 ± 7.0 | 5.2 ± 4.2 |
| 0.85 | 14.1 ± 7.9 | 8.6 ± 8.3 | 13.1 ±12.9 | 21.7 ± 5.8 |
| 0.425 | 10.0 ± 3.3 | 4.0 ± 2.0 | 4.6 ± 2.4 | 7.0 ± 5.5 |
| 0.212 | 2.6 ± 0.9 | 1.5 ± 1.1 | 1.9 ± 1.1 | 2.6 ± 3.4 |
| 0.106 | 1.1 ± 0.4 | 0.8 ± 0.7 | 0.6 ± 0.2 | 0.9 ± 0.8 |
| <0.106 | 1.6 ± 1.4 | 1.3 ± 0.6 | 0.4 ± 0.4 | 0.4 ± 0.4 |

On the July and September sampling dates in 1977, the smaller surface stones were completely covered with sand, leaving only the upper surface of the larger cobbles visible. At the lower Sauk station, the surface of the streambed stones was also covered with a layer of deposited silt. However, the interstices between the surface rocks at both Skagit stations were largely free of sediment on all sampling dates.

### Current Velocity

Mean current velocity at the four depths sampled is shown in Table 11. Current velocity was higher at the two Sauk stations than at the Skagit and Cascade stations, but well within the optimal range for stream invertebrates (Gore 1978). Velocity increased linearly with depth at all stations.

## PERIPHYTON

### Effects of Exposure

Artificial periphyton samplers situated near the edge of the river, in shallow water, were exposed to a greater degree than those near midstream. Stream profiles at the lower Skagit transect along with sampler locations, exposure levels and maximum and minimum water levels during the four 6-week colonization periods, are shown in Figs. 19-20. Low flows exposed all samplers, including the deepest sampler at 38 m from the annual high water line, to desiccation during the first three colonization periods and precluded the collection of data on chlorophyll *a* values under conditions of zero exposure. The sampler nearest

Table 11. Mean bottom current velocity (cm/sec) at sampling stations.

| Station | Depth (cm) | | | |
|---|---|---|---|---|
| | 15 | 25 | 35 | 45 |
| Skagit (upper) | 34 | 46 | 52 | 61 |
| Skagit (lower) | 27 | 40 | 46 | 58 |
| Sauk (upper) | 43 | 52 | 55 | 67 |
| Sauk (lower) | 49 | 58 | 61 | 70 |
| Cascade | 27 | 34 | 49 | 58 |

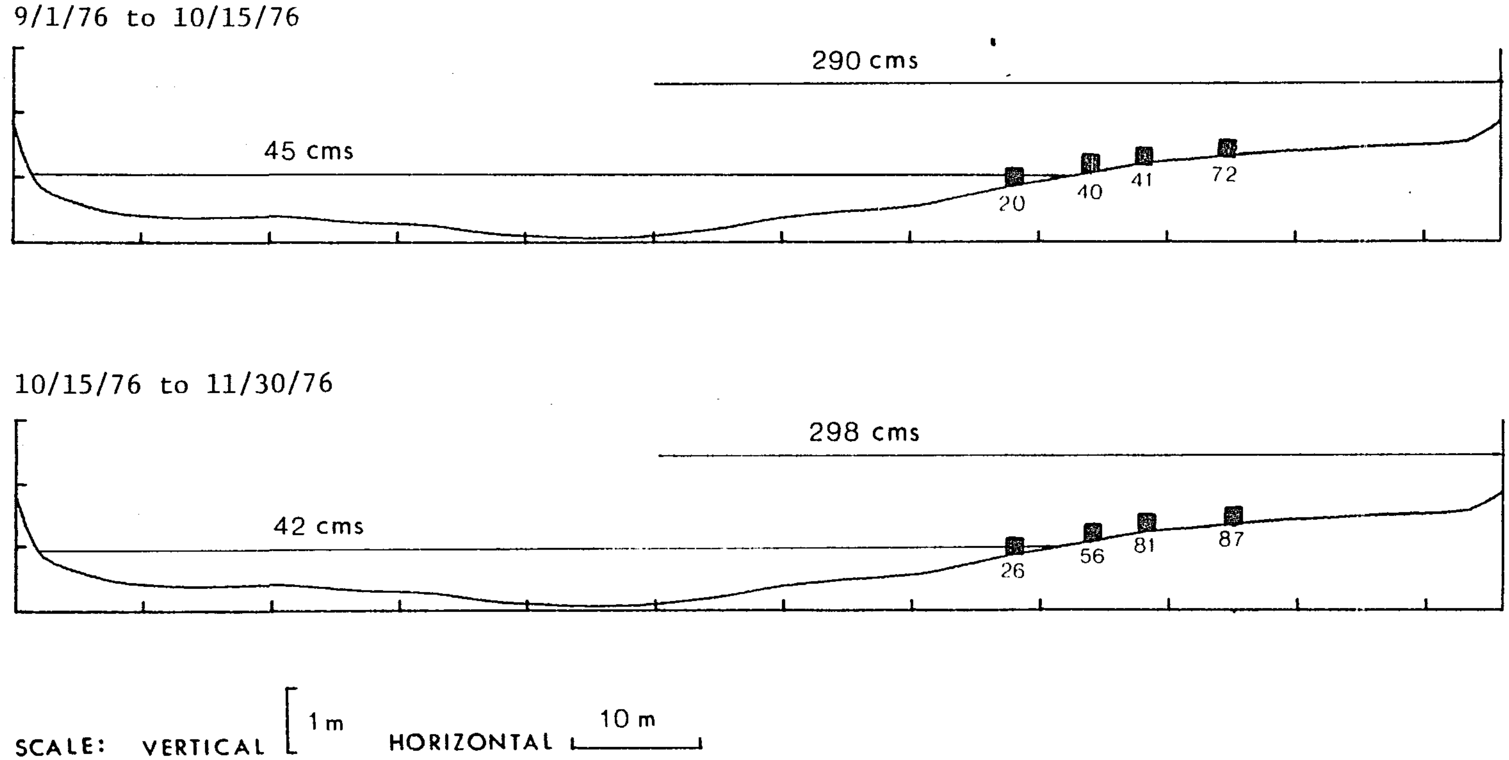


Fig. 19. Stream profiles at the lower Skagit sampling transect showing maximum and minimum water levels during the six-week colonization periods for periphyton samples collected in October and November, 1976. The percentage of time that each periphyton sampler was exposed to desiccation during the colonization period is given below the sampler location, which is indicated by a symbol (■).

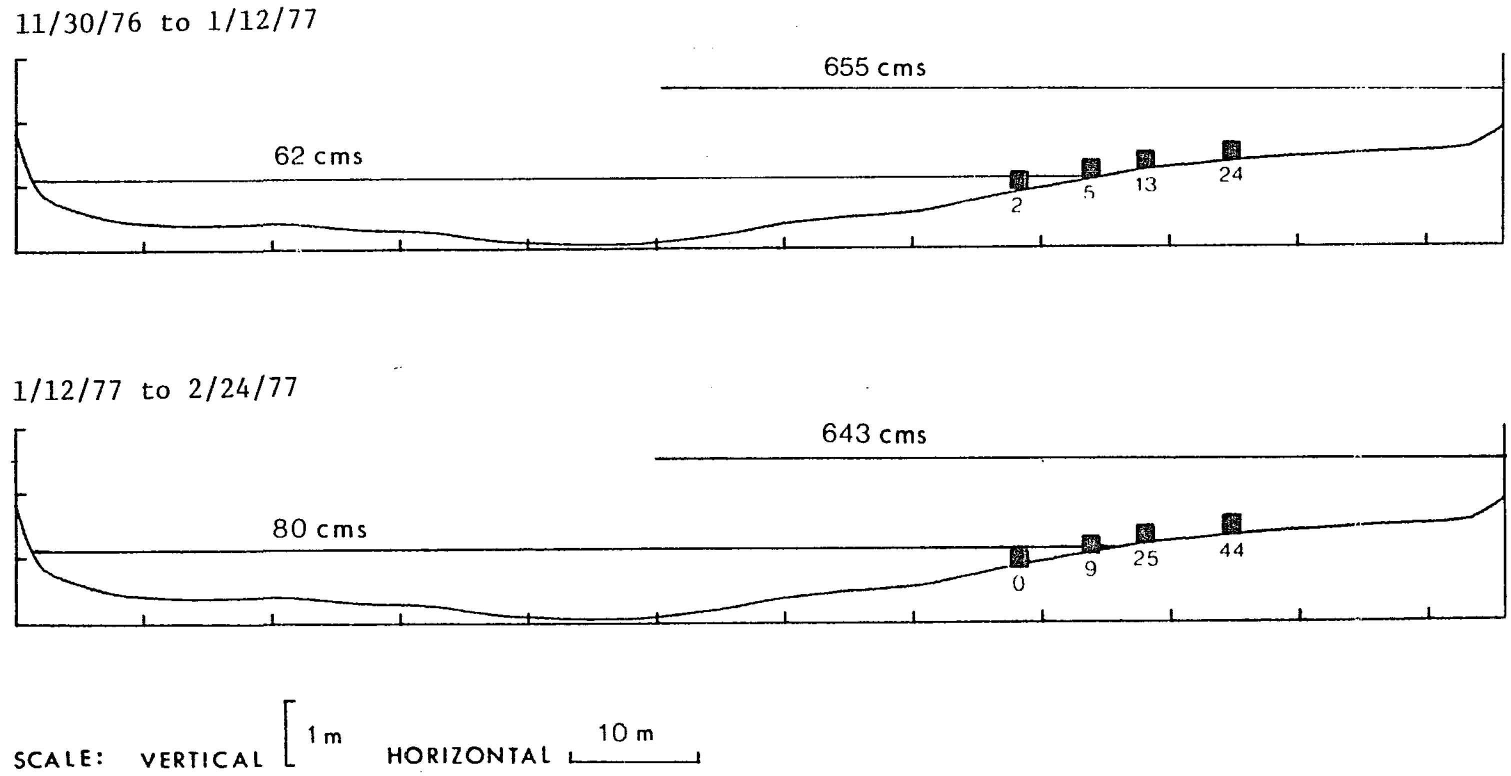


Fig. 20. Stream profiles at the lower Skagit sampling transect showing maximum and minimum water levels during the six-week colonization periods for periphyton samples collected in January and February, 1977. The percentage of time that each periphyton sampler was exposed to desiccation during the colonization period is given below the sampler location, which is indicated by a symbol (■).

the high water line was exposed at flows below 164 $m^3$/sec.

To determine the effects of exposure on periphyton standing crop, the mean chlorophyll a content of the two replicate samples from each periphyton sampler was plotted against percent exposure during the six-week colonization periods. Results from each colonization period are shown in Fig. 21.

In general, there was a trend of increasing chlorophyll a with decreasing exposure to desiccation. This trend was particularly evident in the results from the Skagit River during November 1976 and February 1977. The correlation between exposure time and chlorophyll a was better under conditions of periodic, daily exposure resulting from hydroelectric peaking than under the unregulated flow regime in the Sauk and Cascade rivers, where the samplers may have been exposed for a week and then submerged for a week. It appears that exposure during flow fluctuations limited periphyton standing crop in the margins of all three rivers, and that the amount of periphyton present was related to the degree of exposure, at least in the Skagit River.

The use of artificial substrate samplers may have underestimated the standing crop of filamentous algae in the Skagit River. A dense covering of filamentous Ulothrix sp. was observed on streambed stones at periphyton sampling sites in the Skagit, and on the unexposed concrete base of some of the samplers. Filamentous algae was much less abundant in the Cascade River and was never observed in the Sauk River. The plexiglass slides on unexposed samplers in the Skagit and Cascade were never colonized to the same degree as the streambed

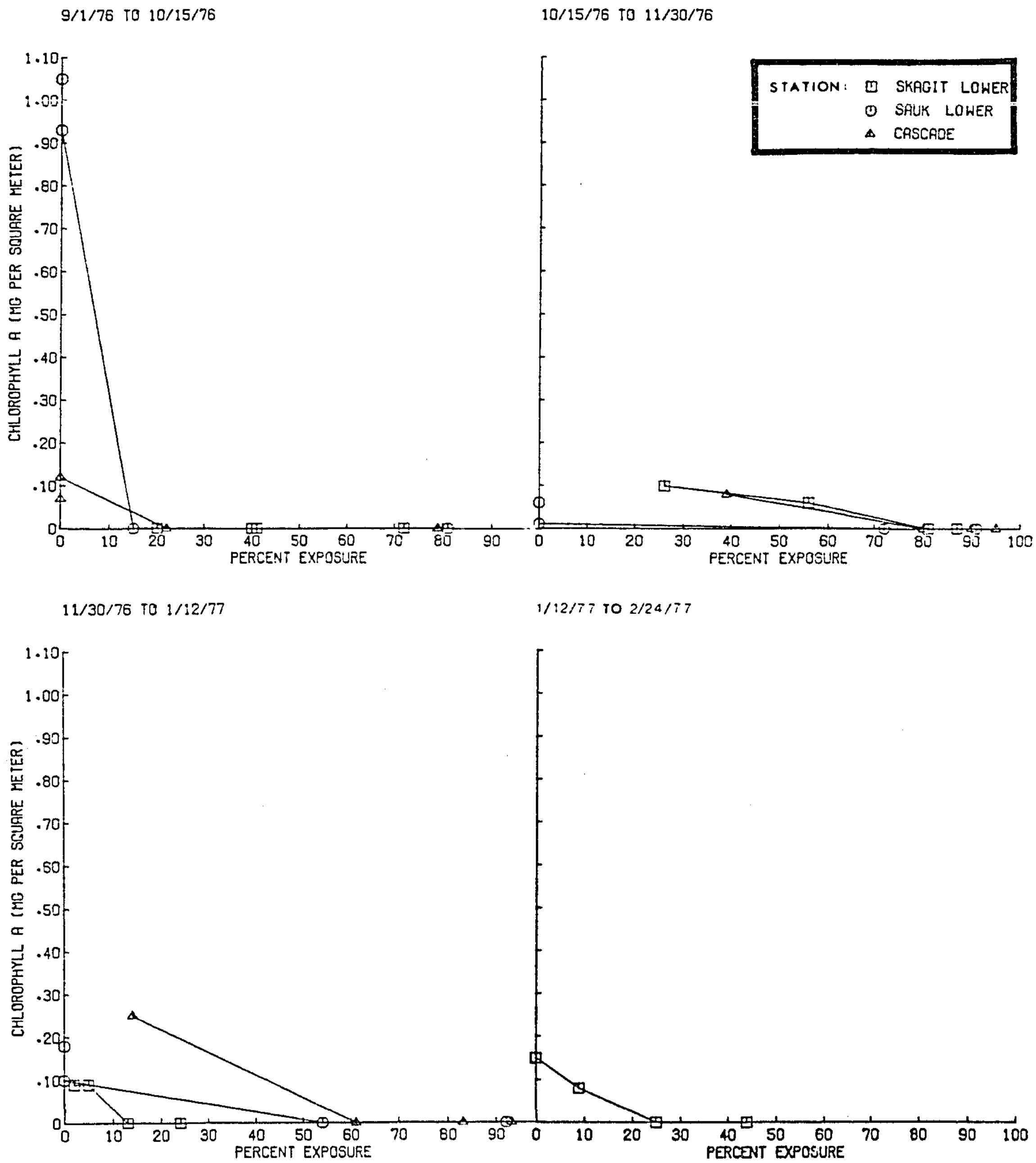


Fig. 21. Chlorophyll a content and exposure level of periphyton samples collected at the lower Skagit, lower Sauk, and Cascade stations from October 1976 through February 1977.

stones. The six week colonization period may have been too short to allow abundant growth of the filaments, or the smooth plexiglass plates may have limited attachment or prevented it completely.

Comparison of the Three Rivers

During the period when periphyton was collected directly from streambed stones, May 1977 to November 1977, the streamflow was relatively stable in all rivers, and there was little or no exposure of the sample sites. Comparisons could be made among stations during this time period, but standing crop at a particular station in 1977 could not be compared with standing crop at the same station in 1976 due to the difference in sampling methods.

The pattern of seasonal variation in periphyton standing crop was different at the four stations during the stable flow period. Chlorophyll a per $m^2$ was low in May and June in both the Sauk (Fig. 22) and Cascade (Fig. 23) rivers, increased during the summer months, and then declined in November. Standing crop at the upper Skagit station (Fig. 23) was also low in May and June, increased during the summer, but continued to increase into November. Standing crop was relatively high at the lower Skagit station (Fig. 22) in May and was variable during the rest of the year.

Analysis of variance was used to compare chlorophyll a levels at the four stations during each of the five months when periphyton was collected from streambed stones. Logarithmic transformation of the data was necessary since the means and variance were not independent (Elliott 1977). If the ANOVA was significant (p = .05), Scheffe's

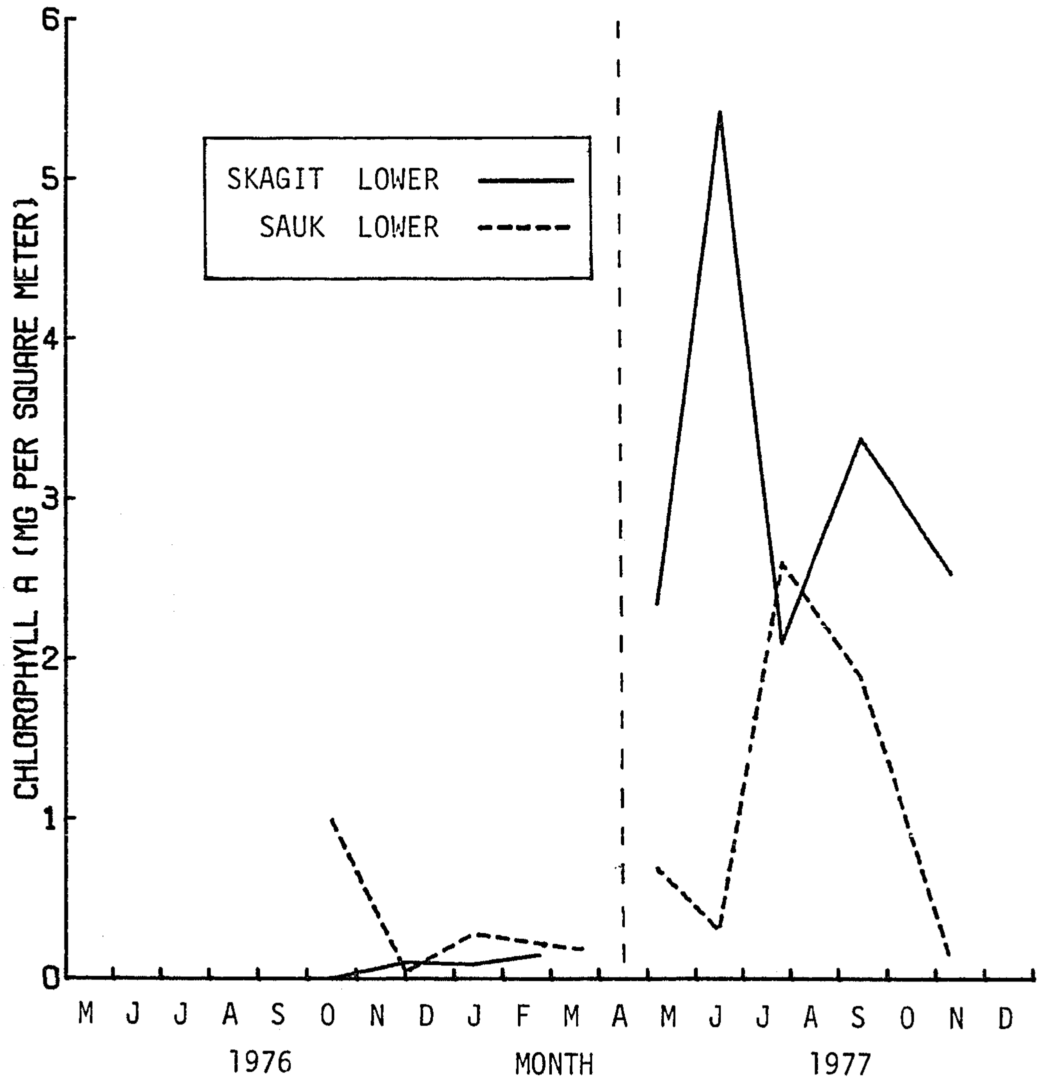


Fig. 22. Periphyton standing crop as indicated by chlorophyll a content of samples collected at the lower Skagit and lower Sauk stations. Two different sampling methods were employed, as indicated in the figure.

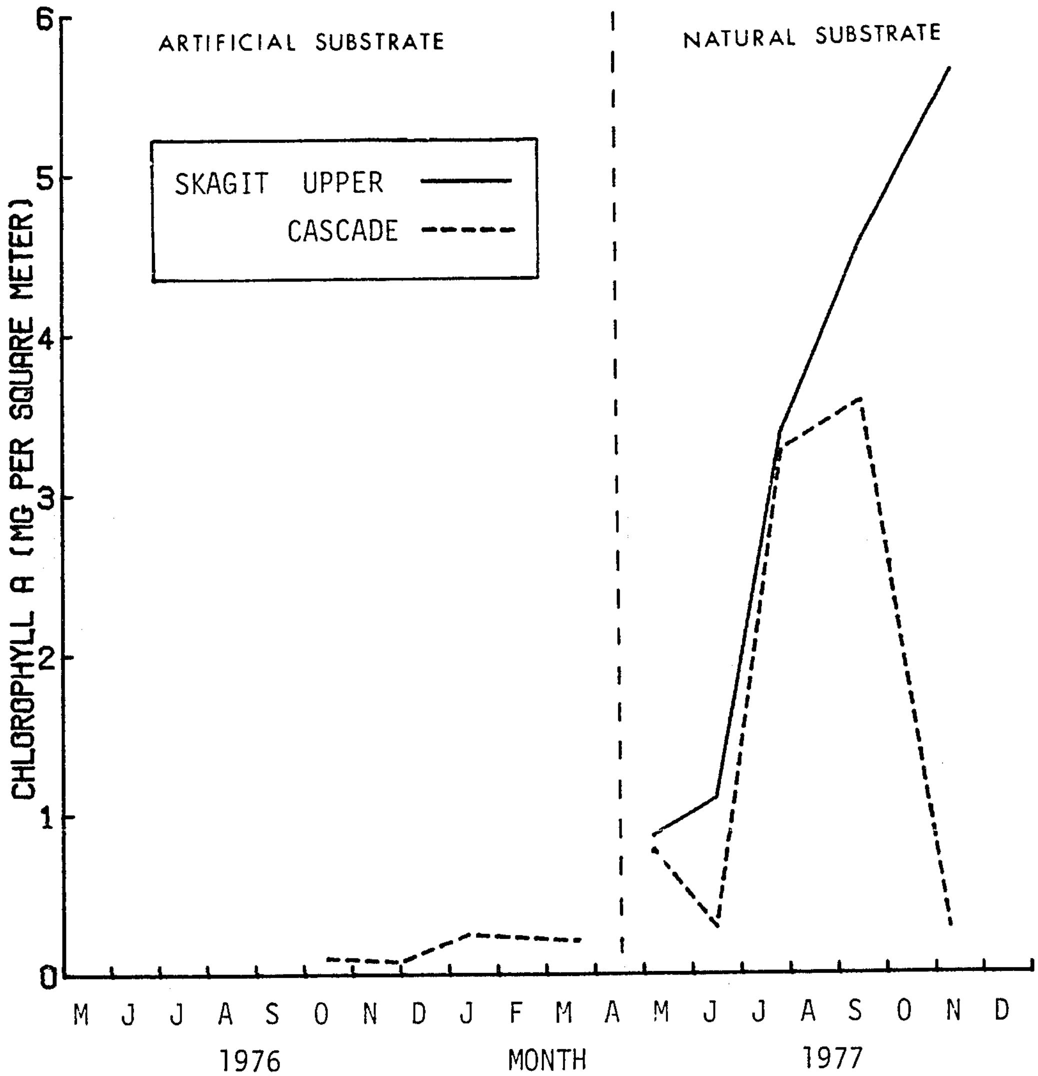


Fig. 23. Periphyton standing crop as indicated by chlorophyll a content of samples collected at the upper Skagit and Cascade stations. Two different sampling methods were employed, as indicated in the figure.

procedure, an *a posteriori* multiple comparison test, was used to determine which individual stations were different from each other.

There was a statistically significant difference among the four stations in all 1977 sampling months except July (Table 12). When stations were different, mean chlorophyll *a* was significantly higher at one or both Skagit River stations than at the lower Sauk station. Mean chlorophyll *a* was significantly higher at the lower Skagit station in May, June and November and higher at the upper Skagit station in September and November. The level of chlorophyll *a* at the Cascade station was intermediate with respect to the other stations, at times similar to the level at the lower Sauk station, at other times similar to the upper and lower Skagit stations.

Although the Sauk was considerably more turbid than the Skagit from June through September 1977, the elevated turbidity did not result in a significant decrease in periphyton standing crop relative to standing crop in the Skagit. Turbidity was almost 20 times greater in the Sauk than in the Skagit during August, but standing crops at the lower Sauk and upper Skagit stations were not significantly different in September, when any reduction due to turbidity should have been evident. However, turbidity may have been responsible for the generally lower levels of chlorophyll *a* in the Sauk and Cascade rivers.

Scouring during high flows occurring one week before sampling was probably responsible for the reduction in standing crop observed at the lower Skagit and lower Sauk stations in November 1977. On November 1, the water level rose over 2.5 m in 24 hours in the Sauk River. The

Table 12. Results of analysis of variance (ANOVA) and multiple comparison tests comparing mean chlorophyll a at sampling stations during the stable flow period. Parentheses were used to indicate homogeneous subsets of station means. The enclosure of station codes within the same pair of parentheses indicates that mean chlorophyll a was not significantly different (p = .05) at those stations. Station codes are listed in the table below, from left to right, in order to increasing chlorophyll a. Station codes: 1- UPPER SKAGIT, 2- LOWER SKAGIT, 4- LOWER SAUK, 5- CASCADE.

| Month | Significance of ANOVA | Results of Multiple Comparison Test |
|---|---|---|
| May 1977 | .004 | (5, 4, 1) (2) |
| June 1977 | < .001 | (4, 5) (5, 1) (2) |
| July 1977 | NS | |
| September 1977 | .01 | (4, 2, 5) (2, 5, 1) |
| November 1977 | < .001 | (4) (5) (2, 1) |

increase in flow was less severe in the upper Skagit River, where water levels rose 1.5 and 1.8 m at the gaging stations near the upper and lower sampling stations. Water level varied only 0.8 m at Newhalem during the same time period.

The observed reduction in periphyton standing crop at the lower Sauk and lower Skagit stations was not due to sampling in previously exposed areas on the November sampling date, since most of the locations had not been exposed for extremely long periods. All sampling locations at the lower Skagit station had been continuously submerged since January, and those at the upper station had been submerged since July. At the lower Sauk station, the shallowest location had been exposed for several days in September and October, but the other three locations had been submerged continuously during 1977. All sampling sites on the Cascade transect were exposed to desiccation prior to sampling, and the reduction in standing crop at this station may have been caused by either exposure or scouring.

Although the November 1 freshet reduced standing crop at the lower Skagit station, it had little impact at the upper station, where standing crop actually increased in November. The maximum discharge during the freshet was slightly lower at the upper station, but it is not likely that such a small difference in streamflow could account for the lower scouring effect at the upper station. Periphyton standing crop was probably reduced at the lower station because there was more sand and silt in the upper surface of the substrate available for suspension during the freshet.

Impoundment has reduced the import of sand and silt from upstream in other rivers (Pearson *et al*. 1968), and it is probable that this phenomenon also occurred in the Skagit. The amount of sand and silt in the substrate would be lowest near the dam and increase downstream due to input from tributary streams. Therefore, one would expect the scouring effect of the November 1 freshet, which was the first freshet after several months of near stable flow, to be lower near Newhalem and increase downstream. Results from the two unregulated streams support this hypothesis. The loss of periphyton due to scouring was much more severe in the Sauk and Cascade rivers, where there was an obvious accumulation of sand and silt in the surface of the streambed, than at the lower Skagit station.

The ranges of chlorophyll *a* values at the lower Skagit, lower Sauk and Cascade stations were compared with the ranges in several other rivers (Table 13). Ranges for each type of substrate used in this study are given separately, and values are from unexposed substrates only. The artificial substrates were used during fall and winter, when periphyton growth is probably at its lowest level, due to reduced light. The natural substrates were used during the seasons of peak periphyton growth.

Results using plexiglass artificial substrates in the Skagit, Sauk and Cascade rivers are comparable to the range of values in Carnation Creek, B.C. (Stockner and Shortreed 1976). Stockner and Shortreed considered the level of chlorophyll in Carnation Creek to be extremely low and attributed this low level to extremely low nutrient concen-

Table 13. Range of chlorophyll _a_ values in the Skagit, Sauk, and several other North American streams.

| Stream | Substrate | Chlorophyll _a_ ($mg/m^2$) |
|---|---|---|
| Logan River, Utah (McConnell and Sigler, 1959) | Streambed rocks | 140 - 1420 |
| Laboratory Stream, Ore. (McIntire and Phinney, 1965) | Streambed rocks | 140 - 2010 |
| Valley Creek, Minn. (Waters, 1961) | Concrete cylinders | 9.2 - 21.1 |
| Carnation Creek, B.C. (Stockner and Shortreed, 1976) | Plexiglass plates | 0.9 - 2.1 |
| Skagit River, Wash. (October 1976 - February 1977) | Plexiglass plates | 0.09 - 0.15 |
| Skagit River, Wash. (May 1977 - November 1977) | Streambed rocks | 0.41 - 8.28 |
| Sauk River, Wash. (October 1976 - March 1977) | Plexiglass plates | 0.01 - 1.05 |
| Sauk River, Wash. (May 1977 - November 1977) | Streambed rocks | 0.07 - 3.92 |
| Cascade River, Wash. (October 1976 - March 1977) | Plexiglass plates | 0.07 - 0.25 |
| Cascade River, Wash. (May 1977 - November 1977) | Streambed rocks | 0.20 - 4.35 |

trations and poor light conditions under the forest canopy. There was no forest canopy at the Skagit, Sauk or Cascade stations, and turbidity was low during 1976 and early 1977. Therefore, one would expect the chlorophyll levels to be higher at these stations. The low values may have resulted from the use of artificial substrates.

The level of chlorophyll _a_ on the streambed rocks was much greater than on the plexiglass plates. This difference may be due to differences in substrate or seasonal effects. The maximum value at the Skagit station, collected from natural substrate, approached the minimum value in Valley Creek Minnesota (Waters 1961). Values from the three rivers examined, even from streambed rocks, were much lower than the minimum value observed in the Logan River, Utah (McConnell and Sigler 1959).

BENTHIC INSECTS

The benthic macroinvertebrate communities in the sections of the Skagit, Sauk and Cascade rivers investigated during this study were dominated by several Ephemeropteran genera and the Dipteran family Chironomidae. The most abundant Ephemeropteran genera were _Baetis_, _Rithrogena_, _Cinygmula_ and _Ephemerella_. The species _Ephemerella inermis_ was particularly abundant. The setipalpian stonefly genera _Alloperla_, _Acroneuria_ and _Arcynopteryx_ were the predominant plecopterans. _Arctopsyche_, _Brachycentrus_ and _Rhyacophila_ were the most abundant trichopterans. No molluscs or benthic crustaceans were collected, and the only non-insect benthic macroinvertebrates of any consequence were the Hydracarina, or water mites. The insect community in all rivers was typical of those found in unpolluted, highly oxygenated, swiftly-flowing streams and was basically similar in terms of dominant taxa to the macroinvertebrate community in the lower section of the Cedar River, Washington (Malick 1977). A list of all insect taxa collected in the Skagit, Sauk and Cascade rivers can be found in Appendix I.

Microdistribution

The width of the unexposed zone at the lower Skagit station during the fluctuating flow period was affected by seasonal changes in streamflow and the magnitude of daily flow fluctuations. As water level in the Skagit increased from May 1976 to July 1976 due to snowmelt, areas of the riverbed that had been exposed by peaking flow fluctuation in May and June became permanently submerged for several weeks. The average daily discharge then decreased through August and September, reaching an annual minimum in October. The width of the unexposed zone declined during this time span, and areas of the river channel that were included in the unexposed zone in July were subjected to daily exposure as a result of the drop in streamflow. These seasonal changes had a significant impact on the distribution of insects along the lower Skagit sampling transect.

A comparison of standing crop at sampling locations along the lower Skagit transect in May and July 1976 revealed the effect of increasing the width of the unexposed zone (Fig. 24). During May, standing crop within 10 m of the annual high water line was low due to the exposure during dewatering. In July, densities were much higher at

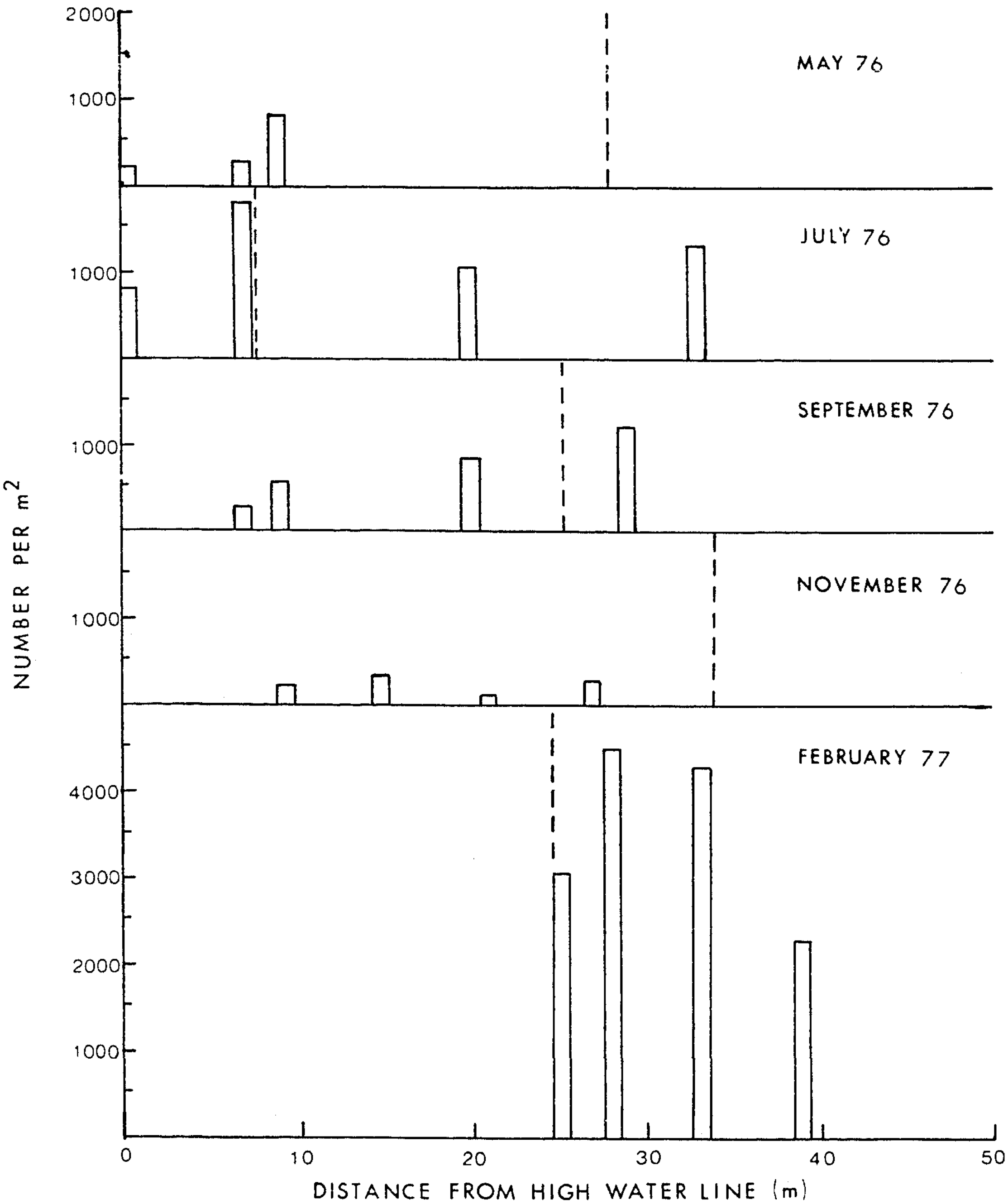


Fig. 24. Density of benthic insects at sampling locations along the lower Skagit transect from May 1976 to February 1977. The vertical dashed line indicates the edge of the wetted area at the minimum flow during the two weeks prior to sampling.

the same locations. Evidently, the previously exposed areas of the stream margin were recolonized by the insects during the period of high discharge prior to sampling. The two sampling locations nearest the high water line were exposed for 4 hours during the night prior to sampling. Without this exposure, densities would have been even higher at these sites.

The effects of the decreasing average streamflow during late summer were apparent in the September sampling period. Areas that were not exposed to desiccation in July were exposed as the discharge declined. Insects that had colonized the margins of the stream channel in July were either killed by stranding or were displaced by drift into the unexposed zone. Continued low water levels in November and daily peaking fluctuation further reduced the benthic standing crop in the exposed zone.

During February 1977, the density of benthic insects at sampling locations in the unexposed zone was relatively high. All four sampling locations along the transect had not been exposed for several months, allowing the insect community to remain undisturbed for a considerable time.

During the stable flow period, mid-April to mid-November, the benthic community in the Skagit was not subject to daily exposure and density was markedly higher during the late summer months of 1977 than during 1976 (Fig. 25). Although the width of the unexposed zone decreased from May to September, the change was gradual, presumably allowing the insects to migrate toward midstream as the flow dropped.

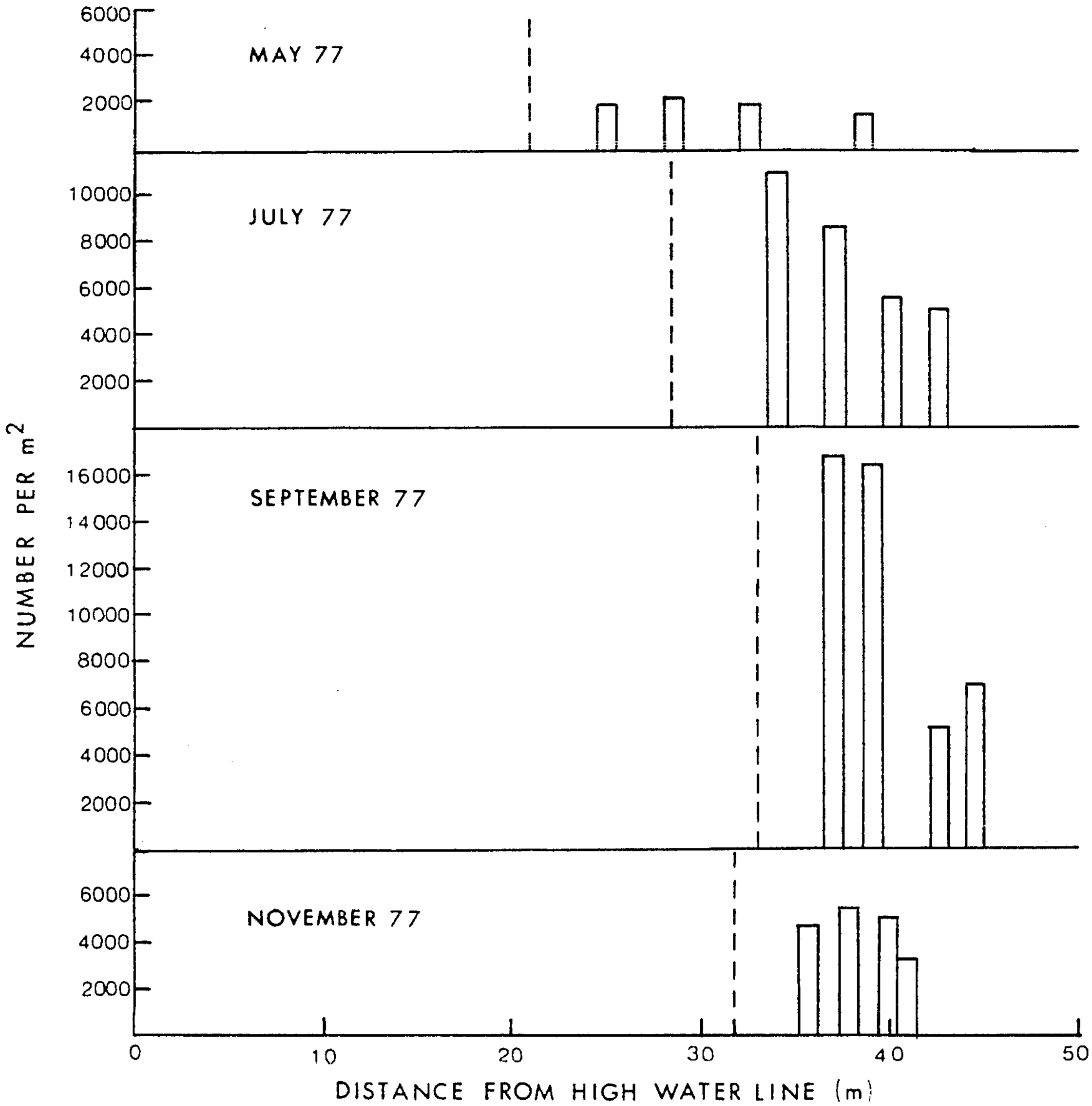


Fig. 25. Density of benthic insects at sampling locations along the lower Skagit transect from May 1977 to November 1977. The vertical dashed line indicates the edge of the wetted area at the minimum flow during the two weeks prior to sampling.

Changes in density were caused by normal seasonal fluctuation in insect populations.

Under fluctuating flow conditions, insect density increased from the water's edge to the deepest point sampled. Peak standing crop was present at unexposed sampling sites in deeper water at midstream. As streamflow became more stabilized in 1977, this microdistributional pattern was reversed. Peak densities were observed at sampling sites in shallow water (15 cm deep) and density decreased with increasing depth.

The transition from the microdistributional pattern found during the fluctuating flow period to the pattern found during stable flow began in May 1977, approximately three weeks after peaking stopped, and was complete by July. Regression lines, with density as the dependent variable and depth as the independent variable, were plotted for May, July and September 1977 (Fig. 26). During May, the slope of the regression equation was not significant at the lower Skagit station, indicating equal densities at all sampling depths along the transect. The regression equation for the upper Skagit station in May had a positive slope, indicating that density still increased with depth, as it did under fluctuating flow conditions. In July and September, the slopes were negative at both stations, indicating decreasing density with increasing depth.

## Effects of Exposure

Stream profiles at the lower Skagit transect, along with sampling locations, exposure levels, maximum and minimum water levels during the

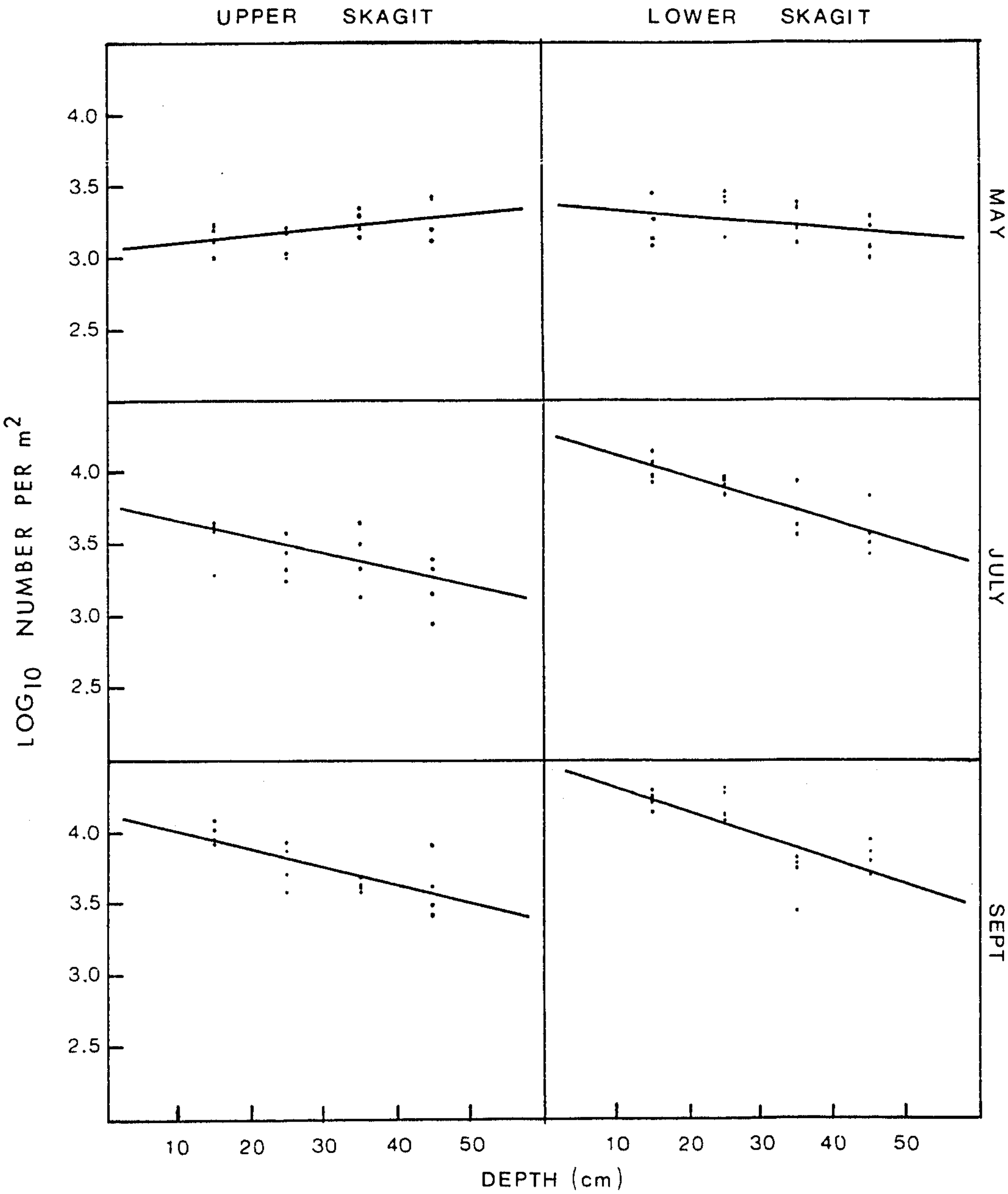


Fig. 26. Relationship between insect density and water depth at the upper and lower Skagit stations during May, July and September 1977.

two weeks prior to sampling, are shown in Figs. 27 and 28.

Benthic insect density and biomass were much lower in shallow areas of the transect, which were subject to high levels of exposure, than in the deeper areas, subject to low exposure (Fig. 29). During May 1976, density and biomass increased along the transect as the exposure level decreased. During July, all sample sites were subject to extremely low levels of exposure (0% to 1%) because daily minimum flows were high prior to sampling. Consequently, density and biomass were high at all sites on the transect. During September and November, the pattern of increasing density and biomass with decreasing exposure was again evident.

Linear regression analysis was used to define the relationship between exposure and insect density at the lower Skagit station from May through November (Fig. 30). The Y-intercept (a) of the regression equation was 2.34, and the slope (b) was -0.003. Density was negatively correlated ($r = -.76$) with the hours of exposure during the two weeks prior to sampling. The coefficient of determination was .58, indicating that 58% of the total variation in density was explained by the regression on exposure time. Most of the unexplained variation was probably due to the effect of season on standing crop over the 7-month period.

Insect density in the Coleman-Hynes basket sampler was much higher than the September 1976 quadrat sampler density estimates. Although the basket sampler was exposed 21%, or 81 hours, during the two weeks prior to removal, insects were present at a density of 4823 per $m^2$.

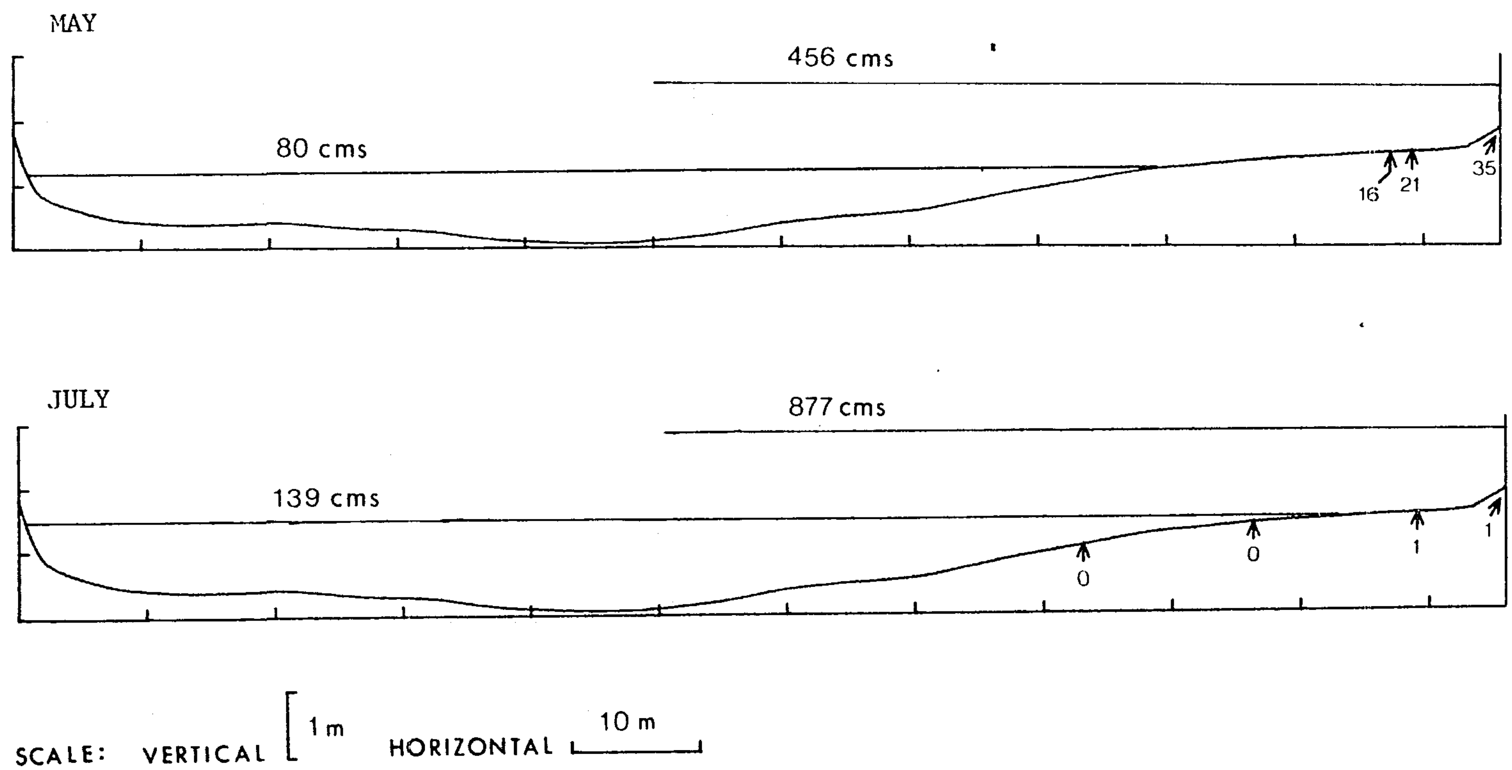


Fig. 27. Stream profiles at the lower Skagit station showing maximum and minimum water levels during the two weeks prior to benthic insect sampling in May and July 1976. The area between the horizontal lines is the area of the riverbed that was periodically exposed and submerged. The locations where replicate benthic samples were collected and percent exposure time are indicated by arrows.

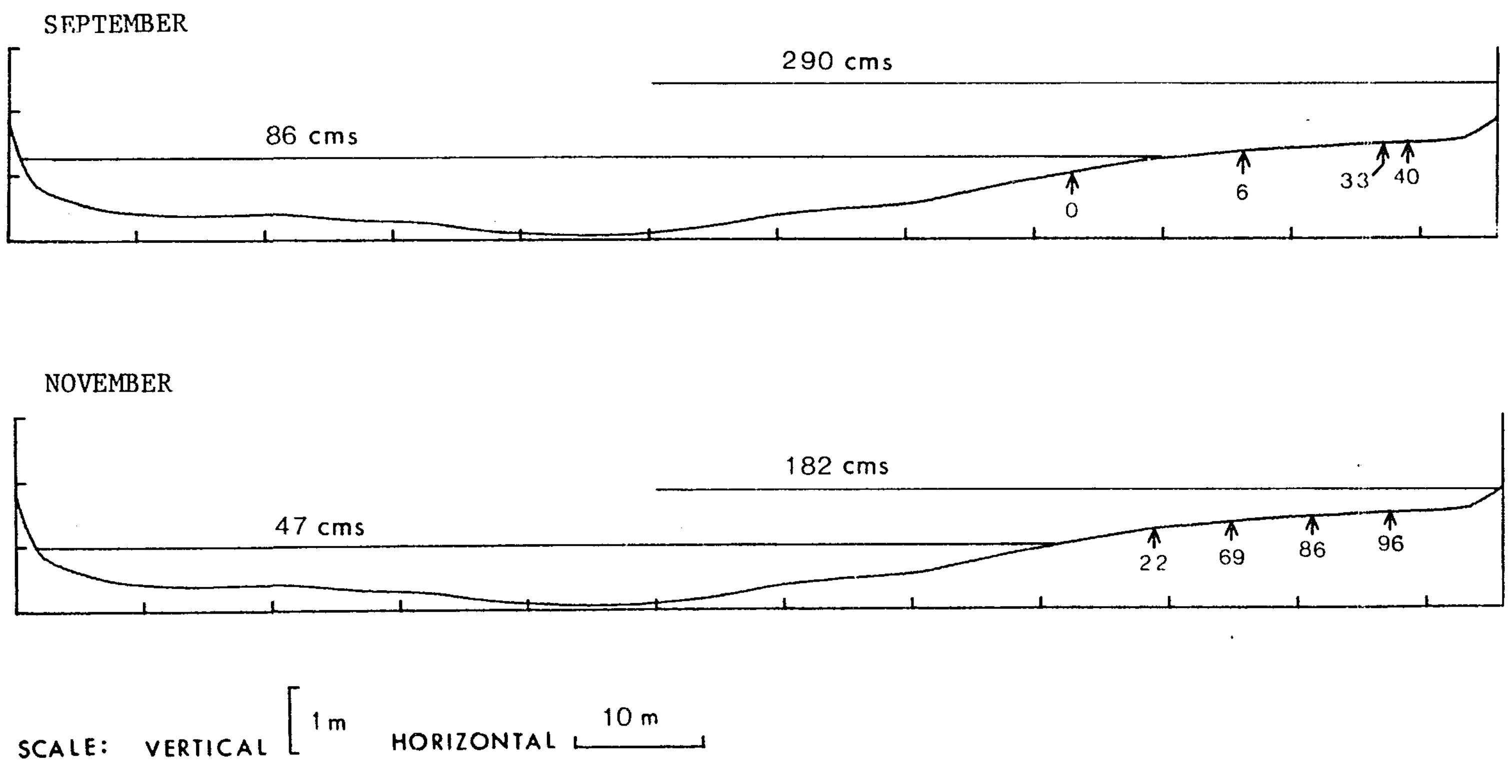


Fig. 28. Stream profiles at the lower Skagit station showing maximum and minimum water levels during the two weeks prior to benthic insect sampling in September and November 1976. The area between the horizontal lines is the area of the riverbed that was periodically exposed and submerged. The locations where replicate benthic samples were collected and percent exposure time are indicated by arrows.

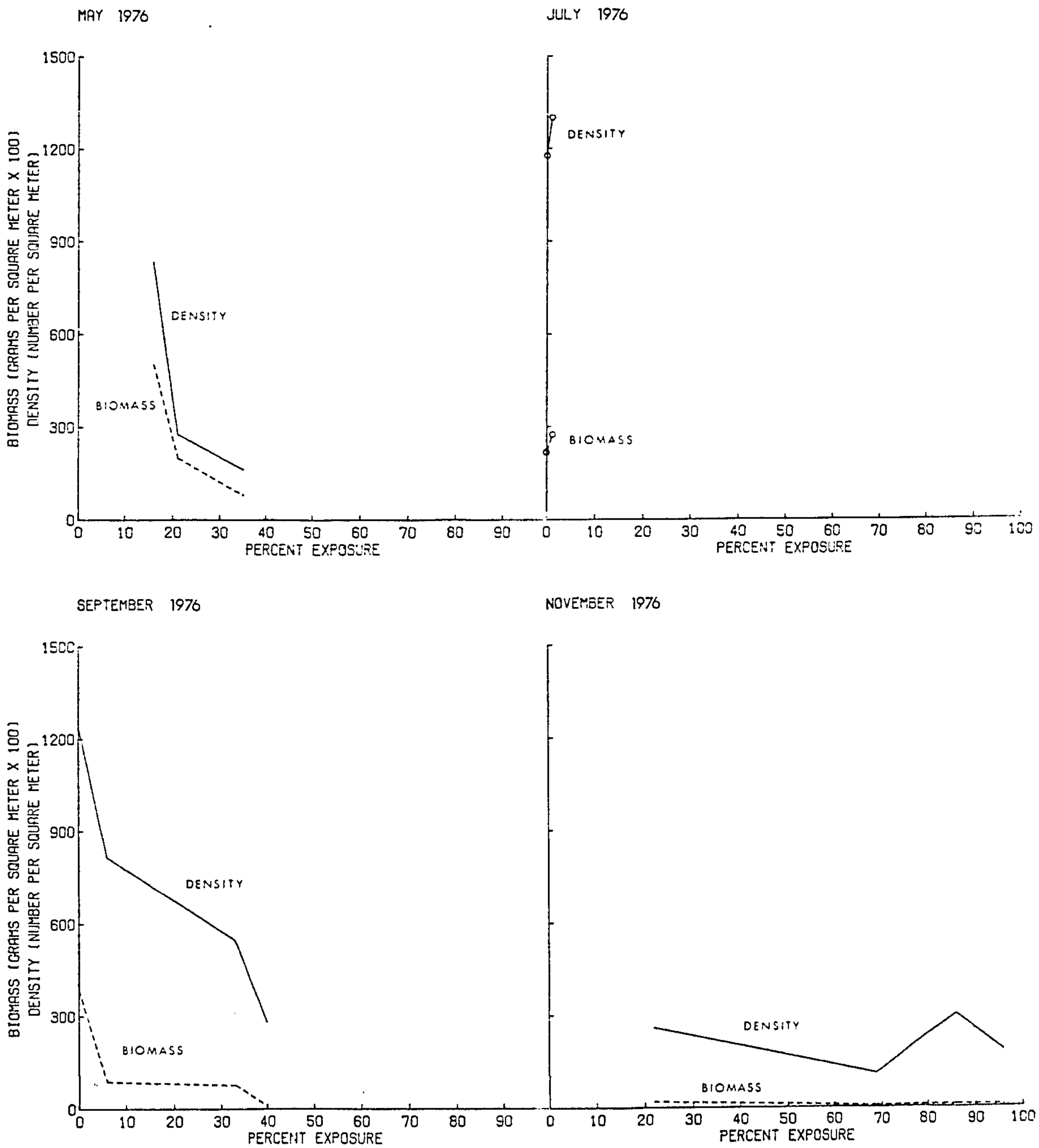


Fig. 29. Density and biomass of benthic insects and exposure levels at sampling locations on the lower Skagit sampling transect during 1976.

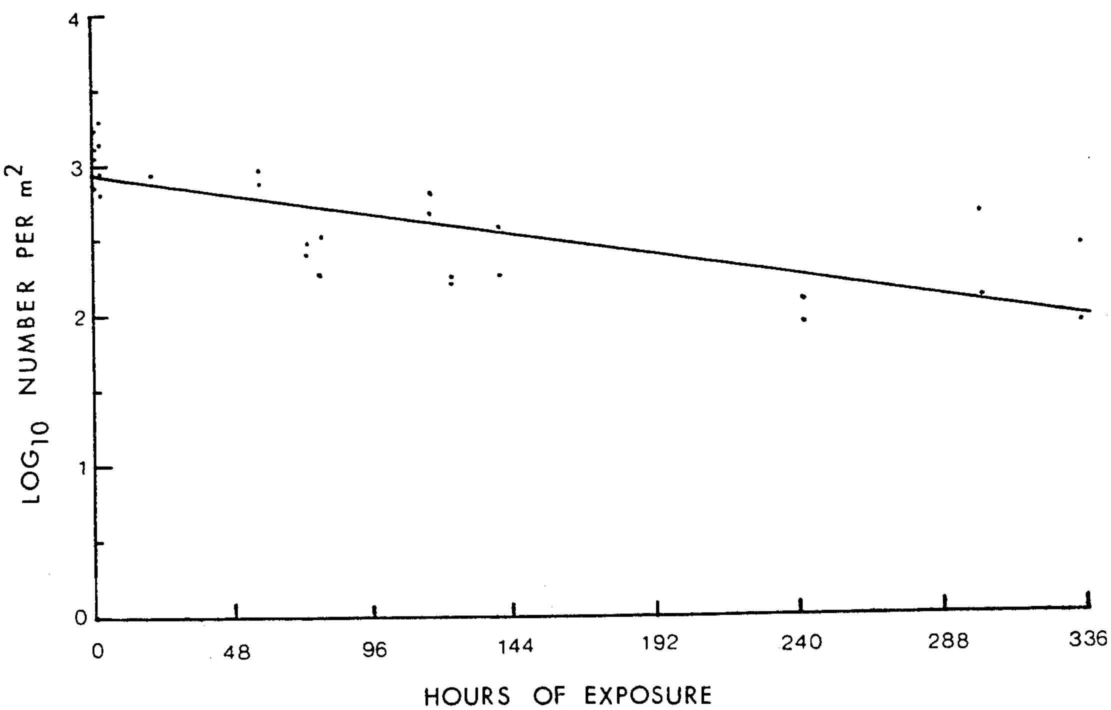


Fig. 30. Relationship between benthic insect density and hours of exposure during the two weeks prior to sampling at the lower Skagit station under fluctuating flow conditions.

Based on quadrat sampling, insect density was only 1236 insects per $m^2$ in the unexposed zone of the stream channel, while it was 816 and 548 insects per $m^2$ at sites exposed 6% and 33%, respectively. The extremely high densities in the basket sampler were due to the large number of chironomids collected.

Chironomidae were present at a density of 4704 per $m^2$, and 89% of all insects were chironomids. The basket sampler contained no Trichoptera larvae and only one mayfly nymph (Ephemeroptera) and two stonefly nymphs (Plecoptera) (Table 14).

The density of chironomids in the quadrat samplers was much lower, but the density of individuals belonging to other orders was similar or higher. Chironomid density at quadrat sampling locations was 478 per $m^2$ in the unexposed zone and even lower at unexposed ocations. Quadrat sampler density estimates for locations exposed 6% and 33%, respectively, were as follows: Ephemeroptera, 34-14; Plecoptera, 204-100; Trichoptera, 22-24 per $m^2$. Basket sampler ephemeropteran density lies between the quadrat density estimates for 6% and 33% exposure as expected, since the basket sampler was exposed 21%. However, plecopteran and trichopteran density in the basket sampler was considerably lower than quadrat sampler density for either exposure level.

The abundance of chironomids in the Coleman-Hynes basket sampler may have been the result of altered pore space. Much of the fine particulate matter is lost when bottom material is removed and replaced in the basket sampler. Thus pore space is altered, and this may lead to unnatural recolonization (Williams and Hynes 1974). Larger pore

Table 14. Number, density and percent composition of insects collected with the Coleman-Hynes basket sampler.

| Taxon | Number | Number per $m^2$ | Percent Composition |
|---|---|---|---|
| Ephemeroptera | 1 | 28 | 0.6 |
| Plecoptera | 2 | 55 | 1 |
| Trichoptera | 0 | 0 | 0 |
| Diptera | 172 | 4740 | 98.4 |
| Coleoptera | 0 | 0 | 0 |

space within the sampler would have resulted in increased intragravel flow down to a substrate depth of 30 cm, creating more favorable conditions for insect colonization. The larger pore space may have also facilitated the penetration of the relatively small, elongated chironomid larvae into the substrate, while barring the larger larvae and nymphs of other taxa. There was no evidence that the quadrat sampler underestimated the density of any order other than Diptera. In fact, it appears that the basket sampler may have underestimated the abundance of Plecoptera and Trichoptera.

The composition of the benthic insect community in the marginal areas of the Skagit River was affected by exposure during flow fluctuation. Composition at each of the sampling sites along the lower Skagit transect and at the lower Sauk and Cascade stations is shown for each sampling date in 1976 in Tables 15 and 16. As the level of exposure increased, Diptera (primarily Chironomidae) formed a progressively greater percentage of the community, while Ephemeroptera formed a progressively smaller percentage. It appears that the ephemeropterans were intolerant of the effects of exposure and were affected more severely than the dipterans. Composition at the Sauk and Cascade stations, under conditions of no exposure, was most similar to composition at the unexposed Skagit sampling sites.

Experimental Studies

Flow Fluctuation Experiments. The effects of experimental flow fluctuations were determined by comparing post-fluctuation density and composition in the two stream channels (Table 17). Since environ-

Table 15. Percent composition of benthic insects at sampling stations during May and July 1976. Composition is presented separately for each sample location at the Skagit lower station. Percent exposure during the two weeks prior to sampling is also given for each location at the Skagit station.

MAY 1976

| | STATION | | | | |
|---|---|---|---|---|---|
| | Skagit (Lower) | | | Sauk | |
| Order | 35% | 21% | 16% | (Lower) | Cascade |
| Ephemeroptera | 43 | 54 | 72 | 53 | 83 |
| Plecoptera | 24 | 22 | 18 | 16 | 11 |
| Trichoptera | 8 | 4 | 1 | 3 | 2 |
| Diptera | 25 | 20 | 9 | 28 | 4 |
| Coleoptera | 0 | 0 | <1 | 0 | 0 |

JULY 1976

| | STATION | | | |
|---|---|---|---|---|
| | (Skagit (Lower) | | Sauk | |
| Order | 1% | 0% | (Lower) | Cascade |
| Ephemeroptera | 16 | 32 | 47 | 83 |
| Plecoptera | 13 | 11 | 19 | 8 |
| Trichoptera | 14 | 9 | 3 | 1 |
| Diptera | 57 | 48 | 31 | 8 |
| Coleoptera | <1 | <1 | <1 | <1 |

Table 16. Percent composition of benthic insects at sampling stations during September and November 1976. Composition is presented spearately for each sample location at the Skagit lower station. Percent exposure during the two weeks prior to sampling is also given for each location at the Skagit station.

SEPTEMBER 1976

| | STATION | | | | | |
|---|---|---|---|---|---|---|
| | Skagit (Lower) | | | | Sauk | |
| Order | 40% | 33% | 6% | 0% | (Lower) | Cascade |
| Ephemeroptera | 0 | 3 | 4 | 37 | 43 | 52 |
| Plecoptera | 7 | 18 | 25 | 12 | 8 | 15 |
| Trichoptera | 1 | 5 | 3 | 7 | 12 | 7 |
| Diptera | 92 | 74 | 67 | 44 | 37 | 26 |
| Coleoptera | 0 | 0 | 1 | 0 | 0 | 0 |

NOVEMBER 1976

| | STATION | | | | | |
|---|---|---|---|---|---|---|
| | Skagit (Lower) | | | | | |
| Order | 96% | 86% | 69% | 22% | (Lower) | Cascade |
| Ephemeroptera | 4 | 4 | 14 | 32 | 54 | 55 |
| Plecoptera | 5 | 1 | 5 | 13 | 24 | 31 |
| Trichoptera | 3 | 1 | 4 | 4 | 10 | 6 |
| Diptera | 88 | 94 | 77 | 51 | 12 | 8 |
| Coleoptera | 0 | 0 | 0 | <1 | 0 | <1 |

Table 17. Mean number of insects per substrate tray in experimental and control artificial stream channels before and after experimental flow fluctuation.

| Experimental Flow Pattern | Pre-fluctuation | Post-fluctuation | |
|---|---|---|---|
| | | Experimental | Control |
| Periodic exposure for one week | 251 | 64 | 194 |
| 48-hr continuous exposure | 536 | 378 | 482 |

mental conditions, except for flow pattern, were identical in both channels, any differences in post-fluctuation density and composition should have been due to the different flow regimes. Density in the control channel at the conclusion of the experiments was always slightly less than pre-fluctuation density because of normal losses from drift, emergence and natural mortality during the experiment.

Approximately equal numbers of insects were present in both channels at the start of the experiments. Pre-fluctuation density in the experimental and control channels was compared using a paired t-test after logarithmic transformation of the data. Density data collected prior to four flow fluctuation experiments conducted in 1976 and 1977 were used. No significant difference between channels was detected.

Post-fluctuation benthic insect density was lower in the experimental channel than in the control channel in both types of flow fluctuation experiment (Table 17). After seven days of periodic exposure, benthic insect density in the fluctuating experimental channel was 67 percent lower than in the nonfluctuating control channel. When the number of insects per substrate tray was compared between channels in a paired t-test, the difference between channels was statistically significant at the .01 level. Following 48 hours of continuous exposure, the density in the experimental channel was 22 percent lower than in the control channel. However, this difference was not statistically significant.

These data indicate that periodic exposure over a one-week period can significantly reduce benthic insect density. The level of exposure to desiccation in the experimental channel during the two weeks prior to sampling was only 30 percent. Flow reductions of similar frequency and duration in the Skagit probably reduced benthic insect density in shaded shoreline areas by a similar amount, either through mortality of stranded insects or drift losses.

The 48 hours of continuous exposure did not reduce density as much as one week of periodic exposure. In the Skagit, shoreline zones that were continuously submerged or exposed periodically during the week may have been exposed continuously for 48 hours on weekends. This type of experiment was intended to duplicate the weekend flow conditions in the Skagit. A 22 percent loss of insects from a particular area of the riverbed would be a sizeable reduction in the amount of food available to the fish. The effect would be even greater if the same area were exposed for 48 hours on several consecutive weekends.

The number of surviving insects in the experimental channel may have been overestimated by the inclusion of dead insects. Due to cool and moist conditions on the exposed substrate trays in the experimental channel, insects dying from exposure to air may not have been decomposed or desiccated after only 48 hours. After preservation in alcohol, these dead insects would have been indistiguishable from insects that were alive at the end of the experiment and would have been included in the counts of insects remaining after 48 hours. Thus, the actual reduction in density was probably greater than 22 percent. The observed 22 percent density reduction was most likely due only to the loss of drifting insects during initial dewatering. During the periodic exposure experiments, any insects killed during exposure would have been washed out of the channel when the substrate was re-submerged.

Benthic insect community structure was altered by one week of periodic exposure (Table 18). Percent composition of each order in the experimental channel was compared with percent composition in the control channel using a Mann-Whitney U-test, the non-parametric alternative to the t-test (Elliott 1977). The percentage of Diptera in the experimental channel was significantly higher than in the control channel, and the percentage of Plecoptera was significantly lower in the experimental channel ($p = .05$). Although the percentage of Ephemeroptera was lower in the experimental channel, the difference between channels was not statistically significant.

Similar changes in composition were observed after 48 hours of continuous exposure (Table 19). The percentage of Diptera was higher in the experimental channel, while the percentages of Ephemeroptera and Plecoptera were lower. However, the differences in composition between channels were not found to be significant, due to the smaller sample size in this unreplicated experiment.

During both flow reduction and increased flow, Ephemeroptera comprised 56-57 percent of the drift, while Diptera comprised 31-36 percent (Table 20). In contrast, the substrate trays contained only 15 percent Ephemeroptera and 73 percent Diptera prior to fluctuation (Table 18). The different proportions of Ephemeroptera and Diptera in the drift and on the bottom of the channel indicate that the Ephemeroptera had a greater propensity to drift during flow fluctuations

Table 18. Percent composition of benthic insects in experimental and control artificial stream channels before and after one week of periodic exposure.

| Order | Pre-fluctuation | Post-fluctuation Experimental | Post-fluctuation Control |
|---|---|---|---|
| Ephemeroptera | 15 | 5 | 7 |
| Plecoptera | 11 | 6 | 13 |
| Trichoptera | 1 | 1 | <1 |
| Diptera | 73 | 88 | 80 |
| Coleoptera | 0 | 0 | 0 |

Table 19. Percent composition of benthic insects in experimental and control artificial stream channels before and after 48 hours of continuous exposure.

| Order | Pre-fluctuation | Post-fluctuation Experimental | Post-fluctuation Control |
|---|---|---|---|
| Ephemeroptera | 11 | 10 | 13 |
| Plecoptera | 4 | 5 | 7 |
| Trichoptera | 1 | <1 | 1 |
| Diptera | 84 | 85 | 79 |
| Coleoptera | 0 | 0 | 0 |

Table 20. Percent composition of drifting aquatic insects in the experimental artificial stream channel during dewatering and rising water and in the control channel during the same time period.

| | Flow Pattern | | |
|---|---|---|---|
| Order | Dewatering | Rising water | Control |
| *Ephemeroptera* | 56 | 57 | 49 |
| *Plecoptera* | 8 | 12 | 11 |
| *Trichoptera* | <1 | <1 | 1 |
| *Diptera* | 36 | 31 | 39 |
| *Coleoptera* | <1 | 0 | 0 |

than Diptera. Apparently the density of Ephemeroptera was reduced by drift during the fluctuations at a greater rate than Dipteran density, resulting in the observed post-fluctuation change in community structure.

Stranding Avoidance. Benthic insects that are unable to avoid stranding during flow reductions and are left on the exposed surface of the riverbed may be killed by desiccation or freezing. Insects may avoid stranding by 1) drifting, 2) migrating with the receding water, 3) migrating from exposed areas to submerged areas or 4) burrowing into wet substrate and waiting for the water level to return. The numbers of insects that avoided stranding by the first three methods were recorded during flow reductions in the artificial stream. The interstices in the substrate in the bottom of the trays were too small to allow any deep burrowing by the species tested.

There were pronounced differences among the three species tested in ability to avoid stranding (Table 21). Only 65 percent of the Ephemerella tibialis nymphs were able to escape stranding, primarily by drifting. Almost all of the stoneflies (Acroneuria pacifica) escaped stranding, mainly by moving to the submerged half of the channel. A total of 96 percent of the caddis larvae (Dicosmoecus sp.) avoided stranding, primarily by drifting.

Both the stonefly and caddis species tested were able to move several centimeters over dewatered substrate to enter the flowing water. Once exposed, the mayfly nymphs did not move more than a centimeter on the exposed substrate.

Table 21. Percentage of aquatic insect larvae stranded and not stranded during experimental flow reductions. The not stranded category includes insects that avoided stranding by moving to the submerged half of the channel or drifting downstream.

| Species | Stranded | Not Stranded Total | (Submerged) | (Drift) |
|---|---|---|---|---|
| Ephemerella tibialis | 35 | 65 | (23) | (42) |
| Acroneuria pacifica | 1 | 99 | (63) | (36) |
| Dicosmoecus sp. | 4 | 96 | (22) | (74) |

The results of the stranding avoidance experiments indicate that mayfly nymphs (Ephemeroptera) are much more likely to become stranded during flow reductions than large stonefly (Plecoptera) nymphs and caddis (Trichoptera) larvae. A reduction in water level at a rate of more than 21 cm per hour, the rate used in the experiments, would probably result in a higher rate of stranding for all three species. Stranding would probably be more severe on gently sloping shoreline areas than on steep river banks.

Desiccation Survival. The ability to survive desiccation on dewatered substrates varied among the three species tested (Table 22). *Dicosmoecus* sp., a case-bearing caddis larva, was the most resistant and survived with no mortality on both dry and damp substrates. All of the *Acroneuria pacifica* nymphs survived on the damp substrate, but 64 percent died on the dry substrate. *Ephemerella tibialis* was the least resistant species and had a high mortality rate of both substrates.

The damp substrate was intended to simulate conditions in shaded areas of the dewatered shoreline areas, or areas dewatered at night or during rain. Conditions on the dry substrate resembled those on areas exposed to sunlight.

The caddis species *Dicosmoecus* sp. had a sand grain case which probably enabled it to survive desiccation with no mortality. Other species with cases would also be expected to have high survival rates on dewatered substrates. Most stonefly species, including *Acroneuria pacifica*, crawl out of the water to emerge and can survive short periods

Table 22. Percent mortality of aquatic insect larvae exposed to desiccation for 24 hours on dry and damp substrates.

| Species | Dry Substrate | Damp Substrate | Control | Maximum Air Temperature (°C) |
|---|---|---|---|---|
| Ephemerella tibalis | 100 | 84 | 2 | 20 |
| Acroneuria pacifica | 64 | 0 | 0 | 20 |
| Dicosmoecus sp. | 0 | 0 | 0 | 14 |

out of the water and would be expected to be more resistant than mayfly nymphs. The desiccation survival experiments, as well as the stranding avoidance experiments, indicate that the mayflies are particularly vulnerable to flow fluctuations.

Effects of Peaking Fluctuation in the Unexposed Zone

Standing Crop. Seasonal changes in the standing crop of benthic insects in the unexposed areas of the streambed are shown in Fig. 31 to 34. The mean of all replicates at all unexposed sample locations, or at locations with minimal exposure, on each sampling date are shown in these figures. The number of replicates used to calculate the station mean during the fluctuating flow period was therefore valuable, and the exact number can be determined by referring to Table 6. Samples were collected only in heavily exposed locations at the lower Skagit station in November 1976 and at the upper Skagit station in February 1977. Results from these stations on the dates mentioned are not presented in the figures.

During the fluctuating flow period, the pattern of seasonal variation differed in the regulated and unregulated rivers. In the Sauk (Fig. 31) and Cascade (Fig. 32), insect density generally increased from May to November 1976, reaching an annual maximum in early autumn, and declined during the winter. Density in the Skagit (Fig. 31) remained nearly constant from May through September and did not exhibit a summer increase, but did increase in February.

The pattern of seasonal variation in biomass (wet weight) was more similar among the three rivers during the fluctuating flow period. At

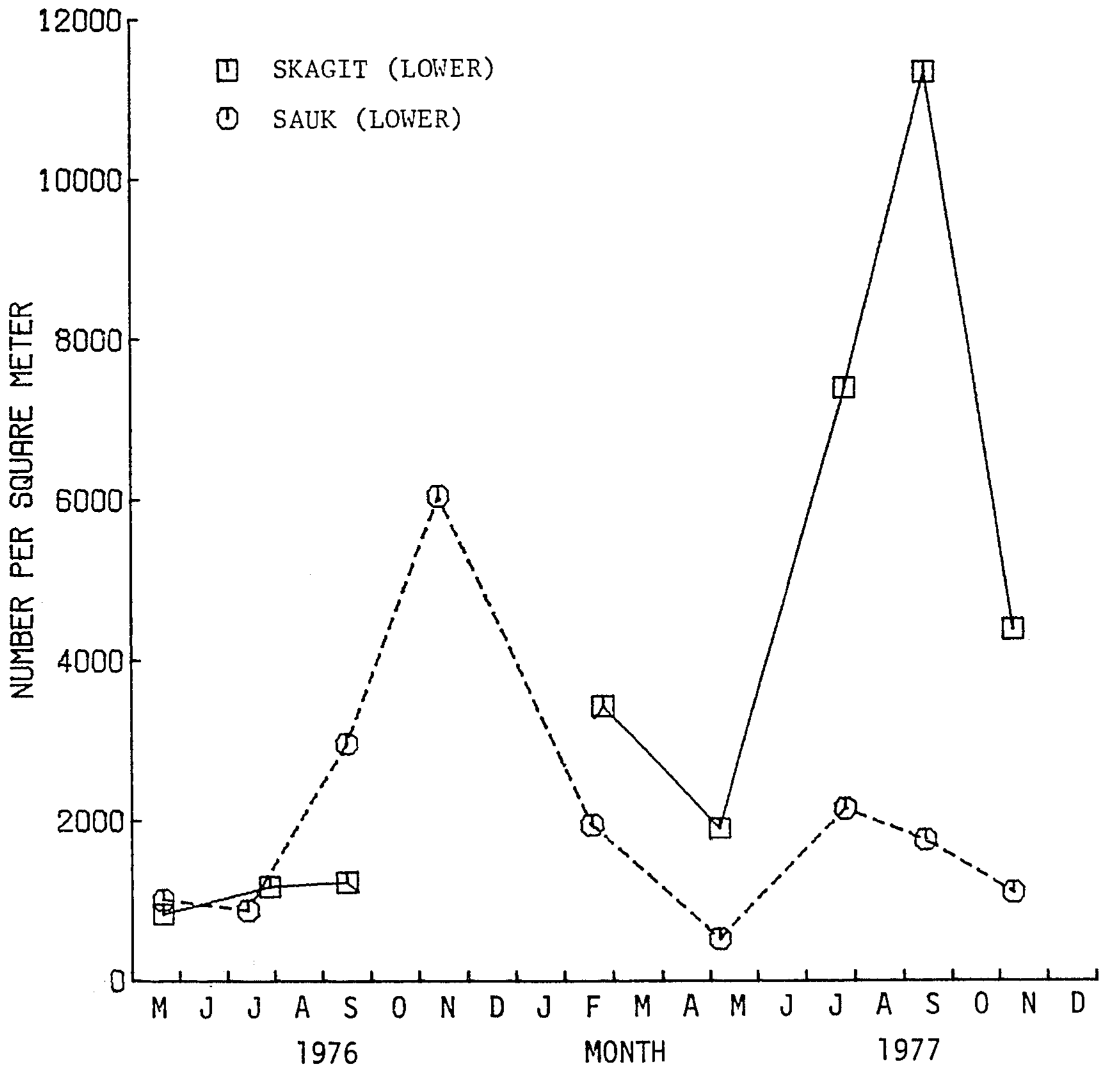


Fig. 31. Benthic insect density at the lower Skagit and lower Sauk sampling stations.

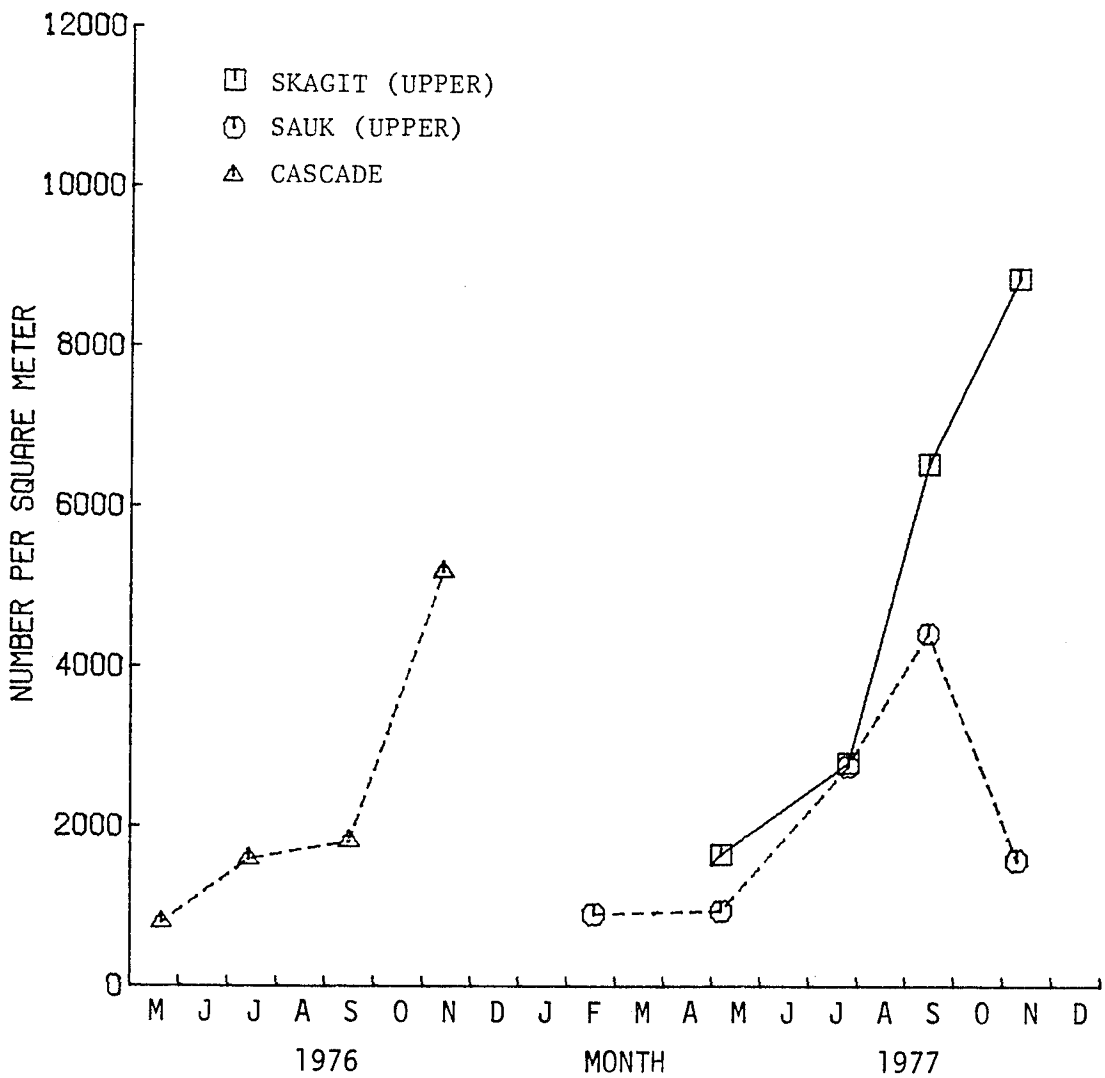


Fig. 32. Benthic insect density at the upper Skagit, upper Sauk, and Cascade sampling stations.

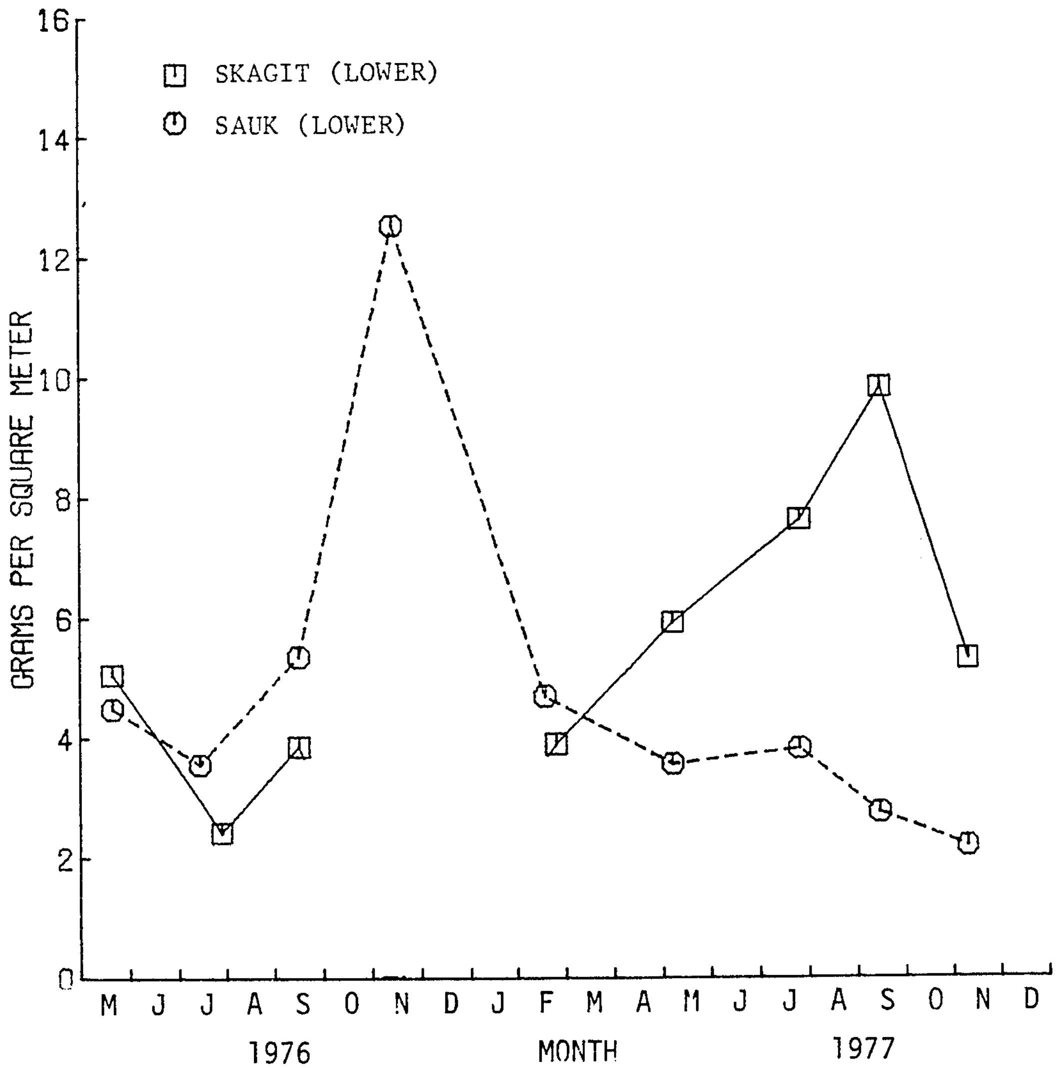


Fig. 33. Benthic insect biomass (wet weight) at the lower Skagit and lower Sauk sampling stations.

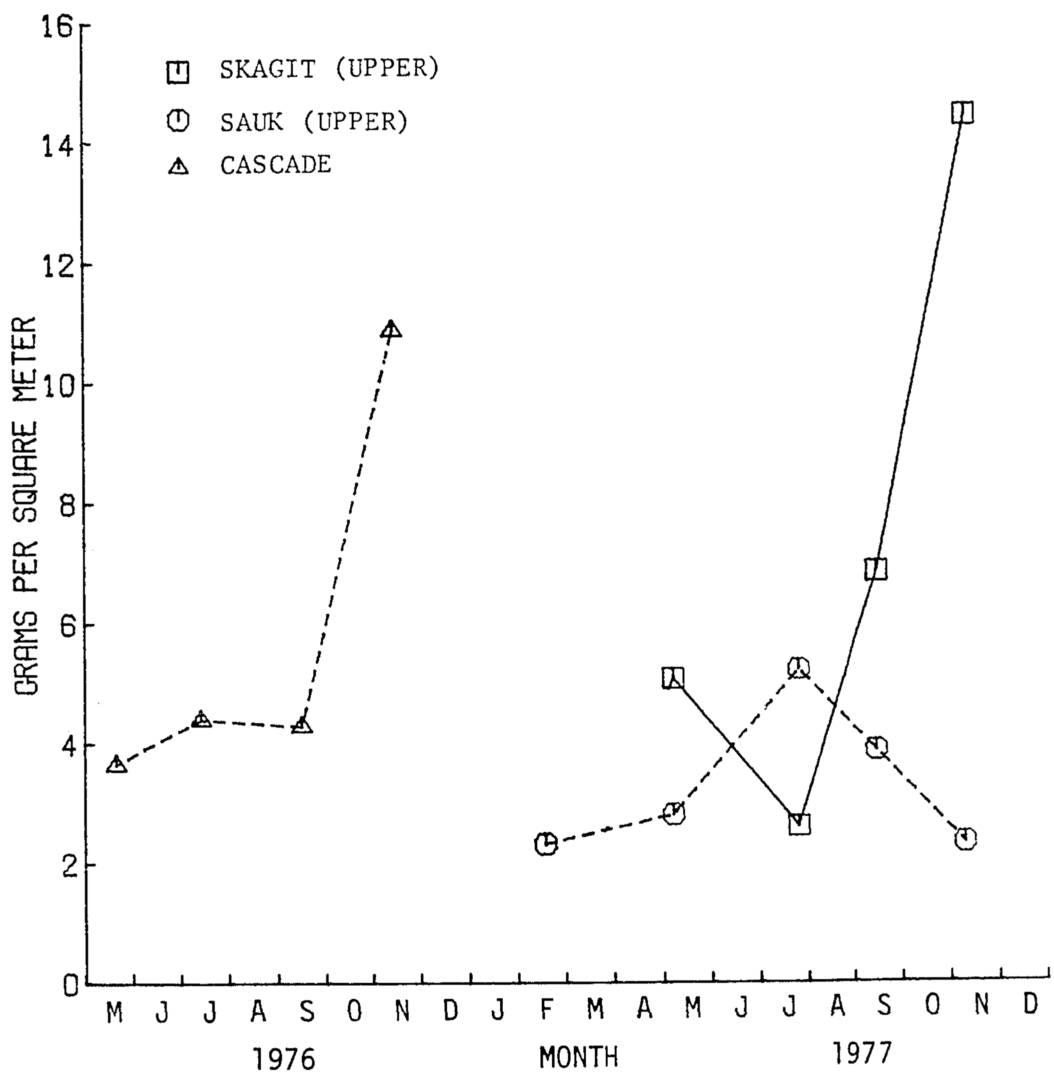


Fig. 34. Benthic insect biomass (wet weight) at the upper Skagit, upper Sauk, and Cascade sampling stations.

both the lower Skagit and lower Sauk stations (Fig. 33), biomass declined in July and increased in September. At the Cascade station (Fig. 34), biomass was more stable from May through September. Biomass at the unregulated stations increased during early autumn, reaching a maximum level in November, and declined during the winter.

The pattern of seasonal fluctuation in insect abundance observed in the unregulated rivers in 1976 resembled the normal pattern of seasonal change. In the typical seasonal cycle described by Hynes (1970), insect numbers are lowest during the late spring, increase during the summer and reach an annual maximum in late autumn. Insect abundance then declines during the winter until spring. Insect abundance in the Skagit under fluctuating flow conditions did not conform to this typical pattern.

During 1977, when Skagit River streamflow was stable for 7 months, seasonal variation in insect numbers at both the upper and lower Skagit stations was similar to the typical pattern. However, density and biomass at the lower Skagit station declined from July through November instead of increasing as it did during 1976.

Seasonal variation in benthic insect density at the lower Skagit and lower Sauk stations during 1977 was compared with seasonal variation in benthic macroinvertebrate standing crop in two other North American streams (Fig. 35). The Skagit, Sauk and Provo rivers had roughly similar patterns of seasonal abundance. Abundance declined from February to May and then increased during the summer. However, there was little seasonal variation in the Kananaskis River.

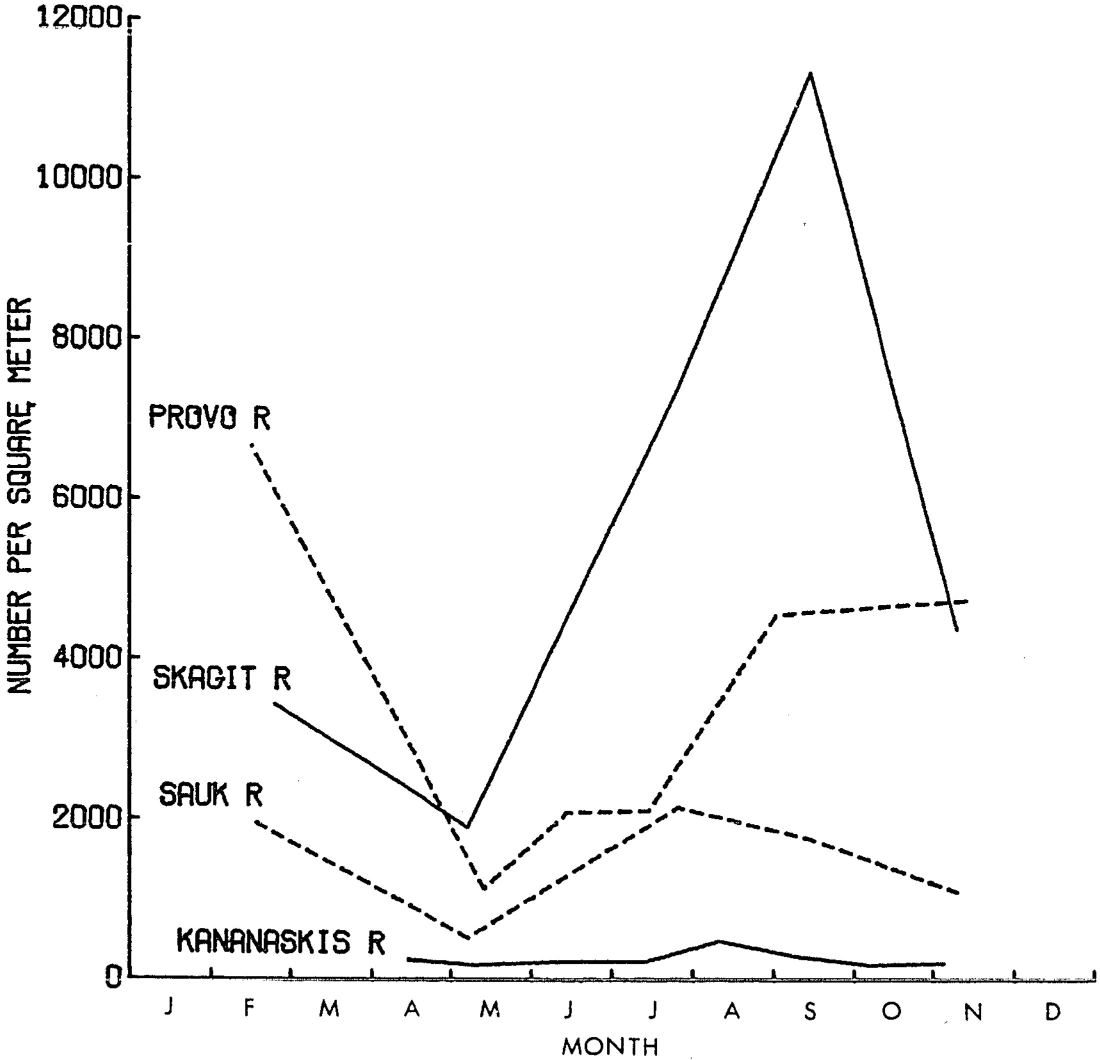


Fig. 35. Seasonal variation in benthic macroinvertebrate density in the Skagit, Sauk, and two other rivers in western North America. The Provo River, Utah (Gaufin, 1959), and the Sauk are unregulated streams. The Skagit River and the Kananaskis River, Alberta (Radford and Hartland-Rowe, 1971), are regulated streams.

The Kananaskis River was subject to considerable seasonal flow fluctuation as well as daily water level fluctuation of 20-32 cm caused by hydroelectric peaking (Radford and Hartland-Rowe 1971). During the eight-month period in which the river was studied (April-November), peak flows (40-50 $m^3$/sec) occurred during May and June as the result of run-off combined with reservoir releases. Low flows (less than 5 $m^3$/sec) occurred in April, July and from mid-August through September, with a minimum flow of 0.3 $m^3$/sec recorded in September. This pattern of seasonal flow fluctuation resembled that of the Skagit River, although the volumes of the high and low flows were different in the two streams.

Benthic macroinvertebrate density in the Kananaskis River increased only slightly during August, but a major increase occurred in the other streams during summer (Fig. 35). The pattern of relatively constant density found in the Kananaskis River is similar to the pattern observed in the Skagit River in 1976 under peaking flow conditions.

Analysis of variance (ANOVA) was used to compare mean benthic density at sampling stations during each sampling month. Results are presented in Table 23. If the ANOVA significant ($p = .05$), Scheffe's procedure was used to determine differences among stations.

There were seasonal changes in the degree of similarity in density in the unexposed zone at sampling stations on the three rivers during the fluctuating flow period. Skagit River standing crop was not significantly different from Sauk and Cascade River standing crop during May and July 1976. In September, standing crop in the Skagit was sig-

Table 23. Results of analysis of variance (ANOVA) and multiple comparison tests comparing mean benthic insect density at sampling stations. Parentheses were used to indicate homogeneous subsets of stations means. The enclosure of station codes within the same pair of parentheses indicates that mean density was not siginificantly different ($p = .05$) at those stations. Station codes are listed in the table below, from left to right, in order ot increasing mean density. Station codes: 1- UPPER SKAGIT, 2- LOWER SKAGIT, 3- UPPER SAUK, 4- LOWER SAUK, 5- CASCADE.

| Month | Significance of ANOVA | Results of Multiple Comparison Test |
|---|---|---|
| May 1976* | NS | |
| July 1976 | NS | |
| September 1976 | .01 | (2) (5, 4) |
| November 1976* | < .001 | (2) (5, 4) |
| February 1977 | < .001 | (3) (4) (2) |
| May 1977 | < .001 | (4) (3) (1, 2) |
| July 1977 | < .001 | (4, 3, 1) (2) |
| September 1977 | < .001 | (4) (3, 1) (1, 2) |
| November 1977 | < .001 | (4, 3) (2) (1) |

* Exposed sites at the Skagit River station were compared with unexposed sites at the other stations during these months.

nificantly lower than standing crop in both unregulated streams. However, density was significantly higher at the lower Skagit station in February 1977.

During the stable flow period, which included the sampling months of May 1977 through November 1977, density at the Skagit stations was nearly always significantly higher than density at the Sauk stations. Lower Skagit density was always significantly higher than density at the upper and lower Sauk stations. Upper Skagit density was significantly higher than lower Sauk density in all months except July.

Although the degree of water level fluctuation at the lower Sauk station was generally similar in 1976 and 1977, standing crop was lower during September and November 1977 than during these same months in 1976. September density was 51 percent lower in 1977. The large amount of silt and sediment deposited on the surface of the streambed during low flow conditions during the summer of 1977 probably caused the September reduction. This contention is supported by the fact that both density and biomass at the upper Sauk station, where the water was less turbid, were higher in September. The reduction in November was probably caused by scouring during a freshet, which also severely reduced the periphyton standing crop in the two unregulated streams.

There was a pronounced difference between the level of standing crop in the Skagit under fluctuating flow conditions in the summer of 1976 and under relatively stable flow in the summer of 1977. Benthic insect density at the lower Skagit station during July and September 1977 was 6 to 9 times greater than density at unexposed sample locations in the same months in 1976.

The freshet on November 1, 1977 also reduced the standing crop at the lower Skagit station, but not at the upper Skagit station. Apparently, scouring was reduced at the upper station due to the effects of impoundment on the import of sand and silt from upstream.

The density of the four major insect orders, Ephemeroptera, Plecoptera, Diptera and Trichoptera, at unexposed locations during the fluctuating flow period was compared with density under stable flow conditions (Fig. 36 and 37). The densities of Ephemeroptera and Diptera were much higher during the stable flow period. Smaller increases in the densities of Plecoptera and Trichoptera were observed. These results indicate that conditions were much more favorable for Ephemeroptera and Diptera under the stable flow regime. It appears that Plecoptera and Trichoptera were not affected as severely by the fluctuating flow regime as Ephemeroptera and Diptera.

Increases in the abundance of the three dominant mayfly taxa, *Ephemerella inermis*, *Baetis* and *Rithrogena*, were responsible for the dramatic increase in total ephemeropteran density in the summer of 1977 (Fig. 38). The standing crops of *E. inermis* and *Rithrogena* were only slightly higher in May and July 1977 than in May and July of 1976. However, densities of all three taxa were several times greater in September of 1977. The late summer increases in the populations of the taxa were due to recruitment from eggs deposited during the spring and early summer. Under fluctuating flow conditions in 1976, this normal late summer population increase did not occur. Peak abundance of

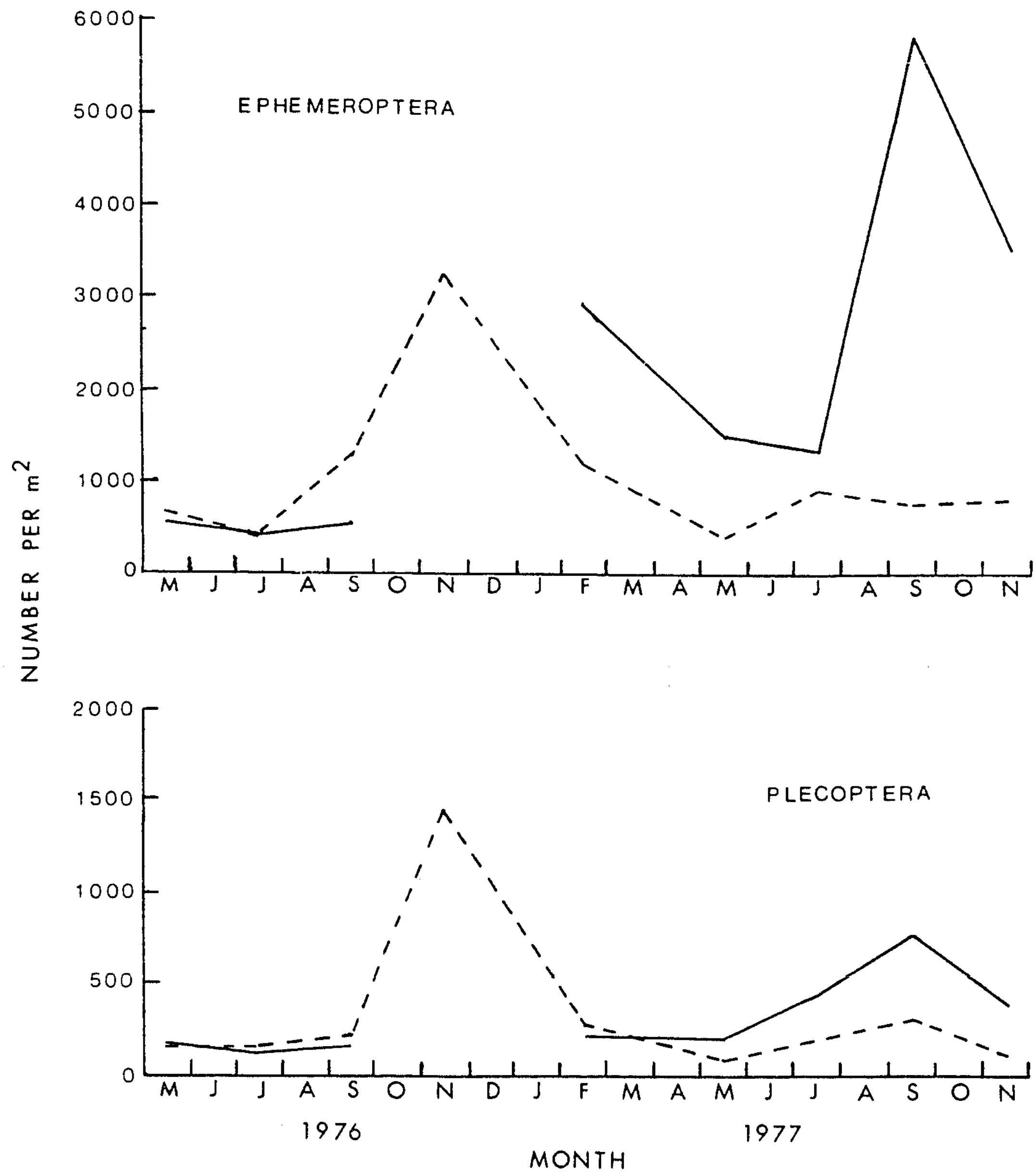


Fig. 36. Density of Ephemeroptera and Plecoptera in the unexposed zone of the Skagit and Sauk Rivers. (solid line = Skagit, dashed line = Sauk)

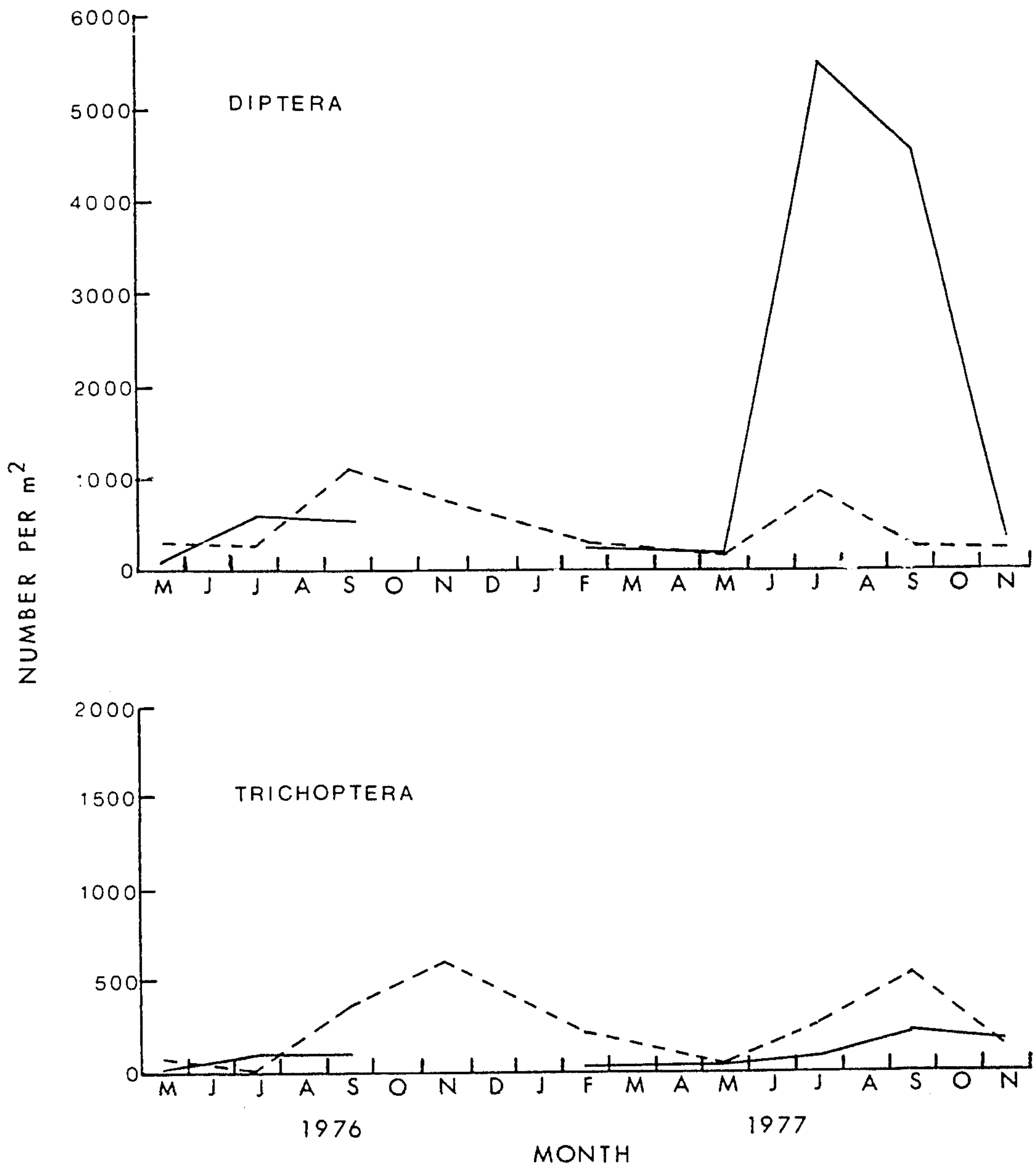


Fig. 37. Density of Diptera and Trichoptera in the unexposed zone of the Skagit and Sauk Rivers. (solid line = Skagit, dashed line = Sauk)

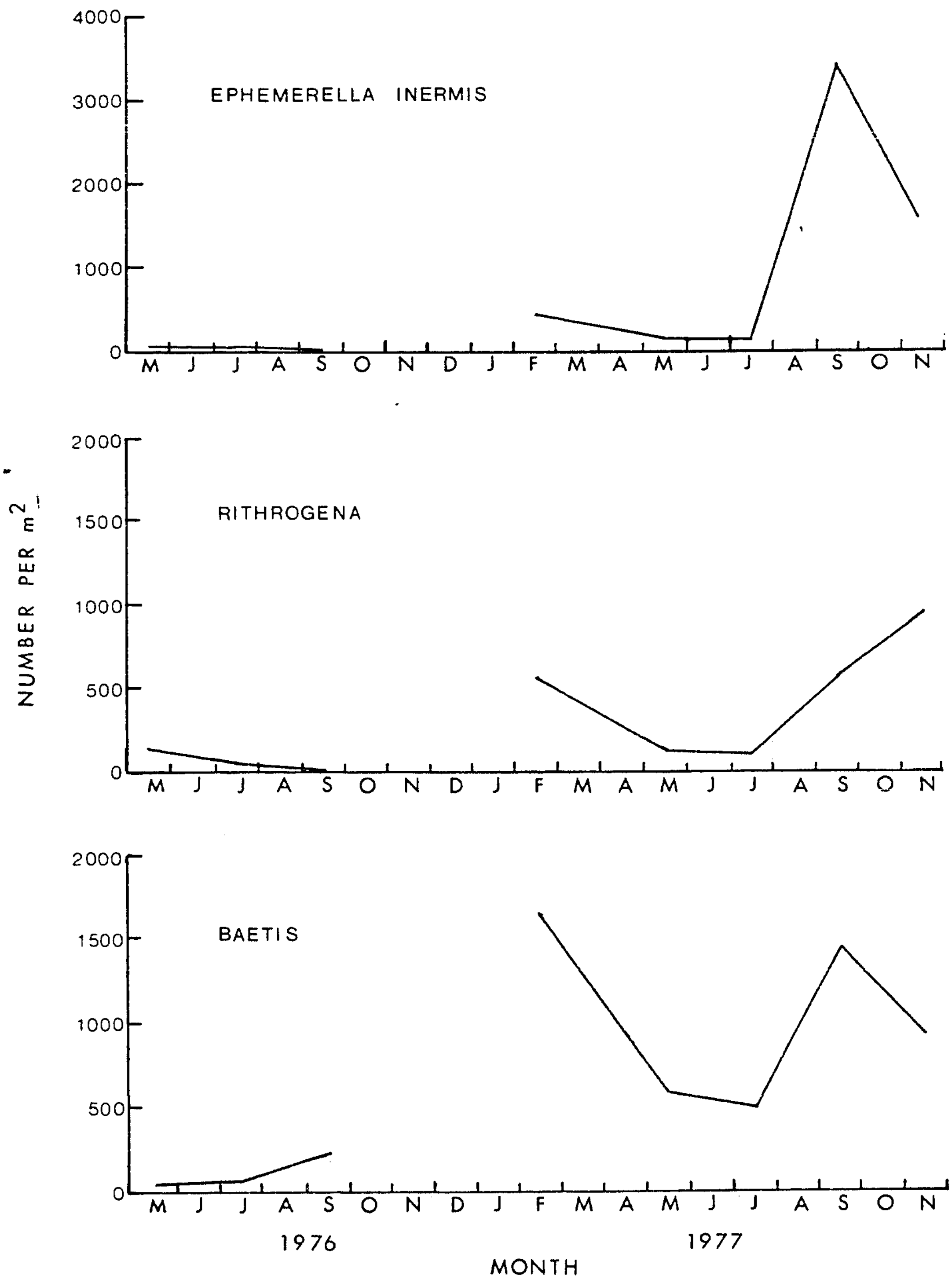


Fig. 38. Density of Ephemerella inermis, Rithrogena and Baetis in the unexposed zone at the lower Skagit station.

Ephemerella tibialis (Fig. 39) was roughly ten times greater in 1977 than in 1976. This species emerges in late summer and autumn, and the September population consisted of near mature and mature nymphs.

The densities of the two dominant plecopteran genera, Alloperla and Acroneuria, were also greater under stable flow conditions (Fig. 39). The species Alloperla forcipata and Acroneuria pacifica both emerged in late summer and early autumn in the Skagit River. During September 1977, the population of Alloperla consisted of mature nymphs while the Acroneuria population consisted of both mature and immature nymphs, as the species A. pacifica requires at least two years to complete its life cycle in the Skagit. Flow fluctuation during the summer of 1976 apparently reduced the numbers of these two taxa.

However, maximum densities of the two dominant trichopteran genera, Arctopsyche and Brachycentrus, were slightly lower under stable flow conditions (Fig. 40). It appears that the populations of these two taxa were not seriously affected by the fluctuating flow regime in 1976.

Taxonomic Composition. An annual pattern of alternating dominance of Ephemeroptera and Diptera was observed in the unexposed zone during both 1976 and 1977 at the Skagit and Sauk River stations (Fig. 41). This pattern was less pronounced at the Sauk stations. Ephemeroptera dominated the insect communities at the Skagit and Sauk stations during winter (February) and spring (May). During July, the numbers of Diptera collected increased. Many of the mayfly nymphs that were present in the winter and spring had emerged, and the Diptera now comprised the

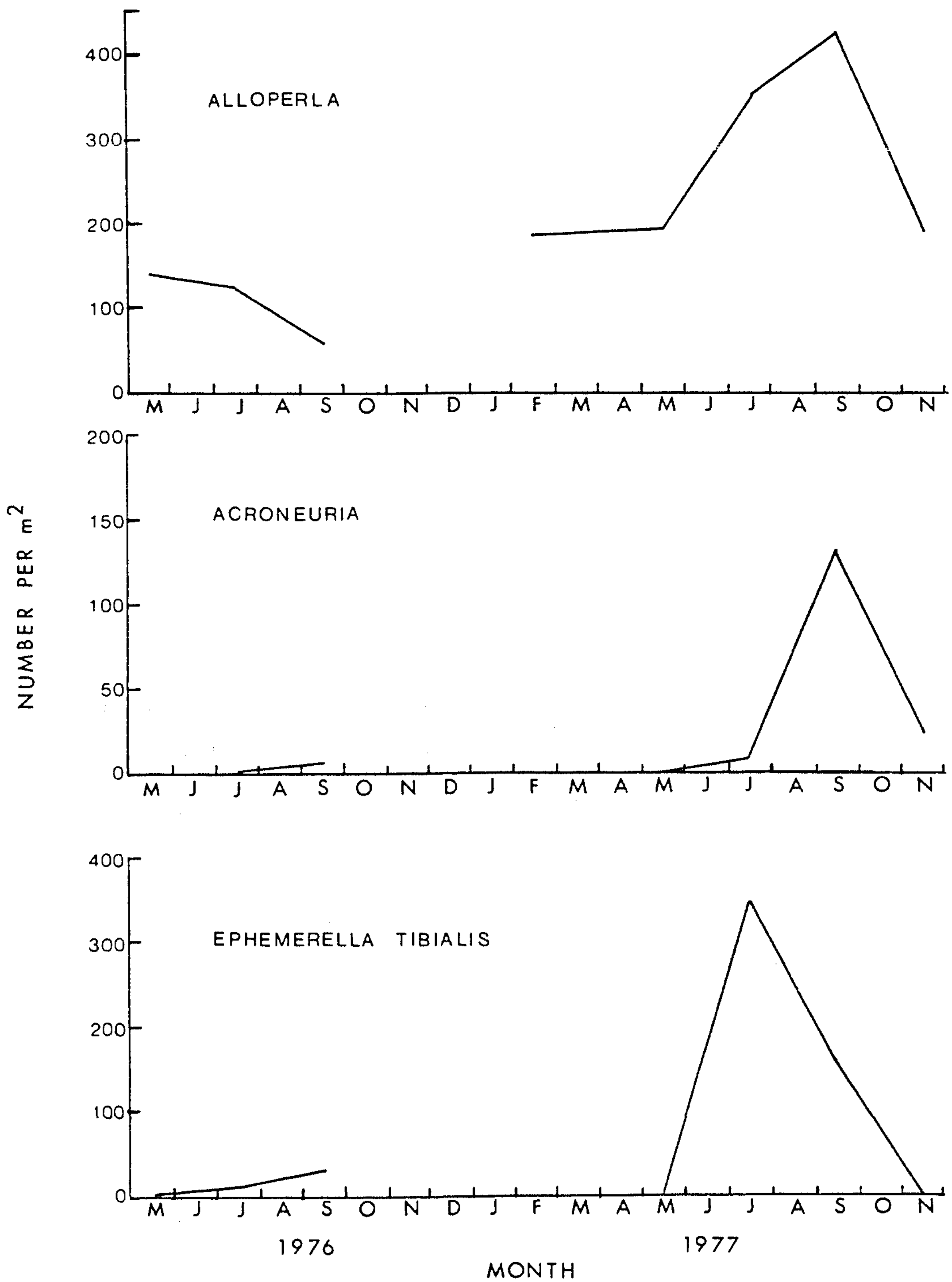


Fig. 39. Density of Alloperla, Acroneuria and Ephemerella tibialis in the unexposed zone at the lower Skagit station.

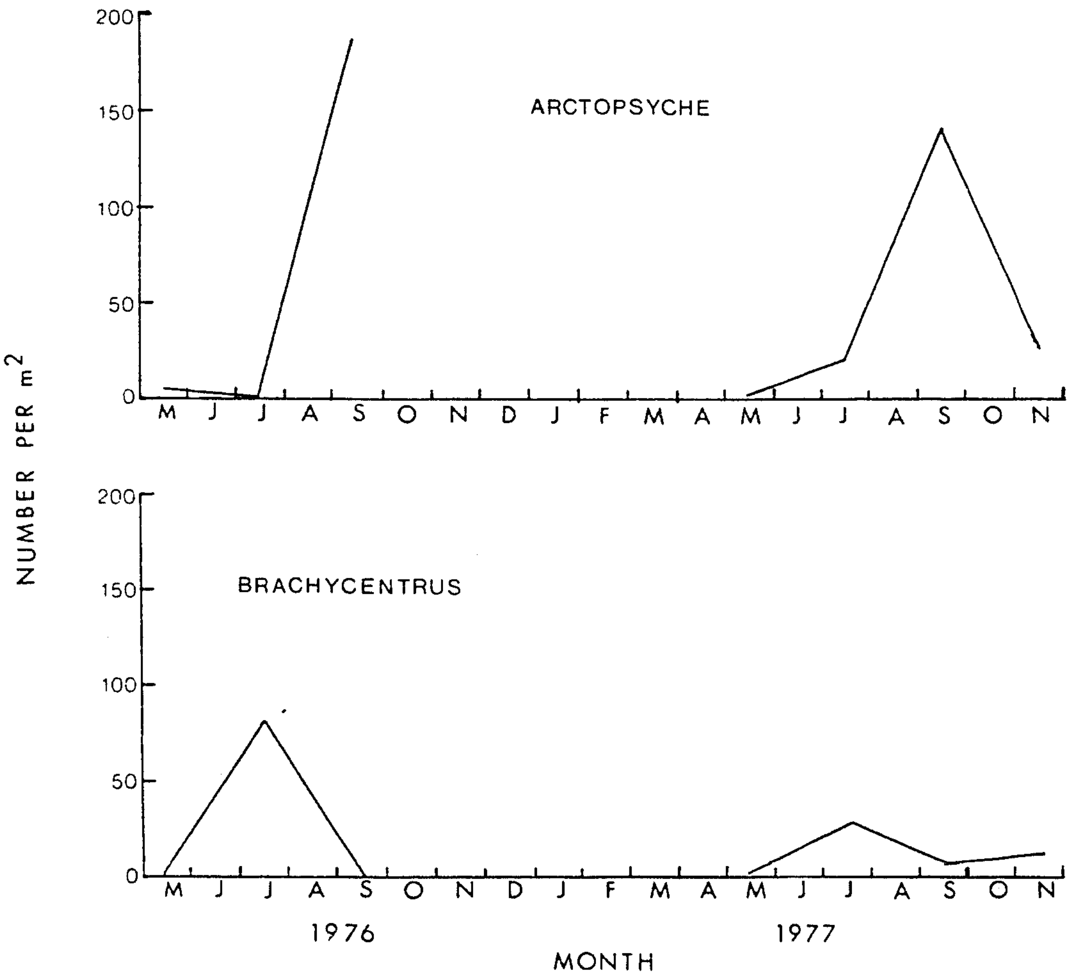


Fig. 40. Density of Arctopsyche and Brachycentrus in the unexposed zone at the lower Skagit station.

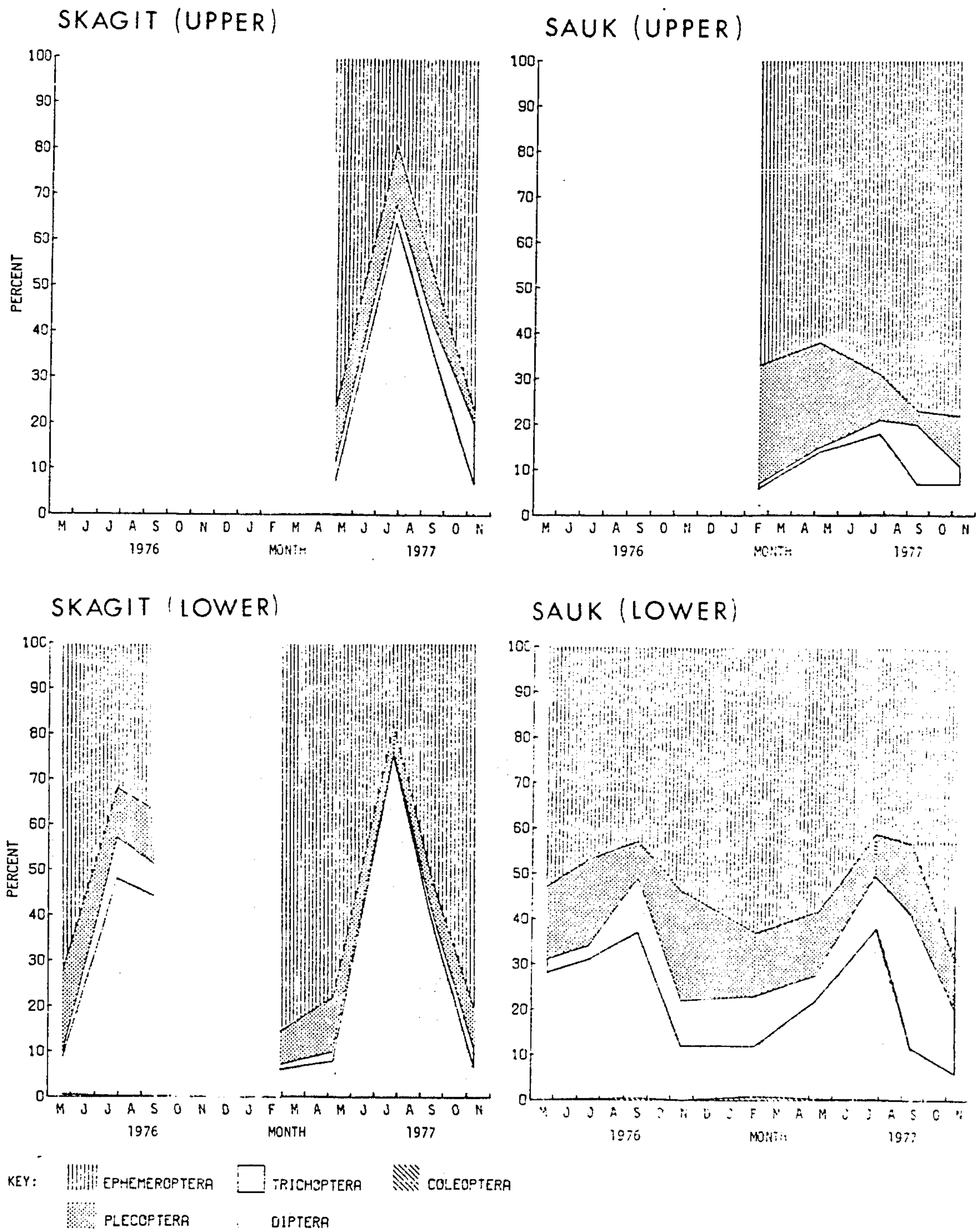


Fig. 41. Percent composition of each benthic insect order at the upper and lower Skagit and upper and lower Sauk stations.

largest proportion of the community. The dominance shifted again to the Ephemeroptera in the late summer and fall due to emergence of many of the chironomids and recruitment of Ephemeroptera.

There was only a slight change in composition at the lower Skagit station under stable flow conditions. During 1977, the percentage of Ephemeroptera, Plecoptera and Trichoptera was generally lower, while the percentage of Diptera increased. The abundance of all groups, except Trichoptera, increased under the stable flow regime. The increase in Diptera (mainly Chironomidae) was proportionately larger, resulting in reduced percentages of Ephemeroptera and Plecoptera.

Seasonal variability in the ability of the 351 μ sampler net to retain insects may have affected the observed composition of the benthic community. Most aquatic insects emerge, mate and deposit eggs in the stream during spring, summer and early fall months. More early instar, newly-hatched larvae are present during these months than during the winter. Consequently, the tendency to underestimate total numbers of all taxa is greatest during late summer and early fall and least during the winter (Barber and Kevern 1974). Most newly-hatched chironomidae have a head capsule width of 60 μ (Mundie 1971) and would have passed through the net until they had grown considerably. However, Ephemeroptera, Plecoptera and Trichoptera have a larger size range (Zelt and Clifford 1972) and larvae would be more likely to be retained immediately or soon after hatching.

The numbers of dipterans, which were primarily chironomids, were probably underestimated on all sampling dates, especially during the summer and fall months when large numbers of newly-hatched larvae were present. The sampler probably captured individuals belonging to other orders much more efficiently. As a result, the actual percentage of Diptera may have been higher during July, September and November. However, sampler efficiency would not affect comparisons among stations and between years, as the same sampler was used throughout the study.

Diversity. Diversity ($\bar{d}$) was calculated after Wilhm and Dorris (1968):

$$\bar{d} = - \sum_{i}^{s} \frac{n_i}{N} \log_2 \frac{n_i}{N}$$

where $s$ = number of taxa

$n_i$ = number of individuals in a particular taxon

and $N$ = total number of individuals

Diversity in the unexposed zone at the upper and lower Skagit and upper and lower Sauk stations is shown in Fig. 42.

During the fluctuating flow period, which included the sampling months May 1976 through February 1977, diversity in the unexposed zone at the lower Skagit station was nearly always lower than at the lower Sauk station. Diversity in the Sauk River was fairly constant and remained above 3.0. Diversity at the lower Skagit station rose above 3.0 only in July, when there was virtually no exposure of the substrate throughout the river channel during the two weeks prior to sampling.

When flow conditions were generally similar in the Skagit and Sauk, from mid-April 1977 to mid-November 1977, the pattern of seasonal variation was also generally similar. Diversity declined at all

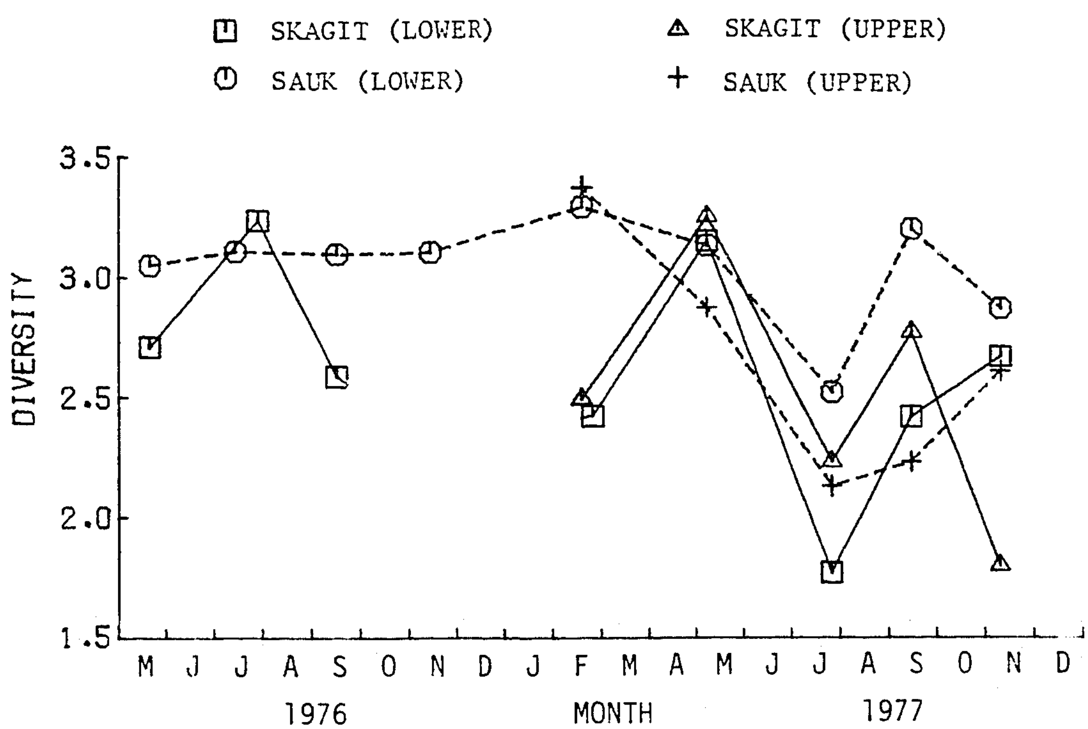


Fig. 42. Diversity at the upper and lower Skagit and upper and lower Sauk stations.

stations from May to July, then increased in September. A similar summer decrease in diversity was also observed in the Cedar River, Washington, by Malick (1977).

The lower diversity values in July 1977 were attributable to the summer increase in chironomid density. The Chironomidae were not identified below the family level and were considered as a single taxon in the computation of diversity. Thus, the benthic community in July was composed of a large number of individuals of a single taxon, Chironomidae, and diversity was consequently lower (Wilhm and Dorris 1968). An enormous increase in chironomid abundance was recorded at the lower Skagit station in July 1977 and diversity dropped below 2.0.

Identification of all insects, particularly the abundant chironomids, to the species level would have yielded higher density values. Thus the results of this study can be compared only with the results of other studies in which insects were identified down to similar levels.

Chironomids were not identified beyond the family level by Mason (1976), Malick (1977) or Siegfried and Knight (1977). All three used the same diversity formula. April samples from a small stream on Vancouver Island, British Columbia, had diversity values ranging from 2.82 to 3.60 (Mason 1976). The annual range of diversity was 0.3 to 2.3 ($\log_e$) in the Cedar River, Washington (Malick 1977) and 0.66 to 2.72 in a small California stream (Siegfried and Knight 1977). The 0.66 value was the result of downstream movement and transport of substrate material during winter flooding.

Both the annual maximum and minimum diversity values in the unexposed zone of the Skagit River were higher than the corresponding annual values in the Cedar River. The lower diversity values in the Cedar River may have resulted from the capture of more chironomids from deeper substrate strata with the Coleman-Hynes basket sampler used by Malick (1977). An increased number of chironomids due to this sampling method would have lowered the diversity index, since chironomids were considered as a single taxon and not identified further.

Trophic Structure. Skagit and Sauk River insects, with the exception of the chironomids, were assigned to a trophic group after the generalized classification scheme of Cummins (1978). Insect taxa in each group are listed in Table 24. There is no sharp distinction between algal grazers and detritivores (Chapman and Demory 1963, Ulfstrand 1968), and many Ephemeropteran and Trichopteran families were included in both the scraper (algal grazer) and collector-gatherer (fine particle detritivore) categories by Cummins (1978). Other references were used to determine the predominant mode of feeding for local taxa of Ephemeroptera (Gilpin and Brusven 1970) and Trichoptera (Mecom 1972, Wiggins 1977), and the taxa were classified accordingly.

The family Chironomidae contains lower taxa which may be either scrapers, collector-filterers, collector-gatherers, shredders or predators (Cummins 1978). Therefore the entire family could not be included under a single trophic category as were the Simuliidae, for example, which are all collector-filterers. To classify the chironomids, it would have been necessary to first identify individuals beyond

Table 24. Trophic classification of aquatic insects (excluding Chironomidae) collected in the Skagit and Sauk rivers.

| SCRAPER | COLLECTOR-GATHERER | COLLECTOR-FILTERER | SHREDDER | PREDATOR |
|---|---|---|---|---|
| EPHEMEROPTERA | EPHEMEROPTERA | TRICHOPTERA | PLECOPTERA | PLECOPTERA |
| Baetidae | Siphlonuridae | Hydropsychidae | Nemouridae | Chloroperlidae |
| *Baetis* sp. | *Ameletus* sp. | *Arctopsyche* sp. | *Nemoura* sp. | *Alloperla* sp. |
| Heptageniidae | Leptophlebiidae | *Hydropsyche* sp. | Capniidae | Perlodidae |
| *Cinygmula* sp. | *Paraleptophlebia* sp. | Brachycentridae | TRICHOPTERA | *Arcynopteryx* sp. |
| *Epeorus* (*Iron*) sp. | Ephemerellidae | *Brachycentrus* sp. | Limnephilidae | *Isoperla* sp. |
| *Rithrogena* sp. | *Ephemerella delantala* | DIPTERA | *Onocosmoecus* sp. | *Isogenus* sp. |
| PLECOPTERA | *Ephemerella hystrix* | Simuliidae | Lepidostomatidae | Perlidae |
| Taeniopterygidae | *Ephemerella coloradensis* | | *Lepidostoma* sp. | *Acroneuria* sp. |
| *Brachyptera* sp. | *Ephemerella doddsi* | | DIPTERA | TRICHOPTERA |
| TRICHOPTERA | *Ephemerella grandis* | | Tipulidae | Rhyacophilidae |
| Glossosomatidae | *Ephemerella inermis* | | *Tipula* sp. | *Rhyacophila* spp. |
| *Glossosoma* sp. | *Ephemerella tibialis* | | | COLEOPTERA |
| Hydroptilidae | PLECOPTERA | | | Dytiscidae |
| *Ochrotrichia* sp. | Chloroperlidae | | | DIPTERA |
| Limnephilidae | *Kathroperla* sp. | | | Tipulidae |
| *Dicosmoecus* sp. | DIPTERA | | | *Hexatoma* sp. |
| COLEOPTERA | Tipulidae | | | *Pedicia* sp. |
| Elmidae | *Antocha* sp. | | | Rhagionidae |
| DIPTERA | Tanyderidae | | | *Atherix variegata* |
| Deuterophlebiidae | Ptychopteridae | | | Empididae |
| Blepharoceridae | | | | Ceratopogonidae |

the family level and then to assign the lower taxa to various trophic categories, a nearly impossible task due to limited taxonomic knowledge of the western Chironomidae and lack of information on feeding habits. For these reasons, the family Chironomidae was considered as a separate trophic group (Chironomidae) when determining trophic structure.

There were similar seasonal changes in the trophic structure within the unexposed zone at all stations (Fig. 43). Scrapers were the dominant trophic group during the winter and spring in both rivers, while Chironomidae were generally dominant in July and September. Predators were the next most important group and comprised a maximum of 45 percent of the insect community at the lower Skagit and upper Sauk stations in May 1977. The percentages of collector-gatherers and collector-filterers were usually less than 20 percent in both rivers. The percentage of shredders was always low, but increased during the fall and winter, when leaf litter was most abundant in the rivers.

Differences in trophic structure under fluctuating and stable streamflow conditions at the lower Skagit station were due mainly to an increase in the importance of chironomids during the summer of 1977. The percentage of Chironomidae was much greater in July 1977 (72 percent) than in July 1976 (39 percent). The percentage of scrapers was slightly lower from May through September 1977, and the percentage of predators was higher in May 1977. The percentage of collector-filterers was also generally lower during the summer months of 1979. Reservoir releases were curtailed in the summer of 1977, and the availability of reservoir phyto- and zooplankton in the river must have been reduced.

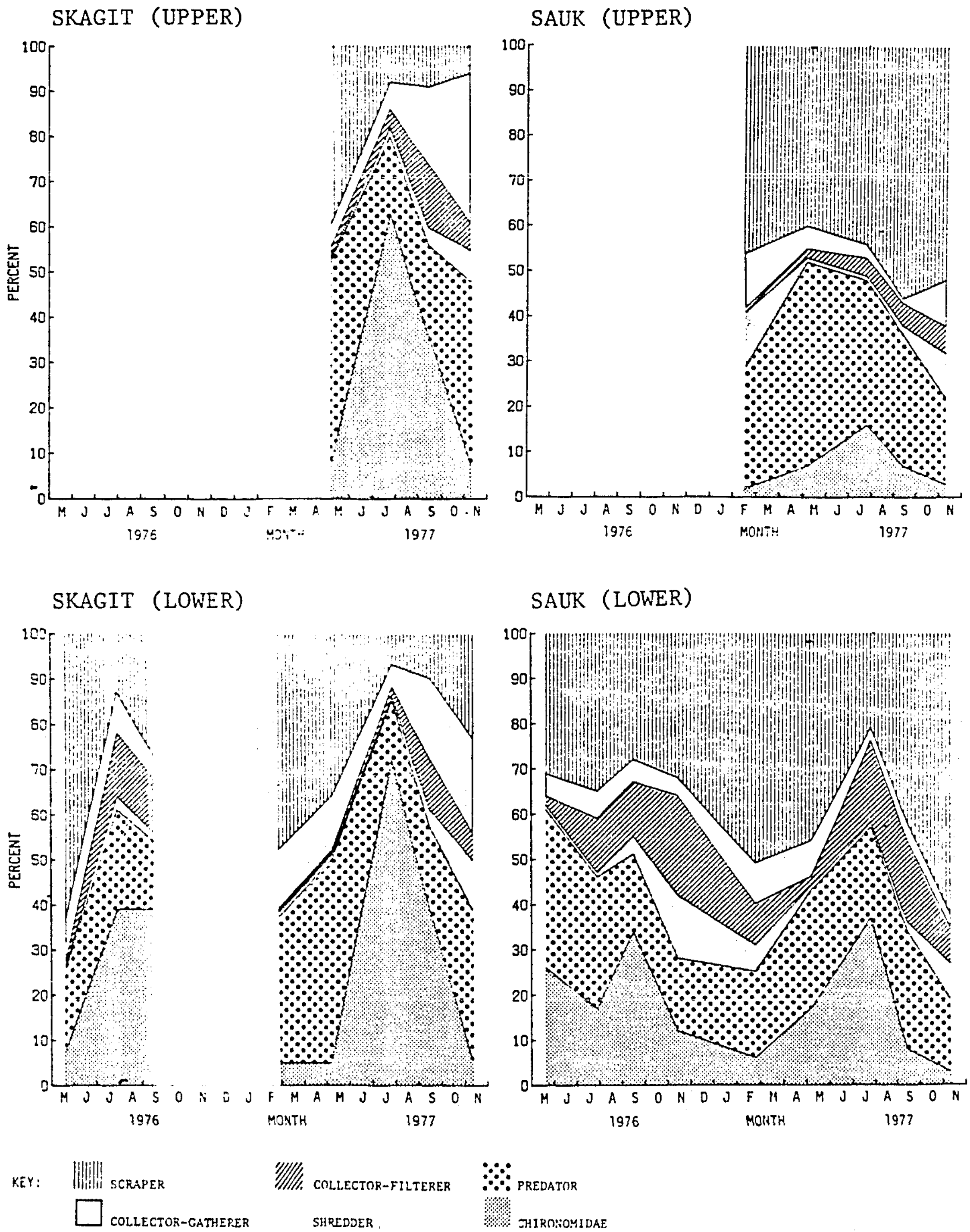


Fig. 43. Percent composition of each benthic insect trophic category at the upper and lower Skagit and upper and lower Sauk stations.

This reduction in the food supply may explain the lower importance of filter feeders in 1977.

There was little difference in trophic structure between years at the lower Sauk station, but there were some overall differences between the Sauk and Skagit. At both Sauk River stations the domination of the summer benthic insect community by Chironomidae was not as great, and scrapers always comprised at least 30 percent of the community at all seasons. Collector-filterers also formed a greater percentage of the community at the lower Sauk Station than at the Skagit River stations in 1977.

# DISCUSSION

## PHYSICAL PARAMETERS

During the course of the study, several beneficial effects of impoundment were observed in the Skagit River. These beneficial effects of regulation were present during both the fluctuating flow period and the stable flow period. Thus, they probably ameliorated the overall impact of peaking flow fluctuation and contributed to the enhancement of benthic insect standing crop under stable flow.

The most significant beneficial effect of impoundment was the reduction of sedimentation of the streambed and consequent reduction of scouring during high flow periods. Impoundment resulted in the settling of suspended inorganic particles and also blocked the downstream movement of coarser bedload material. During seasonal high flow periods, much of the interstitial sand and silt present in the surface of the streambed was washed downstream and was not replaced by import from upstream. During the stable flow period in 1977, these open interstitial spaces in the upper part of the substrate provided a much more favorable habitat for benthic insects than did the compacted substrate of the Sauk River. The lower amount of sand in silt in the surface of the streambed of the Skagit also resulted in reduced scour of periphyton and benthic insects during high flows. Impoundment has reduced scouring and resulted in a more stable substrate in several other streams, with similar beneficial effects (Pearson _et al_. 1968, Armitage 1976).

No disturbance of the surface cobbles was evident after the

November 1977 high flow at any of the Skagit or Sauk River sampling stations. Therefore any standing crop reduction during the high flow was caused by scouring rather than by shifting of the larger substrate particles.

It is not known if the streambed of the Skagit River will remain in its present uncompacted condition. Extreme flood flows during December 1975 may have washed out fine sediment which had previously been contributed to the main stem Skagit by tributary streams, resulting in the absence of interstitial sediment observed during 1976 and 1977. Sediment imported by tributary streams may eventually accumulate in the surface of the streambed and alter benthic insect habitat if it is not removed by the annual peak flows.

Impoundment has also resulted in lower turbidity and contributed to flood control in the Skagit River. However, there was not apparent nutrient enrichment of the type frequently observed below hypolimnial release reservoirs (Neel 1963).

PERIPHYTON

The growth of periphyton at the edge of the Skagit River was limited by exposure to desiccation during periodic dewatering. Current velocity probably limited growth in the unexposed areas of the streambed. Horner (1978) examined the relationship between periphyton growth and current velocity and nutrients in several western Washington streams and found that if phosphorus concentration was above 30-45 μg/l, growth was enhanced by increasing current velocity. However, as velocity increased beyond 50 cm/sec, erosion of periphyton from rock substrates was greater than growth. If nutrient concentration was less than 30 μg/l, growth was inhibited by increasing velocity. Chlorophyll a was always low at velocities approaching 100 cm/sec.

In a large swiftly-flowing stream like the Skagit, where current velocities near mid-stream are greater than 100 cm/sec, most periphyton growth is probably restricted to a band along the river margin where velocity is suitable for growth. In the Skagit and Sauk rivers, bottom current velocity was estimated to be 100 cm/sec at depths of 70 to 90 cm. If we consider 100 cm/sec to be the upper threshold velocity for periphyton growth, most periphyton standing crop in a cross section of the river was probably in the area between the edge of the river and a point 70 to 90 cm deep. Periphyton samples were collected at depths of 45 cm or less, and it was not possible to determine if periphyton was distributed in this manner. However, heavy algal growth was visible in the shoreline areas at the lower Skagit station in aerial photographs, while the deeper midstream areas appeared to be devoid of periphyton.

The location of the periphyton zone, defined as the area of the streambed where bottom current velocity is between 0 and 100 cm/sec, moves laterally as the result of seasonal changes in streamflow. In the three rivers studied, maximum seasonal flows in winter and early summer were followed by periods of lower flow. Periphyton present in shoreline areas during the high flow periods was exposed to desiccation and destroyed as the flow declined. However, under unregulated conditions with low daily fluctuation, the streamflow declined gradually and should have allowed periphyton to become established in midstream areas where high current velocity did not permit growth under higher flow. As streamflow increases in early summer and fall, the periphyton zone would be expected to shift toward the banks of the stream channel as previously dry areas become wetted and current erodes the periphyton near midstream. The width of the periphyton zone would remain roughly constant regardless of the width of the river.

However, daily peaking flow fluctuation in the Skagit River did reduce the width of the periphyton zone. The effect of peaking fluctuation on the width of the periphyton zone is illustrated in Fig. 44. Bottom current velocity was estimated to be 100 cm/sec (95 percent confidence interval of 109-91 cm/sec) at a depth of 86 cm at the lower Skagit station. Therefore severe erosion of periphyton would be expected whenever the depth at any point on the bottom exceeded 86 cm. The width of the periphyton zone is shown during a hypothetical daily range in water level of 0.5 m at the lower Skagit transect. Had streamflow remained stable at either the daily maximum or minimum flow, conditions would have been suitable for periphyton growth along 33 and 29 m of the transect, respectively. At a stable median water level, the width of the periphyton zone would have been 26 m. Due to bottom current velocities above 100 cm/sec along the permanently submerged portion of the transect during daily maximum flow and exposure of the shoreline side of the transect during daily minimum flow, the width of the periphyton zone would have been only 8 m under fluctuating flow conditions. A similar reduction in the width of the periphyton zone

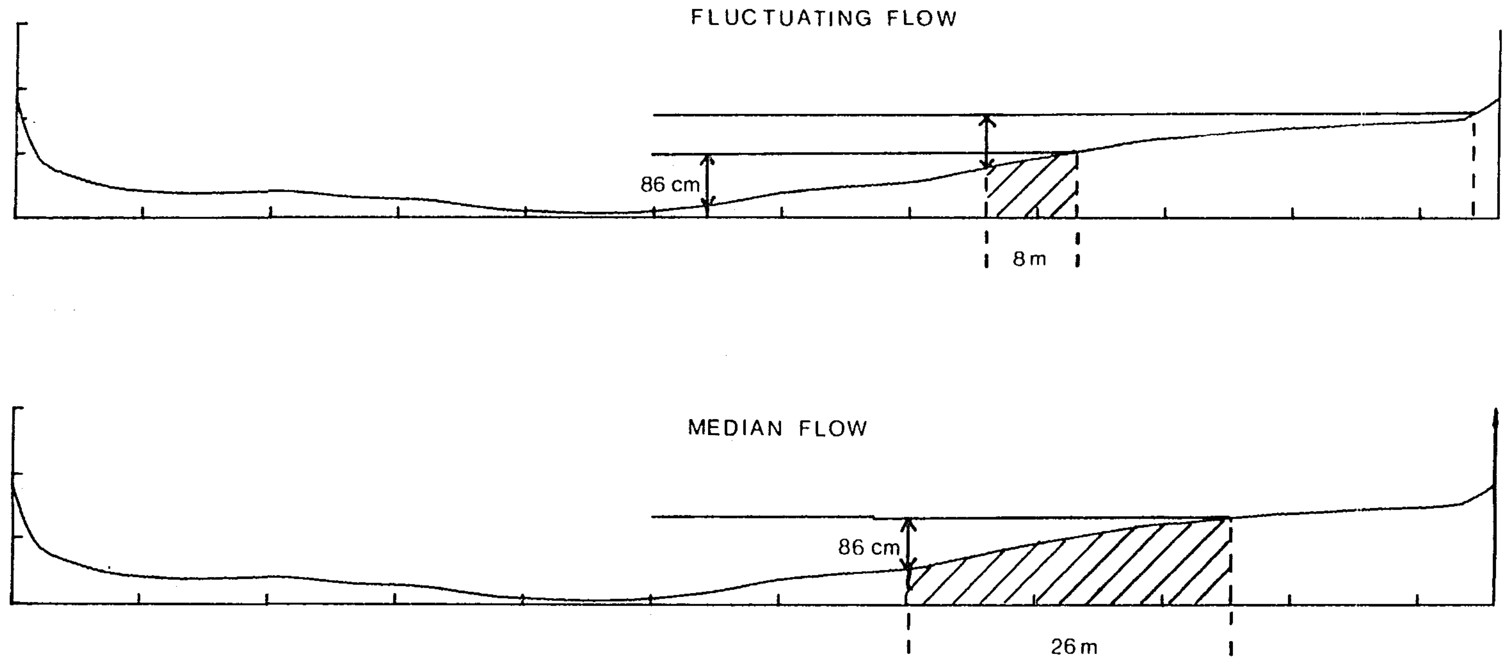


Fig. 44. Width of the periphyton zone during a water level fluctuation of 0.5 m and during stable median flow. The cross-hatched section of the transect is the periphyton zone.

relative to the potential width under stable flow conditions would have occurred in the Skagit regardless of the range of fluctuation, but the magnitude of the reduction would depend on the range of daily flows. If the range of water level fluctuation was greater than 86 m, the entire permanently submerged area of the streambed would have been subjected to current velocities above 100 cm/sec.

BENTHIC INSECTS

Results of the experimental phase of the study explain some of the effects of periodic dewatering on insect standing crop and composition within the zone of exposure. Ephemeropteran nymphs had a much greater propensity to drift during flow reductions in the artificial stream than chironomid larvae. Mayfly nymphs were also susceptible to stranding and were extremely vulnerable to desiccation.

However, chironomids appear to be very resistant to the effects of desiccation on dewatered substrate. Their resistance may be the result of their residence in the hyporheic zone of the streambed. Denham (1938) reported that chironomid larvae were able to survive in mud and sand as long as there was sufficient moisture and observed that larvae burrowed into sand at the bottom of a cylinder in response to experimental dewatering. Chironomid larvae were able to survive 10 weeks of drought in a mountain stream by remaining in the hyporheic zone (Hynes 1958). Sprules (1947) and Brusven et al. (1974) also noted that chironomids were relatively tolerant of desiccation on substrate exposed by flow reduction.

The percentage of Chironomidae in the insect community in the exposed zone of the Skagit was much greater than the percentage in the unexposed zone. The percentage of Ephemeroptera in the exposed zone was lower than in the unexposed zone. During daily flow reductions, many of the mayflies in the exposed zone were presumably stranded and perished, while others were displaced into the unexposed zone by drift. The more resistant chironomids were able to survive desiccation until the river margins were again submerged during daily high flows.

Current velocity was the primary environmental factor controlling the microdistribution of benthic insects within the submerged areas of the Skagit. During stable flow conditions in the summer of 1977, insect density was greatest at a depth of 15 cm and a mean bottom current velocity of 27 cm/sec. Density was negatively correlated with current velocity and decreased with increasing depth and velocity. Since substrate particle size was uniform along the sampling transect, it was not a factor in the cross-stream microdistribution of the benthos.

Several other investigators have also observed that benthic macroinvertebrates are more abundant in the margins of large streams (over 7 m wide) than at midstream (Needham 1934, Needham and Usinger 1956, Kennedy 1967). Kennedy (1967) reported that the majority of benthic organisms in Convict Creek, California, preferred depths between 7.5 and 15 cm and current velocity between 30.5 and 36.6 cm/sec. As depth increased beyond 15 cm, the number of organisms decreased. Gore (1978) concluded that optimal conditions for benthic insects existed at a depth of 28 cm with an average current velocity in the water column above the site (not bottom current velocity) of 76 cm/sec. The results of these studies and the present study clearly indicate a preference for the moderate current velocities found in the margins of large streams and an avoidance of the higher velocities found in the deeper areas.

Greater availability of food at the margins of large streams may have also played a role in insect distribution. As previously discussed, current velocity probably restricted most of the periphyton standing crop to the margins of the Skagit. The distribution of herbivores must have been similarly restricted. Detritus is also particularly abundance in places with reduced current speed (Ulfstrand 1968). In large streams, current speed is lowest in the margins.

Since most of the insects are restricted to a relatively small area along the margins of large streams, a change in the wetted perimeter of the stream would not significantly increase or reduce insect habitat. However, streamflow variations would necessitate a redistribution of insects within the wetted area of the stream channel.

This redistribution was accomplished primarily by the movement of drifting insects. Insect drift is a naturally occurring phenomenon that results in the continuous redistribution of benthic insects throughout the stream (Ulfstrand 1968, Townsend and Hildrew 1976). Insect standing crop at any point in the stream is affected by the immigration rate and the departure rate of drifting insects. Insects that leave the substrate and settle in unsuitable habitat will probably depart at the earliest opportunity (Ulfstrand 1968). Thus, insects are able to control their microdistribution by drifting repeatedly until they settle in suitable habitat. Following a change in the width of a large stream, insects will again be redistributed in the areas of the streambed where current velocity is optimal, if flow remains stable at the higher or lower discharge.

During moderate increases in streamflow in large streams, previously dry areas at the margins of the stream channel are submerged and become accessible to colonization by insects. At the same time, current velocity increases over the submerged areas of the streambed where current velocity was optimal before the flow increase. High flows in smaller streams displaced insects by drift from areas of high current velocity to areas of lower velocity, without any apparent depletion of the bottom fauna (Minckley 1963, Lehmkuhl and Anderson 1972). During higher flows in large streams, insects are probably displaced into the lower velocity areas at the stream margins. Drift unrelated to physical disturbance, including behavioral and constant drift as described by Waters (1972), would also result in the colonization of the newly submerged areas of the stream margin. Some colonization may occur from lateral migration along the bottom and oviposition, but drift is by far the most important colonization mechanism of stream insects (Townsend and Hildrew 1976, Williams and Hynes 1976).

Benthic sampling in the margins of a stream following an increase in discharge and prior to complete colonization would yield a low number of insects. An investigator with no knowledge of the exposure history of the streambed would probably conclude that the stream was extremely unproductive, although benthic insect density in the deeper areas of the stream might be much greater. Samples collected in the stream margins before or after the high flow would have also indicated higher densities in the river. Therefore it is imperative to determine the pre-sampling exposure history of river bottom sample locations in any type of benthic study to avoid erroneous interpretation of the results. This precaution applies to sampling in unregulated coastal streams as well as in streams subject to hydroelectric peaking flow.

During reduction in flow, benthic insects are displaced primarily by drift from the margins toward midstream. Flow reductions in the artificial stream induced drift and similar increases in drift have been observed during flow reductions in natural streams (Minshall and Winger 1968, Pearson and Franklin 1968, Radford and Hartland-Rowe 1971, MacPhee and Brusven 1973). Mobile insects, for example stonefly nymphs and cased caddis larvae, may remain in contact with the bottom as they move laterally. Insects unable to avoid stranding by either of these methods are killed by desiccation. Even during the relatively rapid flow reductions in the artificial stream, many of the insects were able to avoid stranding. Clearly, all insects in the stream margins are not stranded and killed during flow reduction, as stated by Bell (1973). During the general decreases in streamflow observed in the Sauk and Cascade rivers, a considerable number of insects are probably able to escape stranding.

During peaking flow conditions in the Skagit River, both rapid increases in flow and rapid flow reductions usually occurred within the same 24-hour period. Stranding and drift reduced the insect standing crop in the exposed zone. The insect population in the unexposed zone was also reduced in late summer relative to Sauk River standing crop. There are several possible causes for this reduction in the unexposed zone.

Declining discharge following spring runoff combined with daily peaking fluctuation probably contributed significantly to the reduction. As streamflow began to drop, the concentration of insects near the edge of the stream channel during the July sampling period was eventually exposed to desiccation during a daily minimum flow, resulting in stranding losses and dispersal of insects into the unexposed part of the stream channel. However, insects at the edge of the unexposed zone, including many of those that had survived the initial dewatering, were again subjected to stranding by an even lower minimum flow. This process of stranding and dispersal of surviving insects into the ever smaller unexposed zone continued throughout the summer and early autumn due to progressively lower daily minimum flows. The cumulative effect of these stranding losses was evident in September 1976. If the streamflow had dropped gradually, as it did during the summer in the unregulated streams, stranding losses would have been much lower.

Benthic insect standing crop in the unexposed zone may also have been reduced indirectly by stranding without actual exposure of the substrate. Much of the insect drift originating in the unexposed zone undoubtedly settled in the zone of exposure while it was submerged during daily high flows. Considerable colonization of the substrate could have occurred during the relatively brief periods of submergence. Allan (1975) reported that well over 50 percent of individuals and species established in denuded substrate within 24 hours. Mayflies were particularly rapid colonizers. Increased current velocity over the unexposed zone during the daily high flows would have tended to disperse insects into the lower velocity areas at the stream margins. When the flows decreased, the insects that had settled in the exposed zone would have been exposed to potential stranding conditions. Over a period of time this continuous stranding of drifting insects could have significantly reduced the population in the unexposed zone.

Comparison of standing crop in the unexposed zone of the Skagit and Sauk rivers during the fluctuating flow period suggested seasonal variability in the impact of peaking fluctuation on the benthic insect community. The standing crop in unexposed areas of the Skagit was reduced in September 1976, but not in May and July. Skagit River standing crop was higher than Sauk standing crop in February 1977, although peaking was still occurring in the Skagit. The reduction in standing crop in September may be explained by the effect of seasonally declining water level combined with daily peaking fluctuation, but resistance of the different taxa of benthic insects also varies during an annual cycle.

A total of 84 percent of all insects collected during February 1977 at the lower Skagit station belonged to the order Ephemeroptera. Most of the ephemeropterans were members of the genera Baetis, Rithrogena and Cinygmula. These taxa are all morphologically adapted to withstand high current velocity. Rithrogena and Cinygmula, like all the Heptageniidae, have dorso-ventrally flattened bodies enabling them to live in the relatively still boundary layer surrounding streambed stones (Dodds and Hisaw 1924, Hynes 1970). The gills of Rithrogena are also arranged on the underside of the abdomen in a suction cup-like form, a further adaptation to strong current. Baetis has a highly streamlined form, is considered a good swimmer and may be found at current velocities of up to 300 cm/sec (Dodds and Hisaw 1924). Baetids were least affected by early season floods in a small California stream (Siegfried and Knight 1977), and mayflies exhibited a remarkable resistance to winter floods and maintained their populations at increasing levels in another California stream (Briggs 1948).

Due to their relative resistance to high current velocities, the mayflies were able to maintain their position in the unexposed zone during daily maximum flows and were not dispersed into the exposed zone of the river where they might have been stranded. The benthic insect community in May 1976 was also dominated by these same mayfly species, which may have accounted for the reduced impact of flow fluctuation at this time.

Peaking flow fluctuation during the summer months probably has a much greater impact on the mayfly population due to a greater propensity to drift during these months. The abundance of the ephemeropterans increased dramatically during the late summer under stable flow conditions due to the recruitment of nymphs of Ephemerella inermis and Baetis. This normal seasonal peak did not occur in 1976, apparently because these smaller nymphs were destroyed by flow fluctuation. Smaller insects of weak swimming ability are more susceptible to being swept away by high flows than larger individuals (Maciolek and Needham 1951), and high flows have been cited as a mechanism for dispersing the young stages of insects to all habitats in the streams (Anderson and Lehmkuhl 1968, Townsend and Hildrew 1976). Unfortunately, the smaller nymphs were probably dispersed into the zone of exposure in the Skagit where they were stranded. The drift rate of larger, mature mayfly nymphs is also greatest in the period of rapid growth prior to emergence (Elliott 1967), and dispersal into the exposed zone more likely in spring and summer.

Chironomidae may also be more susceptible to the effects of peaking flow fluctuation during the summer, the period of peak emergence. Large numbers of chironomids inhabit the hyporheic zone of the streambed, but these chironomids must migrate to the surface to complete their life cycle. Williams and Hynes (1974) observed downward migration of immature larvae in the winter and upward migration prior to emergence. Chironomid pupae were never found deeper than 10 cm in the substrate. Larvae and pupae near the surface would be susceptible to being swept away by current velocity fluctuation and to becoming stranded during flow reductions. Pupae would be especially vulnerable to desiccation since they would not be able to migrate downward in response to dewatering.

It is possible that the large increase in chironomid abundance under stable flow conditions in 1977 was due to increase in the numbers of surface-dwelling forms. Chironomids were observed in the mats of filamentous algae on the surface of stones in the Skagit and in other rivers (Brusven *et al*. 1974, Brennan *et al*. 1978). The abundance of the stone-surface chironomid fauna was regulated by the amount of fine particulate material available for food and case building in an unregulated stream (Brennan *et al*. 1978). Naturally occurring flow fluctuations periodically removed much of this material and greater chironomid abundance was predicted under more stable flow following impoundment of the stream. The availability of fine particulate material would have been much greater under stable flow in the Skagit River during the summer of 1977, and the chironomids at the surface would not have been exposed to desiccation. These ideal conditions probably resulted in increased abundance in 1977. It appears that the standing

It appears that the standing crop of the dominant Trichoptera genera, *Arctopsyche* and *Brachycentrus*, was not affected by the peaking flow fluctuation. The relative resistance of these genera was probably related to their preference for the higher current velocities associated with deeper areas of the Skagit. Rapid current brings more food per unit time, and it has long been known that faster current favors net-spinning caddis larvae (Philipson 1954, Edington 1965). *Arctopsyche irrorata*, a congener of *Arctopsyche grandis*, the dominant species in the Skagit, prefers current velocity between 105 and 161 cm/sec (Wallace *et al*. 1977). The upper threshold velocity for *Brachycentrus*, a cased filter-feeder, is probably well above 100 cm/sec (Gallep 1977). The resistance of these two genera to high current velocity probably enabled individuals to maintain their position on the bottom in the unexposed zone despite current velocity fluctuation during daily maximum flow. Preference for deeper areas of the stream channel would also be advantageous in avoiding exposure during daily minimum flows.

## IMPLICATIONS FOR FISH FEEDING

The distribution of juvenile chinook salmon, coho salmon and steelhead trout within streams is controlled by current velocity, which generally restricts smaller fish to the margins of large streams (Chapman and Bjornn 1969, Mundie 1969, Bustard and Narver 1975). Juveniles may shift to faster and deeper water as body growth occurs (Bustard and Narver 1975). Under a peaking flow regime, the younger, smaller juveniles must move laterally in order to avoid stranding during flow reductions and to maintain their positions in lower velocity areas at the stream margins during increased flow. During daily maximum flow, the fish are probably distributed within the zone of exposure, where benthic insect standing crop is severely reduced. During the daily low flow period in the peaking cycle, the fish may be in the unexposed zone, where benthic insect densities are much higher, but still reduced below normal levels in the summer.

The availability of drifting insects, as well as the availability of benthos, is probably much lower in the exposed zone. Stream salmonids feed on drifting insects (Mundie 1969), although Waters (1969) has indicated that a substantial proportion of the diet is obtained by bottom foraging. Low drift densities would be expected in the exposed zone. Insects generally drift only for short distances (2-10 m) before returning to the bottom and most are derived from the area of the streambed immediately in front of drift collecting nets (McLay 1970, Elliott 1971, Townsend and Hildrew 1976). An individual fish feeding in the exposed zone would probably be exposed to low drift densities as a result of low benthic densities immediately upstream. However, drifting insects may have been displaced from the unexposed zone by high current velocity and turbulent flow during the daily high flows. Further research is needed to determine the drift densities across the width of large streams during both stable and fluctuating flow over a complete annual cycle.

A concurrent study of the growth and condition of juvenile salmonids (Graybill *et al*. 1979) indicated that the growth patterns of coho and rainbow-steelhead fry reflected the level of benthic insect standing crop in the three rivers. The fish samples were collected at or near the benthic insect sampling stations. From July to December 1976, length and weight of age 0 coho fry increased more rapidly in the Sauk and Cascade rivers than in the Skagit, and the values of these two parameters were also higher in the unregulated rivers. The differences in the growth rate of age 0 rainbow-steelhead fry among the three rivers were not as pronounced as for coho, but the same trends were evident. During the summer of 1977, when benthic insect density was enhanced in the Skagit, Skagit River age 0 coho and rainbow-steelhead fry had much higher condition factors and larger size than during 1976.

## RECOMMENDATIONS

The comparison of benthic insect standing crop under the fluctuating and stable flow regimes clearly indicates the beneficial effects of stabilized flow in the Skagit River. Reduction in the degree of daily peaking fluctuation would greatly enhance insect production in the river. However, a relatively natural seasonal flow regime should be maintained, including the release of large volumes of water at some time during the year, to flush accumulated sediment out of the interstices between substrate particles.

## REFERENCES CITED


Allan, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. Ecology 56:1040-1053.

Allen, R. K., and G. F. Edmunds, Jr. 1959. A revision of the genus Ephemerella (Ephemeroptera: Ephemerellidae). I. The subgenus Timpanoga. Can. Entomol. 91:51-58.

Allen, R. K., and G. F. Edmunds, Jr. 1961a. A revision of the genus Ephemerella (Ephemeroptera: Ephemerellidae). II. The subgenus Caudatella. Ann. Entomol. Soc. Amer. 54:603-612.

Allen, R. K., and G. F. Edmunds, Jr. 1961b. A revision of the genus Ephemerella (Ephemeroptera: Ephemerellidae). III. The subgenus Attenuatella. J. Kansas Entomol. Soc. 34:161-173.

Allen, R. K., and G. F. Edmunds, Jr. 1962. A revision of the genus Ephemerella (Ephemeroptera, Ephemerellidae). V. The subgenus Drunella in North America. Misc. Pub. Entomol. Soc. Amer. 3:145-179.

Allen, R. K., and G. F. Edmunds, Jr. 1963. A revision of the genus Ephemerella (Ephemeroptera: Ephemerellidae). VI. The subgenus Serratella in North America. Ann. Entomol. Soc. Amer. 56:583-600.

Allen, R. K., and G. F. Edmunds, Jr. 1965. A revision of the genus Ephemerella (Ephemeroptera: Ephemerellidae). VIII. The subgenus Ephemerella in North America. Misc. Pub. Entomol. Soc. Amer. 4:243-282.

Allen, R. K., and G. F. Edmunds, Jr. 1976. A revision of the genus Ametropus in North America (Ephemeroptera: Ametropididae). J. Kansas Entomol. Soc. 49:625-635.

American Public Health Association. 1975. Standard methods for the examination of water and wastewater. 14th ed. APHA, Washington, D. C. 1193 pp.

Anderson, N. H., and D. M. Lehmkuhl. 1968. Catastrophic drift of insects in a woodland stream. Ecology 49:198-206.

Armitage, P. D. 1976. A quantitative study of the invertebrate fauna of the River Tees below Cow Green Reservoir. Freshwat. Biol. 6:229-240.

Barber, W. E., and N. R. Kevern. 1974. Seasonal variation in sieving efficiency in a lotic habitat. Freshwat. Biol. 4:293-300.

Bell, M. C. 1973. Fisheries handbook of engineering requirements and biological criteria. Fish. Eng. Res. Prog., U. S. Army Corps Eng., N. Pac. Div., Portland, Oregon.

Brennan, A., A. J. McLachlan and R. S. Wooton. 1978. Particulate material and midge larvae (Chironomidae: Diptera) in an upland river. Hydrobiologia 59:67-73.

Briggs, J. C. 1948. The quantitative effects of a dam upon the bottom fauna of a small California stream. Trans. Amer. Fish. Soc. 78: 70-81.

Brusven, M. A., C. MacPhee and R. Biggam. 1974. Effects of water fluctuation on benthic insects. Pages 67-79 in Anatomy of a river. Pac. N. W. River Basins Comm., Vancouver, Washington.

Brusven, M. A., and K. V. Prather. 1974. Influence of stream sediments on the distribution of macrobenthos. J. Entomol. Soc. British Columbia 71:25-32.

Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). J. Fish. Res. Bd. Can. 32:667-680.

Chapman, D. W., and R. L. Demory. 1963. Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. Ecology 44:140-146.

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153-176 in T. G. Northcote (ed.), Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Coleman, M. J., and H. B. N. Hynes. 1970. The vertical distribution of the invertebrate fauna in the bed of a stream. Limnol. Oceanogr. 15:31-40.

Cordone, A. J., and D. W. Kelley. 1961. The influences of inorganic sediment on the aquatic life of streams. Calif. Fish Game 47: 189-228.

Cummins, K. W. 1974. Structure and function of stream ecosystems. BioScience 24:631-642.

Cummins, K. W. 1975. The ecology of running waters: theory and practice. Pages 277-293 in Proceedings, Sandusky River Basin symposium, May 2-3, 1975. Int. Reference Group on Great Lakes Pollution from Land Use Activities.

Cummins, K. W. 1978. Ecology and distribution of aquatic insects. Pages 29-31 in R. W. Merrit and K. W. Cummins (eds.), An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.

Denham, S. C. 1938. A limnological investigation of the West Fork and common branch of the White River. Invest. Indiana Lakes Streams 1:17-71.

Dodds, G. S., and F. L. Hisaw. 1924. Ecological studies of aquatic insects. I. Adaptations of mayfly nymphs to swift streams. Ecology 5:137-148.

Edington, J. M. 1965. The effect of water flow on populations of net-spinning Trichoptera. Mitt. Int. Verein. Limnol. 13:40-48.

Edmunds, G. F. Jr., S. L. Jensen and L. Berner. 1976. The mayflies of North and Central America. Univ. Minnesota Press, Minneapolis. 330 pp.

Elliott, J. M. 1967. Invertebrate drift in a Dartmoor stream. Arch. Hydrobiol. 63:202-237

Elliott, J. M. 1971. The distances travelled by drifting invertebrates in a Lake District stream. Oecologia 6:191-220.

Elliott, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwat. Biol. Assoc. Sci. Publ. 25, 2nd ed. 160 pp.

Fisher, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U. S. A. Int. Revue ges. Hydrobiol. 62:701-727.

Fisher, S. G., and A. LaVoy. 1972. Differences in littoral fauna due to fluctuating water levels below a hydroelectric dam. J. Fish. Res. Bd. Can. 29:1472-1476.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43:421-439.

Gallep, G. W. 1977. Responses of caddisfly larvae (Brachycentrus spp.) to temperature, food availability and current velocity. Amer. Midl. Nat. 98:59-84.

Gaufin, A. 1959. Production of bottom fauna in the Provo River, Utah. Iowa State Coll. J. Sci. 33:395-419.

Gilpin, B. R., and M. A. Brusven. 1970. Food habits and ecology of mayflies of the St. Maries River Idaho. Melanderia 4:19-40.

Gore, J. A. 1978. A technique for predicting in-stream flow requirements of benthic macroinvertebrates. Freshwat. Biol. 8:141-151.

Graybill, J. P., R. L. Burgner, J. C. Gislason, P. E. Huffman, K. H. Wyman, R. G. Gibbons, K. W. Kurko, Q. J. Stober, T. W. Fagnan, A. P. Stayman and D. M. Eggers. Assessment of the reservoir-related effects of the Skagit Project on downstream fishery resources of the Skagit River, Washington. Univ. Washington, Fish. Res. Inst., Seattle. FRI-UW-7905. 602 pp.

Horner, R. R. 1978. Stream periphyton development in relation to current velocity and nutrients. Ph.D. Thesis, Univ. Washington, Seattle. 273 pp.

Hynes, H. B. N. 1958. The effect of drought on the fauna of a small mountain stream in Wales. Verh. int. Ver. Limnol. 13:826-833.

Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 57:344-388.

Hynes, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press. 555 pp.

Kennedy, H. D. 1967. Seasonal abundance of aquatic invertebrates and their utilization by hatchery-reared rainbow trout. Dept. Interior, Bur. Sport Fish. Wildl. Tech. Paper No. 12. 41 pp.

Kroger, R. L. 1973. Biological effects of fluctuating water levels in the Snake River, Grand Teton National Park, Wyoming. Amer. Midl. Nat. 89:478-481.

Lehmkuhl, D. M., and N. H. Anderson. 1972. Microdistribution and density as factors affecting the downstream drift of mayflies. Ecology 53:661-667.

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

Maciolek, J. A., and P. R. Needham. 1951. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California. Trans. Amer. Fish. Soc. 81:202-217.

MacPhee, C., and M. A. Brusven. 1973. The effects of river fluctuations resulting from hydroelectric peaking on selected aquatic invertebrates. Idaho Water Resour. Res. Inst., Moscow, Idaho. 20 pp.

Malick, J. G. 1977. Ecology of benthic insects of the Cedar River, Washington. Ph.D. Thesis, Univ. Washington, Seattle. 188 pp.

Mason, W. T., J. B. Anderson and G. E. Morrison. 1967. A limestone-filled artificial substrate sampler-float unit for collecting macroinvertebrates in large streams. Prog. Fish. Cult. 29:74.

McConnell, W. J., and W. F. Sigler. 1959. Chlorophyll and productivity in a mountain river. Limnol. Oceanogr. 4:335-351.

McIntire, C. D., and H. K. Phinney. 1965. Laboratory studies of periphyton production and community metabolism in lotic environments. Ecol. Monogr. 35:237-258.

McLay, C. 1970. A theory concerning the distance travelled by animals entering the drift of a stream. J. Fish. Res. Bd. Can. 27:359-370.

McNeil, W. J., and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. U. S. Dept. Interior, Fish. Wildl. Serv. Spec. Sci. Rep.-Fish. No. 469. 15 pp.

Mecom, J. O. 1972. Feeding habits of Trichoptera in a mountain stream. Oikos 23:401-407.

Minckley, W. L. 1963. The ecology of a spring stream, Doe Run, Meade County, Kentucky. Wildl. Monogr. 11. 124 pp.

Minshall, G. W., and P. V. Winger. 1968. The effect of reduction in stream flow on invertebrate drift. Ecology 49:580-582.

Mundie, J. H. 1969. Ecological implications of the diet of juvenile coho in streams. Pages 135-152 in T. G. Northcote (ed.), Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Mundie, J. H. 1971. Sampling benthos and substrate materials, down to 50 microns in size, in shallow streams. J. Fish. Res. Bd. Canada 28:849-860.

Needham, P. R. 1934. Quantitative studies of stream bottom foods. Trans. Amer. Fish. Soc. 64:238-247.

Needham, P. R., and R. L. Usinger. 1956. Variability in the macrofauna of a single riffle in Prosser Creek, California, as indicated by the Surber sampler. Hilgardia 24:383-409.

Neel, J. K. 1963. Impact of reservoirs. Pages 575-593 in D. G. Frey (ed.), Limnology in North America. Univ. Wisconsin Press, Madison.

Nuttal, P. M. 1972. The effects of sand deposition upon the macroinvertebrate fauna of the River Camel, Cornwall. Freshwat. Biol. 2:181-186.

O'Connor, J. F. 1974. An apparatus for sampling gravel substrate in streams. Limnol.Oceanogr. 19:1007-1011.

Pearson, W. D., and D. R. Franklin. 1968. Some factors affecting the drift rates of Baetis and Simuliidae in a large river. Ecology 49:75-81.

Pearson, W. D., R. H. Kramer and D. R. Franklin. 1968. Macroinvertebrates in the Green River below Flaming Gorge Dam, 1964-65 and 1967. Proc. Utah Acad. Sci., Arts, Letters. 45:148-167.

Pfitzer, D. W. 1954. Investigations of waters below storage reservoirs in Tennessee. Trans. N. Amer. Wildl. Conf. 19:271-282.

Philipson, G. N. 1954. The effect of waterflow and oxygen concentrations on six species of caddis fly (Trichoptera) larvae. Proc. Zool. Soc. London 124:547-564.

Powell, G. C. 1958. Evaluation of the effects of a power dam water release pattern upon the downstream fishery. Quart. Rep. Colorado Coop. Fish. Res. Unit 4:31-37.

Radford, D. S., and R. Hartland-Rowe. 1971. A preliminary investigation of bottom fauna and invertebrate drift in an unregulated and a regulated stream in Alberta. J. Appl. Ecol. 8:883-903.

Siegfried, C. A., and A. W. Knight. 1977. The effects of washout in a Sierra foothill stream. Amer. Midl. Nat. 98:200-207.

Smith, S. D. 1968. The Arctopsychinae of Idaho (Trichoptera: Hydropsychidae). Pan-Pacif. Ent. 44:102-112.

Sprules, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ontario. Univ. Toronto Studies, Biol. Series No. 56.

Stanford, J. A. 1973. A centrifuge method for determining live weights of aquatic insect larvae, with a note on weight loss in preservative. Ecology 54:449-451.

Stanford, J. A., and A. R. Gaufin. 1974. Hyporheic communities of two Montana rivers. Science 185:700-702.

Stockner, J. G., and K. R. S. Shortreed. 1976. Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia. J. Fish. Res. Bd. Can. 33:1553-1563.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Trans. Amer. Geophys. Union 38:913-920.

Surber, E. W. 1937. Rainbow trout and bottom fauna production in one mile of stream. Trans. Amer. Fish. Soc. 66:193-202.

Townsend, C. R., and A. G. Hildrew. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. J. Animl Ecol. 45:759-772.

Trotzky, H. M., and R. W. Gregory. 1974. The effects of water flow manipulation below a hydroelectric power dam on the bottom fauna of the upper Kennebec River, Maine. Trans. Amer. Fish. Sco. 103: 319-324.

Ulfstrand, S. 1968. Benthic animal communities in Lapland streams. Oikos Suppl. 10. 120 pp.

United States Geological Survey. 1970-1978. Water resources data for Washington. Yearly volumes. U. S. Geological Survey, Tacoma, Washington.

Usinger, R. L. 1956. Aquatic insects of California with keys to North American genera and California species. Univ. California Press, Berkeley and Los Angeles. 508 pp.

Wallace, J. B., J. R. Webster and W. R. Woodall. 1977. The role of filter feeders in flowing waters. Arch. Hydrobiol. 79:506-532.

Ward, J. V. 1976. Effects of flow patterns below large dams on stream benthos: a review. Pages 235-253 <u>in</u> J. F. Osborn and C. H, Allman (eds.), Instream flow needs symposium, Vol. II. Amer. Fish. Soc.

Waters, T. F. 1961. Notes on the chlorophyll method of estimating the photosynthetic capacity of stream periphyton. Limnol. Oceanogr. 6:486-488.

Waters, T. F. 1964. Recolonization of denuded stream bottom areas by drift. Trans. Amer. Fish. Soc. 93:311-325.

Waters, T. F. 1969. Invertebrate drift-ecology and significance to stream fishes. Pages 121-134 <u>in</u> T. G. Northcote (ed.), Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Waters, T. F. 1972. The drift of stream insects. Ann. Rev. Entomol. 17:253-272.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). Univ. Toronto Press, Toronto and Buffalo. 401 pp.

Wilhm, J. L., and T. C. Dorris. 1968. Biological parameters for water quality criteria. BioScience 18:477-481.

Williams, D. D., and H. B. N. Hynes. 1974. The occurrence of benthos deep in the substratum of a stream. Freshwat. Biol. 4:233-256.

Williams, D. D., and H. B. N. Hynes. 1976. The recolonization mechanisms of stream benthos. Oikos 27:265-272.

Williams, R. W., R. M. Laramie and J. J. Ames. 1975. A catalog of Washington streams and salmon utilization, Vol. 1, Puget Sound Region. Wash. Dept. Fish., Olympia.

Zelt, K. A., and H. F. Clifford. 1972. Assessment of two mesh sizes for interpreting life cycles, standing crop and percentage composition of stream insects. Freshwat. Biol. 2:259-269.

## APPENDIX I

Benthic insect taxa collected in the Skagit, Sauk and Cascade rivers.

| TAXON | RIVER | | |
|---|---|---|---|
| | SKAGIT | SAUK | CASCADE |
| EPHEMEROPTERA | | | |
| Ametropididae | | | |
| *Ametropus ammophilus* | | x | x |
| Baetidae | | | |
| *Baetis* sp. | x | x | x |
| *Pseudocloeon* sp. | x | x | x |
| Heptageniidae | | | |
| *Epeorus* (*Ironopsis*) sp. | x | | x |
| *Epeorus* (*Iron*) *longimanus* | x | x | x |
| *Rithrogena morrisoni* | x | x | x |
| *Rithrogena hageni* | x | x | x |
| *Heptagenia* sp. | | x | |
| *Cinygmula* sp. | x | x | x |
| Ephemerellidae | | | |
| *Ephemerella delantala* | x | | |
| *Ephemerella inermis* | x | x | x |
| *Ephemerella doddsi* | x | x | x |
| *Ephemerella hystrix* | x | x | |
| *Ephemerella grandis* | x | x | x |
| *Ephemerella spinifera* | | x | |
| *Ephemerella hecuba* | | x | |
| *Ephemerella coloradensis* | x | x | x |
| *Ephemerella tibialis* | x | x | x |
| Leptoplebiidae | | | |
| *Paraleptophlebia* sp. | x | x | x |
| Siphlonuridae | | | |
| *Siphlonurus occidentalis* | x | | |
| *Ameletus* sp. | x | x | x |
| PLECOPTERA | | | |
| Perlidae | | | |
| *Acroneuria pacifica* | x | x | x |
| Perlodidae | | | |
| *Arcynopteryx* sp. | x | x | x |
| *Isoperla* sp. | x | x | x |
| *Isogenus* sp. | x | x | x |
| Chloroperlidae | | | |
| *Alloperla forcipata* | x | x | x |
| *Alloperla* sp. | x | x | x |

| TAXON | RIVER | | |
|---|---|---|---|
| | SKAGIT | SAUK | CASCADE |
| Kathroperla sp. | x | | |
| Pteronarcidae | | | |
| Pteronarcys princeps | x | x | x |
| Pteronarcys californica | x | | |
| Peltoperlidae | | | |
| Peltoperla sp. | x | x | x |
| Nemouridae | | | |
| Nemoura sp. | x | x | x |
| Taeniopterygidae | | | |
| Brachyptera sp. | x | x | x |
| Capniidae | x | x | x |
| TRICHOPTERA | | | |
| Rhyacophilidae | | | |
| Rhyacophila sp. "a" | x | x | x |
| Rhyacophila sp. "b" | x | x | x |
| Glossosomatidae | | | |
| Glossosoma sp. | x | x | |
| Limnephilidae | | | |
| Dicosmoecus atripes | x | x | x |
| Onocosmoecus sp. | x | x | x |
| Cryptochia sp. | | x | |
| Lepidostomatidae | | | |
| Lepidostoma sp. | x | x | x |
| Hydropsychidae | | | |
| Hydropsyche sp. | x | x | x |
| Arctopsyche grandis | x | x | x |
| Hydroptilidae | | | |
| Ochrotrichia sp. | x | x | |
| Brachycentridae | | | |
| Brachycentrus sp. | x | x | x |
| DIPTERA | | | |
| Tipulidae | | | |
| Tipula sp. | x | x | x |
| Antocha sp. | x | x | x |
| Hexatoma sp. | x | x | x |
| Pedicia sp. | | x | |
| Simuliidae | x | x | x |
| Chironomidae | x | x | x |
| Ceratopogonidae | x | x | x |
| Tanyderidae | | x | |
| Empididae | x | x | x |
| Rhagionidae | | | |
| Atherix variegata | x | x | x |

| TAXON | RIVER SKAGIT | SAUK | CASCADE |
|---|---|---|---|
| Dolichopodidae | x | | |
| Blepharoceridae | x | x | x |
| Deuterophlebiidae | x | | |
| Ptychopteridae | x | x | x |
| COLEOPTERA | | | |
| Dytiscidae | x | | |
| Elmidae | | | |
| *Lara* sp. | x | x | x |
| *Narpus* sp. | x | x | x |
| MEGALOPTERA | | | |
| Corydalidae | | | |
| *Dysmicohermes* sp. | x | | |
| ODONATA | | | |
| Aeschnidae | | | |
| *Oplonaeschna* sp. | x | | |

# APPENDIX II

Mean chlorophyll a (mg/m$^2$) at unexposed or minimally exposed sample locations at sampling stations with the 96 percent confidence interval.

| Station | Oct 1976 | Nov 1976 | Jan 1977 | Feb 1977 | March 1977 | May 1977 | June 1977 | July 1977 | Sept 1977 | Nov 1977 |
|---|---|---|---|---|---|---|---|---|---|---|
| Skagit (upper) | -- -- | -- -- | -- -- | -- -- | -- -- | 0.87 ± .50 | 1.10 ± .79 | 3.40 ± 1.16 | 4.59 ± 2.29 | 5.64 ± 2.13 |
| Skagit (lower) | 0 | 0.10 ± .32 | 0.09 ± .02 | 0.15 ± .33 | -- -- | 2.36 ± .85 | 5.42 ± 4.23 | 2.15 ± .51 | 3.38 ± 1.01 | 2.54 ± .47 |
| Sauk (lower) | 0.99 ± .38 | 0.04 ± .09 | 0.28 ± .05 | -- -- | 0.18 ± .09 | 0.69 ± .68 | 0.30 ± .15 | 2.60 ± .78 | 1.89 ± .63 | 0.13 ± .10 |
| Cascade | 0.10 ± .10 | 0.08 ± 1.02 | 0.25 ± .38 | -- -- | 0.21 ± .27 | 0.78 ± 1.13 | 0.29 ± .17 | 3.28 ± 1.04 | 3.58 ± 1.35 | 0.29 ± .65 |

# APPENDIX III

Mean number of insects per $m^2$ in the unexposed zone at each sampling station with the 95 percent confidence interval. Since the confidence interval was calculated with log transformed data, it is asymmetrical around the mean (Elliott 1977).

| Station | May 1976 | | July 1976 | | Sept 1976 | | Nov 1976 | | Feb 1977 | | May 1977 | | July 1977 | | Sept 1977 | | Nov 1977 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Skagit (upper) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 1652 | 1374-1845 | 2793 | 1959-3265 | 6521 | 4629-7561 | 8836 | 6755-10,103 |
| Skagit (lower) | 834 | 250-2754 | 1176 | 708-1415 | 1236 | 560-2716 | -- | -- | 3431 | 2542-3953 | 1902 | 1504-2162 | 7392 | 5106-8669 | 11,330 | 7192-13,341 | 4384 | 3214-5094 |
| Sauk (upper) | -- | -- | -- | -- | -- | -- | -- | -- | 900 | 452-1030 | 941 | 741-1072 | 2754 | 1966-3210 | 4406 | 3537-4983 | 1576 | 1042-1847 |
| Sauk (lower) | 1011 | 705-1470 | 881 | 705-1066 | 2962 | 2287-3670 | 6051 | 3802-8510 | 1947 | 1517-2224 | 519 | 499- 695 | 2149 | 1706-2453 | 1756 | 1029-2047 | 1101 | 930-1224 |
| Cascade | 791 | 445-1191 | 1587 | 992-2036 | 1811 | 1235-2456 | 5173 | 4027-6383 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |

# APPENDIX IV

Mean weight of preserved insects ($g/m^2$) in the unexposed zone at each sampling station with the 95 percent confidence interval. Since the confidence interval was calculated with log transformed data, it is asymmetrical around the mean (Elliott 1977).

| Station | May 1976 | | July 1976 | | Sept 1976 | | Nov 1976 | | Feb 1977 | | May 1977 | | July 1977 | | Sept 1977 | | Nov 1977 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Skagit (upper) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- | 5.07 | 3.38-5.91 | 2.60 | 1.88-3.01 | 6.84 | 5.61- 7.68 | 14.43 | 11.47-16.32 |
| Skagit (lower) | 5.06 | 0.26-94.66 | 2.42 | 1.34-3.39 | 3.86 | 0.09-148 | -- | -- | 3.90 | 3.15-4.40 | 5.92 | 4.75-6.69 | 7.63 | 5.40-8.90 | 9.83 | 7.38-11.37 | 5.31 | 3.92- 6.21 |
| Sauk (upper) | -- | -- | -- | -- | -- | -- | -- | -- | 2.31 | 0.97-2.65 | 2.80 | 2.19-3.18 | 5.21 | 3.57-6.00 | 3.86 | 3.00-4.41 | 2.32 | 0.97- 2.85 |
| Sauk (lower) | 4.49 | 2.38-6.97 | 3.56 | 1.95-5.30 | 5.36 | 2.89-8.21 | 12.55 | 6.51-15.84 | 4.70 | 3.87-5.30 | 3.56 | 2.94-3.98 | 3.82 | 2.41-4.45 | 2.76 | 1.35-3.18 | 2.19 | 1.80- 2.46 |
| Cascade | 3.65 | 1.54-6.24 | 4.40 | 3.01-5.91 | 4.28 | 2.69-6.09 | 10.88 | 7.25-13.91 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |

# VITA

Jeffrey Charles Gislason was born on October 16, 1947, in Norfolk, Virginia. His parents are Gene R. and Elayne Gislason. He attended Sault High School in Sault Ste. Marie, Michigan, and Aragon High School in San Mateo, California, graduating in 1965. He received the B.S. degree in fisheries from the University of Michigan in 1969 and the M.S. degree in fisheries from Michigan State University in 1971. After serving in the U.S. Army from 1971 to 1974, he enrolled in the College of Fisheries at the University of Washington, where he received the Ph.D. degree in 1980. He is married to Angelika Gislason, and they have a son, Eric.