



MICHIGAN STATE UNIVERSITY LIBRARIES



3 1293 00882 6376

This is to certify that the

thesis entitled

A COMPARISON OF ACRONEURIA LYCORIAS
(PLECOPTERA) PRODUCTION AND GROWTH RATES IN
NORTHERN MICHIGAN HARD AND SOFT WATER STREAMS
presented by

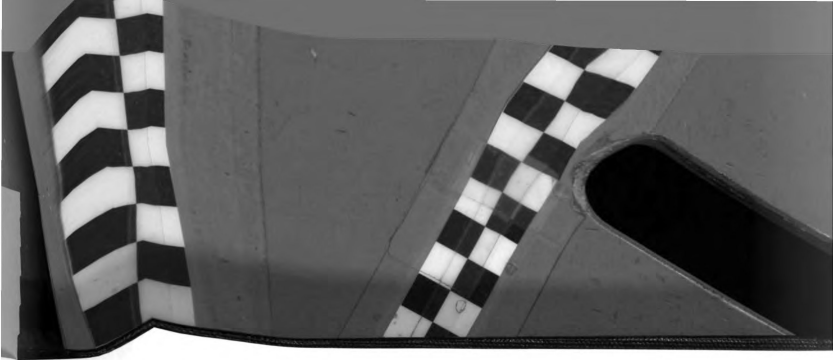
Susan L. Eggert

has been accepted towards fulfillment
of the requirements for

M.S. degree in Fisheries & Wildlife

Major professor

Date 2/14/92



A COMPARISON OF ACRONEURIA LYCORIAS (PLECOPTERA)
PRODUCTION AND GROWTH RATES IN NORTHERN MICHIGAN
HARD AND SOFT WATER STREAMS

By

Susan L. Eggert

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Fisheries and Wildlife

1992

691-6028

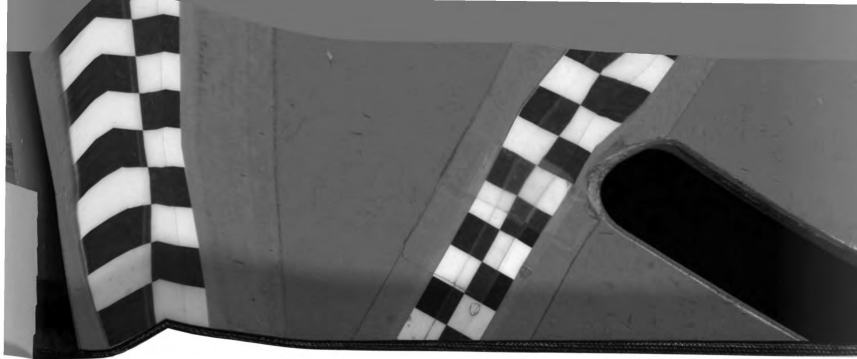
ABSTRACT

A COMPARISON OF ACRONEURIA LYCORIAS (PLECOPTERA)
PRODUCTION AND GROWTH RATES IN NORTHERN MICHIGAN
HARD AND SOFT WATER STREAMS

By

Susan L. Eggert

Annual production and growth rates of Acroneuria lycorias, a predaceous stonefly, were compared between fourth-order hard and soft water streams in Michigan's upper peninsula from 1988 to 1990. Mean annual production of A. lycorias, calculated using the size frequency method, was 5.0 times greater at the hard water site. Mean standing crop biomass was estimated from monthly Hess samples, and was 4.9 times greater at the hard water site. Annual P/B ratios were similar between sites. Monthly growth rates of nymphs living in the streams were calculated from changes in mean weight of cohorts. Growth rates of nymphs were similar at each site for comparable age classes and sexes. Individual growth rates of nymphs reared in the laboratory at high and low water hardnesses with unlimited food and space were not significantly different. Low A. lycorias production estimates at the soft water site resulted from physical, biological or habitat constraints on standing crop biomass, rather than slower growth rates due to low water hardness.



Dedicated to the memory of
Dr. Willard L. Gross



ACKNOWLEDGMENTS

I offer my sincere appreciation to Dr. Thomas M. Burton for his suggesting and supervising this study, and for his patience during the writing of this thesis.

Special thanks go to the members of my committee, Dr. Darrell L. King and Dr. Richard W. Merritt, for their helpful discussions, comments, and suggestions. I thank Dr. Charles E. Cress and Dr. William E. Cooper for their advice on statistical analyses. Dr. William L. Hilsenhoff of the University of Wisconsin-Madison confirmed the identification of A. lycorias specimens collected in this study.

I also wish to thank my fellow graduate students and Dr. Jean Stout for their comments and advice regarding this work. I especially would like to acknowledge the help of Dr. Dennis Mullen, and Dr. Burton in the field. Without their assistance, the winter sampling would have been impossible.

Support for this research was provided in part by the Naval Electronic Systems Command through a subcontract to IIT Research Institute under contract number N00039-88-0065. Other funding was provided by a Grant-in-Aid of Research from Sigma Xi and the Theodore Roosevelt Memorial Fund of The American Museum of Natural History.

TABLE OF CONTENTS

	Page
LIST OF TABLES	vii
LIST OF FIGURES	x
INTRODUCTION	1
Background	1
Study Objectives	5
STUDY ORGANISM	7
Distribution and Habitat	7
Morphology	7
Ecology	8
DESCRIPTION OF STUDY AREAS	13
Site Locations	13
Climate	16
Geology and Soils	18
Riparian Vegetation	24
Water Quality and Hydrology	24
METHODS AND MATERIALS	29
Site Evaluation	29
Streamwater characteristics	29
Substrate composition	32
Riparian vegetation	33
Field Sampling	34
Life history and growth rates	34
Production estimates	37
Laboratory Stream Study	40
RESULTS	43
Streamwater Quality	43
Physical and chemical parameters	43
Nitrogen and phosphorus parameters	50

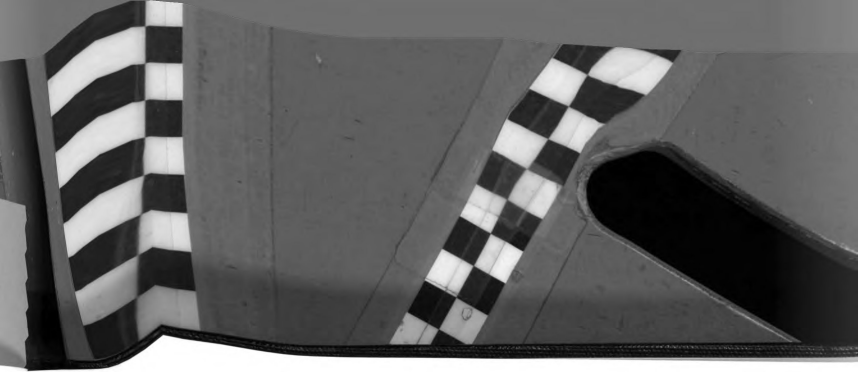


TABLE OF CONTENTS - Continued

	Page
Life History	56
Life cycle	56
Sex ratios	62
Diet	62
Production	64
Density and standing crop biomass	64
Annual production estimates	76
Growth Rates	79
Natural stream growth rates	79
Laboratory stream growth experiment	86
DISCUSSION	95
SUMMARY.	111
APPENDIX A - Physical and Chemical Water Data Tables	113
APPENDIX B - Annual Production Estimate Data Tables	118
LITERATURE CITED	122

LIST OF TABLES

1	Temperature and precipitation data collected at nearest NOAA monitoring station to the Ford and Peshekee River sites from 1951-1980, 1988 and 1989	17
2	Soil classes of townships containing the Ford and Peshekee River study sites	19
3	Selected physical and hydrologic properties of common soils of the Ford River watershed within Dickinson County, Michigan	21
4	Selected physical and hydrologic properties of common soils of the Peshekee River watershed within Baraga County, Michigan	23
5	Calculated importance percentages of riparian vegetation at the Ford River (FS1) site and the Peshekee River (PS1) site	25
6	Percent composition of substrate particle size at the Ford River (FS1) and Peshekee River (PS1) sites	27
7	Summary (mean $\pm$ S.E.) of selected water chemistry parameters for the Ford and Peshekee Rivers, 1988-1990	49
8	Results of paired t-tests between the Ford (FS1 site) and Peshekee (PS1 site) Rivers for selected water chemical, physical and nutrient parameters from July, 1988 to June, 1990	51
9	Gut contents of <u>A. lycorias</u> nymphs of the Ford and Peshekee Rivers, 8/11/90, 10/16/90 and 1/19/91	65
10	Mean density (no. ind./m ²) $\pm$ S.E. of <u>A. lycorias</u> collected from the Ford (FS1) and Peshekee (PS1) Rivers from June, 1988 to June, 1990	67
11	Mean biomass (g dry wt./m ²) $\pm$ S.E. of <u>A. lycorias</u> collected from the Ford (FS1) and Peshekee (PS1) Rivers from June, 1988 to June, 1990	69

LIST OF TABLES - Continued

12	Results of paired t-tests between the Ford River (FS1) and Peshekee River (PS1) for <u>A. lycorias</u> density and biomass from June, 1988 to June, 1990	. 70
13	Results of paired t-tests of <u>A. lycorias</u> densities and standing crop biomass at replicate sites within the Ford and Peshekee Rivers, July, 1989	. 71
14	Mean ecological density (no. ind./m ² rock surface area) ± S.E. of <u>A. lycorias</u> collected from the Ford (FS1) and Peshekee (PS1) Rivers from June, 1988 to June, 1990	. 73
15	Mean ecological biomass (g dry wt./m ² rock surface area) ± S.E. of <u>A. lycorias</u> collected from the Ford (FS1) and Peshekee (PS1) Rivers from June, 1988 to June, 1990	. 74
16	Annual production of <u>A. lycorias</u> at FS1 and PS1 calculated using the size-frequency method for 1988-1989 and 1989-1990	. 77
17	Mean dry weight (mg) ± S.E. by year class of <u>A. lycorias</u> collected at FS1 and PS1, 7/1990 - 1/1991	. 81
18	Monthly growth rates (1/day) ± S.E. by year class of <u>A. lycorias</u> collected at FS1 and PS1, 7/1990 - 1/1991	. 84
19	Chemical and physical characteristics of hard and soft water treatments of laboratory growth study conducted from June to October 1990	. 87
20	Mean laboratory growth rates (1/day) of <u>A. lycorias</u> for 110 day period ± S.E. in soft and hard water treatments	. 90
21	Results of three factor unbalanced analysis of variance of <u>A. lycorias</u> growth in a laboratory stream experiment	. 93
22	Mean prey and predator densities (no./sample) ± S.E. and prey/predator ratios by size class of <u>A. lycorias</u> for the Ford and Peshekee Rivers, 7/15/91	101
23	Results of riffle and pool fish survey of FS1 and PS1 conducted during August 1990	108



LIST OF TABLES - Continued

A-1	Physical and chemical water quality of the Ford River (FS1 site), Michigan, 1988-1990 . . .	113
A-2	Physical and chemical water quality of the Peshekee River (PS1 site), Michigan, 1988-1990 . . .	114
A-3	Cation concentrations (mg/L) of the Ford and Peshekee Rivers from 1988-1990	115
A-4	Nutrient water quality of the Ford River (FS1 site), Michigan, 1988-1990	116
A-5	Nutrient water quality of the Peshekee River (PS1 site), Michigan, 1988-1990	117
B-1	Calculation of production of <u>A. lycorias</u> at the Ford (FS1 site) River, 1988-1989	118
B-2	Calculation of production of <u>A. lycorias</u> at the Ford (FS1 site) River, 1989-1990	119
B-3	Calculation of production of <u>A. lycorias</u> at the Peshekee (PS1 site) River, 1988-1989	120
B-4	Calculation of production of <u>A. lycorias</u> at the Peshekee (PS1 site) River, 1989-1990	121



LIST OF FIGURES

1	Ford River study area and sampling location, Dickinson County, Michigan	14
2	Peshekee River study area and sampling location, Marquette County, Michigan	15
3	Length/dry weight regressions for <u>A. lycorias</u> collected from the Ford (A) and Peshekee (B) Rivers.	36
4	Seasonal variations in water temperature at the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990	44
5	Mean monthly discharge for the Ford (FEX site) and Peshekee (PS1 site) Rivers	46
6	Seasonal variations in pH at the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990	47
7	Seasonal variations in total hardness at the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990	48
8	Cation concentrations (mg/L) for the Ford River (A) and the Peshekee River (B), 1988-1990	52
9	Seasonal variations in orthophosphorus at the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990	54
10	Seasonal variations in nitrate at the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990	55
11	Size-frequency distribution by length of <u>A. lycorias</u> collected from the Ford River (A) and the Peshekee River (B), 7/90	57
12	Size-frequency distribution by length of <u>A. lycorias</u> collected from the Ford River (A) and the Peshekee River (B), 8/90	58
13	Size-frequency distribution by length of <u>A. lycorias</u> collected from the Ford River (A) and the Peshekee River (B), 9/90	59

LIST OF FIGURES - Continued

14	Size-frequency distribution by length of <u>A. lycorias</u> collected from the Ford River (A) and the Peshekee River (B), 10/90	60
15	Size-frequency distribution by length of <u>A. lycorias</u> collected from the Ford River (A) and the Peshekee River (B), 1/91	61
16	Mean gut fullness $\pm$ S.E. of <u>A. lycorias</u> nymphs collected from the Ford (FS1 site) and Peshekee (PS1 site) Rivers; (A) Young of year, (B) Second year, (C) Third year	63
17	Densities (A) and dry weight biomass (B) $\pm$ S.E. of <u>A. lycorias</u> collected from the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990	68
18	Ecological densities (A) and ecological biomass (B) $\pm$ S.E. of <u>A. lycorias</u> collected from the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990	75
19	Annual production of <u>A. lycorias</u> at FS1 and PS1 from 1988-1990	78
20	Total annual <u>A. lycorias</u> densities (A), dry weight biomass (B), and production (C) by year class for 1988-1989 and 1989-1990	80
21	Mean dry weight $\pm$ S.E. by month of young-of-year (A), second year (B), and third year (C) <u>A. lycorias</u> nymphs collected from the Ford and Peshekee Rivers, 7/90-1/91	82
22	Monthly growth rates $\pm$ S.E. of young-of-year (A), second year (B), and third year (C) classes of <u>A. lycorias</u> collected from the Ford and Peshekee Rivers, 8/90-1/91	85
23	Mean log weights $\pm$ S.E. of individual nymphs by sex (M or F), strain (F or P) and treatment (H or S) at start, mid-point and conclusion of laboratory growth experiment	89
24	Mean growth rates of male and female <u>A. lycorias</u> nymphs reared in laboratory streams for 110 days	91



LIST OF FIGURES - Continued

- 25 Mean growth rates of female (A), and male (B)
A. lycorias nymphs reared in laboratory streams
for 110 days 94
- 26 Flow diagram of factors influencing annual production
of A. lycorias nymphs in hard and soft water river
systems 105





INTRODUCTION

Study Background

The association between stream water hardness and invertebrate productivity has been investigated by Tarzwell (1938), Egglshaw (1968), Sutcliffe and Carrick (1973), Arnold et al. (1981), and Collier and Winterbourn (1987, 1990). In each of these studies, greater invertebrate densities were found in streams with higher alkalinities or calcium concentrations. Additionally, Krueger and Waters (1983) reported a positive correlation between alkalinity and both invertebrate production and fish standing stocks in three Minnesota streams. However, none of the studies provided experimental evidence that cation concentrations were the mechanism controlling the observed correlations.

Hynes (1970) discussed a variety of factors that have been demonstrated in the literature to influence benthic invertebrate abundances in streams, including current velocity, temperature, substrate type, dissolved oxygen, acidity, food supply, drought, spates, predation and water hardness. Several studies reviewed by Hynes (1970) regarding the relationship between water hardness and invertebrate productivity suggested that there was no relationship for some Ephemeroptera species (Illies, 1952; Armitage, 1958), Simuliidae (Grenier, 1949) or Sisyridae (Jewell, 1939).



Many mechanisms responsible for the observed relationship between stream water hardness and secondary production have been suggested in the literature. First, a reduced efficiency of osmoregulation may be related to lower invertebrate production in soft water streams. Fiance's (1978) study of Ephemerella growth rates in acidic streams indicated that lowered pH might account for significantly slower growth rates of mayfly larvae. He suggested that the osmoregulatory function in mayflies was affected, resulting in a greater energy expenditure for the maintenance of internal ionic balance. The increase in metabolic rate required to supply energy for active transport might tend to slow the organism's growth rate and overall production. Lechleitner et. al. (1985) also reported an effect on the ionregulatory ability of stonefly nymphs due to acute acidic and alkaline pH. In both cases, osmoregulation was examined under extreme pH conditions for very short periods of time. Possibly, the osmoregulatory functions of invertebrates could also be affected by slightly lowered pH levels under chronic conditions.

The difference in allochthonous inputs from one stream to another may also be related to lower production in soft water streams. Generally, hard water streams are located in primarily deciduous watersheds, while soft water streams are associated with more coniferous type watersheds. Both the timing and nutritional quality of the allochthonous inputs



will vary in coniferous and deciduous watersheds (Fisher and Likens, 1973). Differences between water chemistry parameters such as nitrate and pH may affect the detrital quality in hard and soft water streams. Higher nitrates associated with deciduous inputs in fall may tend to speed up decomposition rates within a hardwater stream (Suberkropp and Klug, 1976; Suberkropp and Chauvet, 1991). Likewise, pH and cation concentrations will determine the precipitation rates of dissolved organic matter (Lush and Hynes, 1973; Lock and Hynes, 1975). By increasing the surface area available for microbial colonization of particulates, a higher quality food source would be available to invertebrates. Additionally, differences in nutrient chemistry between streams may also alter autochthonous energy sources. Levels of primary production within a stream will affect grazer and collector-gatherer populations, and perhaps the higher trophic levels (Krueger and Waters, 1983; Fuller et al., 1986; Lay and Ward, 1987; Collier and Winterbourn, 1987, 1990).

Finally, physical or biological factors may be influencing invertebrate densities and distributions in hard and soft water streams. The effects of temperature on egg diapause, embryonic development, optimal growth and metabolism of aquatic insects has been well documented in the literature (Vannote and Sweeney, 1980; Brittain, 1983; Sweeney and Vannote, 1986; Sweeney et. al., 1986a, 1986b; Lillehammer, 1986; Mutch and Pritchard, 1986; Hauer and

Benke, 1987; Soderstrom, 1988). Differences in water temperatures or degree-day accumulations will alter invertebrate productivity in a stream regardless of water hardness. Likewise, major differences in dissolved oxygen concentrations could play a role in invertebrate distributions within streams of differing water hardnesses (Knight and Gaufin, 1963, 1965, 1966). A large amount of work has been done regarding the effects of current velocity on invertebrate abundances (Kovalak, 1977; Walton et. al., 1977; Orth and Maughan, 1983). Many studies have suggested that hydrologic disturbances such as spates play a major role in determining invertebrate productivity and distribution (Minshall and Minshall, 1977; Siegfried and Knight, 1977; Stout, 1981; Peckarsky, 1983; Statzner and Higler, 1986; Hauer and Benke, 1987; Graesser, 1988; Power et. al., 1988; Resh et. al., 1988; Statzner et. al., 1988). Invertebrates also demonstrate a distinct preference for certain substrate types (Cummins and Lauff, 1969; Walton, 1978; McElhone and Davies, 1983; Reice, 1983, Brown and Brown, 1984; Minshall, 1984; Clements, 1987). Conceivably, differences between invertebrate production of a particular set of streams could be related to differences in hydraulic conditions or the amount of suitable substrate rather than stream water hardness. Finally, biological factors such as competition for food and space, and predation should be considered as controlling mechanisms in the stream community (Allen, 1951;



peckarsky, 1983; Power, 1988; Feltmate and Williams, 1991).

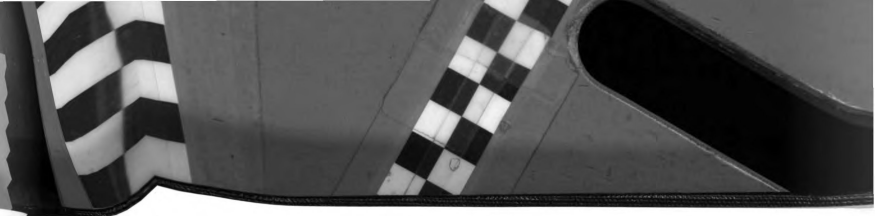
Study Objectives

The goal of this research was to gather quantitative data regarding production and growth of a stream invertebrate predator, Acroneuria lycorias, in matched hard and soft water streams. Specific objectives of the study are the following:

- Compare and contrast physical and chemical characteristics of streamwater, substrate composition, and riparian vegetation at stream sites of a hard and soft water stream.
- Obtain dry weight production estimates of a invertebrate predator common to a hard and soft water stream.
- Determine growth rates of an invertebrate living in its natural habitat, as well as in a controlled laboratory environment at high and low water hardnesses.
- Predict the most likely factor(s) controlling the observed production estimates and growth rates in each stream.

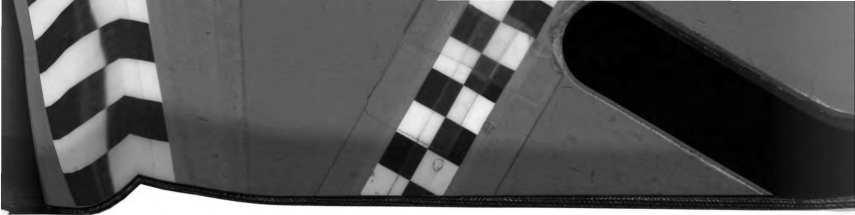
The physical and chemical characteristics of a hard and soft water stream were documented over a two year period. Production estimates were made, which were based on the null hypothesis of no production difference between sites, versus the alternate hypothesis that production would be positively related to stream water hardness. In this study, production was predicted to be greater in the hard water Ford River than in the soft water Peshekee River. A second set of hypotheses were developed to address the study's third objective.





Growth rates were determined for organisms living in the natural environment and in the laboratory in hard and soft water treatments. The null hypothesis stated that growth rates would not differ significantly for organisms living in the natural environment or in the laboratory. The alternate hypothesis predicted that growth rates would be significantly higher in hard water streams and treatments due to less osmoregulatory stress. Finally, production and growth rate data were used to predict likely factors influencing production in each stream.





STUDY ORGANISM

Distribution and Habitat

Acroneuria lycorias was chosen for this study because of its abundance in both the Ford and Peshekee Rivers and the organism's tolerance to handling for laboratory experimental purposes. A. lycorias is distributed over 21 states and provinces throughout the central and eastern United States and Canada (Stark and Gaufin, 1976; Peckarsky, 1979). The stonefly species is commonly found among rubble, and rocks of riffles and rapids in streams of various orders (Knight and Gaufin, 1967).

Morphology

Acroneuria belongs to the family Perlidae, whose diagnostic characteristic is the presence of branched gills on the thoracic segments only. Within the Perlidae family, the genus Acroneuria may be identified by (1) an absence of a setal row on the occiput, (2) a postocular fringe of several thick setae, (3) three ocelli, (4) a basal fringe of setae on the cerci, and (5) a yellow M-shaped mark anterior to the median ocellus (Merritt and Cummins, 1984; Stewart and Stark, 1988). Mature female nymphs may be distinguished from males by their larger size of 17-20 millimeters (15-18 mm for males) and the lack of a complete sternal fringe on the ventral posteromesal margin of sternum eight (Stark and Gaufin, 1976; Stewart and Stark, 1988). A. lycorias nymphs



collected at each site and adults reared in the laboratory were keyed to species using Classen (1931) and Stark and Gaufin (1976). A positive identification of nymphs and adults was made by Dr. William L. Hilsenhoff of the Department of Entomology, University of Wisconsin-Madison. Museum specimens of the nymphs and adults of A. lycorias collected in this study are included in the collection of Dr. Richard W. Merritt of the Department of Entomology, Michigan State University.

Ecology

Knowledge of the life history, growth patterns, trophic interactions and environmental requirements of a species is required to make accurate estimates of production. Frison (1935), Hynes (1976), Barton (1980) and Stewart and Stark (1988) have reviewed the ecology of the Plecoptera. The ecology of the genus Acroneuria has been reviewed by Peckarsky (1979). Detailed accounts of the life history and growth of A. californica and A. carolinensis have been published by Heiman and Knight (1975), Siegfried and Knight (1978) and Schmidt and Tarter (1985). Despite the widespread abundance of A. lycorias, a thorough investigation of the life history of the species has yet to be completed. Peckarsky (1980) and Peckarsky and Dodson (1980) have examined the predator-prey interactions of Acroneuria in the stream community. The following summary of the ecology of



Acroneuria represents observations from studies examining several different species of the genus.

The distribution of Acroneuria is determined by dissolved oxygen concentration, pH, temperature, substrate type and current velocity (Peckarsky, 1979). The genus requires high concentrations of dissolved oxygen. Individuals will become stressed with sharp drops in dissolved oxygen concentrations and exhibit a "push-up" behavior to obtain the necessary oxygen (Knight and Gaufin, 1963, 1965). Because of the requirements for dissolved oxygen, Acroneuria is most abundant in stony substrates associated with riffles and rapids (Walton et al., 1977). Although Kroger (1974) suggested that Hesperoperla, a genus related to Acroneuria, was a strong swimmer, another study indicated that spates can cause the wash-out of Perlidae populations (Siegfried and Knight, 1977). Compared to other stoneflies, A. lycorias is relatively resistant to low pH. Bell and Nebecker (1969) calculated a TLm^{96} of pH 3.32 for A. lycorias. Water temperature has been shown to affect growth and emergence in Acroneuria. Temperature ranges for optimal growth of A. californica nymphs in the summer were 16° - 22° C, 6° - 12° C in the winter and 10° - 18° C during the spring and fall (Heiman and Knight, 1975). Emergence of A. abnormis may be delayed up to two weeks due to cold water temperatures (Harper and Pilon, 1970).



The life cycle of A. lycorias has not been examined in any detail in the literature. Several authors have suggested a three-year life cycle (Peckarsky, 1979; Barton, 1980). Siegfried and Knight (1978) reported an 18-month life cycle for A. californica, while Heiman and Knight (1975) observed a two-year life cycle, and Sheldon (1969) concluded that the same species lived for three years. Other life history studies have documented a 1-year cycle for A. evoluta (Ernst and Stewart, 1985) and a 2-year cycle for A. carolinensis in West Virginia (Schmidt and Tarter, 1985).

Growth rates have been investigated for A. californica (Heiman and Knight, 1975; Siegfried and Knight, 1978) and for A. carolinensis (Schmidt and Tarter, 1985). Field studies of A. carolinensis indicated that female growth was greatest in August, while growth rates for males were highest in October. In this study, as well as in Siegfried and Knight's (1978) study of A. californica, the smallest nymphs exhibited the greatest relative growth rates. Heiman and Knight's (1975) laboratory study of A. californica reported a net growth efficiency of 41%. Growth rates for all nymphs were greatest in the summer, lowest in the winter and intermediate in spring and fall. Maximum laboratory growth rates approximated growth rates calculated from field data.

Emergence of A. lycorias was reported to occur anytime between mid-April to early August by Peckarsky (1979). Barton (1980) collected A. lycorias adults in low numbers in

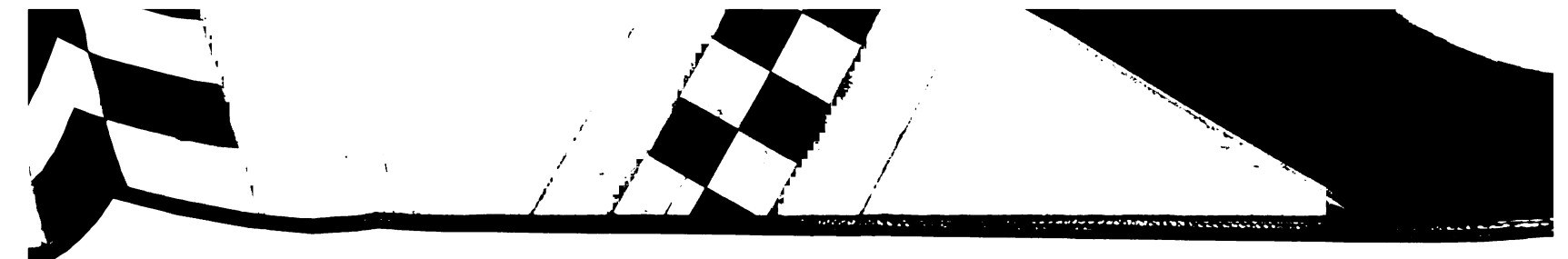


Alberta, Canada in mid-June. Harper and Pilon (1971) found that A. lycorias in Quebec, Canada emerged for an extremely short period of time in early June. They noted that only a few adults were caught in their traps. Likewise, Narf and Hilsenhoff (1974) mentioned difficulties in collecting adult A. lycorias even though nymphs and exuviae were abundant in Otter Creek, Wisconsin. They suggested that the adults inhabited the tree canopy, making the collection of adults difficult. Adults that were reared in their laboratory at an unspecified temperature emerged in May. Data regarding sex ratios, fecundity, and egg development for A. lycorias is non-existent in the literature.

The food habits of Acroneuria is well documented in the literature. Shapas and Hilsenhoff (1976) reported that A. lycorias preyed primarily on Chironomidae and Hydropsychidae. Other sources of food for Acroneuria and related species include Simuliidae and Hydropsychidae for A. californica (Heiman and Knight, 1975), Chironomidae, Hydropsychidae, Tipulidae, Elmidae, Leptophelebiidae, Philopotamidae, and Baetidae for A. abnormis (Johnson, 1981), Baetidae, Chironomidae, Rhyacophilidae, Brachycentridae, Psychomyiidae and Perlidae for A. pacifica (Richardson and Gauvin, 1971), Chironomidae, Capniidae, Leutridae, Nemouridae, Taeniopterygidae, Perlodidae, Baetidae, Ephemerellidae, Glossosomatidae, and Hydropsychidae for A. carolinensis (Schmidt and Tarter, 1985). There is some evidence that



detritus and plant matter makes up a portion of Acroneuria sp. diet. Richardson and Gaufin (1971) found that 11.7 percent of the diet of A. pacifica consisted of plant materials. Siegfried and Knight (1976b) reported that twenty to sixty-two percent of the A. californica foreguts examined contained detritus. Additionally, selectivity of prey items by Acroneuria sp. depends on prey size and availability. Larger nymphs ingest larger prey items, and the proportion of a particular prey item consumed is related to prey populations in the environment (Sheldon, 1969; Siegfried and Knight, 1976a).



DESCRIPTION OF STUDY AREAS

Site Locations

The close proximity of the hard water Ford River and the soft water Peshekee River to one another in Michigan's upper peninsula, along with the fact that both rivers are relatively unimpacted by anthropogenic activities provided a good opportunity for this study. Fourth-order sites on the Ford and Peshekee Rivers were chosen where the physical and chemical water characteristics, riparian vegetation, and land uses were as similar as possible.

The headwaters of the Ford River are located near the county line between Iron and Dickinson County. The stream flows eastward, draining the central and southeastern parts of Dickinson County before entering Green Bay of Lake Michigan (Figure 1). The Peshekee River lies north of Lake Michigamme in Marquette and Baraga County. It originates near Mt. Curwood, the highest point in Michigan, and flows in a southeast direction to Lake Michigamme (Figure 2).

The primary site on the Ford River is located along County 426, approximately 12 miles west of Ralph, Michigan (T. 43 N., R. 29 W., Sec. 16). The site is referred to as Ford Site 1 (FS1) in this report. Peshekee Site 1 (PS1) was the primary soft water sampling site (Figure 2). It lies along County 607, approximately 4 miles north of Lake



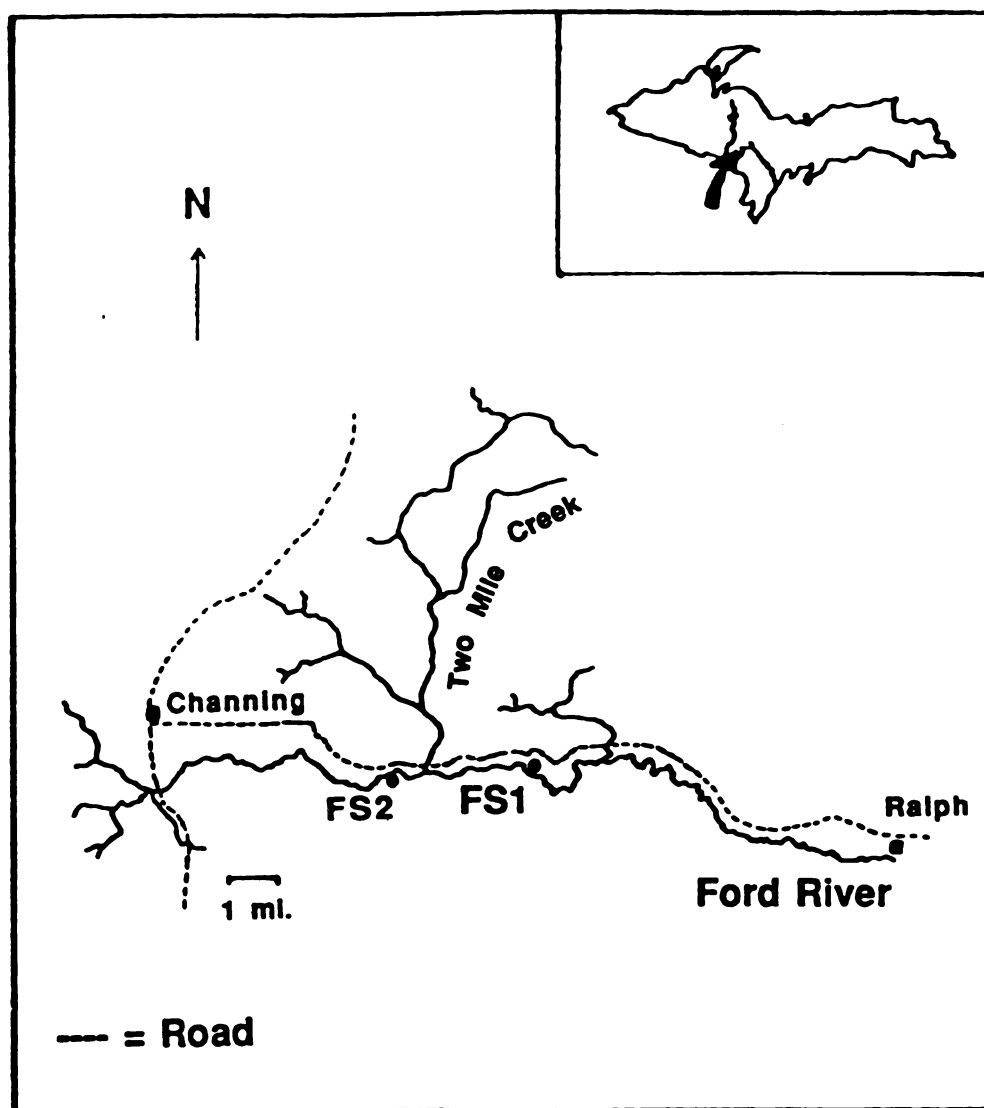


Figure 1. Ford River study area and sampling location, Dickinson County, Michigan.



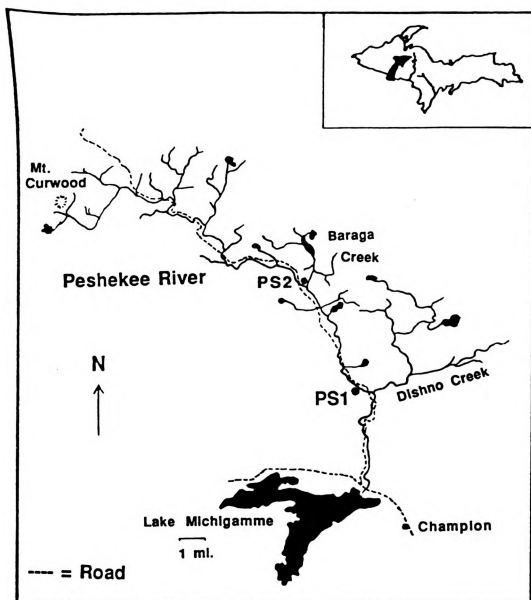


Figure 2. Peshekee River study area and sampling location, Marquette County, Michigan.

Michigamme (T. 49 N., R. 30 W., Sec. 2). FS1 and PS1 were monitored from June, 1988 to June, 1990. In addition to the two primary sites in each river, the invertebrate community was sampled at a second pair of matched sites. The second set of sites were sampled during the summer of 1989.

Climate

In a comparison study such as this one, it is desirable to keep climatic variables such as air temperature, rainfall, and snowfall as similar as possible. Although the distance between watersheds is less than 65 miles, some climatic comparisons should be noted. Climatic data collected at the nearest monitoring station to the Ford River (Crystal Falls) and the Peshekee River (Champion) are presented in Table 1. Historically, the difference in mean daily air temperature between sites has been small. Mean daily air temperatures at both sites during 1988 were approximately 1° F warmer than the daily mean for the period from 1962 to 1980. Temperatures were normal at Crystal Falls during 1989, but were below normal at Champion. Freeze dates (last date 32° F or below in spring and first date 32° F or below in fall) are different for each of the watersheds. With a probability of five years in ten, the last freeze date in spring is seven days later at the Peshekee than at the Ford River. Likewise, the first freeze in fall is seven days earlier at the Peshekee River.

Table 1. Temperature and precipitation data collected at nearest NOAA monitoring station to the Ford and Peshekee River sites from 1951-1980, 1988 and 1989.[†]

Parameter	<u>Station Location</u>	
	Crystal Falls (Ford River)	Champion (Peshekee River)
<u>Air Temperature (°F)</u>		
Average Daily (1951-1980)	38.2 ^a	38.8
Average Daily (1988)	39.8	39.6
Average Daily (1989)	38.3	37.4
Last Freeze in Spring ^b (32 °F or lower)	May 29	June 5
First Freeze in Fall ^b (32 °F or lower)	Sept.17	Sept.10
<u>Precipitation (Inches)</u>		
Average Total Rainfall (1951-1980)	29.8	33.7
Total Rainfall (1988)	28.8	36.0
Total Rainfall (1989)	22.9	26.4
Average Total Snowfall (1951-1980)	70.6	138.0
Total Snowfall (1988)	79.0	143.2
Total Snowfall (1989)	59.0	162.6

[†]Data from NOAA, 1988 and 1989, Berndt, 1988 and Linsemieer, 1989.

^aAverage daily temperature at Crystal Falls recorded 1962-1980.

^bDate represents a probability of five years in ten. Data recorded at Iron Mountain, MI.



Generally, the Peshekee River watershed receives greater amounts of rainfall (Table 1). Average precipitation was below normal during 1988 and 1989 at Crystal Falls and during 1988 at Champion. A large difference between sites is observed when comparing average snowfall totals. The Champion area receives an average 138 inches of snowfall per year, almost twice as much as the amount received in Crystal Falls. During the winter of 1989, the difference in total snowfall between sites increased to almost a three-fold difference. This large difference in snowfall, along with slight differences in freeze dates within each region will directly affect the amount and timing of snowpack runoff each spring.

Geology and Soils

The topography in the Ford River region consists of narrow swampy lowlands with adjacent hills and small areas of exposed bedrock (Table 2). Elevation ranges from 1500 feet above sea level, near the headwaters of the Ford River, to 1100 feet with an average elevation of 1200 feet (Hendrickson and Doonan, 1966). Stream velocities are relatively low, the average drop in elevation is about eight feet per mile (Snider, 1977). Northern portions of Dickinson County are composed of rolling moraines, flatter till plains and outwash plains. The glacial drift consists of sand, limestone fragments, silt, clay, cobbles and boulders (Russell, 1907;



Table 2. Soil classes of townships containing the Ford and Peshekee River study sites.[†]

Soil Class	<u>Area (Square Miles)</u>	
	Ford Site 1 T.43, R.29W	Peshekee Site 1 T.49, R.30W
Swamp and lake	5	5
Rock knobs	5	28
Sandy till	18	--
Sandy gravel	8	3

[†]Data from Leverett, 1911

Hendrickson and Doonan, 1966). Portions of the Ford River studied in this project are underlain by Middle Precambrian igneous, sedimentary and metamorphic rocks (gneiss, granite and schist) and slates, dolomites and quartzites of Cambrian and Ordovician age (Hendrickson and Doonan, 1966; Snider, 1977).

Soils in the Ford River watershed range from mucks of the Carbondale-Cathro and Waucedah-Cathro complexes to sand, with large areas of Pemene and Emmet sandy loam (Table 3) (Linsemier, 1986). Most soils found in this region were formed from glacial till deposited by retreating glaciers. Slopes are not very steep (0-18%). Soils are generally neutral in pH reflecting the large amount of sandy till in the watershed. Hydrologic soil groups and permeability values, useful in estimating runoff from precipitation and characterizing the soil's ability to transmit water, are presented in Table 3. Both parameters indicate the rate of downward movement of water within saturated soils. Most Ford River soils are classified as group A or B, having high to moderate infiltration rates. Permeability ranges from 0.2 to 20 inches of precipitation per hour, with most soils demonstrating moderate permeabilities of 0.2 to 6.0 inches per hour. The high percent organic matter (Table 3) also contributes to the high rates of infiltration.

The Peshekee River watershed is characterized as a region of "hills and bluffs of gneiss separated by lowlands



Table 3. Selected physical and hydrologic properties of common soils of the Ford River watershed within Dickinson County, Michigan.[†]

Soil Name	Extent (%) Within County	Slope (%)	Hydrologic Group ^a	Permeability (In./Hr.)	pH	Organic Matter (%)
Carbondale-Cathro mucks	20.4	0	A/D	0.2-6.0	5.6-8.4	40-85
Emmet fine sandy loam	9.9	6-18	B	0.6-6.0	5.6-8.4	1-3
Pemene fine sandy loam	9.8	6-18	B	0.6-6.0	4.5-7.8	0.5-3
Emmet fine sandy loam	7.2	0-6	B	0.6-6.0	5.6-8.4	1-3
Pemene fine sandy loam	6.8	0-6	B	0.6-6.0	4.5-7.8	0.5-3
Waucedah-Cathro complex	3.4	0	D	0.2-6.0	6.1-8.4	12-30
Rousseau fine sand	1.2	0-6	A	6.0-20	4.5-6.5	1-2
Rubicon sand	0.9	0-6	A	6.0-20	4.5-6.5	0.5-1

[†]Data from Linsemier, 1989.

^aGroup A = High infiltration rate

Group B = Moderate infiltration rate

Group C = Slow infiltration rate

Group D = Very slow infiltration rate

and swamps" (Seaman, 1944). The bluffs have exposed rock surfaces on several sides with vegetation covering most north slopes as well as the bluff tops. The Peshekee Uplands located in the east-central portions of Baraga and western Marquette Counties range in elevation from 1400 to 1890 feet above sea level. The bedrock of the lower Precambrian age is predominately gneiss and Laurentian granite with lesser amounts of schist (Seaman, 1944; Doonan and Byerlay, 1973). Some portions of the region are covered with a very thin layer of glacial drift. The immediate area surrounding the work site on the Peshekee River consists strictly of exposed rock knobs, swamps and sandy gravel (Table 2). Headwaters of the watershed consist of extensive areas of swamps.

Soil types found in the Peshekee Uplands consist largely of nearly level mucks (Carbondale and Tacoosh), hilly Michigamme-Rock outcrop complexes and Champion-Michigamme cobbly silt loams (Table 4) (Berndt, 1983). In contrast with the Ford River soils, the soils associated with the Peshekee River are low in permeability (0-6.0 inches/hour) and belong to hydrologic groups of moderate to very slow infiltration rates. pH of the soil groups are generally acidic (Table 4). The percent organic matter ranges from 0 - 85%, depending on the soil type.

Table 4. Selected physical and hydrologic properties of common soils of the Peshekee River watershed within Baraga County, Michigan. †

Soil Name	Extent (%) Within County	Slope (%)	Hydrologic Group ^a	Permeability (In./Hr.)	pH	Organic Matter (%)
Carbondale- Tacoosh mucks	10.1	0	A/D	0.2-6.0	5.1-7.8	40-75
Champion- Michigamme cobbly silt loam	4.3	15-35	A/D	0.6-2.0	3.6-6.5	1-3
Michigamme-Rock outcrop complex	3.3	15-35	C	0-2.0	3.6-6.5	0-3
Champion- Michigamme cobbly silt loam	3.1	8-15	B/C	0.06-2.0	3.6-6.5	1-3
Witbeck- Tacoosh complex	2.5	0	B/D	0.2-6.0	4.5-7.8	42-75
Dawson and Greenwood peats	1.9	0	A/D	0.2-6.0	3.6-5.5	55-85
Anasa cobbly silt loam	0.2	15-35	B	0-2.0	4.5-6.0	0-3

†Data from Berndt, 1988.

^aGroup A = High infiltration rate

Group B = Moderate infiltration rate

Group C = Slow infiltration rate

Group D = Very slow infiltration rate



Riparian Vegetation

The headwaters of the Ford River are located within areas of vegetation dominated by northern white cedar (Thuja occidentalis) and speckled alder (Alnus rugosa). Extensive tamarack and alder swamps, and sedge meadows characterize the upper reaches of the Peshekee River and its tributaries. At the Ford River site the dominant vegetation, calculated as importance percentages, consists of balsam poplar (Populus balsamifera) and speckled alder (Table 5). Ninety-five percent of the Ford River vegetation is composed of deciduous species, while the majority (52%) of the vegetation at the Peshekee site is made up of coniferous species such as balsam fir, white spruce and white cedar.

Water Quality and Hydrology

The streamwater characteristics of each river is determined by a combination of climatic, geological and vegetative conditions within their respective watersheds. The Ford River flows through ion-rich, high water capacity soils supporting deciduous type vegetation. The brown water, high alkalinity (~ 133 mg CaCO₃/L) stream maintains a stable flow with seasonal fluctuations in spring and fall. Mean annual nitrate concentrations (~ 78 mg NO₃/L) in the Ford are slightly higher than those measured in the Peshekee (~ 75 mg NO₃/L). Mean annual orthophosphorus concentrations are similar in both streams. The low alkalinity (~ 14 mg

Table 5. Calculated importance percentages of riparian vegetation at the Ford River (FS1) site and the Peshekee River (PS1) site.

Ford River	(%)	Peshekee River	(%)
<u>Populus balsamifera</u> (Balsam Poplar)	42	<u>Abies balsamea</u> (Balsam Fir)	37
<u>Alnus rugosa</u> (Speckled Alder)	32	<u>Acer rubrum</u> (Red Maple)	16
<u>Prunus pensylvanica</u> (Pin Cherry)	9	<u>Betula papyrifera</u> (Paper Birch)	16
<u>Betula papyrifera</u> (Paper Birch)	6	<u>Alnus rugosa</u> (Speckled Tag Alder)	14
<u>Abies balsamea</u> (Balsam Fir)	5	<u>Picea glauca</u> (White spruce)	8
<u>Cornus stolonifera</u> (Red-Osier Dogwood)	4	<u>Thuja occidentalis</u> (Northern White Cedar)	7
<u>Ulmus americana</u> (American Elm)	2	<u>Acer spicatum</u> (Mountain Maple)	1



CaCO_3/L) Peshekee River is influenced strongly by its swampy headwaters, which contribute the tannins and lignins that stain the river a dark brown to black color. The watershed's thin poorly drained soils and exposed granitic bedrock account for the river's low cation and anion concentrations, as well as its fluctuating and flashy nature of streamflow. The high spring runoff of a large snowpack can drive a normally neutral pH down to 5.6 (Nancy Fegan, personal communication; Merna and Alexander, 1983). Both rivers maintain the cold water temperatures and high dissolved oxygen concentrations required by sensitive aquatic invertebrate and trout populations.

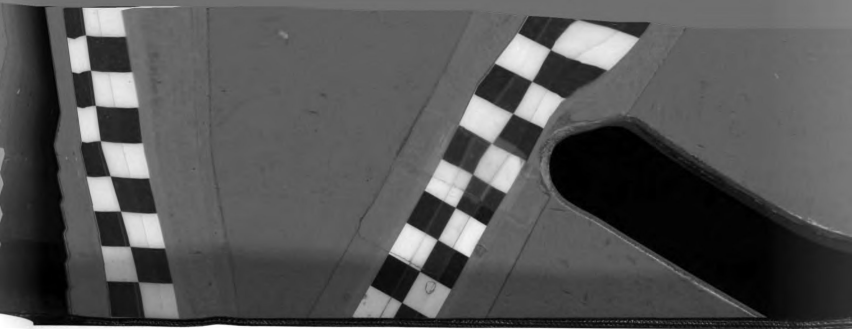
The Ford and Peshekee Rivers have remained relatively free of any anthropogenic disturbances over time. State highway M-95 crosses the Ford River 11 miles upstream of the study site which may be responsible for chloride additions from road salt in the winter. A mink and cattle farm, a possible source of nutrients, is also located near the Ford's headwaters. Both watersheds have been influenced by scattered camps located along the rivers, as well as clearcut logging.

The substrate composition at the study sites within each stream is dominated by cobble (Table 6). A greater proportion of the Peshekee River site consists of boulder substrate, while the Ford River site has a larger percentage of pebble and sand. Personal observations of other sites

Table 6. Percent composition of substrate particle size at the Ford River (FS1) and Peshekee River (PS1) sites. Particle sizes based on the Wentworth classification scheme (after Cummins 1962).

Substrate Particle Category	Percent Composition (%)	
	Ford River (FS1)	Peshekee River (PS1)
Boulder	3	10
Cobble	75	74
Pebble	12	8
Gravel	0	3
Sand	10	5

along the Ford River indicate that the substrate alternates between runs and pools with sand substrate, and riffles with cobble and pebble substrate. In contrast, the Peshekee River consists of long runs with cobble and boulder substrate and occasional pools with sand substrate. Additionally, the smooth cobble and boulder substrate observed in the Peshekee River appeared to be extremely well weathered.



MATERIALS AND METHODS

Site Evaluation

1. Streamwater characteristics

Chemical and nutrient water data were collected in order to match sites as closely as possible for Acroneuria production and growth studies. Water chemistry and physical stream data were measured every two weeks during the summer months of June, July, August and September during 1988, 1989 and 1990. Chemical and nutrient samples were collected every six weeks for the remaining months of the year from September 1988 to June 1990.

Water samples from each site were collected in polyethylene bottles, placed on ice during transport to the the field laboratory and analyzed within six to eight hours for alkalinity, hardness, pH, conductivity and turbidity. Two 250 mL dissolved oxygen samples per site were collected, immediately fixed and later analyzed in the field laboratory. Nutrient samples, also collected in polyethylene bottles, were immediately frozen (or refrigerated for silica) and analyzed six months later using a Technicon® AutoAnalyzer II. Specific analytical procedures used are as follows:

Water Temperature (°C) - Temperature was measured to nearest 0.5 °C in the field with a hand thermometer.

pH - pH was measured using an Orion® Model 407A Ionalyzer.

Conductivity - Conductivity measurements were made using a YSI® Model 31 Conductivity Meter. Values were corrected to 25 °C using the correction factor: Conductivity ($\mu\text{mhos/cm}$) $\times (1 + 0.02 \Delta T)$, where ΔT equals the difference between the observed water temperature reading and 25 °C.

Turbidity - Determinations were made using a Hach® Model 2100A Turbidimeter.

Dissolved Oxygen (D.O.) - D. O. was measured using the sodium azide modification of the Winkler method (APHA, 1980).

Percent Saturation of Dissolved Oxygen - Each D.O. value was converted to percent saturation using the formula: $[\text{D.O.} / (468 / (31.6 + T))] \times 100$, where T equals water temperature (°C) at time of sample collection and D.O. equals dissolved oxygen concentration in ppm.

Alkalinity - Total alkalinity was determined by the titration method described in APHA, 1980.

Hardness - Total hardness was measured by the EDTA titrimetric method (APHA, 1980) using Hach® powder pillows for indicator.

Silica - Determinations were made using the automated molybdosilicate method (U.S.E.P.A., 1979).

Chloride - Chloride measurements were made using the automated ferricyanide method (U.S.E.P.A., 1979).

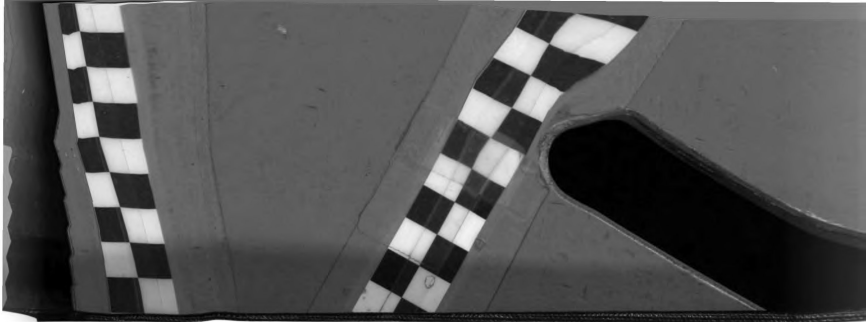
Soluble reactive phosphorus and Total Phosphorus - Phosphorus was measured using the automated ascorbic acid reduction method (U.S.E.P.A., 1979). Soluble reactive phosphorus samples were filtered through 0.45 μm Millipore® membrane filters before freezing and analysis. Organic phosphorus samples were digested with sulfuric acid before analysis.

Nitrate - Nitrate determinations were made using the automated cadmium reduction technique (U.S.E.P.A., 1979).

Nitrite - The automated sulfanilic acid/NED dihydrochloride method was used to determine nitrite concentrations (U.S.E.P.A., 1979).

Ammonia and Total Nitrogen - Ammonia was measured using the automated phenate method (U.S.E.P.A., 1979). Organic nitrogen was digested before analysis with sulfuric acid and measured as for ammonia.

Concentrations of the common cations Ca^{2+} , Mg^{2+} , Na^{+} and K^{+} were measured on a regular basis from 1988 to 1990. Samples were collected in polyethylene bottles, frozen and



later analyzed via atomic absorption spectrophotometry at the Michigan State University Soils Testing Laboratory.

Discharge was measured periodically at each site during the summers of 1988 and 1989 using a Gurley pygmy current meter. Velocity measurements were made at 0.6 of the depth below the water surface, for a minimum of 20 intervals per transect. Discharge was calculated by multiplying depth by interval width by mean velocity for each interval, and summing across the entire transect.

Means $\pm$ standard error for several of the important chemical and physical characteristics of the streamwater at each site were calculated on an annual and seasonal basis. Additionally, these parameters were compared statistically between sites using paired t-tests on the entire data sets using untransformed data. Data were checked for homogeneity of variances using Hartley's test (Ott, 1988).

2. Substrate composition

The composition of substrate particle size was quantified within each site to determine whether substrate differences existed. Approximately 300 meters² of stream bottom at each site were examined. Ten transects, 4 meters apart, were set up across the width of each stream. General particle sizes at ten equidistant intervals along each transect were identified using Wentworth's classification scheme (Cummins,

1962). The percent composition of boulder, cobble, pebble, gravel and sand present was calculated on a per area basis.

Additionally, the surface area of cobble-size rocks per square meter of stream bottom were compared at FS1 and PS1 using rocks collected during Hess sampling for invertebrates. Two measurements, short-axis circumference and long-axis circumference, were recorded for all rocks with a minimum short axis circumference of 80 millimeters. Calculated rock surface areas were determined by multiplying the short-axis circumference by the long-axis circumference for each rock collected. Actual rock surface areas of 45 foil-wrapped rocks from each stream were measured using a LI-COR® leaf area meter. Total rock surface area per sample was determined using calculated rock surface area/actual rock surface area regressions developed for each stream. These data were used in Acroneturia ecological density and biomass calculations described in the field sampling methods.

3. Riparian vegetation

The importance of individual species within the riparian community was estimated by calculating importance values of dominant trees and shrubs at each site (Brower and Zar, 1984). The importance value index is the sum of the relative frequency, density and coverage for a particular species. Five rectangular plots (7 x 14 meters) were randomly chosen along the stream bank up to 150 meters upstream of each

invertebrate sampling site. Each tree, shrub and sapling within a plot was identified and counted. Coverage area was determined from measurements of the diameter of the crown of foliage for each individual plant. Relative frequency, density and coverage for each species was summed and divided by three to obtain an importance percentage. While this calculation has the disadvantage of giving similar values for different combinations of the three relative values, it provides a qualitative estimate of riparian species (Brower and Zar, 1984).

Field Sampling

1. Life history and growth rates

Basic knowledge of aspects of A. lycorias life history was critical for accurate production estimates. Since data were not available in the literature, an effort was made to obtain data regarding the cohort production interval (CPI, Benke, 1979) of A. lycorias found in the northern Michigan geographical region. A series of intensive sampling efforts were made over a six month period, where a minimum of 150 individuals per site were collected using a 1.0 mm mesh kick screen. Individuals larger than 1.0 mm were sorted from debris and other organisms in the field using a white enamel pan and forceps, and were preserved in 90% ethanol. In the laboratory, organisms were measured to the nearest 0.5 mm under 10x power of a dissecting stereomicroscope. The sex of

second and third year nymphs were also recorded. All individuals were saved for stomach content analyses. Cohorts were identified by examining the data for peaks in size-frequency distributions. Mean length and standard errors were calculated for each sex and cohort. Mean dry weight biomass was calculated from length-weight regressions developed for *A. lycorias* nymphs collected from each stream (Figure 3). Growth rates were calculated using the instantaneous rate of growth equation:

$$W_t/W_0 = e^{Gt}$$

where G = instantaneous rate of growth

W_t = weight at time t

W_0 = weight at $t = 0$

t = time (Ricker, 1975)

In this study W_t and W_0 were represented by the mean dry weight biomass of a cohort on each sampling date.

The sex of each mature nymph was determined by examining the posterior fringe of the eighth abdominal segment. The sex ratio of each cohort was calculated by dividing the number of females by the number of males.

Gut contents of all three cohorts of *A. lycorias* were examined from samples collected in August and October, 1990 and January, 1991. The stomach contents were analyzed to provide a cursory look at food habits of various cohorts in each stream. The foreguts of six individuals per cohort per

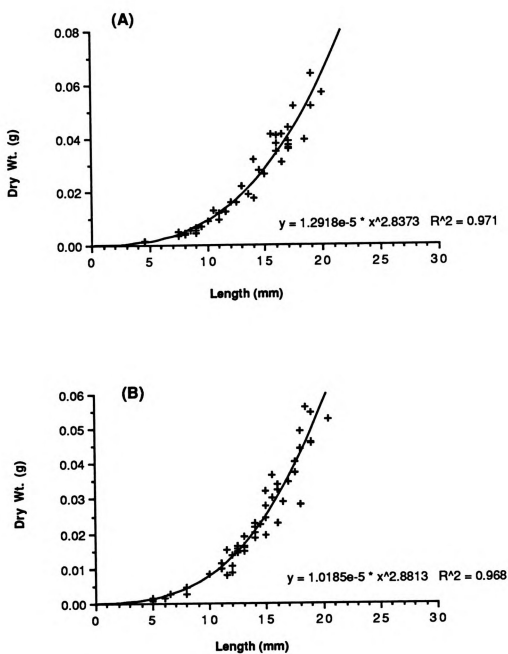


Figure 3. Length/dry weight regressions for *A. lycorias* collected from the Ford (A) and Peshekee (B) Rivers, 1988.

site were removed by cutting the membrane between the head and thorax and pulling the head from the rest of the nymph's body. The foregut usually broke away from the hindgut cleanly. Each gut was gently teased open with a fine probe under a dissecting microscope. Stomach contents were identified to the order level (in some cases to the family level) and enumerated. Foregut fullness was determined by examination only and recorded as empty, 25%, 50%, 75% or 100% full. Mean gut fullness was calculated for each cohort (n = six individuals) and expressed as a proportion.

2. Production estimates

Invertebrate samples were collected with the objective of obtaining a quantitative estimate of A. lycorias production at matched sites in the Ford and Peshekee Rivers. Beginning in the summer of 1988 invertebrate samples were collected with a modified Hess sampler (0.0881 m sample area) at two sites in each stream on an alternating two-week (or once-a-month) schedule. This sampling regime was changed at the end of September to a sample collection at one site per stream every six weeks for the fall, winter and spring seasons of 1988, 1989 and 1990 due to sample processing and ice-cover considerations. Sample collection was increased to a twice-a-month regime at one site per stream during the summer of 1989.

By limiting the sampling regime to two streams, one hard water and one soft water stream, and limiting the sites within each stream to one, this study fell under the definition of a pseudoreplicated study (Hulbert, 1984). Since only one stream of each stream hardness was sampled in this study all conclusions are limited to these particular streams. An additional site in each stream was sampled in July, 1989 to get a general idea of whether FS1 and PS1 were representative of other fourth-order riffles in the streams. Density and standing crop biomass values for A. lycorias nymphs collected at each of these additional sites were compared to values obtained at FS1 and PS1 using a paired t-test after testing for homogeneity of variances.

Six samples were collected in riffle areas from two stratified random transects per site. Three points along each transect were randomly chosen for sample collection, with care taken to avoid sampling in places that had been previously disturbed. Individual rocks were first rubbed by hand to dislodge invertebrates clinging to the rock surfaces, and then removed from the stream for substrate analysis. The remaining substrate was stirred up by hand to a depth of five to seven centimeters for a 30 second time period to allow the current to carry organisms into the sampler's 560 micrometer mesh netting. Samples were preserved immediately in 90% ethanol for later sorting.

In the laboratory, invertebrate samples were sorted for P. lycoctas nymphs, which were counted and measured using a dissecting stereo microscope equipped with an ocular micrometer. The length from the tip of the head to the end of the abdomen of each individual was measured to the nearest 0.5 mm under 10 x power magnification. Nymphs were divided into 0.5 mm size classes, which ranged from 1.0 mm to 24 mm. No attempt was made to identify instars. Length data were converted to dry weight for biomass and production calculations using length/dry weight regressions developed for each stream (Figure 3). Density and biomass values were compared using a paired t-test after testing for homogeneity of variances with Hartley's F-max test. Differences between sites for density and biomass data were compared with unpaired t-tests.

Production was estimated using the size-frequency method (Hynes, 1961; Hynes and Coleman, 1968; Hamilton, 1969). Dry weight biomass losses were summed over the entire sample collection period for each 0.5 mm size class. After multiplying by the total number of size groups, the weight loss of each size group was summed to produce an estimate of total production. Negative weight loss values were included in the final sum. Total production was corrected for the cohort production interval (CPI) by multiplying the estimate by 365/generation time (Benke, 1979). The CPI was determined independently as part of the life history portion of this

study. The cohort turnover ratio (P/B) was calculated by dividing total uncorrected production by the annual dry weight biomass standing crop. The annual turnover ratio (P/B) was calculated by dividing the cohort P/B ratio by the CPI correction (Benke, 1984).

Laboratory Stream Study

Growth studies were conducted in the laboratory to determine growth rates of organisms living in hard and soft water. Transplant experiments were set up in two artificial streams (one stream simulating the Ford River and the other simulating the Peshekee River) in Felch, Michigan during the summer, 1990. The experiment was set up as a three factor factorial design with the strain and sex factors randomized within each treatment. Each stream contained 30 nymphs transplanted from hard water (approximately 15 individuals of each sex) and 30 nymphs taken from soft water (approximately 15 individuals of each sex). Organisms were held individually in cages built from 12 ounce clear plastic cups with screened panels to allow water to flow through the cages. Cages were cleaned and rerandomized within each stream every three days. Each nymph was fed one live waxworm every three days. Nymphs ate the commercially available food source readily in food trials conducted prior to the growth experiment.



Stream water from the Ford and Peshekee Rivers was transported to the field laboratory June 22, 1990 and was added to each recirculating stream. The water temperature was set to 15° C. The temperature was kept constant throughout the experiment. Since the artificial streams were located out-of-doors, the light/dark cycle followed natural photoperiods. The water temperature, pH, conductivity, alkalinity, hardness and dissolved oxygen was monitored at the start, at two-week intervals and at the end of the experiment. The stream water in each stream was exchanged with new stream water from the Ford and Peshekee Rivers at the mid-point of the experiment. The experiment was ended on October 10, 1990 when low ambient air temperatures made it impossible for the stream compressors to maintain 15° C.

An initial, mid-point (41 days) and final (110 days) wet weight measurement was made for each individual. Measurements were made to the nearest 0.0001 gram using a Mettler® analytical balance after blotting nymphs with a paper towel to remove excess moisture. The error associated with using wet weights of nymphs was calculated by weighing a wet nymph fifteen times to obtain a mean weight and standard error. The sex of each nymph was determined using a dissecting microscope after final weight measurements were taken. Growth rates of each individual were calculated using the instantaneous rate of growth equation. Significant differences of individual growth rates between treatments,

sexes, and strains were calculated using a three-way analysis of variance.

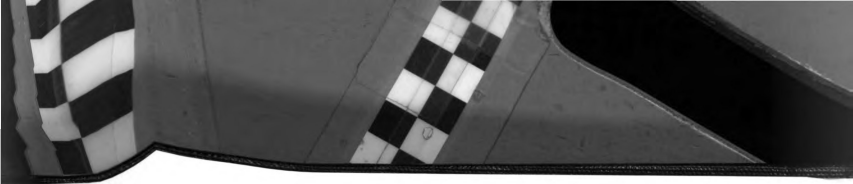
RESULTS

Streamwater Quality

1. Physical and Chemical Parameters

The composite water quality data was collected at Ford Site 1 (FRI) and collected from 1 Fall 1986 to July, 1988 to September, 1988 at two sites, A-1 and A-2. Air and water temperatures (important water quality measurement of each parameter taken on) are shown in Table 1. Data recording instruments such as thermometers and air and water thermometers were not used in this study. However, water temperatures followed similar patterns within each season over the study period (Figure 1). Typically, temperatures of water reached 20°C and above at each site. Although water temperatures during the summer, fall and spring of 1988 were higher at each site than those measured in 1989, it is not clear whether this reflects true temperature differences or is a water quality artifact of the measurement methodology.

Discharge measurements were taken in 1986 and 1987 were inconsistent between sites, a result of the different sampling regime and differences in runoff rates for each measurement. To get an idea of the pattern of discharge for the Kalamazoo River, monthly data were obtained from the Kalamazoo River Survey in Lansing, Michigan for the period 1980-1987 and 1977 (the most recent data available). The data showed



RESULTS

Streamwater Quality

1. Physical and chemical parameters

The complete water chemistry data set collected at Ford Site 1 (FS1) and Peshekee Site 1 (PS1) from July, 1988 to September, 1990 is presented in Tables A-1 and A-2. Air and water temperatures represent an instantaneous measurement of each parameter taken on that date. Continuous data recording instruments such as thermographs or min-max thermometers were not used in this study. Seasonal water temperatures followed similar patterns within each stream over the study period (Figure 4). Typically, temperatures in summer reached 20° C and above at each site. Although water temperatures during the summer, fall and spring of 1989 were higher at each site than those measured in 1988, it is not known whether this reflects true temperature differences, or is merely an artifact of the measurement technique.

Discharge measurements made during 1988 and 1989 were inconsistent between sites, a result of an alternate sampling regime and differences in runoff rates for each watershed. To get an idea of the pattern of discharge for the Peshekee River, monthly data were obtained from the U. S. Geological Survey in Lansing, Michigan for the period between 1975 and 1977 (the most recent data available) for a site located

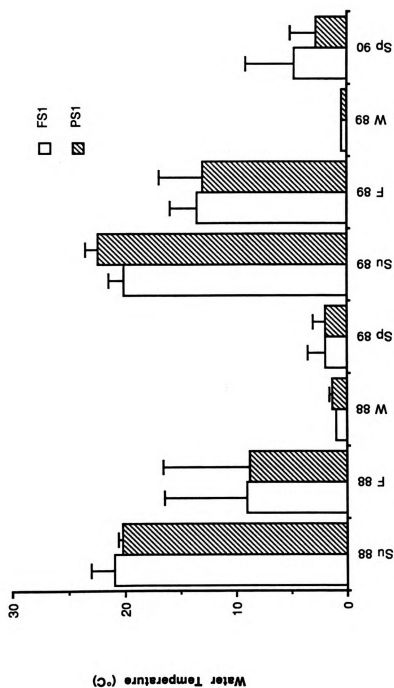


Figure 4. Seasonal variations (mean $\pm$ S.E.) in water temperature at the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990.

downstream of the PS1 site. Since the west branch of the Peshekee, a major tributary, increases the discharge of the river significantly, mean monthly discharge at the PS1 site was estimated using a discharge regression between the sites developed during Summer and Fall 1991 ($y = -0.051263 + 0.43101 x$; $r^2 = 0.99$; $y =$ discharge in m^3/sec at PS1 and $x =$ discharge in m^3/sec at U.S.G.S. site). Discharge for the Ford River was estimated from 1983-1990 data collected continuously from May to November at the FEX site as part of the E.L.F. monitoring project. No major tributaries flow into the Ford River between FEX and FS1. Winter (December through March) discharge data for the Ford River was not available. A plot of mean monthly discharges of the two rivers indicates that the spring and to a lesser extent, fall periods are the most variable (Figure 5). Discharge data plotted for the months of April and May indicate that the snowpack runoff at the Peshekee River is much greater than that at the Ford River.

Variations of conductivity, total alkalinity, total hardness and pH data collected over the entire period and on a seasonal basis reflect their close relationship with stream discharge (Figures 6 and 7, Tables 7, A-1 and A-2). During summer low flow periods, measurements of these four parameters all increased and likewise decreased during periods of high flow. Values for the entire data set for each parameter differed significantly ($p < 0.05$) between



Figure 5. Mean monthly discharge for the Ford (FEX site) and Peshekee (PS1 site) Rivers. Peshekee River data from U.S.G.S., 1975-1977; Ford River data from E.L.F. monitoring study, 1983-1990.



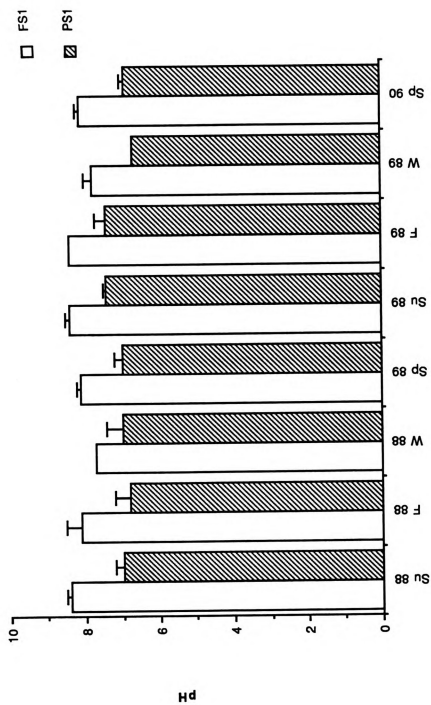


Figure 6. Seasonal variations (mean $\pm$ S.E.) in pH at the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990.

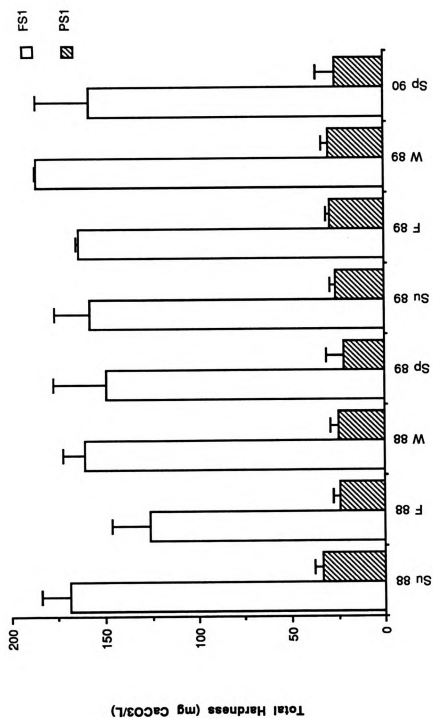


Figure 7. Seasonal variations (mean $\pm$ S.E.) in total hardness at the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990.

Table 7. Summary (two year means $\pm$ S.E.) of selected water chemical, physical and nutrient parameters for the Ford and Peshekee Rivers, 1988-1990.

Parameter	Ford River	Peshekee River
Conductivity (μ mho/cm)	226 $\pm$ 13	34 $\pm$ 3
Dissolved Oxygen (mg/L)	10.6 $\pm$ 0.4	9.9 $\pm$ 0.5
Percent Saturation D.O. (%)	94 $\pm$ 2	87 $\pm$ 1
Total Alkalinity (mg CaCO ₃ /L)	138 $\pm$ 5	15 $\pm$ 1
Silicate (mg SiO ₂ /L)	8.1 $\pm$ 0.4	5.1 $\pm$ 0.5
Chloride (mg Cl/L)	4.8 $\pm$ 0.5	0.5 $\pm$ 0.05
Total Phosphorus (μ g P/L)	50 $\pm$ 18	46 $\pm$ 18
Total Nitrogen (μ g N/L)	571 $\pm$ 74	559 $\pm$ 68
Nitrite-N (μ g N/L)	5.2 $\pm$ 0.4	6.2 $\pm$ 0.6
Ammonium-N (μ g N/L)	62 $\pm$ 8	67 $\pm$ 9

sites (Table 8). pH values for the Peshekee River (PS1 site) never dropped below 6.4, although readings as low as 4.8 have been recorded at the river's mouth during peak spring runoff periods. Dissolved oxygen concentrations remained high year round at both sites with saturation recorded at or near 100% most of the study period (Table 7). These values also represent an instantaneous measurement of dissolved oxygen which will vary with time of day, water temperature and flow. Silica and chloride concentrations averaged higher at the FS1 site than at PS1 (Table 7). Chloride concentrations at FS1 were much higher during September and October 1989 than they were for the same period in 1988 and 1990 (Tables A-1 and A-2). Chloride concentrations of 9-12 mg/L, although high, are considered to be within normal ranges for this geographic region.

Calcium and magnesium constitute the major cations in each stream (Figure 8, Table A-3). Of the four cations measured throughout the study, only potassium did not differ significantly ($p = 0.09$) between streams (Table 8). Calcium levels ranged from two to seven times higher in the Ford River than in the Peshekee, while the mean difference in magnesium was three fold.

2. Nitrogen and phosphorus parameters

Two year means $\pm$ standard errors of total and soluble reactive phosphorus, nitrate-N, nitrite-N, ammonium-N and

Table 8. Results of paired t-tests between the Ford (FS1 site) and Peshekee (PS1 site) Rivers for selected water chemical, physical and nutrient parameters from July, 1988 to June, 1990.

Parameter	df	Paired t-value	Probability
Water Temperature	17	0.078	0.94
pH	17	17.132	0.0001
Total Hardness	17	28.669	0.0001
Calcium	11	4.314	0.001
Magnesium	11	2.990	0.01
Sodium	11	8.519	0.0001
Potassium	11	1.855	0.09
Soluble Reactive Phosphorus	17	-1.398	0.18
Nitrate	17	0.279	0.78

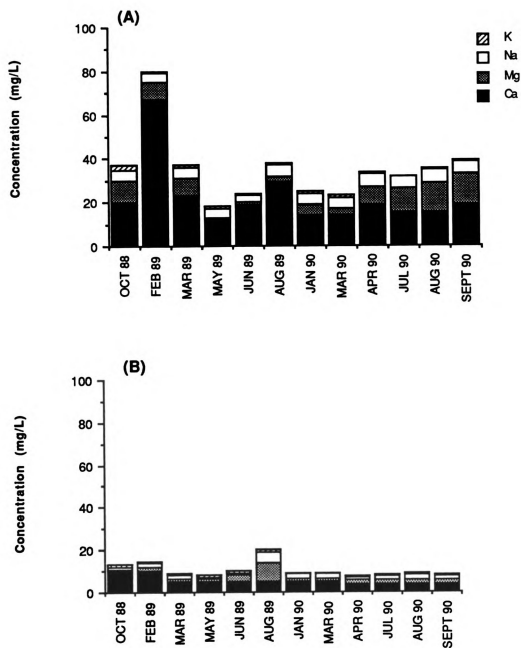
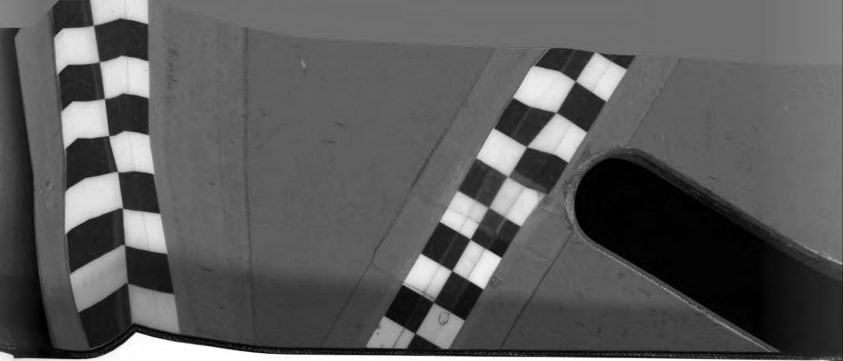


Figure 8. Cation concentrations (mg/L) for the Ford River (A) and the Peshekee River (B), 1988 - 1990.



total nitrogen analyses are presented in Table 7. Soluble reactive phosphorus and nitrate-N concentrations were not found to differ statistically ($p < 0.05$) between sites over the entire study period (Table 8). Concentrations of soluble reactive phosphorus throughout the entire period were never greater than $10 \mu\text{g P/L}$ except for October 1988 at the PS1 site (Tables A1 and A-2). On a seasonal basis, mean soluble reactive phosphorus concentrations at PS1 were slightly greater than those measured at FS1 (Figure 9). Nitrate-N levels were similar in each stream, except for the winter seasons (Figure 10). The higher concentrations of nitrate-N found at FS1 each winter are likely the result of higher deciduous leaf inputs each fall to the Ford River. Mean nitrite-N and ammonium-N concentrations were similar at both sites throughout the study period. Total nitrogen and total phosphorus values varied greatly between sites and in some cases appeared to be inaccurate (Tables A-1 and A-2). Since total nitrogen and total phosphorus concentrations represent the sum of each of their respective forms, totals should never be less than the dissolved concentrations. In this study, several total values were not greater than the dissolved forms, i.e. total phosphorus at PS1 8/5/88, at FS1 7/23/88 and total nitrogen at PS1 3/4/90, at FS1 1/21/90 and 3/3/90. Due to technical problems in the laboratory analysis of these two parameters, results should be viewed with caution.



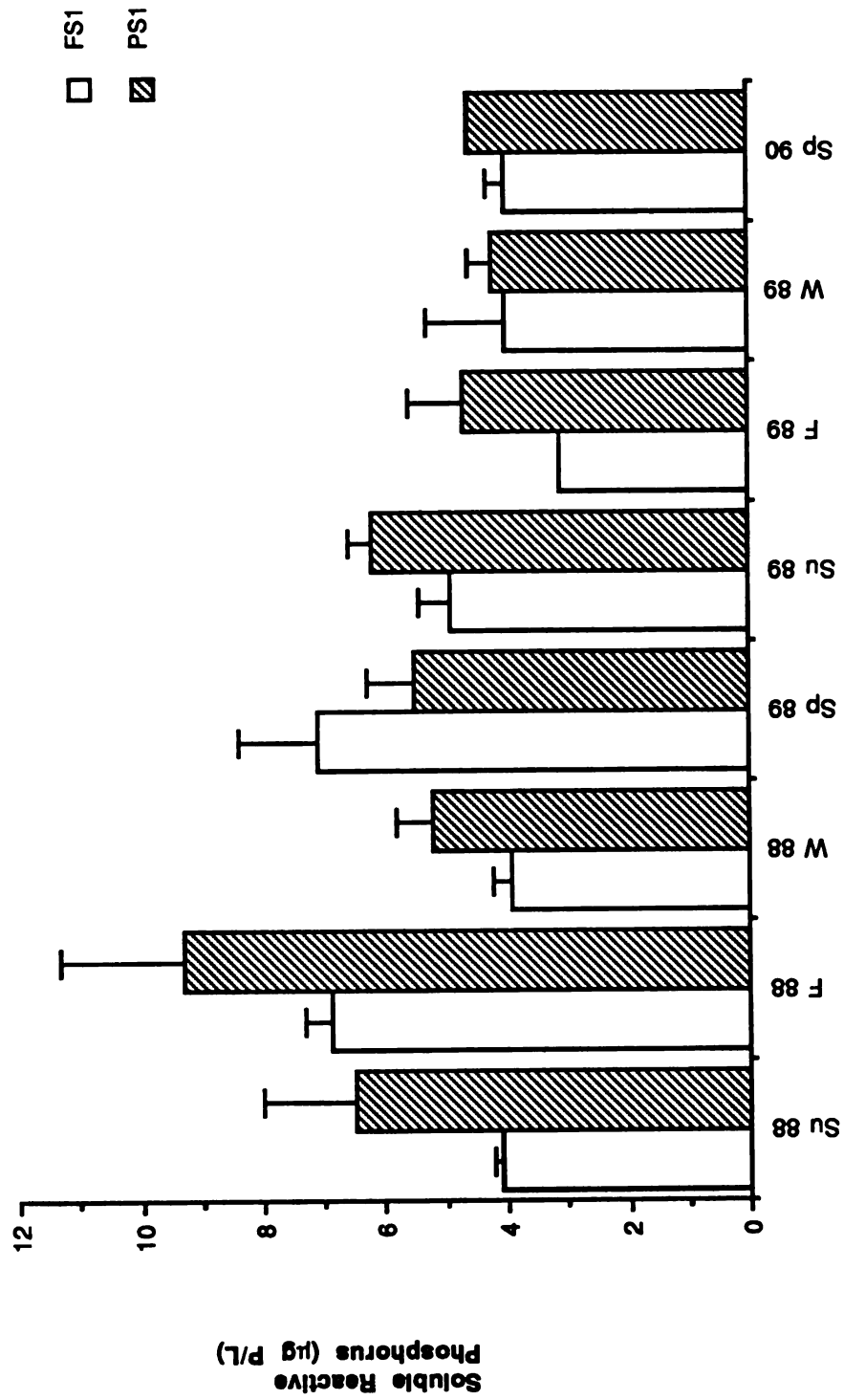


Figure 9. Seasonal variations (mean $\pm$ S.E.) in soluble reactive phosphorus at the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990.



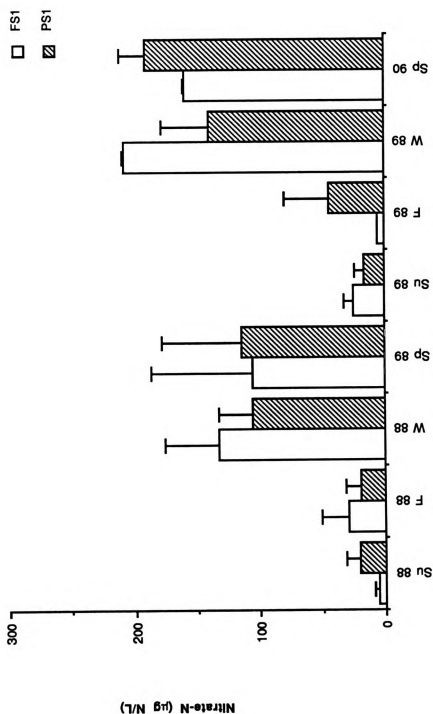


Figure 10. Seasonal variations (mean $\pm$ S.E.) in nitrate at the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990.

Life History

1. Life cycle

Results from the length length-frequency distributions over a seven month period clearly indicate a three-year life cycle for A. lycorias (Figures 11, 12, 13, 14, 15). Nymphs ranging from 2.5 mm to 22.0 mm were collected. Emergence had already occurred at both sites before the July, 1990 sample collection, as only two peaks in the distribution were apparent (Figure 11). A few individuals who had not emerged yet were still evident in July. The merovoltine pattern as described by Pritchard (1983) became obvious when the young-of-year nymphs appeared in August, 1990 (Figure 12). Neither an egg or nymphal diapause was detected for organisms of either stream in this study.

Two patterns were observed after the overall distributions of nymphs were broken down by sex. First, the mean lengths and corresponding dry weights of female nymphs of each cohort are larger than male nymphs of the same age. This trend became more pronounced as the nymphs increased in age from July, 1990 to January, 1991. Secondly, mean lengths of nymphs collected on the same date in each stream indicate that organisms of all size classes from the Peshekee River are slightly larger (Figures 12 and 13). Actual calculations of mean lengths and dry weights are presented later in this section under the heading of natural stream growth rates.

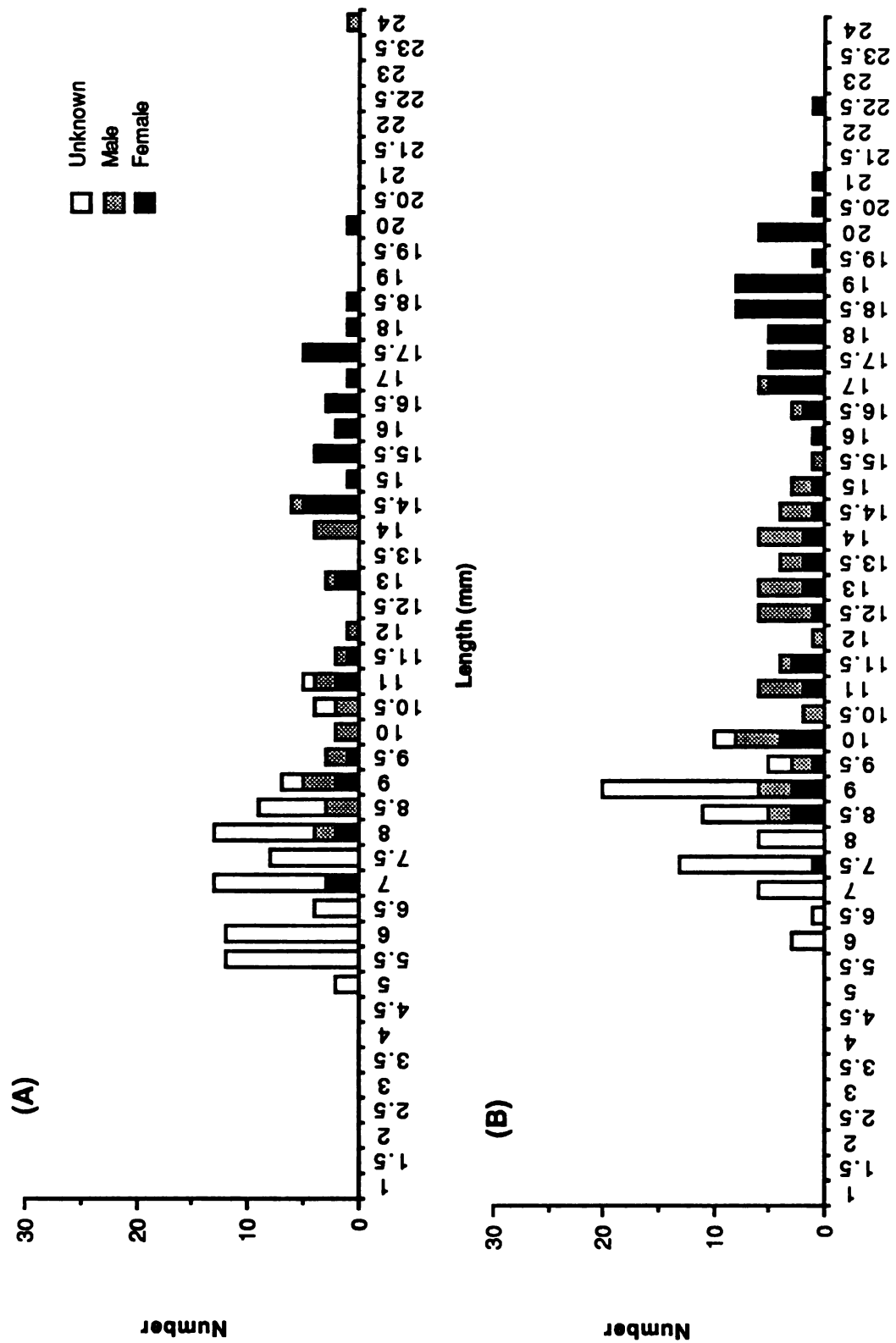


Figure 11. Size-frequency distribution by length of *A. lycorias* collected from the Ford River (A) and the Peshekee River (B), 7/90.



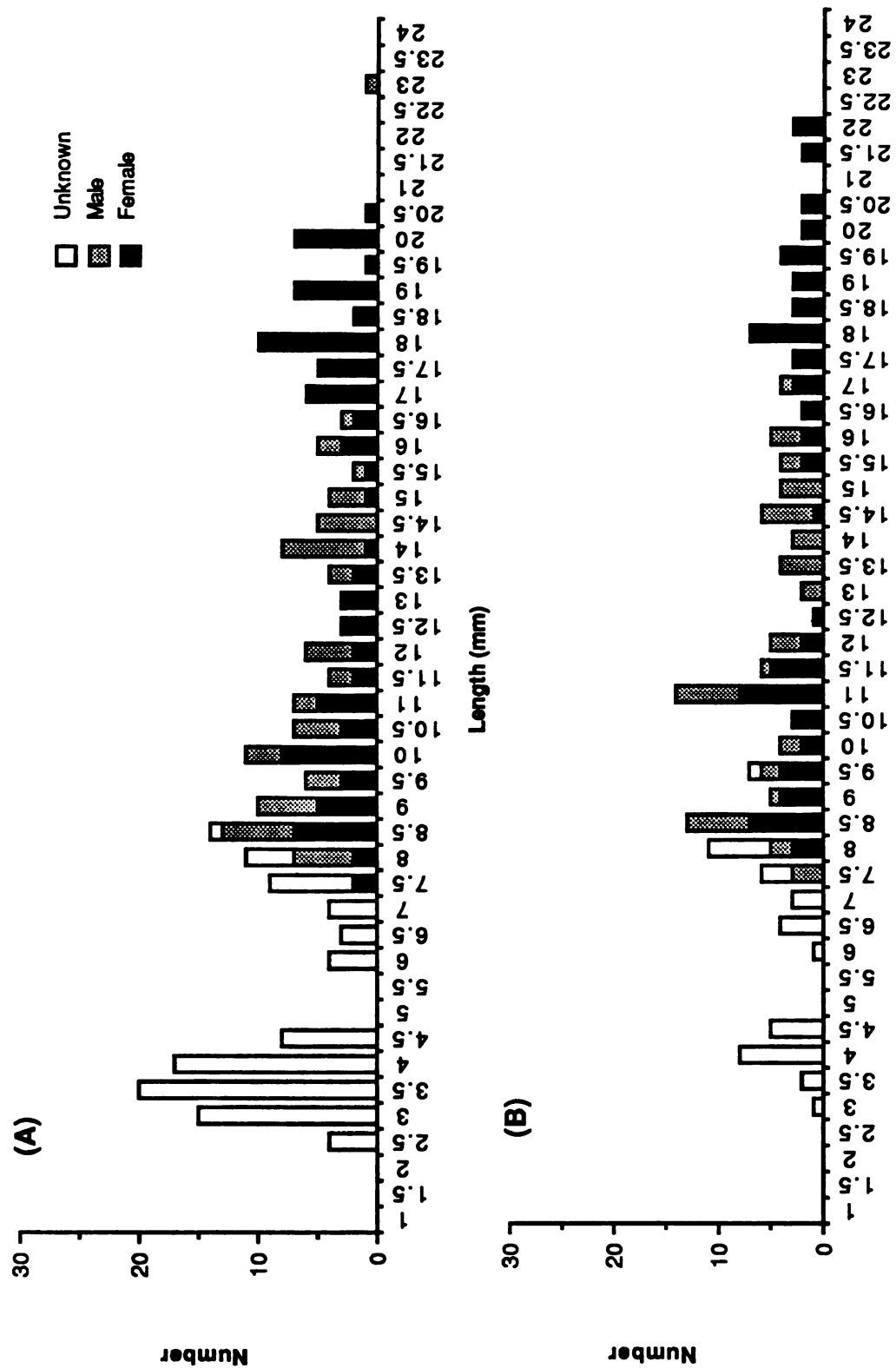


Figure 12. Size-frequency distribution by length of *A. lycorias* collected from the Ford River (A) and the Peshekee River (B), 8/90.

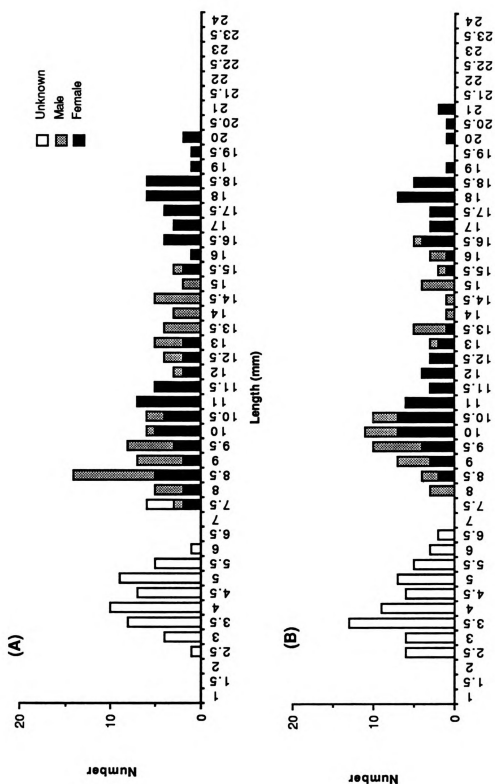
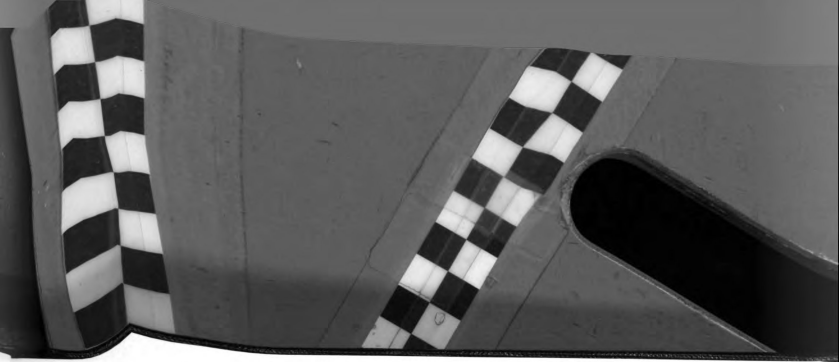


Figure 13. Size-frequency distribution by length of *A. lycorias* collected from the Ford River (A) and the Peshekee River (B), 9/90.

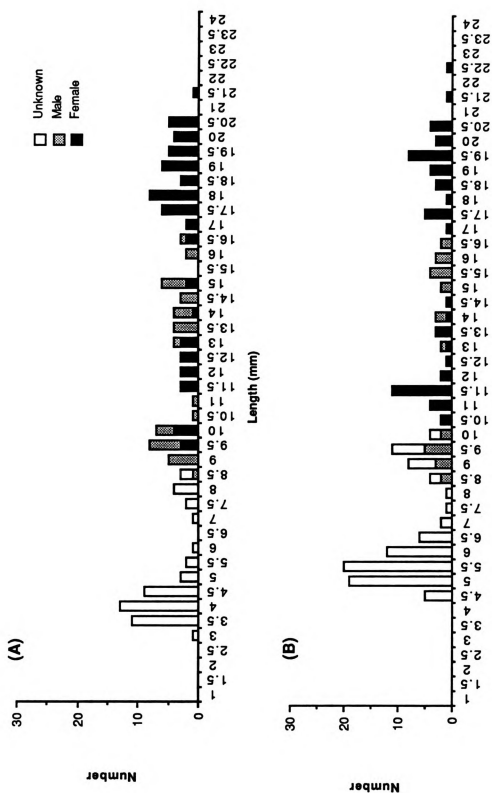


Figure 14. Size-frequency distribution by length of *A. lycorides* collected from the Ford River (A) and Peshekee River (B), 10/90.

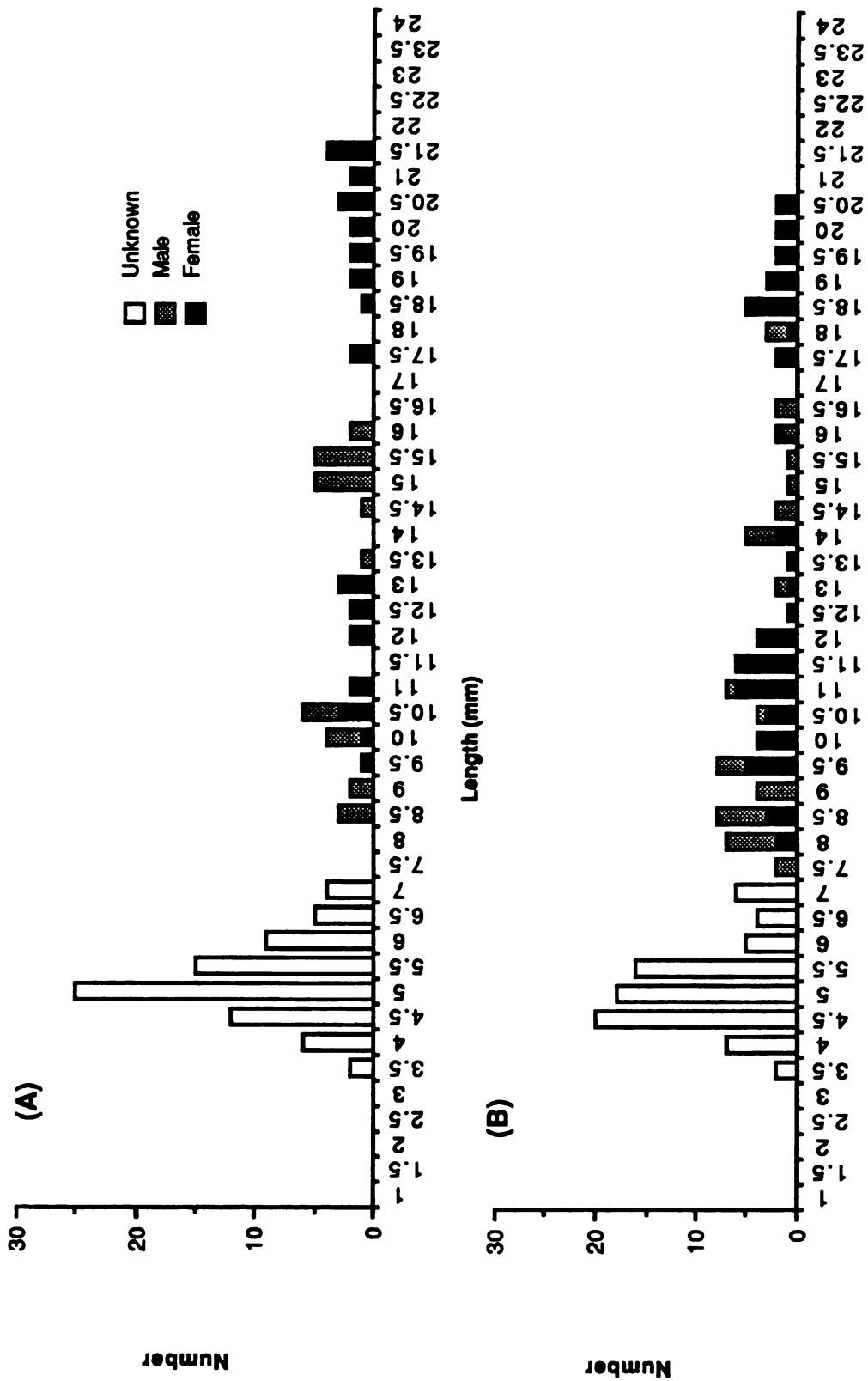


Figure 15. Size-frequency distribution by length of *A. lycorias* collected from the Ford River (A) and Peshekee River (B), 1/91.

2. Sex ratios

Female to male ratios calculated for each size class at FS1 and PS1 varied by size class. Ratios ranged from 0.8:1 for second-year organisms at PS1 and FS1 in July, 1990 to a ratio of 3.7:1 for third-year nymphs at FS1 in July, 1990. In general, second-year class ratios at both sites were 1:1, while mean ratios for third-year class individuals increased to 2:1 at FS1 and PS1.

3. Diet

Mean foregut fullness of young-of-year size classes in each stream depended on time of year (Figure 16). At the time of sample collection in August and October, 1990, young-of-year organisms at FS1 had greater mean gut fullnesses than did those at PS1. Young-of-year gut fullness dropped at both sites in January, 1991. Mean gut fullness for second-year classes in both streams was fairly consistent for all dates sampled. A large difference between gut fullness of third-year nymphs at each site occurred on the August, 1990 date. Average gut fullness of PS1 individuals was 92%, while that of the FS1 nymphs was only 25%. The remaining dates sampled were consistent between sites for the third-year class. Young-of-year organisms in both streams had fuller foreguts on the October, 1990 date than any other year class. Third-

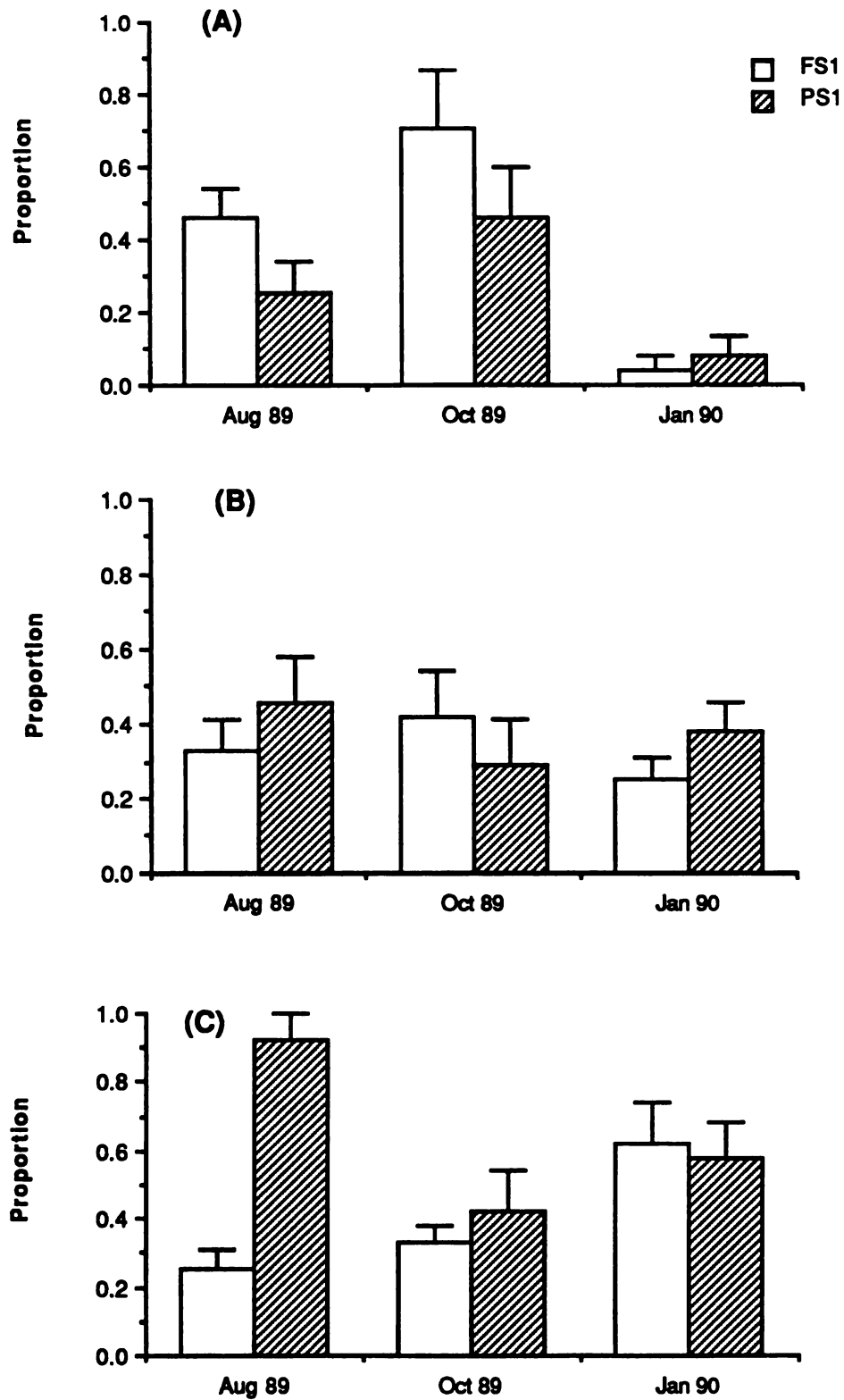


Figure 16. Mean gut fullness $\pm$ S.E. *A. lycorlas* nymphs collected from the Ford (FS1 site) and Peshekee (PS1 site) Rivers; (A) Young of year, (B) Second year, (C) Third year.

year nymphs did the best as far as gut fullness on the January, 1991 date than did the other year classes.

A. lycorias nymphs found in both streams were carnivorous as predicted by earlier studies of Acroneuria in the literature. Insect larvae found in the guts include Ephemeroptera (Heptageniidae, Baetidae, Ephemerellidae), Simuliidae, Chironomidae, Tricoptera (Hydropsychidae, Philopotamidae), Plecoptera (Perlidae, Leuctridae, Perlodidae), Odonata (Gomphidae) and Coleoptera (Elmidae) (Table 9). Organisms of most year classes on all sampling dates had detritus or unidentified organic matter in their foreguts. Ephemeropterans and Plecopterans were found in foreguts consistently from August to January. Chironomidae and Tricoptera were important diet components on the August and January sampling dates, while Simuliidae was found in foreguts of organisms from both streams in October. Rare items such as Gomphidae and Elmidae, as well as the seasonal pattern in food items, indicate that A. lycorias is a opportunist and will eat whatever item is most available. Specific food preferences of A. lycorias were not analyzed in this project.

C. Production

1. Density and standing crop biomass

Mean densities of A. lycorias nymphs at FS1 ranged from 225 individuals/m² in July, 1988 to 26 nymphs/m² in December,

Table 9. Gut contents of A. lycorias nymphs of the Ford and Peshekee Rivers, 8/11/90, 10/16/90 and 1/19/91. YOY = Young of year.

Date	Year Class	Site	Detritus	Ephemeroptera	Simuliidae	Chironomidae	Trichoptera	Plecoptera	Gomphidae	Elmidae
8/11/90	YOY	Ford R. Peshekee R.	X X	X	X	X		X		
	2nd yr	Ford R. Peshekee R.		X X		X X		X		
	3rd yr	Ford R. Peshekee R.	X X	X X	X	X	X	X	X	
10/16/90	YOY	Ford R. Peshekee R.	X X	X X						
	2nd yr	Ford R. Peshekee R.	X X	X X						
	3rd yr	Ford R. Peshekee R.	X X	X X						
1/19/91	YOY	Ford R. Peshekee R.	X X	X X		X		X		
	2nd yr	Ford R. Peshekee R.	X X	X X		X		X		
	3rd yr	Ford R. Peshekee R.	X X	X X				X		

1988 (Table 10, Figure 17). Densities for the PS1 site ranged from 125 nymphs/m² in July, 1988 to 4 organisms/m² in March, 1989. Mean density for the FS1 site over the two year period was 100 individuals/m² compared to 40 organisms/m² at PS1, or 2.5 times more abundant in the hard water stream. Mean dry weight biomass varied between 2.66 g/m² and 0.38 g/m² at FS1, and between 0.98 g/m² and 0.01 g/m² at PS1 during 1988, 1989 and 1990 (Table 11, Figure 17). Mean biomass over the two year period was 1.52 g/m² at FS1 compared to 0.31 g/m² at PS1. This represented a 4.9 fold difference between sites. Differences between sites for untransformed density and biomass data were compared using paired t-tests (Table 12). Yearly and two year comparisons between FS1 and PS1 for both parameters all were significant at $p < 0.05$ or less. Paired t-test comparisons between replicate sites for each stream indicate that no significant differences for density and standing crop biomass occurred (Table 13).

The general pattern of peak density and biomass during summer months was evident at both sites for the two year period (Figure 17). Numbers and dry weights dropped in the fall and spring months, with a secondary peak occurring during winter. In some cases the monthly sampling regime did not reflect true densities and standing crop biomass for that entire month. Sampling was always constrained by the limits of the Hess sampler. Therefore, a disturbance such as a

Table 10. Mean densities (no.ind./m²) $\pm$ S.E. of *A. lycorias* collected from the Ford (FS1) and Peshekee (PS1) Rivers from June, 1988 to June, 1990. N in parentheses.

Date	Density	
	Ford River (FS1)	Peshekee River (PS1)
7/88	225 $\pm$ 14 (6)	125 $\pm$ 10 (6)
8/88	74 $\pm$ 7 (6)	21 $\pm$ 2 (6)
9/88	----	11 $\pm$ 2 (6)
12/88	26 $\pm$ 3 (6)	21 $\pm$ 3 (6)
2/89	28 $\pm$ 5 (6)	23 $\pm$ 2 (6)
3/89	44 $\pm$ 8 (6)	4 $\pm$ 1 (6)
5/89	68 $\pm$ 7 (6)	----
6/89	45 $\pm$ 4 (6)	21 $\pm$ 3 (6)
Mean 88-89	74 $\pm$ 31 (6)	36 $\pm$ 18 (6)
7/89	167 $\pm$ 15 (6)	44 $\pm$ 5 (6)
8/89	183 $\pm$ 8 (6)	87 $\pm$ 7 (6)
9/89	130 $\pm$ 10 (6)	72 $\pm$ 5 (6)
10/89	100 $\pm$ 8 (6)	36 $\pm$ 4 (6)
12/89	114 $\pm$ 7 (6)	42 $\pm$ 12 (6)
1/90	144 $\pm$ 14 (6)	17 $\pm$ 2 (6)
3/90	70 $\pm$ 8 (6)	30 $\pm$ 5 (6)
4/90	83 $\pm$ 5 (6)	----
6/90	49 $\pm$ 4 (6)	13 $\pm$ 2 (6)
Mean 89-90	120 $\pm$ 19 (8)	42 $\pm$ 9 (8)
Mean 88-90	100 $\pm$ 17 (14)	40 $\pm$ 9 (14)

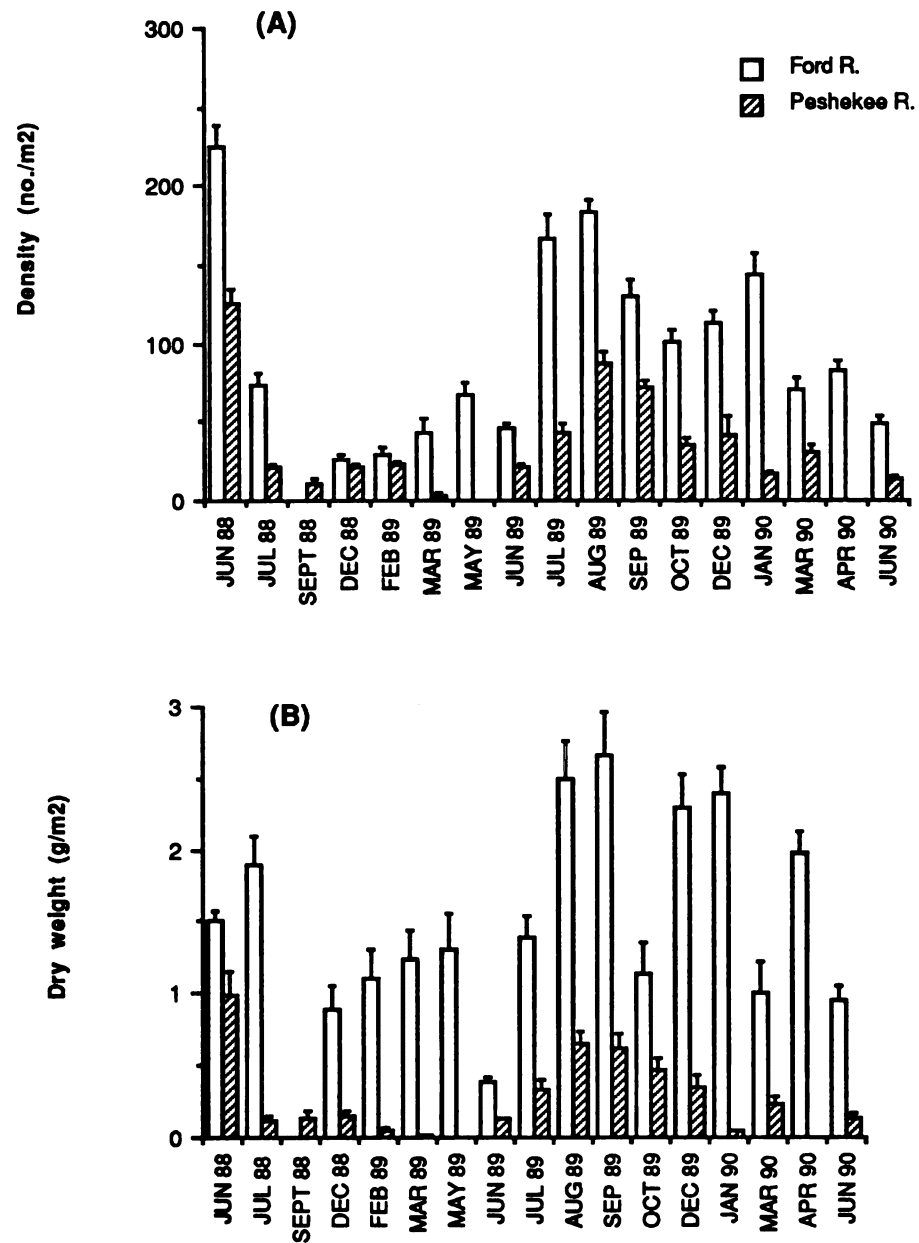


Figure 17. Densities (A) and dry weight biomass (B) $\pm$ S.E. of *A. lycoctas* collected from the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1988-1990.

Table 11. Mean biomass (g dry wt./m²) $\pm$ S.E. of *A. lycorias* collected from the Ford (FS1) and Peshekee (PS1) Rivers from June, 1988 to June, 1990. N in parentheses.

Date	Biomass	
	Ford River (FS1)	Peshekee River (PS1)
7/88	1.51 $\pm$ 0.06 (6)	0.98 $\pm$ 0.17 (6)
8/88	1.89 $\pm$ 0.22 (6)	0.12 $\pm$ 0.03 (6)
9/88	----	0.14 $\pm$ 0.04 (6)
12/88	0.89 $\pm$ 0.16 (6)	0.15 $\pm$ 0.04 (6)
2/89	1.10 $\pm$ 0.20 (6)	0.05 $\pm$ 0.01 (6)
3/89	1.24 $\pm$ 0.21 (6)	0.01 $\pm$ 0.00 (6)
5/89	1.30 $\pm$ 0.26 (6)	----
6/89	0.38 $\pm$ 0.04 (6)	0.13 $\pm$ 0.01 (6)
Mean 88-89	1.17 $\pm$ 0.21 (6)	0.24 $\pm$ 0.15 (6)
7/89	1.38 $\pm$ 0.15 (6)	0.34 $\pm$ 0.06 (6)
8/89	2.50 $\pm$ 0.27 (6)	0.65 $\pm$ 0.10 (6)
9/89	2.66 $\pm$ 0.27 (6)	0.63 $\pm$ 0.10 (6)
10/89	1.14 $\pm$ 0.31 (6)	0.47 $\pm$ 0.07 (6)
12/89	2.30 $\pm$ 0.22 (6)	0.35 $\pm$ 0.09 (6)
1/90	2.39 $\pm$ 0.22 (6)	0.05 $\pm$ 0.01 (6)
3/90	1.01 $\pm$ 0.20 (6)	0.24 $\pm$ 0.04 (6)
4/90	1.98 $\pm$ 0.21 (6)	----
6/90	0.96 $\pm$ 0.15 (6)	0.13 $\pm$ 0.04 (6)
Mean 89-90	1.79 $\pm$ 0.26 (8)	0.36 $\pm$ 0.08 (8)
Mean 88-90	1.52 $\pm$ 0.19 (14)	0.31 $\pm$ 0.08 (14)

Table 12. Results of paired t-tests between the Ford River (FS1) and Peshekee River (PS1) for *A. lycorias* density and biomass from June, 1988 to June, 1990.

Parameter	df	Paired t-value	Probability NS = $p > 0.05$
Density			
1988-1989	5	2.618	$p < 0.05$
1989-1990	7	6.211	$p < 0.001$
1988-1990	13	5.732	$p < 0.001$
Ecological density			
1989-1990	7	8.647	$p < 0.001$
Biomass			
1988-1989	5	4.218	$p < 0.01$
1989-1990	7	6.035	$p < 0.001$
1988-1990	13	7.005	$p < 0.001$
Ecological biomass			
1989-1990	7	4.663	$p < 0.005$

Table 13. Results of paired t-tests of *A. lycorias* densities and standing crop biomass at replicate sites within the Ford and Peshekee Rivers, July, 1989.

Parameter	Probability NS = $p > 0.05$	
	FS1 vs. FS2	PS1 vs. PS2
Density (no./m ²)	NS	NS
Ecological Density (no./m ² rock surf. area)	NS	NS
Standing Crop Biomass (g/m ²)	NS	NS
Ecological Biomass (g/m ² rock surf. area)	NS	NS

major discharge event would postpone sampling to a later date at which time populations could have differed from pre-flood conditions. Also, density and standing crop values obtained at certain points in the life history such as emergence and the hatching of nymphs were influenced by the sampling regime.

Ecological or effective habitat densities (number of individuals/rock surface area) and biomass standing crop values (biomass/rock surface area) (Resh, 1979) were calculated for each riffle due to possible differences in substrate types between the sites. Regressions between known rock surface areas and the product of long and short axis circumferences were calculated for PS1 ($y = 1.695 + 0.384x$, $r^2 = 0.99$; y = rock surface area, x = product of circumferences) and FS1 ($y = -2.195 + 0.394x$, $r^2 = 0.98$) to determine rock surface areas for each sample. Mean differences between sites over the two year period for ecological density and ecological biomass were similar (2.6 and 4.8-fold differences, respectively) to the density and biomass calculations based on stream bottom area (Tables 14 and 15). The pattern of ecological density and biomass at each site for the period from June, 1989 to March, 1990 paralleled the patterns observed earlier (Figure 18). Ecological density and biomass differed significantly, $p < 0.001$ and $p < 0.005$ respectively, between sites for the period between June, 1989 and March, 1990 (Table 12). No

Table 14. Mean ecological densities (no.ind./m² rock surface area) $\pm$ S.E. of *A. lycorias* collected from the Ford (FS1) and Peshekee (PS1) Rivers from June, 1988 to June, 1990. N in parentheses.

Date	Ecological Density	
	Ford River (FS1)	Peshekee River (PS1)
6/89	27 $\pm$ 1 (6)	7 $\pm$ 1 (6)
7/89	61 $\pm$ 6 (6)	19 $\pm$ 3 (6)
8/89	61 $\pm$ 3 (6)	31 $\pm$ 2 (6)
9/89	59 $\pm$ 3 (6)	28 $\pm$ 1 (6)
10/89	50 $\pm$ 5 (6)	27 $\pm$ 5 (6)
12/89	58 $\pm$ 2 (6)	13 $\pm$ 3 (6)
1/90	57 $\pm$ 6 (6)	18 $\pm$ 3 (6)
3/90	31 $\pm$ 3 (6)	13 $\pm$ 3 (6)
Mean 89-90	51 $\pm$ 5 (7)	20 $\pm$ 3 (7)



Table 15. Mean ecological biomass (g dry wt./m² rock surface area) $\pm$ S.E. of A. lycorias collected from the Ford (FS1) and Peshekee (PS1) Rivers from June, 1988 to June, 1990. N in parentheses.

Date	Ecological Biomass	
	Ford River (FS1)	Peshekee River (PS1)
6/89	0.25 $\pm$ 0.02 (6)	0.05 $\pm$ 0.01 (6)
7/89	0.53 $\pm$ 0.06 (6)	0.16 $\pm$ 0.03 (6)
8/89	0.85 $\pm$ 0.10 (6)	0.22 $\pm$ 0.03 (6)
9/89	1.10 $\pm$ 0.12 (6)	0.26 $\pm$ 0.04 (6)
10/89	0.47 $\pm$ 0.08 (6)	0.26 $\pm$ 0.04 (6)
12/89	1.20 $\pm$ 0.09 (6)	0.12 $\pm$ 0.03 (6)
1/90	0.98 $\pm$ 0.08 (6)	0.04 $\pm$ 0.01 (6)
3/90	0.40 $\pm$ 0.06 (6)	0.09 $\pm$ 0.02 (6)
Mean 89-90	0.72 $\pm$ 0.12 (7)	0.15 $\pm$ 0.03 (7)

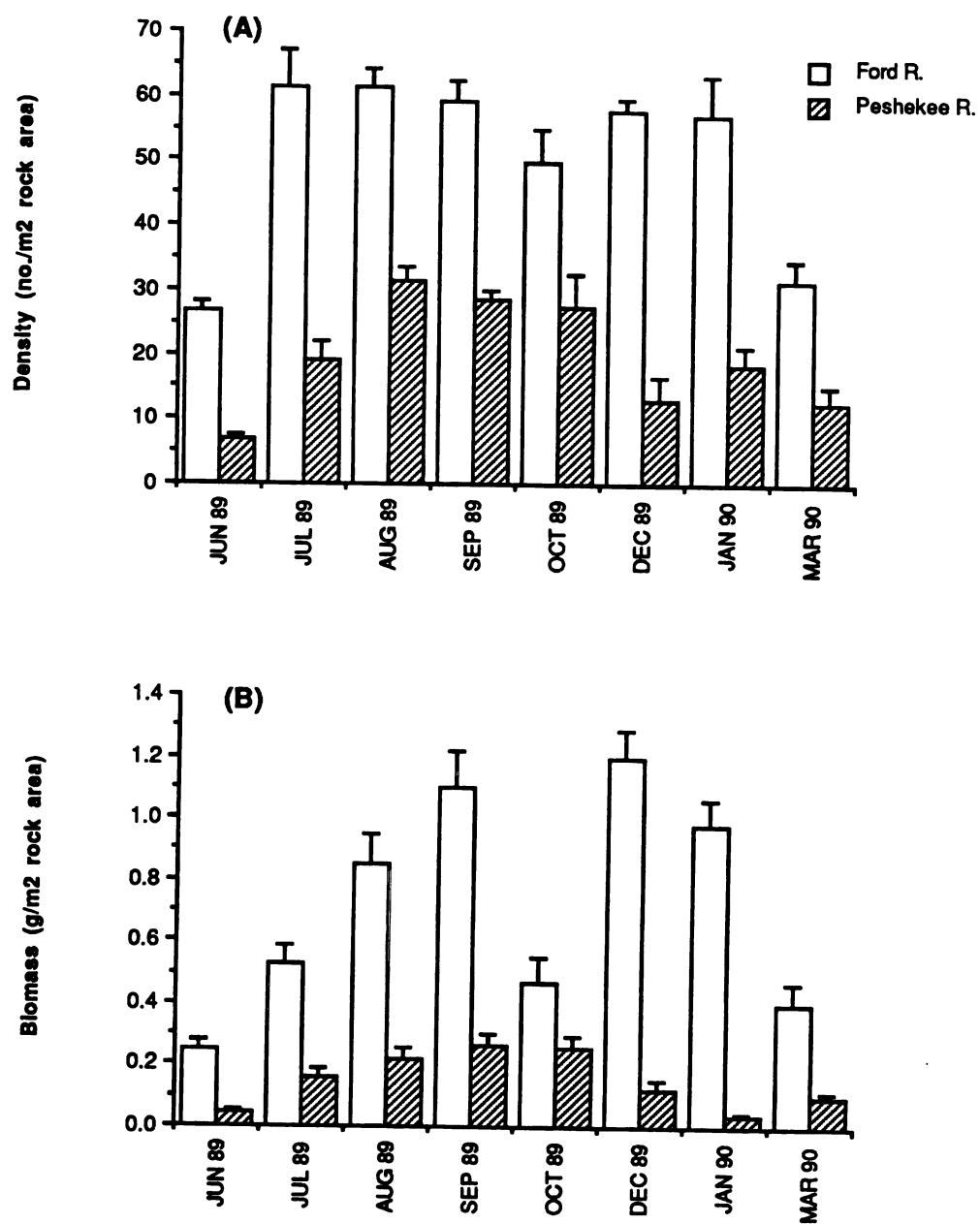


Figure 18. Ecological densities (A) and ecological biomass (B) $\pm$ S.E. of *A. lycorias* collected from the Ford (FS1 site) and Peshekee (PS1 site) Rivers, 1989-1990.

significant differences occurred between replicate sites for ecological density or biomass values (Table 13).

2. Annual production estimates

Mean annual production of A. lycorias corrected with a CPI factor of 0.333 at PS1 between 1988 and 1990 was 0.43 g dry weight m^{-2} (Table 16, Figure 19). For the same time period, mean annual production at FS1 was 2.18 g dry weight m^{-2} , or 5.0 times the amount calculated at PS1. Production estimates at PS1 were slightly higher from 1988-1989 than from 1989-1990. At FS1 production estimates for A.lycorias were greater from 1989-1990.

Annual production estimates were calculated from standing stock biomass and biomass turnover rates (Benke, 1984). Mean annual P/B ratios over the two year period were similar; 1.42 yr^{-1} for FS1 and 1.58 yr^{-1} for PS1 (Table 16). Differences in production estimates between sites, therefore, were the result of differences in standing crop biomass. Mean annual total biomass at FS1 was 1.54 g dry weight m^{-2} (Tables B-1 and B-2). At the soft water site, mean annual total biomass was 5.5 times less, averaging 0.28 g dry weight m^{-2} (Tables B-3 and B-4). The difference in biomass standing crop between sites accounted for the large difference in production estimates.

Table 16. Annual production of *A. lycorias* at FS1 and PS1 calculated using the size-frequency method for 1988-1989 and 1989-1990.

	Total Production (g/m ²)	Cohort P/B	Annual P/B (1/yr)	N
<u>Ford River (FS1)</u>				
1988-1989	1.73	4.37	1.45	7 dates
1989-1990	2.62	4.15	1.38	8 dates
Mean $\pm$ S.E.	2.18 $\pm$ 0.44	4.26 $\pm$ 0.11	1.42 $\pm$ 0.04	2 years
<u>Peshekee River (PS1)</u>				
1988-1989	0.41	5.47	1.82	7 dates
1989-1990	0.45	4.00	1.33	7 dates
Mean $\pm$ S.E.	0.43 $\pm$ 0.02	4.74 $\pm$ 0.74	1.58 $\pm$ 0.24	2 years

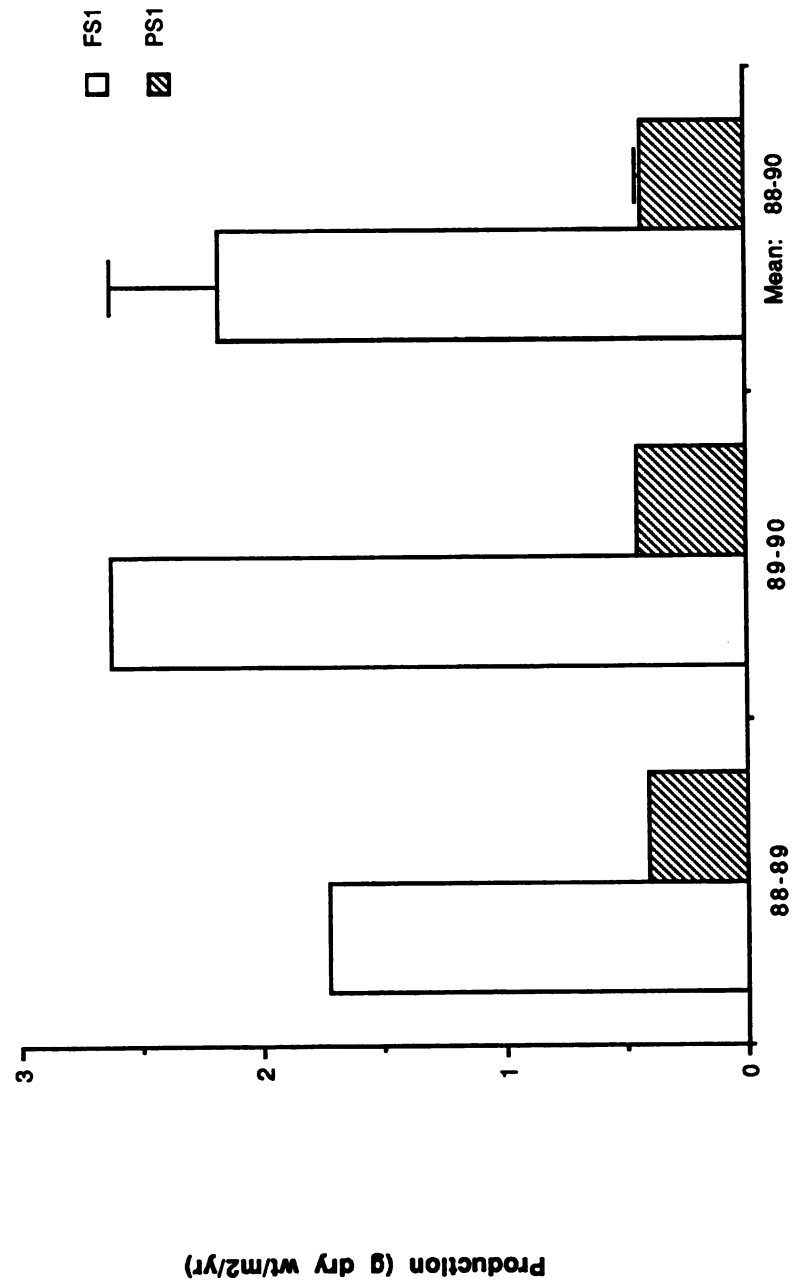


Figure 19. Annual production of *A. lyctorias* at the Ford River (FS1) and Peshekee River (PS1) from 1988-1990.

Further analysis of the production data yielded differences in annual density and biomass standing crop among the year classes. Nymphs were divided into age classes based on total length; young-of-year = 0-6 mm, second year = 7-12 mm, third year = 12-25 mm. Total annual density or biomass for each age class was calculated and plotted (Figure 20). The young-of-year class made up the largest proportion of total nymphs per square meter per year at each site, but contributed only a minor portion of the total biomass per square meter per year. The third year class made up a substantial portion of total annual biomass and production in each stream.

Growth Rates

1. Natural stream growth rates

Mean dry weights of each year class of A. lycorias collected on each sampling date between August, 1990 and January, 1991 were calculated from length/weight regressions (Figure 3). Standard errors associated with length measurements and the dry weights were less than 0.05 mg (Table 17). A plot of mean dry weights revealed two trends in the data (Figure 21). First, female nymphs of the second and third year classes weighed more than the male nymphs of their corresponding classes. This difference in weight between the sexes increased with age. Secondly, with the

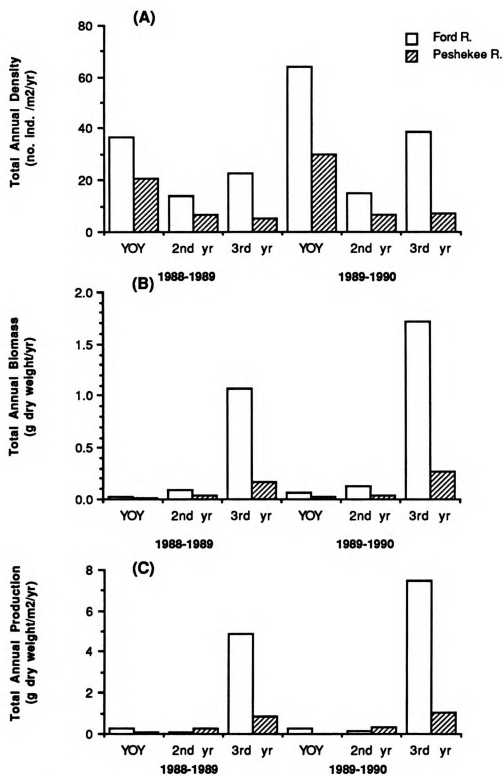


Figure 20. Total annual *A. lycorix* densities (A), dry weight biomass (B), and production (C) by year class for 1988-1989 and 1989-1990.

Table 17. Mean dry weight (mg) $\pm$ S.E. by Year Class of *A. lycockias* Collected at FS1 and PS1, 7/1990 - 1/1991. YOY = Young-of-year, 2 = Second year class, 3 = Third year class. M = Male, F = Female. N in parentheses.

Date	Site	YOY	2nd Year		3rd Year	
			M	F	M	F
7/6/90	FS1	---	4.0 $\pm$ 0.0 (52)	4.5 $\pm$ 0.0 (44)	21.4 $\pm$ 0.0 (7)	34.1 $\pm$ 0.0 (26)
	PS1	---	5.7 $\pm$ 0.0 (46)	6.7 $\pm$ 0.0 (41)	22.3 $\pm$ 0.0 (24)	44.1 $\pm$ 0.0 (52)
8/11/90	FS1	0.5 $\pm$ 0.0 (64)	6.0 $\pm$ 0.0 (64)	9.2 $\pm$ 0.0 (52)	25.8 $\pm$ 0.0 (22)	47.4 $\pm$ 0.0 (46)
	PS1	0.7 $\pm$ 0.0 (16)	6.2 $\pm$ 0.0 (41)	8.6 $\pm$ 0.0 (42)	26.0 $\pm$ 0.0 (24)	50.6 $\pm$ 0.0 (39)
09/5/90	FS1	0.8 $\pm$ 0.0 (45)	6.1 $\pm$ 0.0 (29)	9.6 $\pm$ 0.0 (41)	22.2 $\pm$ 0.0 (21)	43.3 $\pm$ 0.0 (27)
	PS1	1.6 $\pm$ 0.0 (52)	6.7 $\pm$ 0.0 (26)	10.7 $\pm$ 0.0 (43)	26.1 $\pm$ 0.0 (15)	45.1 $\pm$ 0.0 (27)
10/16/90	FS1	0.7 $\pm$ 0.0 (40)	6.5 $\pm$ 0.0 (24)	12.6 $\pm$ 0.0 (21)	25.4 $\pm$ 0.0 (18)	51.4 $\pm$ 0.0 (44)
	PS1	1.7 $\pm$ 0.0 (66)	7.0 $\pm$ 0.0 (26)	14.1 $\pm$ 0.0 (28)	29.5 $\pm$ 0.0 (14)	56.6 $\pm$ 0.0 (31)
1/19/91	FS1	1.4 $\pm$ 0.0 (78)	7.8 $\pm$ 0.0 (11)	13.2 $\pm$ 0.0 (14)	29.0 $\pm$ 0.0 (14)	63.4 $\pm$ 0.0 (18)
	PS1	1.3 $\pm$ 0.0 (78)	6.0 $\pm$ 0.0 (21)	11.0 $\pm$ 0.0 (38)	30.1 $\pm$ 0.0 (14)	54.6 $\pm$ 0.0 (17)

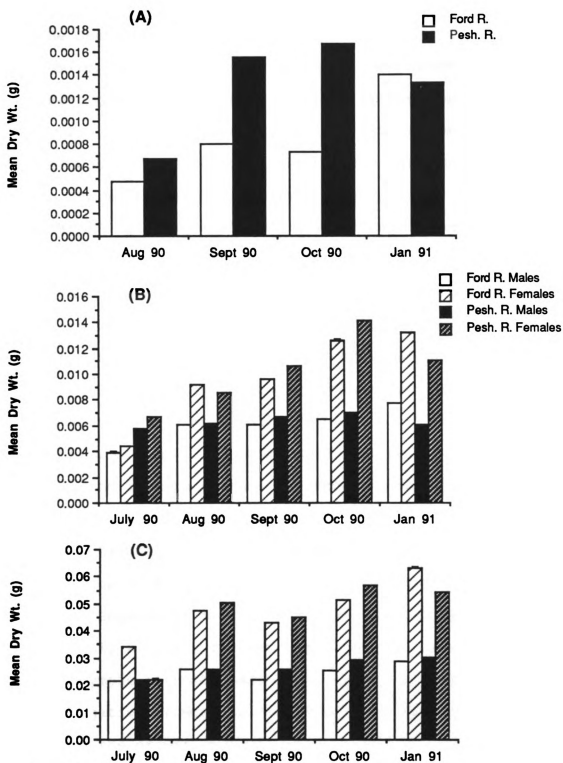


Figure 21. Mean dry weight $\pm$ S. E. by month of young-of-year (A), second year (B) and third year (C) *A. lycorides* nymphs collected from the Ford and Peshekee Rivers. 7/90-1/91.

exception of the January date, nymphs of all year classes from the Peshekee River were larger.

Monthly growth rates for young-of-year nymphs at both sites were greater than rates of older nymphs (Table 18, Figure 22). Young-of-year nymphs from PS1 grew at a faster rate throughout the fall than did their counterparts at FS1. Between the months of October and January, young-of-year nymphs at FS1 grew at a slightly faster rate. Some cases of negative growth rates occurred in the data set. Negative growth rates resulted for months where mean weights for a year class did not increase from the previous month. These negative rates are likely the result of sampling biases or the loss of larger, heavier individuals from the population between successive sample collections.

Growth patterns varied by month and by sex for older nymphs living in each stream. Second and third year female nymphs at FS1 at each site grew faster than male nymphs (Table 18, Figure 22). Growth rates of third year male and female nymphs dropped drastically at both sites between August and September, but rates for second year nymphs differed only slightly between sites for the same time period. Nymphs of both sexes from the PS1 site exhibited zero or negative growth for the October to January period, similar to the growth pattern of young-of-year nymphs described above.

Table 18. Monthly growth rates (day^{-1}) $\pm$ S.E. by year class of *A. lyctorias* collected at FS1 and PS1, 7/1990 - 1/1991. YOY = Young-of-year, 2 = Second year class, 3 = Third year class, M = Male, F = Female.

Date	Site	YOY	2nd Year		3rd Year	
			M	F	M	F
8/11/90	FS1	---	.0117 $\pm$ 1.8 E-5	.0200 $\pm$ 1.3 E-5	.0052 $\pm$ 2.0 E-6	.0092 $\pm$ 1.1 E-5
	PS1	---	.0020 $\pm$ 1.2 E-5	.0072 $\pm$ 6.0 E-6	.0045 $\pm$ 5.0 E-6	.0040 $\pm$ 2.3 E-5
9/5/90	FS1	.0203 $\pm$ 2.0 E-6	.0003 $\pm$ 1.0 E-5	.0018 $\pm$ 2.0 E-5	-.0061 $\pm$ 3.0 E-6	-.0037 $\pm$ 5.0 E-6
	PS1	.0338 $\pm$ 2.0 E-6	.0037 $\pm$ 1.0 E-5	.0088 $\pm$ 8.0 E-6	.0002 $\pm$ 4.0 E-6	-.0046 $\pm$ 2.0 E-5
10/16/90	FS1	-.0021 $\pm$ 0.0	.0016 $\pm$ 2.0 E-6	.0067 $\pm$ 9.0 E-6	.0034 $\pm$ 2.0 E-6	.0042 $\pm$ 6.0 E-6
	PS1	.0016 $\pm$ 1.0 E-6	.0008 $\pm$ 1.0 E-6	.0068 $\pm$ 6.0 E-6	.0030 $\pm$ 3.0 E-6	.0055 $\pm$ 4.0 E-6
1/19/91	FS1	-.0069 $\pm$ 1.0 E-6	.0019 $\pm$ 1.0 E-6	.0004 $\pm$ 4.0 E-6	.0014 $\pm$ 1.0 E-6	.0022 $\pm$ 6.0 E-6
	PS1	-.0023 $\pm$ 1.0 E-6	-.0015 $\pm$ 1.0 E-6	-.0026 $\pm$ 4.0 E-6	.0002 $\pm$ 4.0 E-6	-.0004 $\pm$ 2.0 E-6

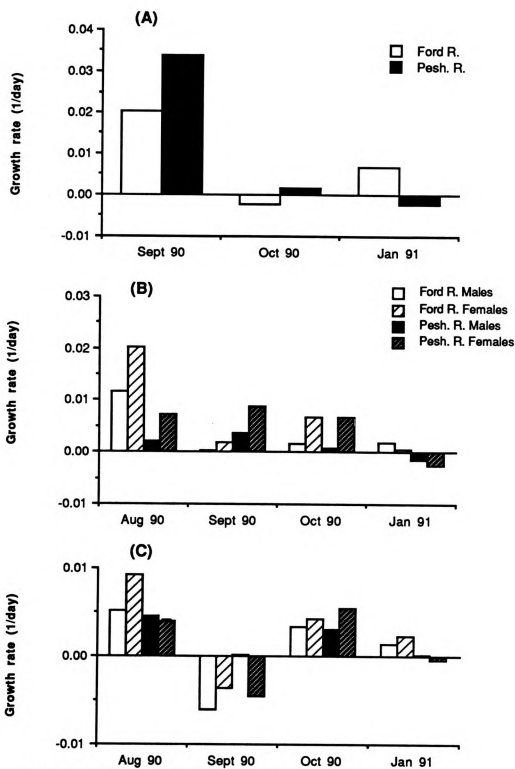


Figure 22. Monthly growth rates $\pm$ S.E. of young-of-year (A), second year (B), and third year (C) classes of *A. lycoctis* collected from the Ford and Peshekee Rivers, 8/90-1/91.

Statistical analyses of monthly growth rates were not possible, since rates were calculated from monthly mean weights rather than individual weights. Although growth patterns of nymphs differed between sites from one month to the next, the difference in magnitude of growth rates between sites for the entire sampling period was not greater than expected.

2. Laboratory stream growth experiment

The pH, conductivity, alkalinity, and hardness of the streamwater of the soft water and hard water treatments reflected typical water chemistry of the natural streams during low flow conditions (Table 19). The six-fold difference in hardness between the two streams provided a good contrast in water chemistries to test the hypothesis of increased growth rates with increased water hardness. Mean dissolved oxygen concentrations maintained in each stream were high (9.2 mg/L). Even though the temperature controls were set at 15° C for both streams, there was a slight difference in mean water temperature between streams. Water in the soft water treatment averaged 0.5° C warmer than in the hard water treatment. A min-max thermometer in each stream recorded temperatures between 12° C and 16° C. Since growth is affected by water temperature, growth rates could have been biased in favor of the organisms living in the soft water stream.

Table 19. Chemical and physical characteristics of hard and soft water treatments of *A. lycoctas* laboratory growth study conducted from June to October, 1990. Mean $\pm$ S.E.; range in parentheses.

Parameter	Water Source		t-test Significance
	Ford River	Peshekee River	
Temperature (°C)	14.0 $\pm$ 0.4 (12.0-16.0)	14.5 $\pm$ 0.4 (12.0-16.0)	NS
pH	8.4 $\pm$ 0.0 (8.3-8.4)	7.4 $\pm$ 0.1 (7.1-7.5)	p < 0.001
Conductivity * (μ mhos)	240 $\pm$ 14 (213-269)	37 $\pm$ 6 (23-50)	p < 0.001
Alkalinity (mg CaCO ₃ /L)	122 $\pm$ 9 (107-144)	14 $\pm$ 2 (10-20)	p < 0.001
Hardness (mg CaCO ₃ /L)	143 $\pm$ 8 (126-169)	24 $\pm$ 2 (19-30)	p < 0.001
Diss. Oxygen (mg O ₂ /L)	9.2 $\pm$ 0.4 (8.9-9.6)	9.2 $\pm$ 0.4 (8.8-9.5)	NS

* μ mhos corrected to 25° C.

Mortality rates for the duration of the experiment were lower than mortality rates experienced during previous attempts to rear A. lycorias nymphs in the laboratory. Three percent of the Ford River nymphs died and 20% of the Peshekee River organisms were lost in the hard water treatment. Twenty-three percent of organisms from both streams died or escaped in the soft water treatment. Nymphs lost during the experiment were not replaced with new organisms.

Individual growth rates were measured under conditions of unlimited space and food in the laboratory environment. A log plot of mean weights of each group of organisms by treatment and sex at time zero, day 41 and day 110 demonstrates that growth approximated a straight line or constant rate over the experimental period (Figure 23). Therefore, individual laboratory growth rates over the 110 day period of A. lycorias nymphs may be described using the instantaneous growth equation.

Hartley's test for homogeneity of variances of mean growth rates was non-significant at the 0.05 level. Untransformed data were analyzed using $2 \times 2 \times 2$ unbalanced form of analysis of variance. Nymphs taken from both the Ford and Peshekee Rivers grew at a slightly faster rate in the high hardness water than in low hardness (Table 20, Figure 24). Organisms originally from the Peshekee River grew at a slightly faster rate than Ford River nymphs regardless of water hardness. Results from the analysis of

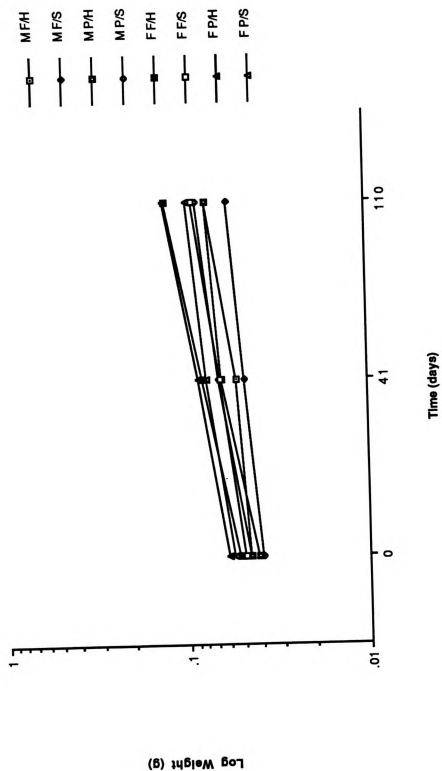


Figure 23. Mean log weights $\pm$ S.E. of individual nymphs by sex (M or F), strain (F or P), and treatment (H or S) at start, mid-point and conclusion of laboratory growth experiment.

Table 20. Mean A. lycorias laboratory growth rates (day^{-1}) for 110 day period $\pm$ S.E. in soft (20 mg CaCO_3/L) and hard (135 mg CaCO_3/L) water treatments. N in parentheses.

Water Hardness			
		20 mg CaCO_3/L	135 mg CaCO_3/L
Peshekee River			
Male		0.0061 $\pm$ 0.0006 (14)	0.0060 $\pm$ 0.0004 (14)
Female		0.0063 $\pm$ 0.0007 (15)	0.0070 $\pm$ 0.0007 (13)
Mean		0.0062 $\pm$ 0.0006 (29)	0.0064 $\pm$ 0.0004 (27)
Ford River			
Male		0.0058 $\pm$ 0.0006 (20)	0.0056 $\pm$ 0.0004 (20)
Female		0.0062 $\pm$ 0.0008 (9)	0.0073 $\pm$ 0.0008 (10)
Mean		0.0059 $\pm$ 0.0005 (29)	0.0061 $\pm$ 0.0004 (30)

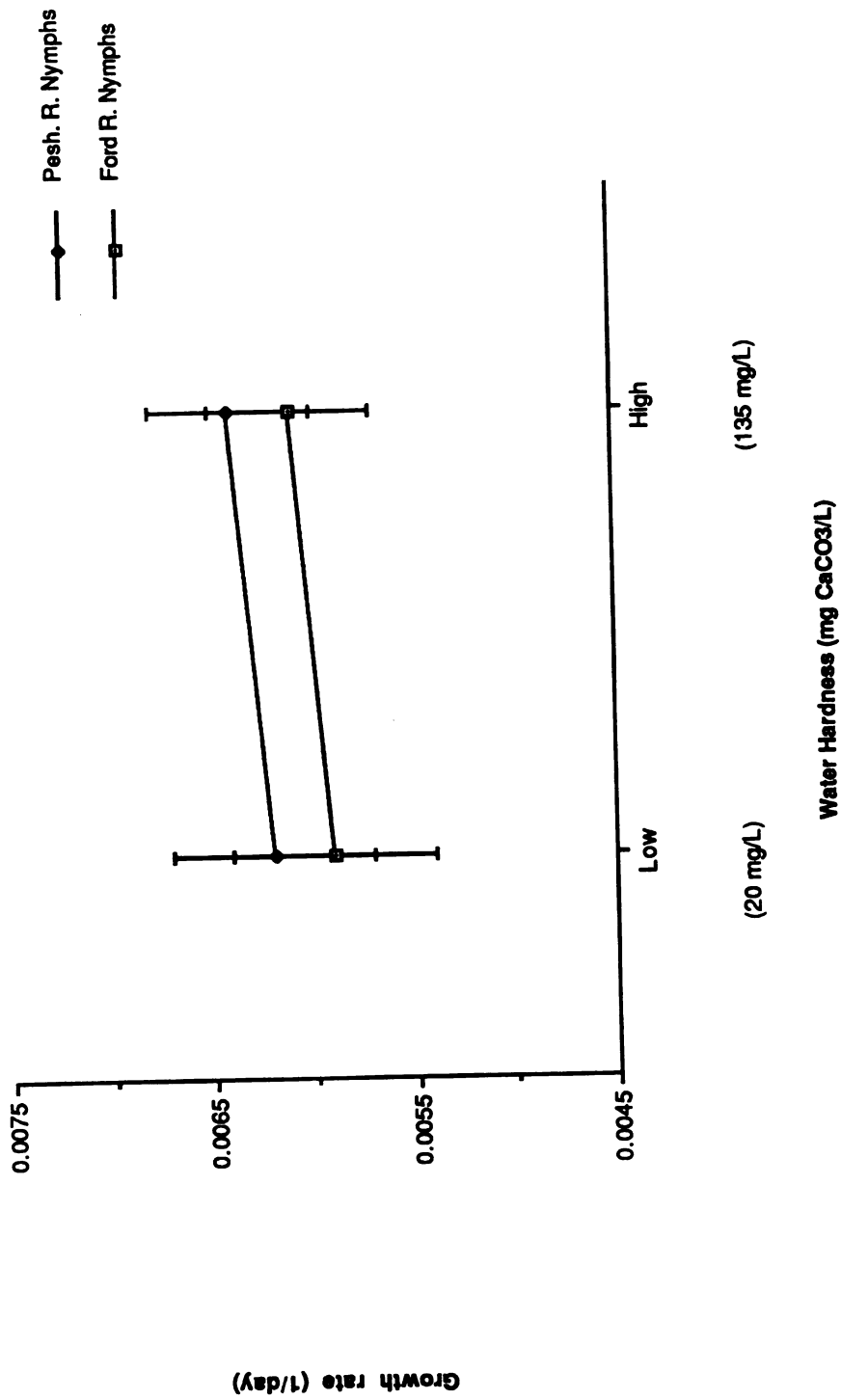


Figure 24. Mean growth rates of male and female A. lycorias nymphs reared in laboratory streams for 110 days.

variance calculated from growth data after 110 days indicate that no significant ($p < 0.05$) differences in growth existed in this experiment (Table 21). Probabilities of the three-factor and two-factor interactions were all highly non-significant. Of the strain, sex and treatment factors, only sex was relatively important in explaining the variance (Table 21). After separating growth data by sex of the nymphs, it became apparent that only the female nymphs grew faster in the hard water treatment (Table 20, Figure 25). Males of both strains grew at nearly equal rates in either treatment (Table 20, Figure 25). Female nymphs of both strains grew at faster rates than male nymphs.

Table 21. Results of three factor unbalanced analysis of variance on *A. lycoridis* growth in a laboratory stream experiment. ANOVA based on final growth measurements.

Source	df	SS	MS	F	Probability
Strain (A)	1	1.89 E-6	1.89 E-6	0.36	0.55
Sex (B)	1	1.81 E-5	1.81 E-5	3.42	0.07
AB	1	1.02 E-6	1.02 E-6	0.19	0.66
Treatment (C)	1	1.38 E-6	1.38 E-6	0.26	0.61
AC	1	1.41 E-6	1.41 E-6	0.27	0.61
BC	1	7.59 E-6	7.59 E-6	1.43	0.23
ABC	1	6.86 E-7	6.86 E-7	0.13	0.72
Error	104	5.52 E-4	5.31 E-6		

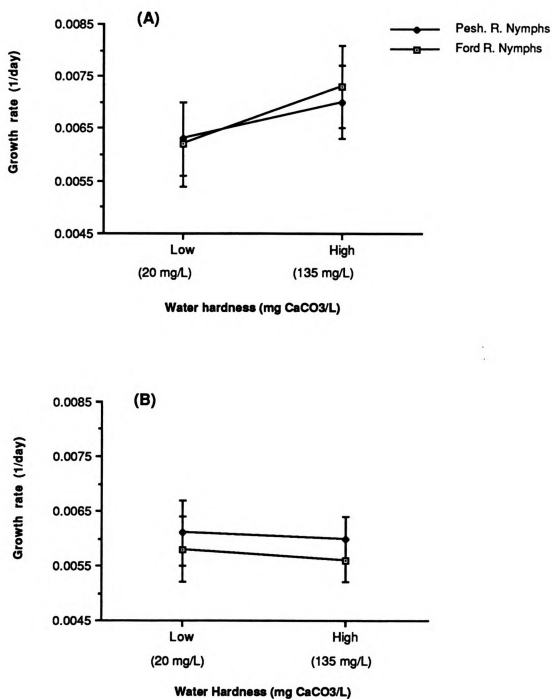


Figure 25. Mean growth rates of female (A) and male (B) *A. lycorias* nymphs reared in laboratory streams for 110 days.

DISCUSSION

The first objective of this study was to compare and contrast physical and chemical characteristics of stream water at the Ford and Peshekee River sites. Values obtained for conductivity, pH, total alkalinity, total hardness and cation concentrations varied significantly, as expected, between the two study sites. Water temperatures and dissolved oxygen concentrations, although not monitored on a continuous basis, varied only slightly between sites over the course of the study. Current velocities within each study riffle were similar at sample collection times. Discharge data, climatic data and personal observations of discharge response at each site provided some evidence that large snowpack runoff, topography and soil type contributed to a more variable, less stable flow regime at PS1. Future work at these two sites will require a closer examination of differences in flow regimes within each stream. Both streams were relatively nutrient-poor. Mean orthophosphorus and nitrate concentrations were similar between sites over the two year period. Burton et. al. (1991) reported higher orthophosphorus and nitrate concentrations along a continuum in the Peshekee River as compared to the Ford River. These data reflected nutrient levels during the month of August only. Data collected throughout the year from 1988 to 1990 in

the present study suggested that no mean differences existed with regard to nutrient availability. However, seasonal variability in nutrient concentrations between sites did occur and might have influenced primary productivity during certain seasons of the year.

Substrate composition was described at the FS1 and PS1 sites only. The substrate was predominately cobble at both sites which was one of the criteria examined when site selection took place. However, substrate composition at the sites may not necessarily reflect that of the entire stream channel. Although substrate composition along the stream continuum was not quantified, personal observations indicated that large areas of cobble substrate were common along fourth-order sections of the Peshekee River. In contrast, a greater portion of the Ford River consists of sand substrate, a poor habitat for most invertebrates. Other factors that would play an important role in invertebrate distribution and were not considered in this study include substrate stability, heterogeneity, texture and pore size (Minshall, 1984).

Riparian vegetation surveys suggested that immediate vegetation surrounding FS1 was dominated by deciduous species, while coniferous species were more common at PS1. Terrestrial vegetation, like substrate, varied along a continuum at each river. A complete riparian survey has not been conducted for either stream. Differences between the

Ford and Peshekee Rivers along this continuum would be expected to influence invertebrate densities downstream in the form of differential allochthonous inputs, shading and dissolved organic material concentrations.

Life history characteristics such as nymphal development length and emergence periods of A. lycorias living in each stream were similar to those reported in the literature for other Acroneuria species. The three-year life cycle reported by Peckarsky (1979) and Barton (1980) was consistent with data collected for A. lycorias in this study. This three-year cycle is one year longer than those found for Acroneuria species observed in California and West Virginia (Heiman and Knight, 1975; Schmidt and Tarter, 1985). Emergence was observed for A. lycorias during growth studies in the laboratory, but not at either field site. Narf and Hilsenhoff (1974) mentioned difficulties in collecting emerging A. lycorias nymphs in the field. It is assumed that the emergence period in the present study was extremely short, synchronous and occurred sometime between May and July, the months of final presence of mature nymphs and first appearance of young-of-year nymphs. The switch from a 1:1 sex ratio to a 2:1 ratio favoring mature female nymphs may be related to some unknown mortality factor following the second year. The deviation in sex ratios has not been reported in the literature before for A. lycorias nymphs and will require more research to fully explain the observed ratios.

The pattern of greater mean weights of female nymphs over male nymphs in both stream is not unusual. Sexual dimorphism in size has been documented in the literature (Pritchard, 1976; Sweeney, 1978; Vannote and Sweeney, 1980). In most cases, the extra weight achieved by female nymphs is associated with eggs in the abdomen (Butler, 1984), but data from the present study indicated that this sexual dimorphism in size appeared early in nymphal development. Butler (1982) offered one hypothesis based on studies with Chironomus that male nymphs stop feeding and growing much earlier than female nymphs do, but still continue with development. This hypothesis was not supported by foregut content data of A. lycorias of the Ford and Peshekee Rivers. All third-year nymphs, male and female, contained prey items of some sort during the month of January, only four months before emergence.

The fact that nymphs of all size classes collected from the soft water stream were slightly larger in size than hard water organisms is important in that positive correlations between size and fecundity has been reported in the literature (Sweeney and Vannote, 1981). Implications of the size/fecundity correlation to this study suggest that mature female nymphs of the Peshekee River could produce more eggs per adult nymph than those nymphs reproducing in the Ford River. In theory, potential recruitment per individual female nymph is greater in the Peshekee River. Overall

recruitment, however, is probably balanced by the fact that fewer mature nymphs exist within the Peshekee River population. Unfortunately, fecundity data is not available to support or refute this idea.

Food items found in the foreguts of A. lycorias collected from the Ford and Peshekee Rivers were very similar to diets reported for other species of Acroneuria collected within North America (Heiman and Knight, 1975; Shapas and Hilsenhoff, 1976; Johnson, 1981; Schmidt and Tarter, 1985). Additionally, the types of prey items taken by A. lycorias in each stream were similar for each of the size classes. Although prey availability and selectivity was not examined, seasonal trends in foregut contents indicated that the diets of A. lycorias nymphs, like the Acroneuria nymphs studied by Sheldon (1969) and Siegfried and Knight (1976a), were quite flexible. By having diets which can vary with changes in prey densities, A. lycorias nymphs were able to maintain mean gut fullnesses of at least 25%. The exception to this was observed in the month of January when young-of-year nymphs at both sites, the largest size class by numbers, were found to have empty to near empty foreguts.

One of the hypotheses for lower productivity in soft water rivers was described in the introduction as being food quantity or quality related. Two studies, one conducted in the Ford and Peshekee River watersheds and the other in New Zealand streams, suggested that this may indeed be a valid

hypothesis. Burton et. al. (1991) found that diatom densities and chlorophyll a standing crops were greater at sites along the Ford River than along the Peshekee River, suggesting that the algal food base is stronger during the month of August in the hard water stream. Data from separate unpublished studies by T. M. Burton and R. J. Stout at unrelated sites at the Ford and Peshekee Rivers in July, 1985 indicate that A. lycorias prey densities were similar at both sites (Table 22). Prey/predator ratios (prey items available to each size class of A. lycorias divided by the number of A. lycorias nymphs of each size class) were very different however, because of the low A. lycorias densities found in the soft water stream. In a set of New Zealand hard and soft water streams, Collier and Winterbourn (1990) concluded that higher grazing rates by Deleatidium reflected lower quality of epilithic food in the soft water streams. Clearly, the question regarding food quality or quantity differences between the Ford and Peshekee Rivers for the various trophic levels will require further research.

The second objective of this research was to estimate as accurately as possible, the annual production of A. lycorias nymphs in each study stream. At the start of the study, I predicted as an alternate hypothesis that annual A. lycorias production would be positively related to stream water hardness. Greater production should be found in the Ford River than in the Peshekee River. This prediction was true

Table 22. Mean prey and predator densities (no./sample[†]) $\pm$ S.E. and prey/predator ratios by size class of *A. lycorias* for the Ford¹ and Peshekee² Rivers, 7/15/1985. Prey items = Chironomidae, Heptageniidae, Hydropsychidae, and Simuliidae. Predator = *A. lycorias*. YOY = Young-of-year.

Year Class	Prey Items (no./sample)	<i>A. lycorias</i> (no./sample)	Prey/Predator Ratio
Ford River			
YOY	1173.6 $\pm$ 170.3	17.8 $\pm$ 2.1	65.9
2nd Year	1427.2 $\pm$ 155.7	1.2 $\pm$ 0.2	1189.3
3rd Year	1427.2 $\pm$ 155.7	0.8 $\pm$ 0.5	1784.0
Peshekee River			
YOY	916.0 $\pm$ 146.4	4.8 $\pm$ 1.4	190.8
2nd Year	1070.8 $\pm$ 153.3	3.0 $\pm$ 0.4	356.9
3rd Year	1072.8 $\pm$ 153.0	0.4 $\pm$ 0.2	2682.0

¹Ford River data collected at FEX by R. J. Stout, 1985.

²Peshekee River data collected at McCormick Tract Bridge by T. M. Burton, 1985.

[†]All samples consisted of 18x28x10 cm half-cylinder baskets filled with substrate which were allowed to be colonized for 28 days.

for the period between 1988 and 1990 at the Ford and Peshekee River sites. Mean annual production of A. lycorias was 5.6 times greater at the FS1 site than at the PS1 site. The difference in standing crop biomass between sites, rather than biomass turnover was the major factor responsible for the observed production estimates.

The difference in production levels of a stream invertebrate between the Ford and Peshekee Rivers is higher than those reported in several other studies of this kind. Krueger and Waters (1983) reported a 2.3 fold difference in annual production by invertebrate carnivores and a 4.4 fold difference in herbivore-detritivore production in a hard and soft water stream. They presented production values for an Acroneuria species found in the Blackhoof River (mean alkalinity = 83 mg CaCO_3/L) of 0.2 g/m² as wet mass. This value was less than dry weight production values obtained for the Peshekee River with a mean alkalinity of 14 mg CaCO_3/L . The Acroneuria species was not present in the other two Minnesota streams studied by Krueger and Waters, so correlations between stream water hardness and Acroneuria production could not be made. Annual production of Deleatidium larvae was 4.2 times greater in an alkaline stream than in an acid stream (Collier and Winterbourn, 1990). Results from their study also reflected higher standing crop biomass in the alkaline sites, with relatively constant P/B ratios across all sites. Populations of

Deleatidium at the least productive sites were characterized as having very few late larval instars, a pattern similar to that found for the A. lycorias population structure at the Ford and Peshekee River sites.

The study's third objective was to determine natural stream growth rates of A. lycorias nymphs in hard and soft water as well as growth rates under controlled conditions in the laboratory at high and low water hardnesses. Growth rates were expected to be lower for organisms living in the soft water stream and the low hardness laboratory stream, since low cation concentrations would require the nymphs to divert more energy towards osmoregulatory functions than towards growth (Fiance, 1978). Growth rates of nymphs collected from the hard and soft water sites between July, 1990 and January, 1991 were similar at each site for comparable age classes and sexes. Laboratory growth rates of A. lycorias nymphs reared at high and low water hardnesses with unlimited space and food were also not significantly different. While these results reflected the annual P/B ratios calculated from production estimates, they were not predicted by the osmoregulation hypothesis.

When laboratory growth rates of second-year nymphs were compared to field growth rate data for the same age class, a slight difference in rates was observed. Mean stream growth rates for the June to October period of 1990 were calculated by averaging available monthly growth rates data collected

from July, 1990 to October, 1990 (Table 18). Mean laboratory growth rates for female and male nymphs removed from the Ford River and reared in hard water laboratory streams were lower than those calculated from field data; 0.0061 day^{-1} in the laboratory, compared to 0.0070 day^{-1} in the field. Peshekee River organisms grew slightly better in the laboratory stream (0.0062 day^{-1}) than in the field (0.0050 day^{-1}). Since the laboratory stream water temperatures were maintained at a constant temperature unlike that in the field, it is not possible to determine whether differential intraspecific or interspecific competition for food or space exists for second year nymphs in each stream. A method for measuring growth rates for individual nymphs living in the streams would have to be developed before any conclusions regarding competition could be made with certainty. Other growth rate data for Acroneturia species in the literature are limited. Other published studies dealing with Acroneturia growth rates used methods that were not comparable to those used in this study (Heiman and Knight, 1975; Siegfried and Knight, 1978; Schmidt and Tarter, 1985). In a growth study of a pleurocerid snail conducted in six Alabama streams of different alkalinities, Huryn (1991) found that natural stream growth rates were not correlated with alkalinity.

Within the context of this study's hypotheses and results, possible factors regulating secondary production at the FS1 and PS1 sites can be examined (Figure 26). The first

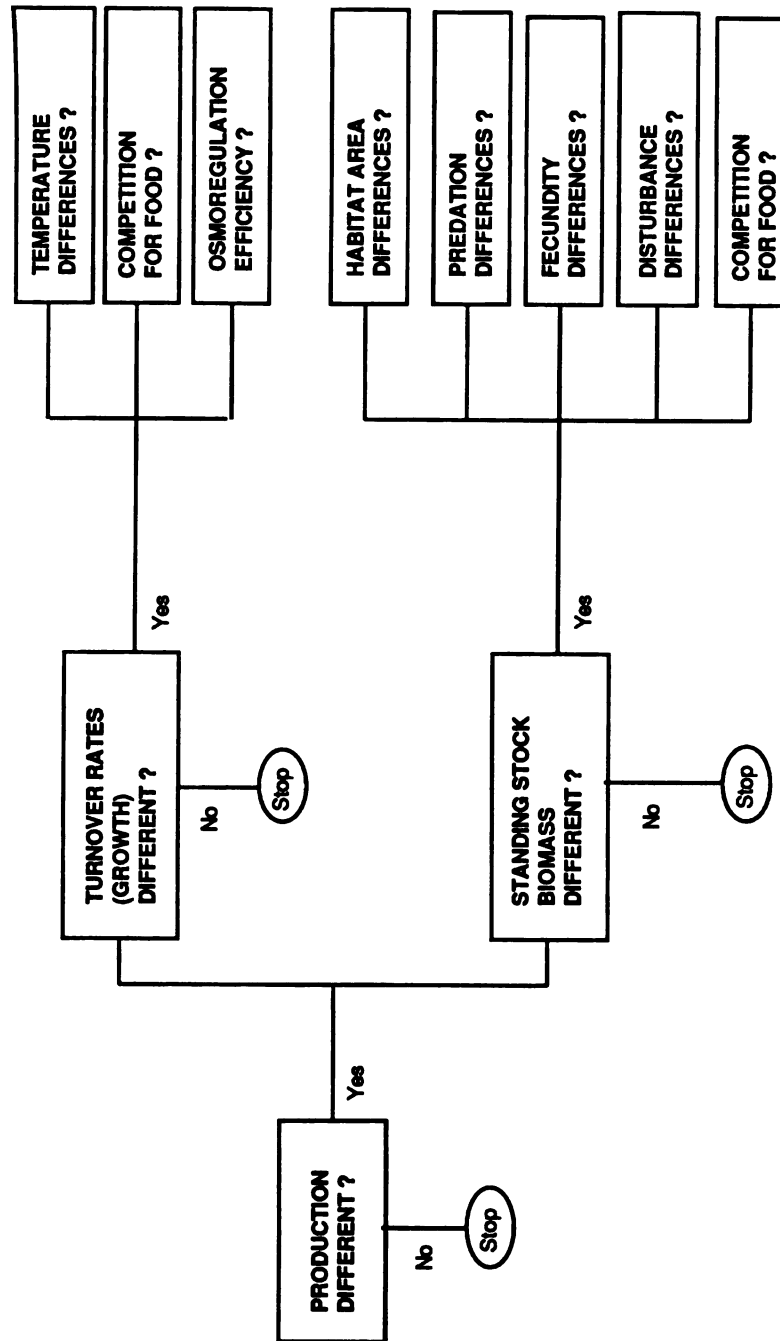


Figure 26. Flow diagram of factors influencing annual production of *A. lycorlas* nymphs in hard and soft water river systems.

question, asking whether production was really different between the two sites, was clearly answered. Production at FS1 was greater than that at PS1. By separating the production estimates into the components of standing stock biomass and turnover ratios, it was evident that differences in standing stock biomass between sites were greater than the differences in turnover ratios. This lack of inter-site difference in turnover ratios was substantiated by growth rate data collected in the field and in the laboratory. Therefore, factors such as stream water temperature differences, competition differences and osmoregulatory efficiencies are not strongly affecting growth rates.

The next logical step would be to determine what factors are influencing the standing stock biomass at each site (Figure 26). Several of these factors were given a cursory examination in the present study. The ratios of effective habitat area to bottom area were determined to be similar at each site. This determination was made for the riffle habitat at each site and may not be extended to the entire stream continuum. A greater predation risk for A. lycorias by other invertebrates and fish at the PS1 site is an alternate explanation. Fish predation was found to significantly reduce Paraquatina densities (Feltmate and Williams, 1991). An electrofishing survey conducted at each site in August, 1990 indicated that on the sampling date, fish predation would likely have a greater impact on A.

lycorias standing stocks at FS1 rather than PS1 (Table 23). This conclusion, based on fish density data collected on one sampling date is weak, but consistent with personal observations made over the entire study period. Fecundity of third-year nymphs in each stream, as discussed earlier, is a trade-off between nymphal size and total number of reproducing nymphs. Before this factor can be eliminated, fecundity data will have to be collected.

Differences between sites concerning disturbance and competition for food were not determined in this study. However, these two factors represent the most likely route towards answering the question of why the stream productivity/water hardness correlation exists. Seasonal disturbances will reduce abundances of Acroneuria species (Siegfried and Knight, 1977) and determine the distribution of stream invertebrates (Stout, 1981; Peckarsky, 1983; Reice, 1985; Statzner and Higler, 1986; Marmonier and Creuze' des Chatelliers, 1991). The quantity and quality of food has been proposed as the "single most important factor limiting animal abundance" (White, 1978). Algal standing crops and production have been shown to limit secondary production (Benke and Wallace, 1980; Lamberti and Resh, 1983; Huryn and Wallace, 1985). Densities of filter feeding invertebrates have been correlated with fine organic particulate matter (Wallace and Merritt, 1980; Wotton, 1987). Shredder populations were shown to be food limited (Richardson, 1991),

Table 23. Results of riffle and pool fish survey of FS1 and PS1 conducted during August 1990. Pool habitat sampled qualitatively only.

FS1	Density (no./m ²)	PS1	Density (no./m ²)
<u>Riffle</u>		<u>Riffle</u>	
Rhinichthys cataractae (Longnose dace)	0.66	Rhinichthys atratulus (Blacknose dace)	0.06
Cottus bairdi (Mottled sculpin)	0.18	Cottus bairdi (Mottled sculpin)	0.02
Rhinichthys atratulus (Blacknose dace)	0.12	Phoxinus neogaeus (Finescale dace)	0.01
Etheostoma flabellare (Fantail darter)	0.07	Micropterus dolomieu (Smallmouth bass)	0.004
Percina maculata (Blackside darter)	0.04		
Salvelinus fontinalis (Brook trout)	0.01		
Etheostoma nigrum (Johnny darter)	0.003		
Lota lota (Burbot)	0.003		
<u>Pool</u>		<u>Pool</u>	
Catostomus catostomus (White sucker)		Semotilus atromaculatus (Creek chub)	
Rhinichthys atratulus (Blacknose dace)		Cottus bairdi (Mottled sculpin)	
Rhinichthys cataractae (Longnose dace)		Micropterus salmoides (Largemouth bass)	
Semotilus atromaculatus (Creek chub)			
Lota lota (Burbot)			
Etheostoma nigrum (Johnny darter)			
Etheostoma flabellare (Fantail darter)			

and fish production has been limited by food resources (Cada et. al., 1987).

Disturbance and competition may also act together to limit production in streams. Peckarsky (1983) proposed the harsh-benign model to explain the role of biotic and abiotic factors in stream community structure. The model predicts the relative importance of abiotic factors, competition and predation on community structure over a gradient of environmental conditions ranging from harsh to benign. Initial research has shown that the model is a good predictor of predator impact on prey species (Peckarsky et. al., 1990). Recently, Hemphill (1991) demonstrated experimentally that seasonal disturbances, along with competition, played roles in regulating Hydropsyche and Simulium abundances in a California stream. Collier and Winterbourn (1990) reported lower production of Deleatium in acid streams compared to alkaline streams, and concluded that lower quality epilithic food in the acid stream was responsible for the lower production values. However, evidence presented in their paper of differential flow regimes and stream channel stability were not factored into their conclusions.

The final objective of this study was to narrow the scope of the problem for future research regarding the stream productivity/water hardness correlation. From data presented in this study, it is clear that the lower production estimates of A. lycorias at the soft water site are a result

of physical, biological or habitat constraints on standing crop biomass, rather than slower growth rates due to cation concentrations. These constraints, particularly disturbance and competition for food and habitat, will form the basis of future hypotheses developed to determine specific factors regulating secondary production in a hard and soft water stream.



SUMMARY

1. The life history, density, standing crop biomass, production and growth of a stonefly, Acroneuria lycorias were compared between fourth-order hard and soft water streams in Michigan's upper peninsula from 1988 to 1990.
2. Conductivity, pH, total alkalinity and total hardness, and Ca^{2+} Mg^{2+} , Na^{+} concentrations varied significantly between the hard water Ford River ($\sim 133 \text{ mg CaCO}_3/\text{L}$) and the soft water Peshekee River ($\sim 14 \text{ mg CaCO}_3/\text{L}$). Water temperature, dissolved oxygen, soluble reactive phosphorus and nitrate concentrations were similar at sites in each stream. Discharge was found to fluctuate more during spring and fall seasons in the soft water stream than in the hard water stream.
3. A. lycorias nymphs exhibited a three-year life cycle in each stream. Mean weights of female nymphs of second and third year cohorts were greater than male nymphs of the same age. Nymphs of all size classes at the soft water site were slightly larger than those at the hardwater site. Foregut contents of nymphs from both streams indicated that A. lycorias was a predator, and an opportunist type feeder.

4. Mean densities of nymphs were higher (100 ind./m²) at the hard water site than at the soft water site (40 ind./m²). Mean standing crop biomass for organisms at the hard water site over the two year period was 1.52 g dry weight m⁻² compared to 0.31 g dry weight m⁻² for nymphs at the soft water site.
5. Mean annual production of A. lycorias was 5.0 times greater at the hard water site (2.18 g dry weight m⁻²) between 1988 and 1990 than that at the soft water site (0.43 g dry weight m⁻²).
6. Growth rates of A. lycorias nymphs collected from the hard and soft water sites between July 1990 and January 1991 were similar at each site for comparable age classes and sexes.
7. Laboratory growth rates of A. lycorias nymphs reared at high and low water hardnesses with unlimited space and food were not significantly different.
8. Low A. lycorias production estimates at the soft water site were a result of physical, biological or habitat constraints on standing crop biomass, rather than slower growth rates due to low water hardness.

APPENDIX A

PHYSICAL AND CHEMICAL WATER DATA TABLES

Table A-1. Physical and chemical water quality of the Ford River (FS1 site), Michigan, 1988-1990.

Date	Air Temp. (°C)	Water Temp. (°C)	Conductivity (µmhos/cm)	Turbidity	Diss. Oxygen (mg/L)	Percent Saturation (%)	pH	T. Alkalinity (mg/L)	T. Hardness (mg/L)	SiO ₂ (mg/L)	Cl ⁻ (mg/L)
1988											
7/23	39.5	23.0	265	1.0	8.7	102	8.5	170	184	7.5	3.6
8/6	36.0	21.5	230	2.1	8.1	92	8.2	114	144	--	--
8/13	25.0	22.0	280	1.3	8.4	96	8.4	152	163	9.4	4.0
8/30	16.0	16.5	210	1.3	8.9	91	8.4	137	162	9.2	4.2
9/7	21.5	16.5	200	1.0	10.1	104	8.5	122	146	9.9	3.8
10/29	2.0	1.5	120	1.6	13.0	92	7.6	78	105	8.0	4.0
12/28	-9.0	1.0	214	0.9	12.3	86	7.6	132	150	9.9	4.1
1989											
2/11	-3.0	1.0	203	1.0	11.5	80	7.7	148	173	9.7	4.9
3/20	-1.5	0.5	199	0.6	13.2	91	7.9	138	178	9.1	4.4
5/6	1.5	3.5	120	0.7	12.6	95	8.2	86	120	4.0	3.8
6/22	23.5	18.0	165	1.5	8.4	89	8.2	106	128	5.8	3.0
7/6	19.5	23.0	250	1.1	7.8	90	8.5	145	162	6.8	3.0
7/23	26.5	20.5	230	1.2	9.1	101	8.4	160	176	6.4	3.0
8/5	36.0	24.5	260	1.3	8.4	101	8.5	158	175	7.8	4.5
8/19	31.0	16.5	298	1.4	10.0	103	8.3	163	180	7.5	4.3
9/2	22.5	16.0	298	1.4	9.5	97	8.4	145	165	8.4	9.1
10/28	18.5	11.0	256	1.2	10.8	98	8.4	141	163	8.0	12.3
12/10	-0.5	0.5	272	1.1	11.2	77	7.6	159	187	--	4.8
1990											
1/21	-0.1	0.5	291	1.7	12.7	87	7.9	156	185	10.3	4.3
3/3	-0.5	0.5	281	2.0	13.0	89	8.0	125	186	8.7	4.3
4/21	25.0	9.0	203	0.7	11.3	98	8.2	106	130	5.0	5.4
6/28	37.0	23.0	235	0.8	8.7	102	8.3	124	149	6.7	3.9
7/21	20.0	19.0	296	1.1	8.5	92	8.4	155	175	7.1	4.0
8/29	22.5	19.0	282	1.6	10.1	109	8.3	163	180	8.9	3.5
9/27	21.0	11.5	237	1.0	10.6	98	8.2	137	159	8.0	4.6

Table A-2. Physical and chemical water quality of the Peshokee River (PSI site), Michigan, 1988-1990.

Date	Air Temp. (°C)	Water Temp. (°C)	Conductivity (µhos/cm)	Turbidity	Diss. Oxygen (mg/L)	Percent Satura. (%)	pH	T. Alkalinity (mg/L)	T. Hardness (mg/L)	SiO ₂ (mg/L)	Cl ⁻ (mg/L)
1988											
7/30	25.0	20.5	63	0.7	7.5	83	7.2	32	38	4.6	0.6
8/5	26.5	21.5	54	1.2	7.5	85	6.9	16	32	5.2	0.6
8/21	21.5	18.5	32	0.8	7.9	85	6.8	10	25	4.8	1.0
9/3	17.0	16.5	34	1.0	8.4	86	7.1	17	28	6.3	0.4
10/29	1.0	1.0	18	0.5	12.6	88	6.4	6	20	4.8	0.7
12/29	-7.0	1.5	27	0.8	12.0	85	6.6	12	21	7.2	0.4
1989											
2/12	-3.0	1.0	28	0.5	11.9	83	7.4	14	29	7.7	0.4
3/21	-4.0	1.0	26	0.6	11.9	83	6.8	16	31	8.0	0.4
5/6	2.0	3.0	11	0.6	11.7	87	7.2	14	13	2.9	0.3
6/22	32.5	21.0	30	1.2	7.9	89	7.2	14	21	2.6	0.5
7/6	38.0	23.5	34	1.4	7.2	87	7.2	19	29	4.2	0.5
7/23	30.0	24.5	46	0.8	7.3	92	7.6	22	30	4.2	0.7
8/4	32.0	25.5	48	1.0	7.3	89	7.6	20	30	4.1	0.7
8/18	33.0	19.0	38	0.6	8.5	92	7.4	14	27	3.8	0.7
9/1	25.5	17.0	41	0.8	--	--	7.6	19	31	4.1	0.6
10/28	15.5	9.0	36	2.1	10.0	87	7.1	12	26	2.2	0.8
12/10	-0.5	0.5	33	0.7	11.2	77	6.7	12	27	6.4	0.6
1990											
1/21	-0.5	0.5	37	0.6	12.3	84	6.7	15	33	7.3	0.2
3/4	-0.5	0.5	43	0.9	--	--	6.9	18	37	8.7	0.2
4/21	16.5	5.0	21	0.7	11.0	86	6.8	5	16	--	0.2
6/28	35.0	22.0	31	0.8	7.5	86	7.2	13	22	2.7	0.4
7/21	24.0	21.0	35	1.0	8.1	91	7.0	14	30	4.4	0.4
8/24	27.0	21.0	49	1.3	8.2	92	7.3	24	32	6.0	0.3
9/26	23.0	13.0	32	0.8	9.2	88	6.7	11	24	4.8	0.6

Table A-3. Cation concentrations (mg/L) of the Ford and Peshekee Rivers from 1988 - 1990.

River	Date	Ca ⁺²	Mg ⁺²	Na ⁺	K ⁺
Ford	Oct. 88	20.0	10.0	5.0	2.0
	Feb. 89	67.0	8.0	4.0	1.0
	Mar. 89	23.0	8.0	5.0	1.0
	May 89	12.0	1.0	4.0	1.0
	June 89	19.0	1.0	3.0	1.0
	Aug. 89	29.0	3.0	5.0	1.0
	Jan. 90	14.0	5.0	5.0	1.0
	Mar. 90	14.0	3.0	5.0	1.0
	Apr. 90	19.1	7.6	6.2	0.4
	Jul. 90	15.3	11.2	5.0	0.4
	Aug. 90	13.6	13.6	5.8	0.4
	Sept 90	19.1	14.0	5.4	0.4
Peshekee	Oct. 88	10.0	1.0	1.0	1.0
	Feb. 89	10.0	1.7	2.0	1.0
	Mar. 89	5.0	1.0	2.0	1.0
	May 89	5.0	1.0	1.0	1.0
	June 89	5.0	3.0	1.0	1.0
	Aug. 89	5.0	9.0	5.0	1.0
	Jan. 90	5.0	1.5	2.0	0.3
	Mar. 90	5.0	1.6	2.0	0.4
	Apr. 90	3.8	1.8	1.5	0.4
	Jul. 90	3.8	1.8	1.9	0.4
	Aug. 90	3.8	1.8	2.7	0.4
	Sept 90	3.8	1.8	1.9	0.4

view of the Ford River (FSI site), Michigan, 1988-1990.

Table A-4. Nutrient water quality of the Ford River (FS1 site), Michigan, 1988-1990.

Date	Sol. Reactive Phosphorus (µg P/L)	Total Phosphorus (µg P/L)	Nitrate-N (µg N/L)	Nitrite-N (µg N/L)	Ammonium-N (µg N/L)	Total Nitrogen (µg N/L)
1988						
7/23	4.2	3.9	3.0	5.1	3.0	150
8/13	3.7	10.2	11.9	5.2	10.0	140
8/30	4.2	138.4	4.4	4.1	10.0	1110
9/7	6.5	180.2	6.4	4.1	9.0	640
10/29	7.3	286.8	51.2	4.3	30.0	270
12/28	4.2	46.9	90.4	4.5	30.0	390
1989						
2/11	3.6	22.3	175.2	3.8	69.0	520
3/20	8.3	15.8	187.2	3.8	64.0	570
5/6	5.8	27.1	25.5	4.5	66.0	870
6/22	5.8	41.4	32.2	4.8	57.0	880
7/6	6.0	26.6	22.5	5.5	68.0	660
7/23	3.0	-	38.2	3.8	67.0	760
8/5	4.7	15.5	3.5	3.5	66.0	700
8/19	4.3	9.1	20.2	2.8	61.0	960
9/2	3.1	22.0	6.2	3.8	61.0	900
10/28	3.1	38.5	3.9	3.1	69.0	1310
12/10	2.8	-	156.5	3.5	71.0	480
1990						
1/21	5.3	8.6	259.9	10.6	92.3	127
3/3	3.7	16.9	249.2	9.0	107.7	127
4/21	4.2	9.5	70.2	8.3	105.1	476
6/28	6.9	11.9	37.0	8.3	136.1	397
7/21	-	9.5	17.7	6.7	25.2	380
8/29	3.7	13.6	15.6	6.0	22.3	310
9/27	4.2	9.5	10.2	6.3	22.3	511

Table A-5. Nutrient water quality of the Peshekee River (PS1 site), Michigan, 1988-1990.

Date	Sol. Reactive Phosphorus ($\mu\text{g P/L}$)	Total Phosphorus ($\mu\text{g P/L}$)	Nitrate-N ($\mu\text{g N/L}$)	Nitrite-N ($\mu\text{g N/L}$)	Ammonium-N ($\mu\text{g N/L}$)	Total Nitrogen ($\mu\text{g N/L}$)
1988						
7/30	5.0	5.4	10.9	4.2	50.0	140
8/5	6.9	4.2	53.5	4.3	40.0	270
8/21	9.1	33.4	8.4	4.6	30.0	490
9/3	7.3	151.4	6.8	4.6	50.0	1040
10/29	11.3	50.4	31.4	4.7	40.0	470
12/29	5.8	284.8	77.9	3.9	30.0	310
1989						
2/12	4.6	-	133.2	3.8	48.0	830
3/21	4.7	20.7	178.2	3.8	51.0	720
5/6	6.3	37.7	19.9	4.2	59.0	390
6/22	6.5	30.1	19.2	4.8	52.0	860
7/6	6.4	25.2	43.2	4.8	45.0	920
7/23	4.5	31.7	5.8	4.2	53.0	790
8/4	6.3	-	7.5	4.5	45.0	660
8/18	6.7	15.8	0.0	5.8	56.0	590
9/1	5.6	28.0	7.8	4.2	56.0	980
10/28	3.8	19.9	79.8	5.2	49.0	850
12/10	3.7	20.4	101.5	4.5	59.0	630
1990						
1/21	4.6	8.6	178.5	8.7	94.8	1035
3/4	4.6	10.3	211.7	8.0	141.2	153
4/21	-	8.6	171.0	13.0	149.0	327
6/28	6.4	11.1	37.0	11.0	141.2	572
7/21	6.4	10.3	43.4	13.0	38.1	799
8/24	4.3	11.1	37.0	8.7	51.0	616
9/26	5.9	12.8	25.2	11.6	38.1	1043



APPENDIX B

ANNUAL PRODUCTION ESTIMATE DATA TABLES

Table B-1. Calculation of production of A. lycorias at the Ford (FS1) site River, 1988-1989.

Length (mm)	N (no./m ²)	W (g)	B (g/m ²)	No. loss/m ²	Wt at loss Ave W	Wt loss Ave WAN	X 25 (g/m ² /yr)
0 - 1	0.27	0.0000	0.0000				
1 - 2	0.54	0.0001	0.0001	-0.2714	0.0000	0.0000	-0.0003
2 - 3	5.67	0.0002	0.0014	-5.1286	0.0001	-0.0008	-0.0189
3 - 4	17.58	0.0006	0.0099	-11.9086	0.0004	-0.0047	-0.1169
4 - 5	9.21	0.0011	0.0096	8.3658	0.0008	0.0068	0.1710
5 - 6	3.26	0.0019	0.0058	5.9571	0.0015	0.0087	0.2186
6 - 7	4.06	0.0029	0.0124	-0.8000	0.0024	-0.0019	-0.0478
7 - 8	2.99	0.0043	0.0130	1.0714	0.0036	0.0039	0.0971
8 - 9	2.71	0.0061	0.0165	0.2715	0.0052	0.0014	0.0354
9 - 10	0.54	0.0083	0.0045	2.1714	0.0072	0.0156	0.3902
10 - 11	1.63	0.0109	0.0181	-1.0857	0.0096	-0.0104	-0.2606
11 - 12	2.17	0.0141	0.0304	-0.5429	0.0125	-0.0068	-0.1695
12 - 13	1.89	0.0177	0.0348	0.2857	0.0159	0.0045	0.1134
13 - 14	1.90	0.0219	0.0437	-0.0143	0.0198	-0.0003	-0.0071
14 - 15	3.53	0.0268	0.0972	-1.6285	0.0244	-0.0397	-0.9917
15 - 16	0.81	0.0323	0.0265	2.7143	0.0295	0.0801	2.0026
16 - 17	2.44	0.0384	0.0938	-1.6286	0.0353	-0.0575	-1.4384
17 - 18	2.71	0.0453	0.1223	-0.2714	0.0418	-0.0114	-0.2839
18 - 19	2.99	0.0529	0.1588	-0.2715	0.0491	-0.0133	-0.3331
19 - 20	1.90	0.0613	0.1153	1.0857	0.0571	0.0620	1.5493
20 - 21	1.36	0.0705	0.0959	0.5429	0.0659	0.0358	0.8942
21 - 22	1.63	0.0806	0.1349	-0.2715	0.0755	-0.0205	-0.5126
22 - 23	1.09	0.0915	0.1144	0.5429	0.0860	0.0467	1.1677
23 - 24	0.27	0.1034	0.0288	0.8143	0.0975	0.0794	1.9839
24 - 25	0.00	0.1162	0.0000	0.2714	0.1098	0.0298	0.7451
				1.1880			
							5.1880

Total Production = 5.1880 x 0.333 (CPI correction) = 1.728 g/m²/yr

Table B-2. Calculation of production of A. lycorias at the Ford (FS1 site) River, 1989-1990.

Length (mm)	N (no./m ²)	W (g)	B (g/m ²)	No. loss / m ²	Wt at loss Ave W	Wt loss Ave WAN	X 25 (g/m ² /yr)
0 - 1	0.00	0.0000	0.0000				
1 - 2	1.42	0.0001	0.0001	-1.4188	0.0000	-0.0001	-0.0013
2 - 3	14.30	0.0002	0.0036	-12.8812	0.0001	-0.0019	-0.0475
3 - 4	12.65	0.0006	0.0075	1.6500	0.0004	0.0006	0.0162
4 - 5	25.41	0.0011	0.0291	-12.7563	0.0008	-0.0104	-0.2607
5 - 6	10.19	0.0019	0.0183	15.2188	0.0015	0.0223	0.5583
6 - 7	3.21	0.0029	0.0096	6.9812	0.0024	0.0167	0.4171
7 - 8	2.61	0.0043	0.0113	0.5938	0.0036	0.0022	0.0538
8 - 9	1.31	0.0061	0.0081	1.3062	0.0052	0.0068	0.1701
9 - 10	1.78	0.0083	0.0155	-0.4750	0.0072	-0.0034	-0.0854
10 - 11	2.73	0.0109	0.0305	-0.9438	0.0096	-0.0091	-0.2265
11 - 12	3.44	0.0141	0.0489	-0.7187	0.0125	-0.0090	-0.2243
12 - 13	2.14	0.0177	0.0389	1.3063	0.0159	0.0207	0.5187
13 - 14	3.56	0.0219	0.0792	-1.4250	0.0198	-0.0283	-0.7064
14 - 15	5.11	0.0268	0.1378	-1.5438	0.0244	-0.0376	-0.9401
15 - 16	6.06	0.0323	0.1988	-0.9500	0.0295	-0.0280	-0.7009
16 - 17	4.63	0.0384	0.1796	1.4250	0.0353	0.0503	1.2585
17 - 18	5.69	0.0453	0.2560	-1.0625	0.0418	-0.0444	-1.1112
18 - 19	3.92	0.0529	0.2075	1.7750	0.0491	0.0871	2.1776
19 - 20	1.54	0.0613	0.0960	2.3750	0.0571	0.1356	3.3891
20 - 21	1.66	0.0705	0.1184	-0.1187	0.0659	-0.0078	-0.1955
21 - 22	2.49	0.0806	0.1972	-0.8313	0.0755	-0.0628	-1.5696
22 - 23	1.78	0.0915	0.1766	0.7125	0.0806	0.0574	1.4350
23 - 24	0.00	0.1034	0.0000	1.7813	0.1034	0.1842	4.6044
24 - 25	0.24	0.1162	0.0316	-0.2375	0.1098	-0.0261	-0.6520
			1.9000				7.8775

Total Production = 7.8775 x 0.333 (CPI correction) = 2.623 g/m²/yr

Table B-3. Calculation of production of A. lycorias at the Peshekee (PSI site) River, 1988-1989.

Length (mm)	N (no./m ²)	W (g)	B (g/m ²)	No. loss/m ²	Wt at loss Ave W	Wt loss Ave W ^N	X 25 (g/m ² /yr)
0 - 1	0.00	0.0000	0.0000				
1 - 2	1.63	0.0001	0.0001	-1.6285	0.0000	-0.0001	-0.0013
2 - 3	4.33	0.0002	0.0010	-2.7001	0.0001	-0.0003	-0.0083
3 - 4	8.91	0.0005	0.0041	-4.5857	0.0003	-0.0015	-0.0375
4 - 5	4.61	0.0009	0.0042	4.3001	0.0007	0.0030	0.0742
5 - 6	1.09	0.0016	0.0017	3.5286	0.0012	0.0044	0.1100
6 - 7	1.09	0.0025	0.0029	-0.0001	0.0020	0.0000	0.0000
7 - 8	1.09	0.0037	0.0038	0.0000	0.0031	0.0000	0.0000
8 - 9	1.36	0.0053	0.0070	-0.2714	0.0045	-0.0012	-0.0306
9 - 10	1.09	0.0072	0.0078	0.2715	0.0063	0.0017	0.0424
10 - 11	1.63	0.0096	0.0162	-0.5429	0.0084	-0.0046	-0.1138
11 - 12	0.27	0.0123	0.0031	1.3571	0.0110	0.0149	0.3716
12 - 13	1.36	0.0156	0.0209	-1.0857	0.0140	-0.0152	-0.3795
13 - 14	0.27	0.0194	0.0050	1.0857	0.0175	0.0190	0.4755
14 - 15	0.27	0.0238	0.0067	0.0000	0.0216	0.0000	0.0000
15 - 16	0.54	0.0287	0.0155	-0.2714	0.0262	-0.0071	-0.1780
16 - 17	1.09	0.0343	0.0386	-0.5429	0.0315	-0.0171	-0.4274
17 - 18	0.27	0.0405	0.0105	0.8143	0.0374	0.0304	0.7612
18 - 19	0.54	0.0474	0.0256	-0.2714	0.0440	-0.0119	-0.2983
19 - 20	0.54	0.0551	0.0298	0.0000	0.0513	0.0000	0.0000
20 - 21	0.00	0.0635	0.0000	0.5428	0.0593	0.0322	0.8047
21 - 22	0.27	0.0727	0.0203	-0.2714	0.0681	-0.0185	-0.4622
22 - 23	0.00	0.0828	0.0000	0.2714	0.0778	0.0211	0.5276
23 - 24	0.00	0.0937	0.0000	0.0000	0.0883	0.0000	0.0000
24 - 25	0.00	0.1055	0.0000	0.0000	0.0996	0.0000	0.0000
			0.2249				1.2302

Total Production = 1.2302×0.333 (CPI correction) = $0.410 \text{ g/m}^2/\text{yr}$

Table B-4. Calculation of production of A. lycorias at the Peshekee (PS1 site) River, 1989-1990.

Length (mm)	N (no./m ²)	W (g)	B (g/m ²)	No. loss/m ²	Wt at loss Ave W	Wt loss Ave WΔN	X 25 (g/m ² /yr)
0 - 1	0.54	0.0000	0.0000				
1 - 2	2.57	0.0001	0.0002	-2.0286	0.0000	-0.0001	-0.0016
2 - 3	3.12	0.0002	0.0007	-0.5499	0.0001	-0.0001	-0.0017
3 - 4	8.51	0.0005	0.0041	-5.3929	0.0003	-0.0018	-0.0442
4 - 5	7.98	0.0009	0.0070	0.5357	0.0007	0.0004	0.0092
5 - 6	7.31	0.0016	0.0118	0.6648	0.0012	0.0008	0.0207
6 - 7	0.81	0.0025	0.0020	6.4995	0.0020	0.0133	0.3319
7 - 8	1.90	0.0037	0.0073	-1.0857	0.0031	-0.0034	-0.0845
8 - 9	1.22	0.0053	0.0063	0.6785	0.0045	0.0031	0.0764
9 - 10	0.54	0.0072	0.0040	0.6786	0.0063	0.0042	0.1060
10 - 11	1.09	0.0096	0.0103	-0.5428	0.0084	-0.0046	-0.1138
11 - 12	0.95	0.0123	0.0118	0.1357	0.0110	0.0015	0.0372
12 - 13	0.95	0.0156	0.0149	0.0000	0.0140	0.0000	0.0000
13 - 14	1.22	0.0194	0.0246	-0.2715	0.0175	-0.0048	-0.1189
14 - 15	0.81	0.0238	0.0190	0.4072	0.0216	0.0088	0.2198
15 - 16	0.41	0.0287	0.0118	0.4071	0.0262	0.0107	0.2670
16 - 17	0.27	0.0343	0.0093	0.1357	0.0315	0.0043	0.1068
17 - 18	1.09	0.0405	0.0451	-0.8143	0.0374	-0.0304	-0.7612
18 - 19	0.81	0.0474	0.0399	0.2714	0.0440	0.0119	0.2983
19 - 20	0.68	0.0551	0.0364	0.1358	0.0513	0.0070	0.1740
20 - 21	0.00	0.0635	0.0000	0.6785	0.0593	0.0402	1.0059
21 - 22	0.41	0.0727	0.0292	-0.4071	0.0681	-0.0277	-0.6933
22 - 23	0.27	0.0828	0.0294	0.1357	0.0778	0.0106	0.2638
23 - 24	0.00	0.0937	0.0000	0.2714	0.0883	0.0240	0.5988
24 - 25	0.14	0.1055	0.0147	-0.1357	0.0996	-0.0135	-0.3380
			0.3396				1.3587

Total Production = 1.3587×0.333 (CPI correction) = $0.452 \text{ g/m}^2/\text{yr}$



LITERATURE CITED

LITERATURE CITED

- Allen, K. R. 1951. The Horokiwi Stream. A study of a trout population. New Zealand Marine Department Fisheries Bulletin 10:1-238.
- American Public Health Association. 1980. Standard methods for the examination of water and wastewater, 15th edition. American Public Health Association. Washington, D.C., 1134 pp.
- Armitage, K. B. 1958. Ecology of riffle insects of the Firehole River, Wyoming. Ecology 39:571-580.
- Arnold, D. E., P. M. Bender, A. B. Hale, and R. W. Light. 1981. Studies on infertile, acidic Pennsylvania streams and their benthic communities, pp. 15-33. In: R. Singer (ed.) Effects of Acidic Precipitation on Benthos, Proceedings of a Symposium, Colgate University, August 8-9, 1980. North American Benthological Society.
- Barton, D. R. 1980. Observations on the life histories and biology of Ephemeroptera and Plecoptera in northeastern Alberta. Aquatic Insects 2:97-111.
- Bell, A. L., and A. V. Nebeker. 1969. Preliminary studies on the tolerance of aquatic insects to low pH. Journal of the Kansas Entomological Society 42:230-236.
- Benke, A. C. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnology and Oceanography 24:168-171.
- Benke, A. C. 1984. Secondary production of aquatic insects, pp. 289-322. In: V. H. Resh and D. M. Rosenberg (eds.) The Ecology of Aquatic Insects. Praeger Scientific, New York.
- Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology 61:108-118.
- Berndt, L. W. 1988. Soil survey of Baraga County area, Michigan. United States Department of Agriculture, Soil Conservation Service. 306 pp.

- Brittain, J. E. 1983. The influence of temperature on nymphal growth rates in mountain stoneflies (Plecoptera). *Ecology* 64:440-446.
- Brower, J. E., and J. H. Zar. 1984. Field and laboratory methods for general ecology (2nd ed.). Brown Publishers, Dubuque, IA 226 pp.
- Brown, A. V., and K. B. Brown. 1984. Distribution of insects within riffles of streams. *Freshwater Invertebrate Biology* 3:2-11.
- Burton, T. M., M. P. Oemke, and J. M. Molloy. 1991. Effects of stream order and alkalinity on the composition of diatom communities in two northern Michigan river systems. (In Press).
- Butler, M. G. 1982. Morphological and phenological delimitation of *Chironomus prior* sp. n. and *C. tardus* sp. n. (Diptera: Chironomidae), sibling species from arctic Alaska. *Aquatic Insects* 4:219-235.
- Butler, M. G. 1984. Life histories of aquatic insects, pp. 24-55. In: V. H. Resh and D. M. Rosenberg (eds.) *The Ecology of Aquatic Insects*. Praeger Scientific, New York.
- Cada, G. F., J. M. Loar, and M. J. Sale. 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. *Transactions of the American Fisheries Society* 116:692-702.
- Claassen, P. W. 1931. *Plecoptera Nymphs of America* (North of Mexico). Thomas Say Foundation. Charles C. Thomas Publisher. Springfield, Illinois.
- Clements, W. H. 1987. The effect of rock surface area on distribution and abundance of stream insects. *Journal of Freshwater Biology*. 4:83-91.
- Collier, K. J., and M. J. Winterbourn. 1987. Faunal and chemical dynamics of some acid and alkaline New Zealand streams. *Freshwater Biology* 18:227-240.
- Collier, K. J., and M. J. Winterbourn. 1990. Population dynamics and feeding of mayfly larvae in some acid and alkaline New Zealand streams. *Freshwater Biology* 23:181-189.
- Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *American Midland Naturalist* 67:477-504.

- Cummins, K. W., and G. H. Lauff. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia* 34:145-181.
- Doonan, C. J., and J. R. Byerley. 1973. Ground water and geology of Baraga County, Michigan. Water Investigation 11. State of Michigan Department of Natural Resources-Geological Survey Division. Lansing, Michigan. 26 pp.
- Egglishaw, H. J. 1968. The quantitative relationship between bottom fauna and plant detritus in streams of different calcium concentrations. *Journal of Applied Ecology* 5:731-740.
- Ernst, M. R., and K. W. Stewart. 1985. Emergence patterns and an assessment of collecting methods for adult stoneflies (Plecoptera) in an Ozark foothills stream. *Canadian Journal of Zoology* 63:2962-2968.
- Feltmate, B. W., and D. D. Williams. 1991. Evaluation of predator-induced stress on field populations of stoneflies (Plecoptera). *Ecology* 72:1800-1806.
- Fiance, S. B. 1978. Effects of pH on the biology and distribution of Ephemerebella funeralis (Ephemeroptera). *Oikos* 31:332-339.
- Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* 43:421-439.
- Frison, T. H. 1935. The stoneflies, or Plecoptera, of Illinois. *Illinois Natural History Survey Bulletin* 20:281-471.
- Fuller, R. L., J. L. Roelofs, and T. J. Fry. 1986. The importance of algae to stream invertebrates. *Journal of North American Benthological Society* 5:290-296.
- Graesser, A. K. 1988. Invertebrate drift in three flood-prone streams in South Westland, New Zealand. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen* 23:1422-1426.
- Grenier, P. 1949. Contribution a l'etude biogique des Simuliides de France. *Physiologia comp. Oecol.* 1:165-330.
- Hamilton, A. L. 1969. On estimating annual production. *Limnology and Oceanography* 14:771-782.

- Harper, P., and J. C. Pilon, 1971. Annual patterns of emergence of some Quebec stoneflies. *Canadian Journal of Zoology* 48:681-694.
- Hauer, F. R., and A. C. Benke. 1987. Influence of temperature and river hydrograph on black fly growth rates in a subtropical blackwater river. *Journal of the North American Benthological Society* 6:251-261.
- Heiman D. R., and A. W. Knight. 1975. The influence of temperature on the bioenergetics of the carnivorous stonefly nymph, Acroneuria californica Banks (Plecoptera: Perlidae). *Ecology* 56:105-116.
- Hemphill, N. 1991. Disturbance and variation in competition between two stream insects. *Ecology* 72:864-872.
- Hendrickson, G. E., and C. J. Doonan. 1966. Ground-water resources of Dickinson County, Michigan. Water Investigation 5. State of Michigan Department of Conservation-Geological Survey Division. Lansing, Michigan. 49 pp.
- Hulbert, S. H. 1984. Psuedoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187-211.
- Huryn, A. D. 1991. Growth of pleurocerid snails in streams draining regions of contrasting geology. Paper presented at the 39th Annual Meeting of the North American Benthological Society, 20-24 May, 1991.
- Huryn, A. D., and J. B. Wallace. 1985. Life history and production of Goerita semata Ross (Tricoptera: Limnephilidae) in the southern Appalachian Mountains. *Canadian Journal of Zoology* 64:2604-2611.
- Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. *Archiv fur Hydrobiologia* 57:344-388.
- Hynes, H. B. N. 1970. *The Ecology of Running Waters*. University of Toronto Press, Canada.
- Hynes, H. B. N. 1976. Biology of Plecoptera. *Annual Review of Entomology* 21:135-153.
- Hynes, H. B. N., and M. J. Coleman. 1968. A simple method of assessing the annual production of stream benthos. *Limnology and Oceanography* 13:569-573.
- Illies, J. 1952. Die Molle. Faunistisch-okologische Untersuchungen an einem Forellenbach in Lipper Bergland. *Archiv fur Hydrobiologie* 46:424-612.

- Jewell, M. E. 1939. An ecological study of the fresh-water sponges of Wisconsin II. The influence of calcium. *Ecology* 20:11-28.
- Johnson, J. H. 1981. Food habits and dietary overlap of perlid stoneflies (Plecoptera) in a tributary of Lake Ontario. *Canadian Journal of Zoology* 59:2030-2037.
- Knight, A. W., and A. R. Gaufin. 1963. The effect of water flow, temperature, and oxygen concentration on the Plecoptera nymph, Acroneturia pacifica Banks. *Proceedings of the Utah Academy of Sciences* 40:175-184.
- Knight, A. W., and A. R. Gaufin. 1967. Stream type selection and associations of stoneflies (Plecoptera) in a Colorado River drainage system. *Journal of the Kansas Entomological Society* 40:347-352.
- Knight, A. W., and A. R. Gaufin. 1965. Function of stonefly gills under reduced dissolved oxygen concentration. *Proceedings of the Utah Academy of Sciences* 42:186-190.
- Knight, A. W., and A. R. Gaufin. 1966. Oxygen consumption of several species of stoneflies (Plecoptera). *Journal of Insect Physiology* 12:347-355.
- Kovalak, W. P. 1977. Relationship between size of stream insects and current velocity. *Canadian Journal of Zoology* 56:178-186.
- Kroger, R. L. 1974. Invertebrate drift in the Snake River, Wyoming. *Hydrobiologia* 44:369-380.
- Krueger, C. C., and T. F. Waters. 1983. Annual production of macroinvertebrates in three streams of different water quality. *Ecology* 64:840-850.
- Lamberti, G. A., and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. *Ecology* 64:1124-1135.
- Lay, J. A., and A. K. Ward. 1987. Algal community dynamics in two streams associated with different geological regions in the southeastern United States. *Archiv fur Hydrobiologie* 108:305-324.
- Lechleitner, R. A., D. S. Cherry, J. Cairns, Jr., and D. A. Stetler. 1985. Ionregulatory and toxicological responses of stonefly nymphs (Plecoptera) to acidic and alkaline pH. *Archives of Environmental Contamination and Toxicology* 14:179-185.

- Leverett, F. 1911. Surface geology of the northern peninsula of Michigan. Michigan Geological and Biological Survey. Publication 7. Geological Series 5. Wynkoop Hallenbeck Crawford Co., Lansing, Michigan. 91 pp.
- Lillehammer, A. 1986. The effect of temperature on the egg incubation period and nymphal growth of two Nemoura species (Plecoptera) from subarctic Fennoscandia. *Aquatic Insects* 8:223-235.
- Linsemier, L. H. 1989. Soil survey of Dickinson County, Michigan. United States Department of Agriculture, Soil Conservation Service. 177 pp.
- Lock, M. A., and H. B. N. Hynes. 1975. The disappearance of four leaf leachates in a hard and soft water stream in southwestern Ontario, Canada. *Internationale Revue gesamten Hydrobiologie* 60:847-855.
- Lush, D. L., and H. B. N. Hynes. 1973. The formation of particles in freshwater leachate of dead leaves. *Limnology and Oceanography* 18:968-977.
- Marmonier, P., and M. Creuze' des Chatelliers. 1991. Effects of spates on interstitial assemblages of the Rhone River. *Hydrobiologia* 210:243-251.
- McElhone, M. J., and R. W. Davies. 1983. The influence of rock surface area on the microdistribution and sampling of attached riffle dwelling tricoptera in Hartley Creek, Alberta. *Canadian Journal of Zoology* 61:2300-2304.
- Merna, J. W., and G. R. Alexander. 1983. Effects of snowmelt runoff on pH and alkalinity of trout streams in northern Michigan. Technical Report No. 83-2. Michigan Department of Natural Resources-Fisheries Division. 14 pp.
- Merritt, R. W., and K. W. Cummins, eds. 1984. An introduction to the aquatic insects of North America. Kendall/Hunt. Iowa. 722 pp.
- Minshall, G. W. 1984. Aquatic insect-substrate relationships, pp. 358-400. In: V. H. Resh and D. M. Rosenberg (eds.) *The Ecology of Aquatic Insects*. Praeger Scientific, New York.
- Mutch, R. A., and G. Pritchard. 1986. Development rates of eggs of some Canadian stoneflies (Plecoptera) in relation to temperature. *Journal of North American Benthological Society*. 5:272-277.

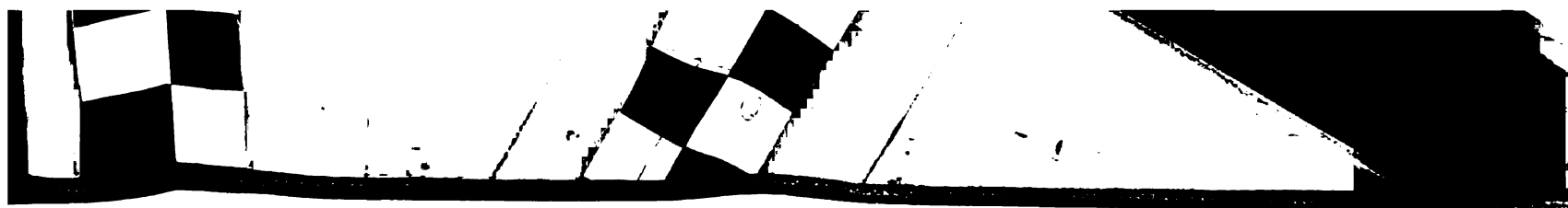
- Narf, R. P., and W. L. Hilsenhoff. 1974. Emergence patterns of stoneflies (Plecoptera) in Otter Creek, Wisconsin. *The Great Lakes Entomologist* 7:117-125.
- National Oceanic and Atmospheric Administration. 1988. Climatological data annual summary, Michigan. National Climatic Data Center, Asheville, North Carolina. Vol.103, No.13.
- National Oceanic and Atmospheric Administration. 1989. Climatological data annual summary, Michigan. National Climatic Data Center, Asheville, North Carolina. Vol.104, No.13.
- Orth, D. J., and O. E. Maughan. 1983. Microhabitat preferences of benthic fauna in a woodland stream. *Hydrobiologia* 106:157-168.
- Ott, L. 1988. An introduction to statistical methods and data analysis. 3rd edition. PWS-KENT Publishing, Boston, MA 835 pp.
- Peckarsky, B. L. 1979. A review of the distribution, ecology, and evolution of the North American species of Acroneturia and six related genera (Plecoptera: Perlidae). *Journal of the Kansas Entomological Society* 52:787-809.
- Peckarsky, B. L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. *Ecology* 61:932-943.
- Peckarsky, B. L. 1983. Biotic interactions or abiotic limitations? A model of lotic community structure, pp. 303-323. In: Fontaine III, T. D. and S. M. Bartell (eds.) *Dynamics of Lotic Ecosystems*. Ann Arbor Science Publishers, Ann Arbor, MI.
- Peckarsky, B. L., and S. I. Dodson. 1980. Do stonefly predators influence benthic distributions in streams? *Ecology* 61:1275-1282.
- Peckarsky, B. L., S. C. Horn, and B. Statzner. 1990. Stonefly predation along a hydraulic gradient: a field test of the harsh-benign hypothesis. *Freshwater Biology* 24:181-191.
- Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, B. Statzner, and I. R. Wais De Badgen. 1988. Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* 7:456-479.

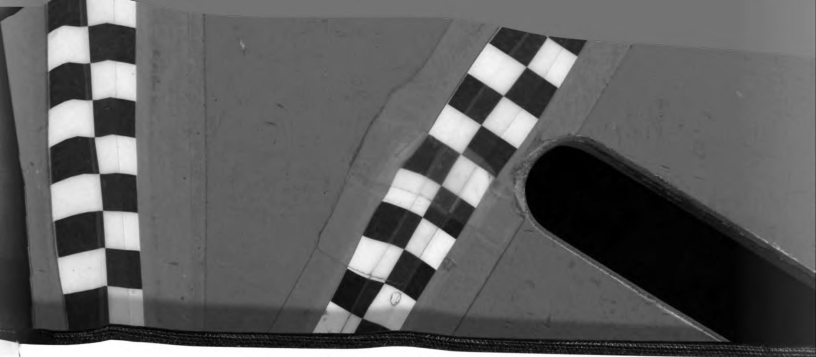
- Pritchard, G. 1976. Growth and development of larvae and adults of Tipula sacra Alexander (Insecta: Diptera) in a series of abandoned beaver ponds. Canadian Journal of Zoology 54:266-284.
- Pritchard, G. 1983. Biology of Tipulidae. Annual Review of Entomology 28:1-22.
- Reice, Seth R. 1983. Predation and substratum: factors in lotic community structure, pp. 325-345. In: Fontaine III, T. D. and S. M. Bartell (eds.) Dynamics of Lotic Ecosystems. Ann Arbor Science Publishers, Ann Arbor, MI.
- Reice, Seth R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. Oecologia 67:90-97.
- Resh, V. H. 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect studies. Journal of the Fisheries Research Board of Canada 36:290-311.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433-455.
- Richardson, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology 72:873-887.
- Richardson, J. W., and A. R. Gaufin. 1971. Food habits of some western stonefly nymphs. Transactions of the American Entomological Society 97:91-121.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin 191. Department of the Environment, Fisheries and Marine Service. Ottawa, Canada. 382 pp.
- Russell, I. C. 1907. The surface geology of portions of Menominee, Dickinson, and Iron Counties, Michigan. Report of the State Board of Geological Survey of Michigan for the year 1906. 601 pp.
- Schmidt, D. A., and D. C. Tarter. 1985. Life history and ecology of Acroneuria carolinensis (Banks) in Panther Creek, Nicholas County, West Virginia (Plecoptera: Perlidae). Psyche 92:393-406.

- Seaman, W. A. 1944. Geology of the Spruce River and Peshekee River areas-Baraga and Marquette Counties. Progress Report 11. State of Michigan Department of Conservation-Geological Survey Division. 12 pp.
- Shapas, T. J., and W. L. Hilsenhoff. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera, and Tricoptera. Great Lakes Entomologist 9:175-188.
- Sheldon, A. L. 1969. Size relationships of Acroneuria californica (Perlidae, Plecoptera) and its prey. Hydrobiologia 34:85-94.
- Siegfried, C. A., and A. W. Knight. 1976a. Trophic relations of Acroneuria (Calineuria) californica (Plecoptera: Perlidae) in a Sierra foothill stream. Environmental Entomology 5:575-581.
- Siegfried, C. A., and A. W. Knight. 1976b. Prey selection by a setipalpiian stonefly nymph, Acroneuria (Calineuria) californica Banks (Plecoptera: Perlidae). Ecology 57:603-608.
- Siegfried, C. A., and A. W. Knight. 1977. The effects of washout in a Sierra foothill stream. American Midland Naturalist 98:200-207.
- Siegfried, C. A., and A. W. Knight. 1978. Aspects of the life history and growth of Acroneuria (Calineuria) californica in a Sierra foothill stream. Annals of the Entomological Society of America 71:149-154.
- Snider, D. W. 1977. A ground investigation of an aeromagnetic anomaly, Dickinson County, Michigan. Report of Investigation 16. Michigan Department of Natural Resources-Geology Division. 18 pp.
- Soderstrom, O. 1988. Effects of temperature and food quality on life-history parameters in Parameletus chelifera and P. minor (Ephemeroptera): a laboratory study. Freshwater Biology 20:295-303.
- Stark, B. P., and A. R. Gaufin. 1976. The nearctic species of Acroneuria (Plecoptera: Perlidae). Journal of the Kansas Entomological Society 49:221-253.
- Statzner, B., J. A. Gore and V. H. Resh. 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of the North American Benthological Society 7:307-360.

- Statzner, B., and B. Higler. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology* 16:127-139.
- Stewart, K. W., and B. P. Stark. 1988. Nymphs of North American stonefly genera (Plecoptera). Vol. 12. Thomas Say Foundation, 460 pp.
- Stout, R. J. 1981. How abiotic factors affect the distribution of two species of tropical predaceous aquatic bugs (Family Naucoridae). *Ecology* 62:1170-1178.
- Suberkropp, K., and E. Chauvet. 1991. Effects of water chemistry on aquatic hyphomycetes growing on leaves. Paper presented at the 39th Annual Meeting of the North American Benthological Society, 20-24 May, 1991.
- Suberkropp, K., and M. J. Klug. 1976. Fungi and bacteria associated with leaves during processing in a woodland stream. *Ecology* 57: 707-719.
- Sutcliffe, D. W., and T. R. Carrick. 1973. Studies on mountain streams in the English Lake District. *Freshwater Biology* 3:437-462.
- Sweeney, B. W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. *Limnology and Oceanography* 23:461-477.
- Sweeney, B. W., and R. L. Vannote. 1981. Ephemerella mayflies of White Clay Creek: bioenergetic and ecological relationships among six coexisting species. *Ecology* 62:1353-1369.
- Sweeney, B. W., and R. L. Vannote. 1986. Growth and production of a stream stonefly: influences of diet and temperature. *Ecology* 67: 1396-1410.
- Sweeney, B. W., R. L. Vannote, and P. J. Dodds. 1986a. Effects of temperature and food quality on growth and development of a mayfly, Leptophlebia intermedia. *Canadian Journal of Fisheries and Aquatic Sciences* 43:12-18.
- Sweeney, B. W., R. L. Vannote, and P. J. Dodds. 1986b. The relative importance of temperature and diet to larval development and adult size of the winter stonefly, Soyedina carolinensis (Plecoptera: Nemouridae). *Freshwater Biology* 16:39-48.
- Tarzwel, C. M. 1938. Factors influencing fish food and fish production in southwestern streams. *Transactions of the American Fisheries Society* 67:246-255.

- U.S. Environmental Protection Agency. 1979. Methods for chemical analysis of water and wastes. EPA-600/4-79-020, Environmental Monitoring and Support Laboratory, U.S. Environmental Protection Agency. Cincinnati, OH.
- Vannote, R. L. and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist* 115:667-695.
- Wallace, J. B., and R. W. Merritt. 1980. Filter-feeding ecology of aquatic insects. *Annual Review of Entomology* 25:103-132.
- Walton, Jr., O. E., S. R. Reice and R. W. Andrews. 1977. The effects of density, sediment particle size and velocity on *Acroneuria abnormis* (Plecoptera). *Oikos* 28:291-298.
- Walton, Jr., O. E. 1978. Substrate attachment by drifting aquatic insect larvae. *Ecology* 59:1023-1030.
- White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. *Oecologia* 33:71-86.
- Wotton, R. S. 1987. Lake outlet blackflies-the dynamics of filter feeders at very high population densities. *Holarctic Ecology* 10:65-72.





MICHIGAN STATE UNIV. LIBRARIES



31293008826376