WHOI-Q-83-002

WHOI-84-29

Woods Hole
Oceanographic
Institution

The Matamek Research Program: Annual Report for 1983

by

Robert J. Naiman

July 1984

Technical Report

Funding was provided by:
Matamek and Education Programs of
the Woods Hole Oceanographic Insitution
NOAA, Office of Sea Grant, Grant NA 80-AA-D-00077
National Science Foundation, Grant DEB 81-05677
Tai Ping Foundation
National Scientific and Engineering Research Council, Canada
Atlantic Salmon Association
Department of Recreation, Fish and Game Province of Quebec
University of Waterloo, Waterloo, Ontario
Natural Environment Research Council, United Kingdom

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ANNUAL REPORT FOR 1983

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Robert J. Naiman

WOODS HOLE OCEANOGRAPHIC INSTITUTION
Woods Hole, Massachusetts 02543

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TECHNICAL REPORT

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Natural Environment Research Council, United Kingdom

Approved for Distribution: _____

John M. Teal, Chairman
Department of Biology

ABSTRACT

This report summarizes activities associated with the Institution's Matamek Research Station during 1983. Research was conducted on the biological, chemical and physical environment of streams and rivers, principally in the Moisie and Matamek River watersheds, on the effects of beaver in shaping the dynamics of aquatic ecosystems, on salmonid ecology, on decomposition dynamics, on invertebrate community dynamics, on sedimentary diatom responses to acid precipitation, and on microbial production. Canadian universities, American universities, the University College of North Wales, the Quebec government, and the Woods Hole Oceanographic Institution cooperated in this program.

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INTRODUCTION

The 1983 scientific program at the Matamek Research Station can best be characterized as a time of change. In October it was learned that the Director and Trustees of the Woods Hole Oceanographic Institution were seriously considering the future involvement of the Institution in the Matamek Research Program after fall 1985. Nevertheless, funding and support from the National Science Foundation, NOAA (Office of Sea Grant), the Tai-Ping Foundation, North Atlantic Treaty Organization, the National Scientific and Engineering Research Council of Canada, National Research Council (U.K.), the Atlantic Salmon Association, the Ministére du Loisir, de la Chasse, et de la Pêche du Québec, the Woods Hole Oceanographic Institution, the University of Waterloo, the University of North Carolina, and the University College of North Wales all combined to produce a program of broad scope and high quality that is described in the following report. As established in 1979, the present program continued to emphasize river ecosystem dynamics from a watershed perspective and salmonid ecology. With the addition of a new research laboratory provided by the Province of Québec, the quality of our programs were vastly improved. In 1983 the research group consisted of 29 persons, with 8-12 additional researchers utilizing the station for various periods. These personnel represent a diverse array of interests within our cohesive program, with the results amplified in the adjoining research summaries.

The integrated ecosystem analysis of streams and rivers included historical records of acidity through diatom analysis, invertebrate community organization and production, microbial production, decomposition dynamics of wood, leaves and macrophytes, nature and quantity of allochthonous inputs, the role of beaver in influencing the dynamics of aquatic ecosystems, monitoring rainwater chemistry, and the chemistry of stream water. These studies, in total, explore the trophic basis for salmonid production and are now being used to construct a conceptual model describing the environmental basis for fish production in boreal forest rivers. Several of these studies were extensions of projects mostly completed during the 1982 field season (e.g., leaf decomposition, allochthonous inputs). The watershed analysis is continuing in the other areas, however, especially on the role of beaver and forming a major portion of the present program.

The salmonid ecology program continued to monitor adult and juvenile life history characteristics. This provides continuity with studies conducted in previous years, with the complete data base being used to construct a general model of complex life history patterns. We continued to investigate the relative roles of size, age and photoperiod in determining the osmoregulatory ability of brook trout in both field and laboratory situations, as well as the influence of riparian vegetation on the ecology of brook trout fry. A new project, examining fish community production dynamics as a function of stream size, was begun and yielded favorable results.

Graduate student projects include a comparative life history study of Atlantic salmon in response to river harshness (jointly funded with the Atlantic Salmon Association), and insect production dynamics as a function of stream size. Student interns investigated the long-term changes in the demography of brook trout and the colonization of stream benthos after severe disturbance.

The Matamek Research Program offers a unique opportunity for North American researchers and students to join in a common scientific effort. The location of the Matamek Research Station in close proximity to a variety of pristine lakes and rivers, in conjunction with the endowed nature of the program, provides a unique opportunity for development of significant programs of long duration. The cooperation this Program has received from university scientists and the Quebec Ministry of Recreation, Fish and Game has been exceptional. We are most grateful for the continued support and assistance given us by the Quebec Government and our Canadian colleagues.

Robert J. Naiman
Scientific Director
Matamek Research Program

19 July 1984

MATAMEK PERSONNEL 1983

Administration
- Dr. Robert J. Naiman, Scientific Director
- Dr. John M. Teal, Department Chairman
- Mrs. Judith L. Kleindinst, Executive Assistant
- Ms. Eileen Klopfer, Data Management

Scientists
- Dr. Hamish Duthie, University of Waterloo
- Dr. Christiane Hudon, University of Waterloo
- Dr. Seth R. Reice, University of North Carolina
- Dr. Maurice A. Lock, University College of North Wales
- Dr. Jerry M. Melillo, Marine Biological Laboratory
- Dr. John E. Hobbie, Marine Biological Laboratory
- Dr. Jean-Marie Dubois, Université de Sherbrooke
- Dr. Hal Caswell, Woods Hole Oceanographic Institution
- Mr. Roderick Morin, Woods Hole Oceanographic Institution

Graduate Students
- Dr. Stephen D. McCormick, MIT/WHOI
- Dr. Timothy Ford, University College of North Wales
- Ms. Elizabeth M. Conners, MIT/WHOI
- Ms. Jill Scharold, MIT/WHOI
- Mr. Rob Edwards, University of North Carolina
- Mr. Alex Bielak, University of Waterloo

Field and Laboratory Staff
- Ms. Barbara Farr, Technician
- Mr. Donald McDowell, Technician
- Ms. Rossana Sallenave, Technician
- Mr. Alain Cloutier, Technician
- Mr. Alan McNeil, Technician
- Mr. Monte Foil, Technician
- Ms. Sandra Ditner, Technician
- Ms. Margaret Francis, Technician
- Ms. Cynthia Trowbridge, Student Intern
- Ms. Genia Kedney, Student Intern

Support Staff
- Mr. Harold Gallienne, Gardien
- Mrs. Alfonsine Gallienne, Cook
- Mrs. Marlida Rock, Cleaning Services
- Mr. Marcel Poulin, Maintenance
- Ms. Elaine M. Lynch, Secretary
- Ms. Dianne Steele, Secretary
- Ms. Teresa Lynch, Secretary
- Mr. James Mitchell, Facilities
- Mr. Harold VanSicklen, Finances
- Ms. Cookie Sharpe, Travel

Visiting Scientists and Educational Groups

McGill University
Université de Sherbrooke
University of Waterloo
University of Georgia
Canada Centre for Inland Waters, Ontario
Fisheries and Oceans Canada
Sept-Iles Regional Schools

RESEARCH AWARDS - 1983

Principal Investigator	Affiliation	Title of Project	Award
Hamish Duthie	University of Waterloo	Determination of pH changes in the Matamek watershed based on sedimentary diatom analysis. II. Multivariate analysis.	$9,580 C
Maurice A. Lock	University College of North Wales	A watershed analysis of the dissolved and colloidal organic component of river water and its catabolism by benthic sediments.	$10,500 US
Seth R. Reice	University of North Carolina	The role of fish in the regulation of benthic invertebrate communities in Québec streams.	$5,860 US

PUBLICATIONS - 1983

Matamek Contribution No.

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MANUSCRIPTS ACCEPTED FOR PUBLICATION - 1983

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NITROGEN BUDGET OF A SUBARCTIC STREAM ALTERED BY BEAVER (CASTOR CANADENSIS)*

Robert J. Naiman and Jerry M. Melillo
Woods Hole Oceanographic Institution and
The Ecosystem Center, Marine Biological Laboratory

ABSTRACT

Beaver (Castor canadensis) influence stream ecosystems through their wood cutting and dam building activities. To quantify this influence we have used measured rates of nitrogen dynamics to construct a nitrogen budget for a section of a second order stream in eastern Québec and a beaver dam in that stream. The budget demonstrates the importance of sediment accumulations and an expanded wetted area to the annual nitrogen economy and to pathways of nitrogen cycling. Major changes after impoundment (per unit area) include a reduction in allochthonous nitrogen inputs and an increase in nitrogen fixation by sediment microbes. Overall, the beaver-modified stream section accumulated ~10^3 times more nitrogen than before alteration. The ecosystem implications of beaver activity suggest that current concepts of patterns and processes in running waters require modification.

INTRODUCTION

Beaver (Castor canadensis) affect the structure and dynamics of stream ecosystems by transferring organic matter from the terrestrial to the aquatic system and by building dams. The more noticeable effects are the retention of sediment, organic matter, and water by the dam, an increase in wetted surface area, modification of nutrient cycling and decomposition dynamics, and alterations to the riparian zone (Naiman et al. 1984; Francis et al. 1984). These changes have a long-lasting influence on the nature of stream ecosystems, on wetlands, and on the surrounding forest. Nevertheless, there are few instances where changes in any ecosystem component by beaver have been quantified (see literature reviews by Yeager and Hay 1955; Jenkins and Busher 1979; Hodgdon and Larson 1980).

Historically, beaver were extraordinarily abundant and widely dispersed in North America. Prior to the arrival of Europeans the population was estimated to be about 60 million individuals ranging over 15.5

*We thank B. S. Farr, M. M. Francis, and N. Corwin for assistance in the field and laboratory. J. E. Hobbie, R. W. Howarth, B. Peterson, and J. M. Teal kindly reviewed the manuscript. Research support by NSF grant DEB 81-05677 and the Woods Hole Oceanographic Institution. This is Contribution No. 5565 from the Woods Hole Oceanographic Institution and No. 88 from the Institution's Matamek Research Station.

million km^2 (Seton 1929; Jenkins and Busher 1979). The density was about 4 beaver/km^2, which is in accord with densities in remote regions today (Naiman, unpublished data). Since near extinction around 1900 A.D., the beaver population has increased substantially throughout its former range. Beaver are again becoming a significant component of aquatic ecosystems.

In Québec, beaver influence a substantial percentage of the total stream length within catchment basins; in some cases as much as 30-50% of the total length of second to fourth order streams is affected. This alteration has important implications for sediment movement, biogeochemical processes, and aquatic communities. Compared to a typical riffle, beaver activities produce an alteration to nutrient cycling and decomposition dynamics through entrainment of sediment and organic matter, there is an alteration to the light regime through the opening of the forest canopy, and there are alterations to precipitation, throughfall, and the character of allochthonous inputs (Fig. 1). Concomitant with these changes, the extent of wetted surface area increases, influencing the nature and intensity of interactions between the stream channel, biological components of the ecosystem, and the surrounding forest. The objectives of this paper are to quantify the influence of beaver activities on the nitrogen dynamics of a small, nutrient poor, subarctic stream and to examine this influence in reference to current perspectives in running waters ecology.

STUDY SITE

We studied nitrogen dynamics in both a beaver pond and a riffle in Beaver Creek, a second order stream located ~25 km east of Sept Iles, Québec, Canada. This region is Precambrian Shield with waters characterized by low nutrient concentrations (<0.3 mg N/L as nitrate and <0.003 mg P/L as orthophosphate), 5-15 mg C/L of dissolved organic carbon, about 2100 degree days annually (°C/yr), and generally acidic brown waters (pH: 4.8-7.2).

The Beaver Creek drainage is a pristine watershed with no evidence of human disturbance. The forest is predominantly black spruce (Picea mariana) and balsam fir (Abies balsamea), with paper birch (Betula papyrifera), trembling aspen (Populus tremuloides), speckled alder (Alnus rugosa), and willow (Salix sp.) composing the riparian community. The catchment of drains 1.8 km^2, has a large beaver pond in its headwaters, and over its 1.4 km length there are 12 abandoned or recolonized dams separated by riffles. Mean annual discharge is ~0.113 m^3/s. Several geomorphological, hydrological, and biological components of this stream have been described by Naiman (1982, 1983a,b,c), Melillo et al. (1983, 1984), Conners and Naiman (1984), Francis et al. (1984), and Naiman et al. (1984).

METHODS

The entire stream was mapped using standard survey techniques. Sediment accumulations behind each dam were estimated by using trigonometric interpolations of valley contour and measuring channel slope, pond width, pond length, dam height, and the bulk density and percentage organic matter of sediment cores taken from ponds. Accumulation of woody debris >10 cm diameter was measured, by species, over a 1383 m transect. Woody debris between 1-10 cm diameter was measured, also by species, in 1 m wide transects every 10 m for 300 m (Naiman et al. 1982). The erosion rate of particulate organic carbon (POC: >0.5 μm) suspended in the water column was reported by Naiman (1982). The amount of nitrogen associated with this carbon was estimated from C:N ratios given by Naiman (1983c) for Beaver Creek seston. Water samples for total dissolved nitrogen, and nitrogen in precipitation and throughfall under riparian zone species, were collected regularly between 1979-1983 and analyzed for total nitrogen by the method of D'Elia et al. (1977). Nitrate, nitrite, and ammonia in stream water were determined by the methods of Solorzono (1969) and Wood et al. (1967). The sum of nitrate, nitrite, and ammonia (dissolved inorganic nitrogen; DIN) was substracted from total nitrogen to estimate dissolved organic nitrogen (DON). Allochthonous inputs were collected from riffles and dam sites, sorted into component types, and the percentage nitrogen determined by the Kjeldahl technique or taken from the literature (Conners and Naiman 1984; Melillo et al. 1983). Nitrogen fixation associated with wood species and sediments was measured using the acetylene reduction technique (Hardy et al. 1973; Francis et al. 1984). Insect emergence was estimated using surface traps and literature data on percentage nitrogen associated with major insect groups (Naiman et al. 1984; Allen et al. 1974).

RESULTS AND DISCUSSION

From measurements of nitrogen dynamics at a number of dam and riffle sites along Beaver Creek and similar streams we have constructed composite nitrogen budgets for a beaver pond and a stream riffle. For this exercise we assumed a situation where beaver have taken a 100 m reach of Beaver Creek, which has an average width of 1 m and a mean water depth of 15 cm, and transformed it into a pond with an average width of 7 m and a mean water depth of 150 cm. Further, the riffle has 1 kg/m^2 of sediment and 15.9 kg/m^2 of wood; the beaver pond has 125 kg/m^2 of sediment and 12.9 kg/m^2 of wood. These dimensions, amounts of material, and general assumptions are in agreement with actual field data from 2nd and 3rd order streams of this region (Naiman et al. 1982). In that study we made detailed surveys of five streams covering ~4.3 km and 42 beaver dams. The details of the nitrogen budget are given in Table 1.

Budget Calculations

Standing Stock. Per unit area, the standing stock of nitrogen in the water column and associated with woody debris is similar in the riffle and beaver pond (Fig. 2). The water column contains 0.1-0.5 g N/m^2 and woody debris accounts for >14.5-17.8 g N/m^2. The amount of wood-associated nitrogen in the beaver pond is a minimal estimate since wood buried in sediments was not measured. However, per linear meter of channel, there are substantial differences between the two habitat types. The water column in the beaver pond contains 37 times more nitrogen than the riffle and the wood sequesters at least six times more nitrogen (Fig. 3).

The standing stock of nitrogen in sediments differs greatly between the riffle and pond (Figs. 2, 3). This is solely a function of the amount of accumulated sediment since cores taken from both sites had an average nitrogen content of 0.43% as dry weight. The beaver pond stores approximately 1000 times more nitrogen in sediments, per linear meter of stream channel, than does the riffle (Fig. 3).

Throughflow. The average annual discharge since 1979 in Beaver Creek is 1.04×10^6 m^3/yr (Naiman 1982 and unpublished data). Since 1979 we have monitored dissolved nitrogen (DIN and DON) concentrations in a riffle; in 1981 water leaving a beaver pond was added to the biweekly sampling program. We found the average concentrations to be statistically identical (riffle DIN = 0.066 mg N/L, DON = 0.304 mg N/L; pool DIN = 0.071 mg N/L, DON = 0.323 mg N/L). Most of the dissolved nitrogen is organic (riffle = 82.1%, pond = 81.5%). Using average concentrations, the throughflow of DIN available to the 100 m^2 of riffle is 712 g $N/m^2/yr$ versus 102 g $N/m^2/yr$ for the 700 m^2 beaver pond (Fig. 2); the corresponding values for DON are 3265 g $N/m^2/yr$ and 467 g $N/m^2/yr$. The difference between the riffle and pond in available nitrogen is due to the larger surface area of the pond.

Every 2nd or 3rd order stream in this region has significant beaver activity. Therefore, we have no control by which to judge how upstream activity has influenced nitrogen concentrations entering the study reach. We do have data on a small 1st order stream (First Choice Creek) with no history of beaver activity (Naiman 1982, 1983a,c). Between 1979 and 1983 the average concentration of DIN in that stream was 0.050 mg N/L, 72% of the level measured in the beaver influenced watershed; DON was 0.134 mg N/L, only 43% of that measured in Beaver Creek. Since we were unable to detect a significance difference in total dissolved nitrogen between water entering and leaving a beaver pond, we can only speculate that perhaps a series of ponds is required to raise the nitrogen concentration and, once a stabilized level is reached, no further increases can be detected. Water exiting the Beaver Creek watershed has essentially the same DIN and DON concentrations as water in large rivers downstream (Naiman 1982, 1983a). For the present budget we are assuming net changes in DIN or DON cannot be detected as water passes through a single beaver pond.

The situation for particulate organic nitrogen (PON) is similar. From 1980 to 1982 we monitored PON suspended in water entering and leaving a beaver pond and could not detect any net change. Using the average concentration (0.083 mg N/L), the total amount of particulate nitrogen in stream water available annually to the riffle is 861 g N/m^2 compared to 123 g N/m^2 to the beaver pond (Fig. 2). Again, we are not certain how upstream activity has influenced suspended particulate nitrogen concentrations since we could not locate a similar stream lacking beaver activity. Indications are, however, that beaver activity may significantly increase the export of particulate nitrogen since First Choice Creek has an export rate of only 0.54 g $C/m^2/yr$ compared to 3.37 g $C/m^2/yr$ for Beaver Creek (Naiman 1982). We suspect that the higher export rate may result from the increased organic matter loading caused by beaver feeding activities and that the water must pass through a series of ponds in order to raise the concentration.

The throughflow of dissolved and particulate nitrogen is large compared to that in storage or received via other pathways (see below). This represents a fundamental problem in budget calculations (Meyer and Tate 1983; Cummins et al. 1983). Since we cannot calculate error estimates for the throughflow components, we cannot be certain if there was a significant difference between the input and export of nitrogen. We conclude, as did Cummins et al. (1983), that a budget approach towards comparing two stream ecosystems may be inappropriate if one is trying to assess differences in biological processes. An input-output budget for nitrogen obscures important in-stream processes such as organic nitrogen formation and utilization.

Meterologic Inputs. The beaver pond receives only direct precipitation since the forest canopy has been completely opened by flooding and cutting. Between 1979 and 1982 the 109 cm/yr of rainwater and snow averaged 0.625 mg N/L. This is an annual input of 0.7 g N/m^2 or 4.9 g N/m of stream channel (Figs. 2, 3). For the riffle segment, precipitation during the leaf-off period (approximately 1 October - 15 May) averages 65.5 cm. This amounts to an annual nitrogen input of 0.4 g N/m^2.

The riffle section of Beaver Creek is heavily shaded by speckled alder from about 15 May to 1 October. During this period an average of 43.5 cm of rain falls. Water dripping from alder leaves between 1980-1983 averaged 1.031 mg N/L, nearly 65% greater than unaltered precipitation, resulting in an estimated input of 0.5 g $N/m^2/yr$ (Fig. 2). Annually, the pond receives 0.7 g N/m^2 from precipitation while the riffle receives 0.9 g N/m^2 from precipitation and throughfall.

Allochthonous inputs are an important source of nitrogen for small streams (Conners and Naiman 1984). Most direct inputs of nitrogen to the riffle is in the form of alder, birch, and aspen leaves; together they account for 3.9 g $N/m^2/yr$ (Table 1, Fig. 2). Since there is no canopy over the beaver pond, direct inputs of allochthonous material are less (1.6 g $N/m^2/yr$), but the collecting width of the channel is 7 times that

of the riffle, with the amount collected per linear meter of channel being large (11.4 g N/m/yr; Fig. 3).

Beaver, by opening the canopy and expanding the width of the stream channel, effectively increase the stream order from 2 to 3 in terms of annual direct inputs of allochthonous organic matter. Second order streams with a closed canopy receive ~260 g AFDM/m^2/yr of litter whereas, in the ponded reach, the annual input averages ~110 g AFDM/m^2, a level predicted for 3rd order streams in this region (Conners and Naiman 1984). Nevertheless, alder, birch, and aspen leaves remain the dominant litter types.

Lateral inputs of organic matter from the forest floor are less than direct allochthonous inputs (Conners and Naiman 1984). For the riffle, nearly 81% of the annual 119 g AFDM/m was leaves or tree products (e.g., seeds and catkins) and 19% was fine wood. This amounts to an input of 1.9 g N/m^2/yr (Table 1; Fig. 2). For the beaver pond, 76% of the annual 63 g AFDM/m was leaves or tree products, and 24% was fine wood, accounting for an annual input of only 0.1 g N/m^2. The annual input per unit of stream channel was 1.0 g N/m (Fig. 3).

One form of allochthonous input not directly measured in this study was the annual contribution of nitrogen in coarse wood. This is a difficult contribution to accurately measure in streams. Nevertheless, an estimate can be made for the beaver pond. An individual beaver requires about a metric ton of wood for growth and maintenance annually (Howard 1982), and a pond of this size would contain one lodge with a minimum of six beaver (Jenkins and Busher 1979). Feeding activities by these beaver could contribute as much as 10.3 g N/m^2/yr if their diet consists entirely of paper birch and trembling aspen and if all of that wood is transferred to the pond. This gives a minimum turnover time of 1.4 yr for the standing stock of wood in the pond, which is in agreement with estimates of wood decay rates made in Beaver Creek by Melillo et al. (1983), especially when the inherent uncertainties in our assumptions are considered. This estimated input rate for coarse wood mediated by beaver is more than twice that estimated for other forms of allochthonous inputs and for nitrogen fixation (see below).

In-Stream Processes. Francis et al. (1984) examined nitrogen fixation associated with wood and sediment in riffles and ponds on Beaver Creek. Wood, in general, had low and patchy fixation rates, accounting annually for 0.2 g N/m^2 in the riffle and <0.1 g N/m^2 in the pond (Fig. 2). This despite the fact that both sites had substantial standing stocks of woody debris (e.g., 12.9 to 15.9 kg/m^2).

For sediment, mass specific nitrogen fixation rates did not differ significantly ($P > 0.10$) between aerobic and anaerobic sediment or between riffles and ponds. Fixation rates remained at approximately 3.3×10^{-3} μmoles C_2H_4 g $AFDM^{-1}hr^{-1}$ during the ice-free season. The difference between riffles and ponds in the absolute amount of nitrogen fixed results

from the substantial amount of sediment accumulated behind the beaver dam. In riffles, with only about 1 kg/m^2 of sediment, the annual nitrogen fixation is <0.1 g N/m^2 (Fig. 2); ponds average about 125 kg/m^2 of sediment with organisms fixing 5.1 g N/m^2 annually or 35.7 g N/m of channel length (Figs. 2, 3).

Other than erosion (see above) there appears to be only two major pathways for loss of nitrogen from streams: denitrification and insect emergence. Denitrification was not measured in this study. However, in other studies it has ranged between 0.2-14.0 g N/m^2/yr (Sain et al. 1977; Chatarpaul et al. 1980; Smith and DeLaune 1983; P. A. Steudler, unpublished data).

The exit of insects from the water column represent a small annual loss of nitrogen during the ice-free season (Table 1; Naiman et al. 1984). In both the riffle and the beaver pond, annual insect emergence accounts for 0.1 g N/m^2, and only 0.4 g N/m of stream length from the pond. These are minimal rates since insect emergence from stream margins has not been measured.

Budget analysis. If the large annual throughflow of nitrogen suspended in stream water is excluded and only in-stream processes examined, it is clear that fundamental pathways of nitrogen cycling have been altered by beaver (Table 2). In riffles, 83.3% of the annual nitrogen inputs (7.2 g N/m^2) are accounted for by allochthonous inputs either as direct (56.9%) or as lateral inputs from the forest floor (26.4%). Nearly all this nitrogen enters the stream in the form of leaves, most of which is speckled alder. Precipitation, throughfall, and nitrogen fixation are not especially important to the riffle's nitrogen budget. Together they account for only 16.7% of the annual nitrogen inputs (Table 2). Cycling of nitrogen is rapid in the riffle, with a turnover time of 3.1 yr; sediment nitrogen turns over faster (0.6 yr) than that of wood (~ 90 yr).

In the beaver pond, most of the annual input (7.7 g N/m^2) is accounted for by nitrogen fixation associated with accumulated sediment (66.2%); direct allochthonous inputs have been reduced to 22.1% and lateral inputs to 1.3% of the budget. Precipitation contributes 9.1% but throughfall and nitrogen fixation associated with wood are negligible (<1.3%). The turnover time for nitrogen is a slow 72.4 yrs. It appears that much of the nitrogen is sequestered in sediments until the site is abandoned, the dam decays and the pond dries. Only when the pond dries does it appear that the nitrogen is released to higher trophic levels (Naiman et al. 1984). This scenario is similar when considered per unit length of channel.

In one other nitrogen budget study DON was also the major form of throughflow (Watershed 10, Oregon; Triska et al. 1983). In that study the dissolved nitrogen fraction consisted of 95% DON and 5% DIN which contrasts sharply with Meyer et al. (1981) who found that only 13% of the dissolved nitrogen in Bear Brook, New Hampshire, was DON. Watershed 10

had annual allochthonous input rates (3.1 g N/m^2) slightly less, and nitrogen fixation rates on a variety of organic materials (0.8 g N/m^2), that were slightly higher than those measured in our study. Overall, the nitrogen budget reported by Triska et al. (1983) is similar to that reported here for the riffle.

Ecosystem implications

Historically, small streams throughout North America had different features than they do today (Morgan 1868; Sedell and Froggett 1984). Beaver undoubtly exerted a much stronger and wider influence on ecosystem structure and dynamics by ponding headwater streams and by intensifying interactions between the terrestrial and aquatic environments. The fact that large amounts of sediment and nitrogen were sequestered high up in the watershed, rather than being eroded downstream, suggests that watercourses throughout North America were significantly altered by the removal of beaver long before extensive research began. In fact, the influence of beaver activity can still be seen today in the terrestrial vegetation of meadowlands centuries after extirpation (Ives 1942, Neff 1957).

Beaver mediated alterations to streams have far reaching implications when viewed in an ecosystem perspective. In pristine and semi-pristine regions of Oregon and Québec, nearly 1500 km of stream have been surveyed recently with the conclusion that today beaver may directly influence ~30% of that length (J. R. Sedell and R. J. Naiman, unpublished data). In Wyoming, Smith (personal communication) recently surveyed 1,840 km of stream and found that beaver dams averaged 0.8/km. In these studies only dams of significant size and water ponding were counted. If this was a general situation throughout the historical range of beaver, as we suspect, then nitrogen fixation by sediment organisms, long-term cycles of nitrogen storage and release, and elevated nitrogen concentrations in waters flowing downstream would have been dominant features of running waters. These features would have had strong effects on community composition and productivity, especially in regions where nitrogen is a limiting nutrient.

Finally, the storage of sediment and nitrogen by beaver dams has strong implications for the river continuum concept (Vannote et al. 1980), the nutrient spiraling concept (Elwood et al. 1983) and the intermediate-disturbance hypothesis (Connell 1978; Ward and Stanford 1983). Specifically, the continuum concept must be modified to include numerous zones of beaver altered reaches in small order streams, and concomitant changes in community processes and composition. Nutrient retention is increased within streams altered by beaver as nitrogen is sequestered for longer time periods, thus decreasing spiraling length and increasing ecosystem retention and processing efficiency. Beaver ponds also increase the diversity of habitat available for aquatic organisms. As ponds pass through their ontogeny from formation to erosion, they act to enhance the biotic diversity of headwater streams by creating small "disturbance" zones analogous to those in marine intertidal areas. Overall, these

features suggest that beaver, through their feeding and dam building activities, act as a keystone species (sensu Paine 1966) to affect ecosystem structure and dynamics far beyond their immediate requirements for food and space. This being the case, the role of beaver in influencing interactions between terrestrial and aquatic ecosystems, and in the structuring of those ecosystems, deserves serious consideration.

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Table 1. Details of nitrogen budgets calculated for a riffle and a beaver pond in Beaver Creek, Québec.

NITROGEN SOURCE	RIFFLE[1] ($g\ N \cdot m^{-2} \cdot yr^{-1}$)	BEAVER POND[2] ($g\ N \cdot m^{-2} \cdot yr^{-1}$)	BEAVER POND[2] ($g\ N \cdot m^{-1} \cdot yr^{-1}$)
Throughflow			
Dissolved inorganic	712	102	712
Dissolved organic	3265	467	3265
Particulate	861	123	861
Standing Stock (gN/m^2 or gN/m)			
Water column	0.1	0.5	3.7
Woody debris	17.8	>14.5	>101.2
Sediment	4.3	542.5	3797.5
Precipitation	0.4	0.7	4.9
Throughfall	0.5	0	0
Allochthonous inputs			
Direct fall	4.1	1.7	11.4
Aspen	(0.4)	(0.1)	(0.5)
Birch	(0.8)	(0.4)	(2.7)
Alder	(2.6)	(1.1)	(7.6)
Conifer needles	(<0.1)	(<0.1)	(0.1)
Seeds and flowers	(0.2)	(<0.1)	(0.1)
Fine wood	(<0.1)	(0.1)	(0.4)
Lateral movement	1.9	0.1	1.0
Leaves	(1.9)	(0.1)	(1.0)
Fine wood	(<0.1)	(<0.1)	(<0.1)
Nitrogen fixation			
Woody debris	0.2	<0.1	0.1
Aspen	(<0.1)	(<0.1)	(<0.1)
Birch	(0.2)	(<0.1)	(<0.1)
Alder	(<0.1)	(<0.1)	(<0.1)
Balsam fir	(<0.1)	(<0.1)	(<0.1)
Spruce	(<0.1)	(<0.1)	(<0.1)
Sediment	<0.1	5.1	35.7
Denitrification	?	?	?
Insect emergence	0.1	0.1	0.4

[1]Surface area 100 m^2; 1 kg/m^2 sediment, and 15.9 kg/m^2 woody debris.
[2]Surface area 700 m^2; 125 kg/m^2 sediment, and 12.9 kg/m^2 woody debris.

Table 2. Percentage composition of major nitrogen sources when the throughflow of nitrogen suspended in the water is excluded.

NITROGEN SOURCE	RIFFLE (%)	BEAVER POND (%)
Precipitation	5.6	9.1
Throughfall	6.9	0.0
Allochthonous Inputs		
Direct	56.9	22.1
Lateral	26.4	1.3
Nitrogen Fixation		
Wood	2.8	1.3
Sediment	1.4	66.2
Total Standing Stock (g N/m^2)	22.2	557.5
Annual Input (g N/m^2)	7.2	7.7
Turnover Time (yr)	3.1	72.4

FIGURE CAPTIONS

Figure 1. The activities of beaver influence stream ecosystem components primarily by opening of the forest canopy, by increasing the water surface area, and by increasing the amount of sediment and organic matter in the channel. The schematic drawing depicts ecosystem components addressed in this study.

Figure 2. The nitrogen budget of a riffle is compared to that of a beaver pond, per unit of area. See Table 1 for specific details of the budget.

Figure 3. The nitrogen budget of a riffle is compared to that of a beaver pond, per unit of channel length. See Table 1 for specific details of the budget.

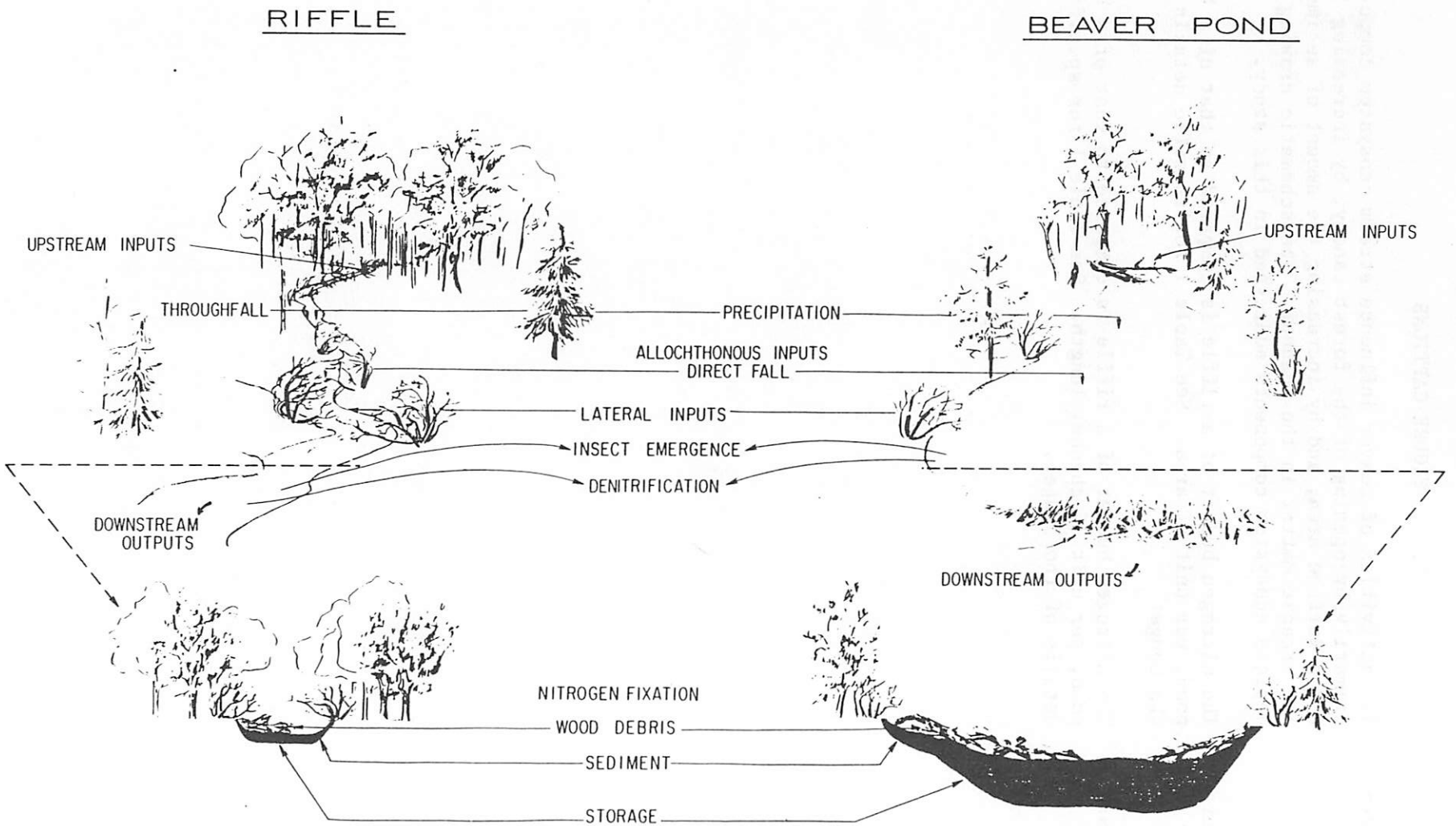
RIFFLE
BEAVER POND
UPSTREAM INPUTS
UPSTREAM INPUTS
THROUGHFALL
PRECIPITATION
ALLOCHTHONOUS INPUTS
DIRECT FALL
LATERAL INPUTS
INSECT EMERGENCE
DENITRIFICATION
DOWNSTREAM OUTPUTS
DOWNSTREAM OUTPUTS
NITROGEN FIXATION
WOOD DEBRIS
SEDIMENT
STORAGE

Fig. 1

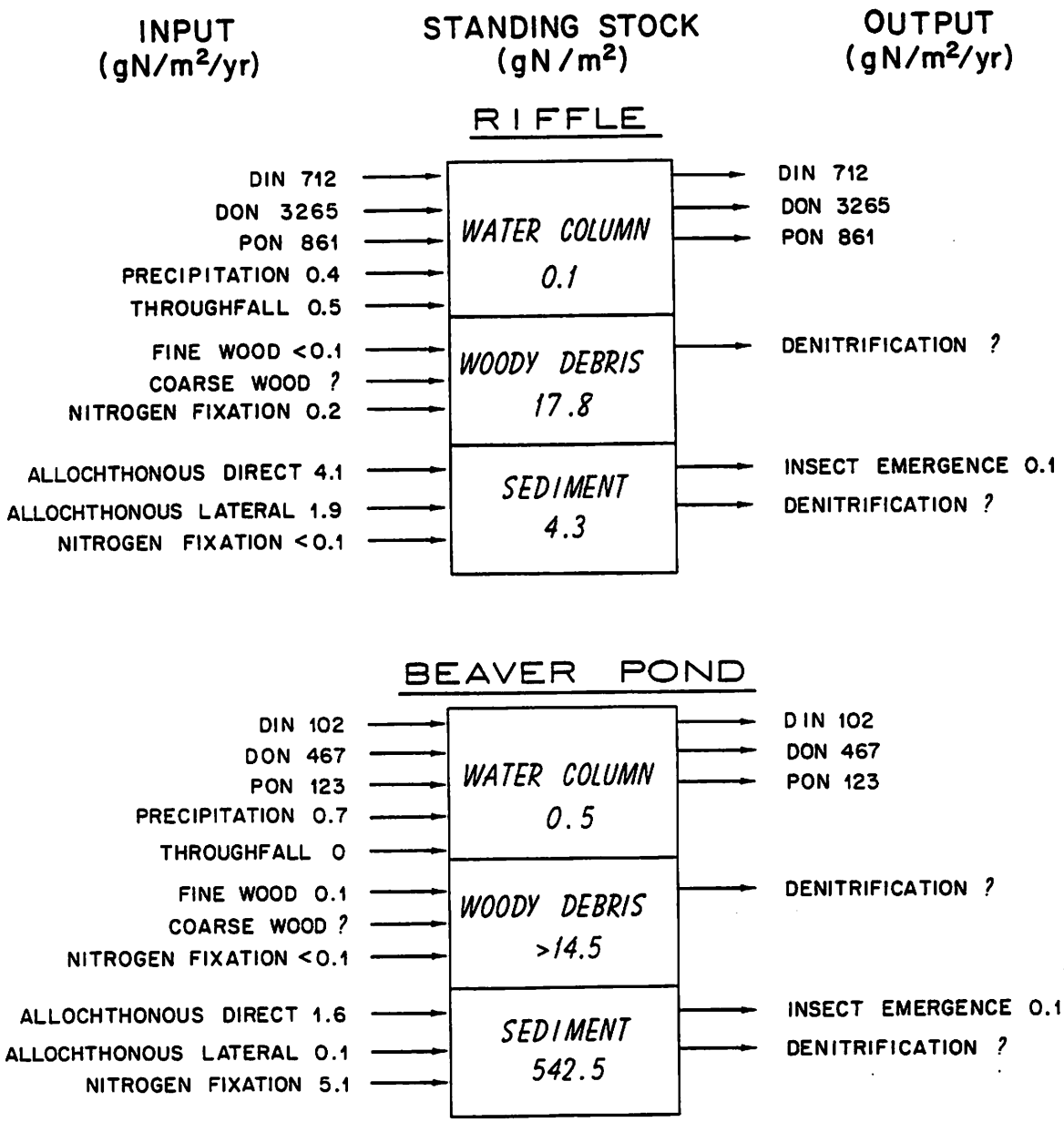
INPUT
(gN/m²/yr)
STANDING STOCK
(gN/m²)
OUTPUT
(gN/m²/yr)
RIFFLE
DIN 712
DON 3265
PON 861
PRECIPITATION 0.4
THROUGHFALL 0.5
WATER COLUMN
0.1
DIN 712
DON 3265
PON 861
FINE WOOD <0.1
COARSE WOOD ?
NITROGEN FIXATION 0.2
WOODY DEBRIS
17.8
DENITRIFICATION ?
ALLOCHTHONOUS DIRECT 4.1
ALLOCHTHONOUS LATERAL 1.9
NITROGEN FIXATION <0.1
SEDIMENT
4.3
INSECT EMERGENCE 0.1
DENITRIFICATION ?
BEAVER POND
DIN 102
DON 467
PON 123
PRECIPITATION 0.7
THROUGHFALL 0
WATER COLUMN
0.5
DIN 102
DON 467
PON 123
FINE WOOD 0.1
COARSE WOOD ?
NITROGEN FIXATION <0.1
WOODY DEBRIS
>14.5
DENITRIFICATION ?
ALLOCHTHONOUS DIRECT 1.6
ALLOCHTHONOUS LATERAL 0.1
NITROGEN FIXATION 5.1
SEDIMENT
542.5
INSECT EMERGENCE 0.1
DENITRIFICATION ?

Fig. 2

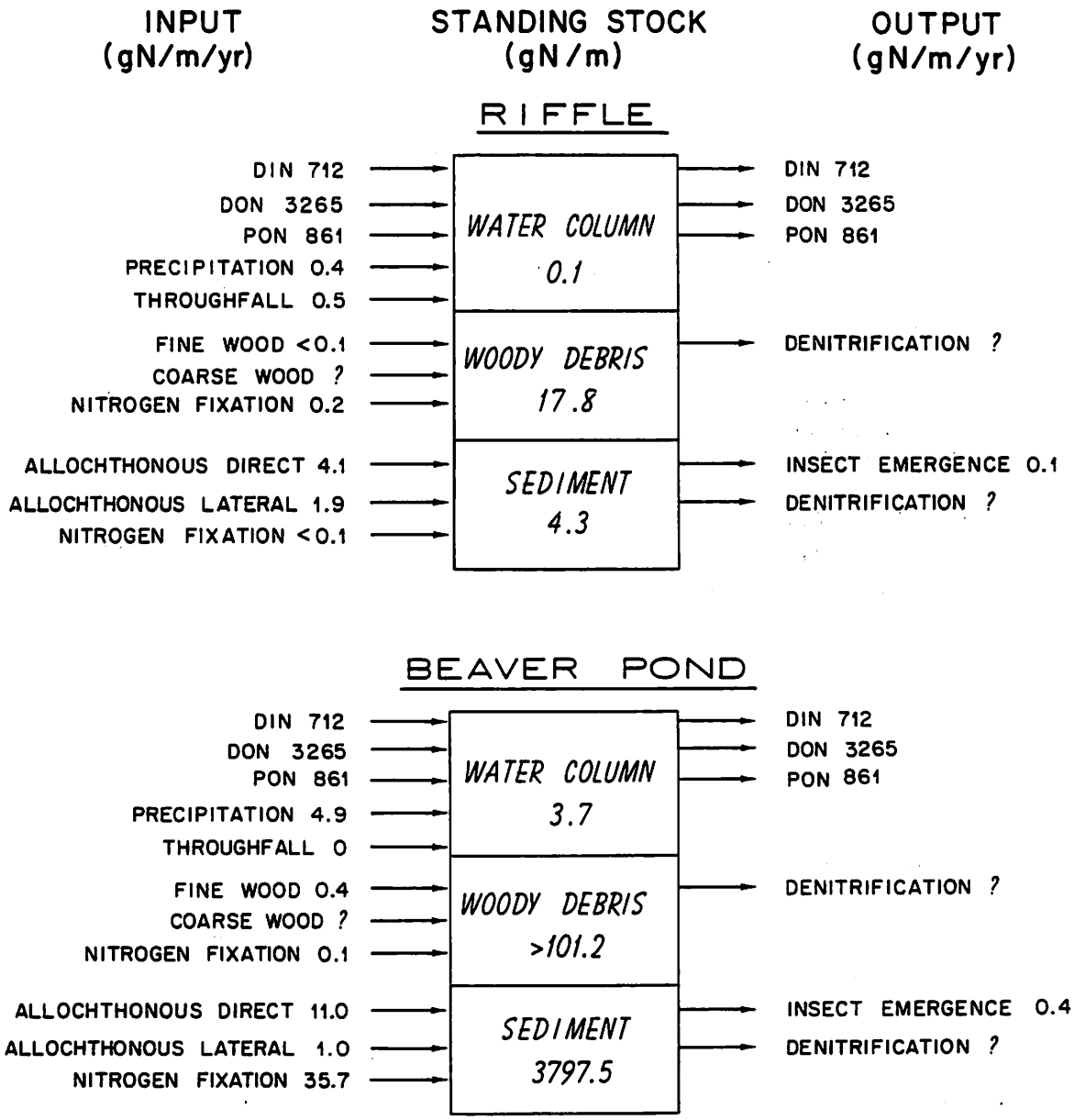
INPUT (gN/m/yr)
STANDING STOCK (gN/m)
OUTPUT (gN/m/yr)
RIFFLE
DIN 712
DON 3265
PON 861
PRECIPITATION 0.4
THROUGHFALL 0.5
WATER COLUMN 0.1
DIN 712
DON 3265
PON 861
FINE WOOD <0.1
COARSE WOOD ?
NITROGEN FIXATION 0.2
WOODY DEBRIS 17.8
DENITRIFICATION ?
ALLOCHTHONOUS DIRECT 4.1
ALLOCHTHONOUS LATERAL 1.9
NITROGEN FIXATION <0.1
SEDIMENT 4.3
INSECT EMERGENCE 0.1
DENITRIFICATION ?
BEAVER POND
DIN 712
DON 3265
PON 861
PRECIPITATION 4.9
THROUGHFALL 0
WATER COLUMN 3.7
DIN 712
DON 3265
PON 861
FINE WOOD 0.4
COARSE WOOD ?
NITROGEN FIXATION 0.1
WOODY DEBRIS >101.2
DENITRIFICATION ?
ALLOCHTHONOUS DIRECT 11.0
ALLOCHTHONOUS LATERAL 1.0
NITROGEN FIXATION 35.7
SEDIMENT 3797.5
INSECT EMERGENCE 0.4
DENITRIFICATION ?

Fig. 3

DYNAMICS OF PLANT LITTER DECAY IN NORTHERN STREAMS

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ABSTRACT

In this paper we consider the influences of initial litter quality, exogenous nutrient supply, temperature and oxygen tension on decay rates and nutrient immobilization potentials of plant litter materials decomposing in northern streams. We review a new method of estimating nitrogen and phosphorus immobilization potentials in decaying litter. And we discuss the mechanisms responsible for nitrogen immobilization.

Initial litter quality is the dominant factor that influences decay rate. Materials rich in nitrogen and poor in lignin generally decay most rapidly. Addition of nitrogen and/or phosphorus to the water often result(s) in increased decay rate as does elevation of water temperature. While low oxygen tension retards the decay of lignin and related compounds, it is not clear that low oxygen tension slows the rate of decay of more labile compounds.

Initial litter quality is also the dominant factor that influences nitrogen immobilization potential. Materials poor in both nitrogen and lignin generally have the highest immobilization potentials. Addition of nitrogen to the water increases the immobilization potential of a litter material. Plant litter decomposing under anaerobic conditions immobilizes less nitrogen than the same litter decomposing under aerobic conditions. And, all other conditions being equal, temperature changes will influence nitrogen immobilization rate but not its maximum amount.

The Amount of nitrogen directly associated with microbial biomass makes up only a small fraction of the total nitrogen mass in decomposing litter. Microbes appear to be important agents in the nitrogen immobilization process on decaying litter. The microbes produce exoenzymes which in turn cause the degradation of large molecules such as polyphenolics and lignins. Some of these degradation products, such as the "reactive phenolics", recondense with nitrogen containing compounds. The degradation-recondensation cycle continues throughout litter decay, with the ultimate product being nitrogen-rich humic substances.

The writing of this manuscript was supported by NSF Grants DEB-80- 05081, DEB-81-05677 and DEB-82-07055.

Table 1. Laboratory study of elm leaf litter decay in aquatic microcosms (Kaushik and Hynes (1971). % OM remaining, % N in remaining tissue, and incubation time.

Time (wk)	% OM	% N
0	100	1.02
0.25	97.5	0.96
0.50	91.5	1.10
1	84	1.36
2	76	1.61
3	73.5	1.70
4	72.5	1.81
6	65	1.90
8	62	2.16

Table 2. Observed and estimated maximum net N immobilization (mg N/g initial material) for five decomposing plant materials (Richards and Norman 1931).

Material	Nmax Observed (mg N/g initial material)	Nmax Estimated (mg N/g initial material)
Flax straw (normal)	5.7	5.4
Flax straw (retted)	1.2	1.8
Flax fiber	3.4	4.0
Willow peel	10.3	16.9
Oat straw	8.0	8.2

Table 3. Initial litter quality parameters and correlation coefficients, slopes and intercepts of the inverse linear functions relating mass loss and the N concentration in the remaining material for each of five wood chip types decomposing in a first order stream in Quebec.

Material	Initial Lignin (%)	Nitrogen (%)	Inverse Linear Function (OM vs N) r	Slope	Intercept
alder wood	13.1	0.32	-0.89	-39.18	106.29
birch wood	8.2	0.14	-0.99	-33.71	102.03
aspen wood	12.0	0.08	-0.88	-43.46	104.09
spruce wood	25.9	0.06	-0.91	-49.20	104.93
fir wood	24.6	0.04	-0.97	-52.96	105.18

Table 4. Estimates of N_{max} for a set of hypothetical litter materials that have a range of initial nitrogen and lignin concentrations and that are decomposing in a first order stream in eastern Quebec. The calculations were made using Equation (5). The N_{max} values are reported in mg N immobilized per g initial tissue.

Initial nitrogen concentration	Initial Lignin Concentration		
	10%	15%	20%
(%)			
0.02	6.55	5.83	5.26
0.20	5.69	4.98	4.40
0.40	4.80	4.10	3.54

FIGURE CAPTIONS

Figure 1. a) Annual decay rates (k) of Spartina alterniflora leaves from plants grown under different fertilizer regimes expressed as a function of the initial nitrogen concentrations of the materials (redrawn from Marinucci et al. 1983). The studies were carried out in laboratory microcosms.

b) Annual decay rates (k) of three hardwood leaf litter materials (willow, sycamore, and oak) expressed as a function of their initial nitrogen concentrations (data of Mathews and Kowalczewski 1968). The studies were carried out in the River Thames, England.

Figure 2. a) Annual decay rates (k) of five wood chip materials (alder aspen, birch, spruce and fir) express as a function of the initial lignin concentrations, for the materials decomposing in a 9th order stream in Quebec, and

b) k expressed as a function of initial lignin to nitrogen ratio in a 1st order stream in Quebec, Canada (after Melillo et al. 1983).

Figure 3. Design of the microcosms used for the study of decomposition in the laboratory (after Melillo et al. 1984).

Figure 4. The percentage of original mass of alder and spruce wood shavings remaining as a function of time (weeks) under both high and low levels of exogenous phosphorus supply. Data from a laboratory study of decay (Melillo et al. unpublished).

Figure 5. a) Percentage of original elm leaf litter mass remaining as a function of time (weeks). Data from a decomposition study conducted in the laboratory at a constant temperature of 22°C and with the addition of exogenous nitrogen (Kaushik and Hynes 1971).

b) Nitrogen concentration in remaining elm leaf litter as a function of time (weeks).

c) Percentage of original elm leaf litter mass remaining expressed as a function of the nitrogen concentration in the remaining material.

Figure 6. a) Percentage of original oak leaf litter mass remaining expressed as a function of the nitrogen concentration in the remaining material. Data from a decomposition study conducted in a Michigan Stream (Suberkropp et al. 1976).

b) Percentage of original birch wood mass remaining expressed as a function of the nitrogen concentration in the remaining material. Data from a decomposition study conducted in a Quebec stream (Melillo et al. 1983).

c) Percentage of original Calamagrostis leaf and stem litter mass remaining expressed as a function of the nitrogen concentration in the remaining material. Data from a decomposition study conducted in the laboratory (Melillo et al. 1984).

Figure 7. Percentage of original Typha leaf and stem litter mass remaining expressed as a function of the phosphorus concentration in the remaining material. Data from a decomposition study conducted in the laboratory (Melillo et al. 1984).

Figure 8. Slopes of the inverse linear functions relating mass loss and nitrogen concentration in the remaining material expressed as a function of the initial lignin concentrations of the materials. Five wood ship chip types were used - alder, aspen, birch, fir and spruce. Data from a decomposition study conducted in a first order stream in Quebec, Canada (Melillo et al. 1983).

Figure 9. Percentage of original alder wood chip mass remaining expressed as a function of the phosphorus concentration in the remaining material. The lower line (steep slope) resulted from decay under low (1X) P enrichment. The upper line (shallow slope) resulted from decay under high (50X) P enrichment. The same initial material was used in the two cases. Data from a decomposition study conducted in laboratory microcosms (Melillo et al. unpublished).

Figure 10. Percentage of birch wood mass remaining as a function of the nitrogen concentration in the remaining material. The same type of initial material was placed in four Quebec streams 1st, FCC; 2nd order, BC; 6th order, MA; and 9th order, MO).

Figure 11. Percentage of original rice straw mass remaining as a function of the nitrogen concentration in the remaining material. Data from a decomposition study conducted in laboratory microcosms at the Fermentation Department, Rothamsted Experimental Station, Harpenden Herts, England (Acharya 1935).

Figure 12. Percentage of original elm leaf litter mass remaining as a function of time (weeks). Data from a decomposition study conducted in the laboratory at two temperatures (10°C and 22°C) and with the addition of exogenous nitrogen (Kaushik and Hynes 1971).

Figure 13. Distribution of nitrogen in decaying alder wood chips as a function of time. Upper points (circles) = amount of N in total detrital complex (including microbes and microbial products). Middle points (triangles) = amount of N associated with original material. Lower points (squares) = amount of nitrogen associated with fungal biomass.

Figure 14. Model of phases of nitrogen immobilization and mineralization as litter material decays and humic substances are formed and degraded (after Melillo et al. manuscript).

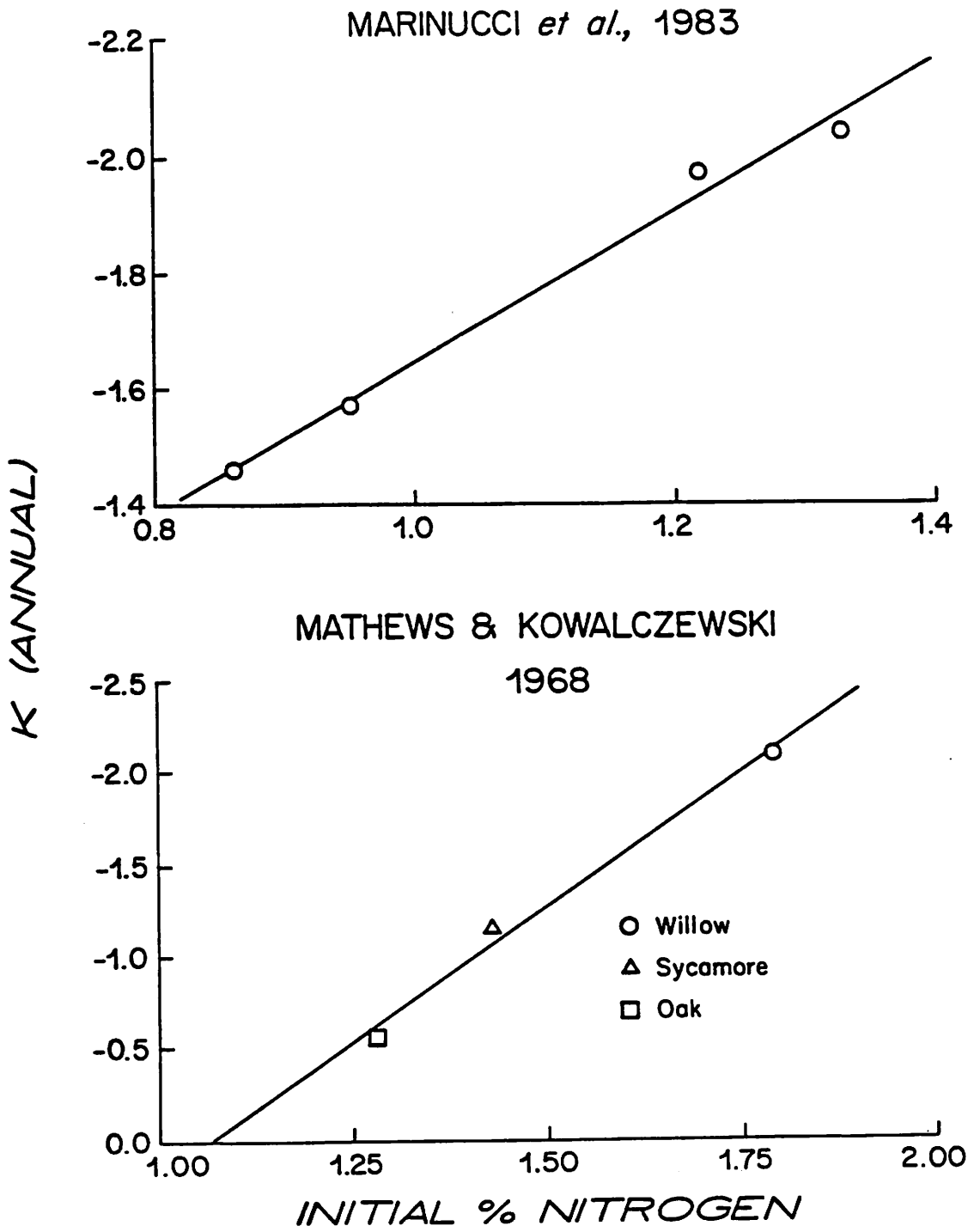
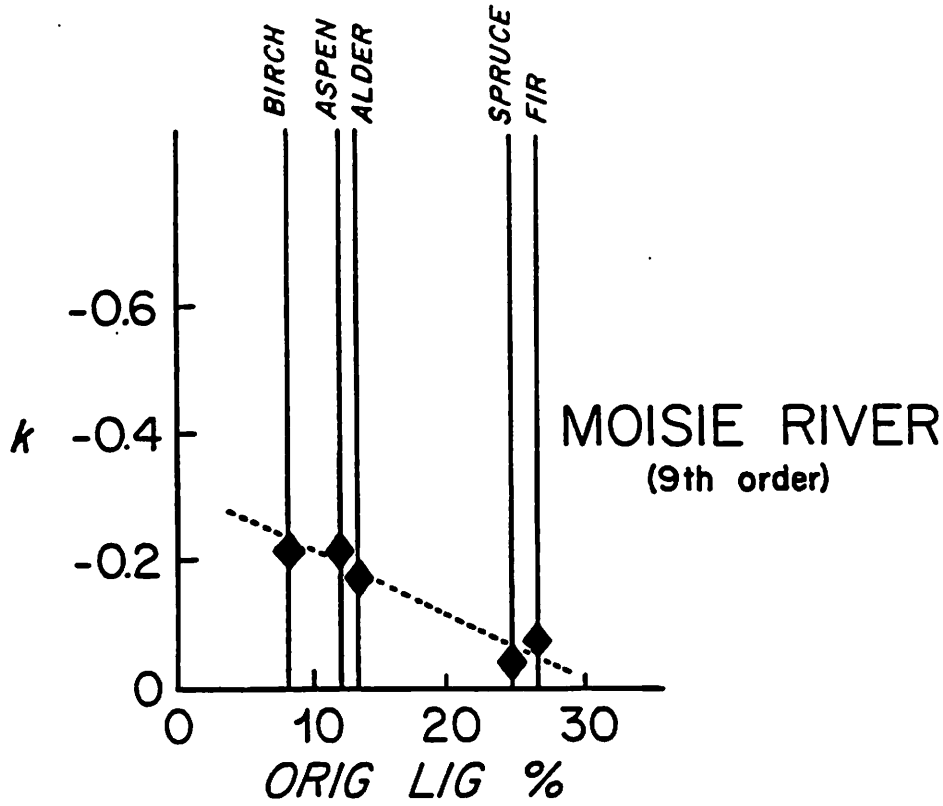

MARINUCCI et al., 1983
-2.2
-2.0
-1.8
-1.6
-1.4
0.8
1.0
1.2
1.4
MATHEWS & KOWALCZEWSKI
1968
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
1.00
1.25
1.50
1.75
2.00
Willow
Sycamore
Oak
K (ANNUAL)
INITIAL % NITROGEN

Fig. 1


BIRCH
ASPEN
ALDER
SPRUCE
FIR
-0.6
-0.4
-0.2
0
k
MOISIE RIVER
(9th order)
0
10
20
30
ORIG LIG %

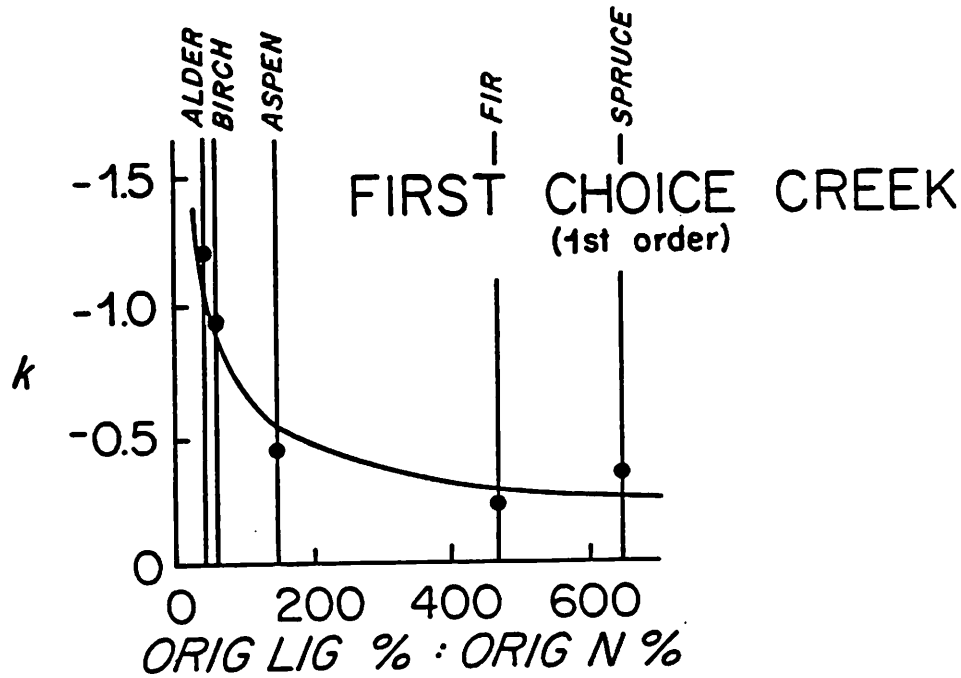

ALDER
BIRCH
ASPEN
FIR
SPRUCE
-1.5
-1.0
-0.5
0
k
FIRST CHOICE CREEK
(1st order)
0
200
400
600
ORIG LIG % : ORIG N %

Fig. 2

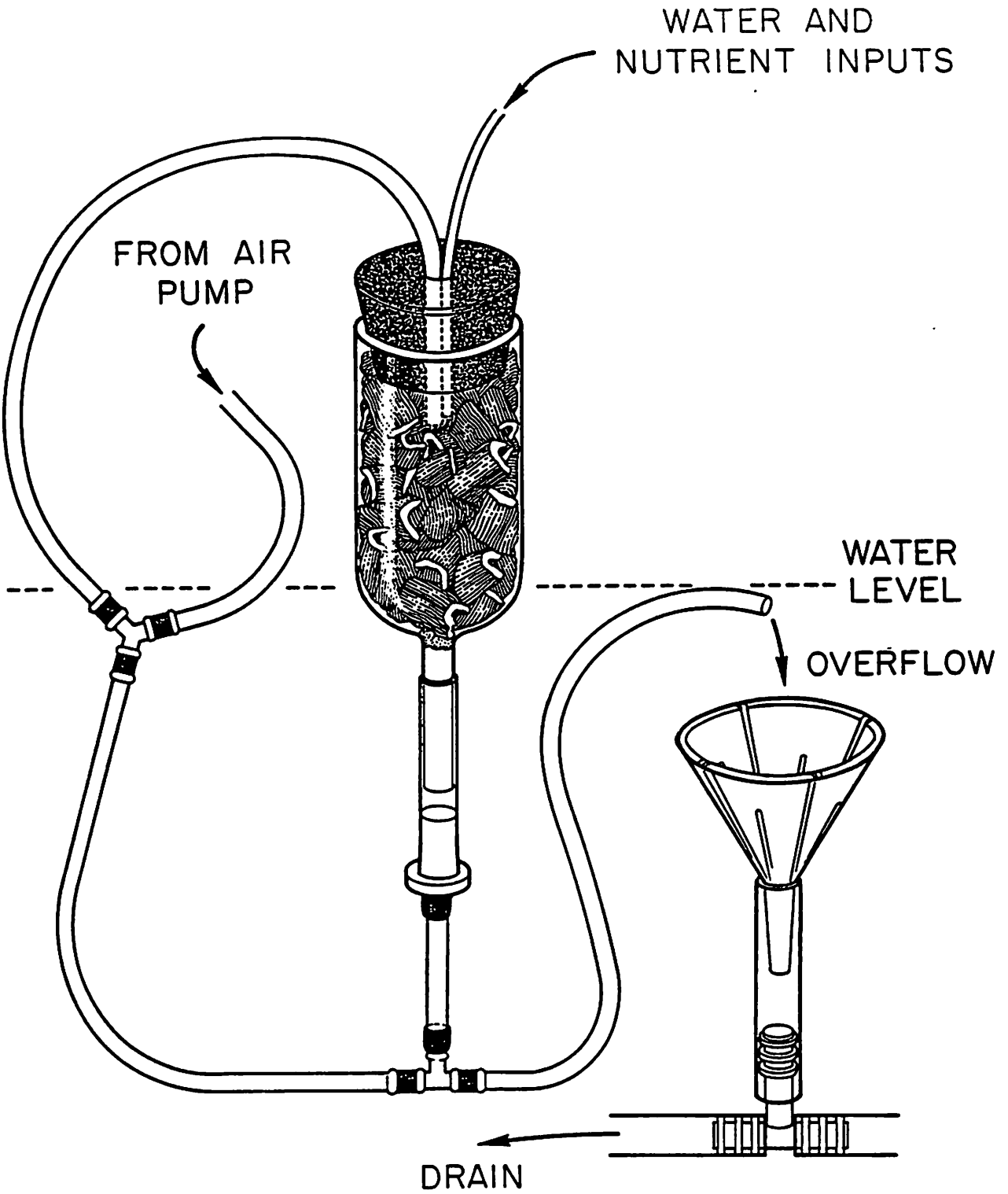

WATER AND
NUTRIENT INPUTS
FROM AIR
PUMP
WATER
LEVEL
OVERFLOW
DRAIN

Fig. 3

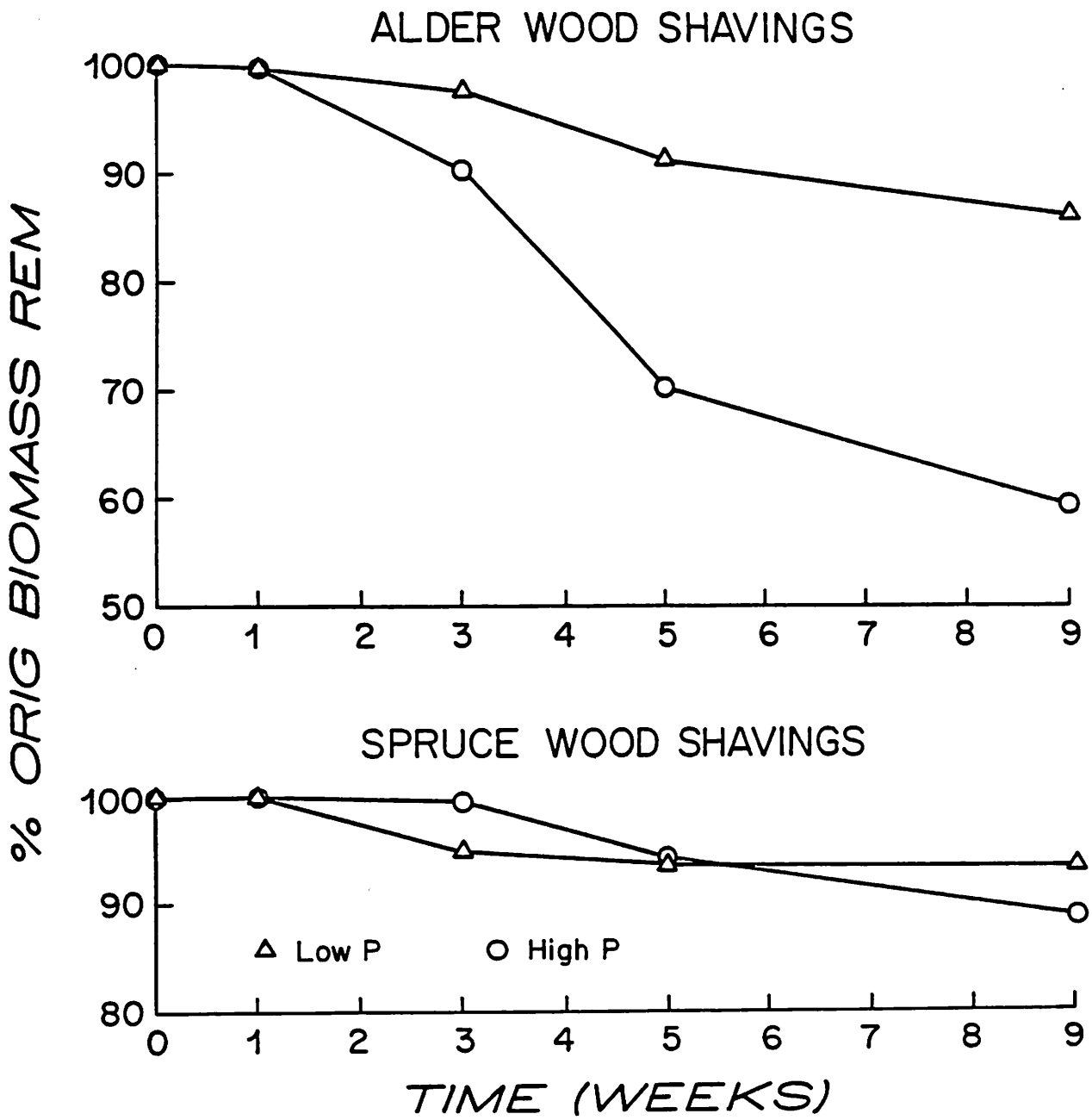

ALDER WOOD SHAVINGS
100
90
80
70
60
50
0
1
2
3
4
5
6
7
8
9
% ORIG BIOMASS REM
SPRUCE WOOD SHAVINGS
100
90
80
Δ Low P
O High P
0
1
2
3
4
5
6
7
8
9
TIME (WEEKS)

Fig. 4

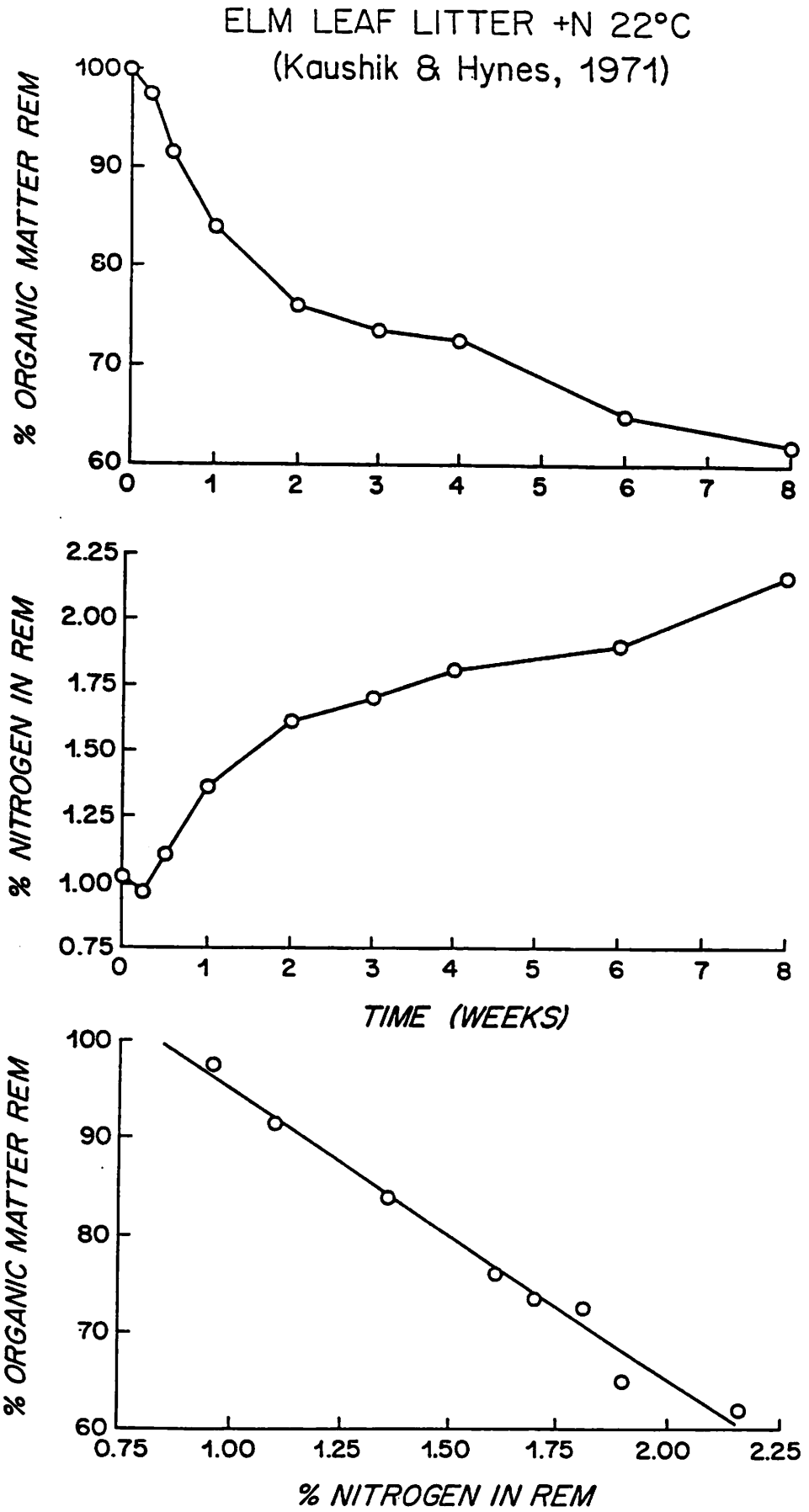

ELM LEAF LITTER +N 22°C
(Kaushik & Hynes, 1971)
% ORGANIC MATTER REM
100
90
80
70
60
0
1
2
3
4
5
6
7
8
% NITROGEN IN REM
2.25
2.00
1.75
1.50
1.25
1.00
0.75
TIME (WEEKS)
% ORGANIC MATTER REM
% NITROGEN IN REM

Fig. 5

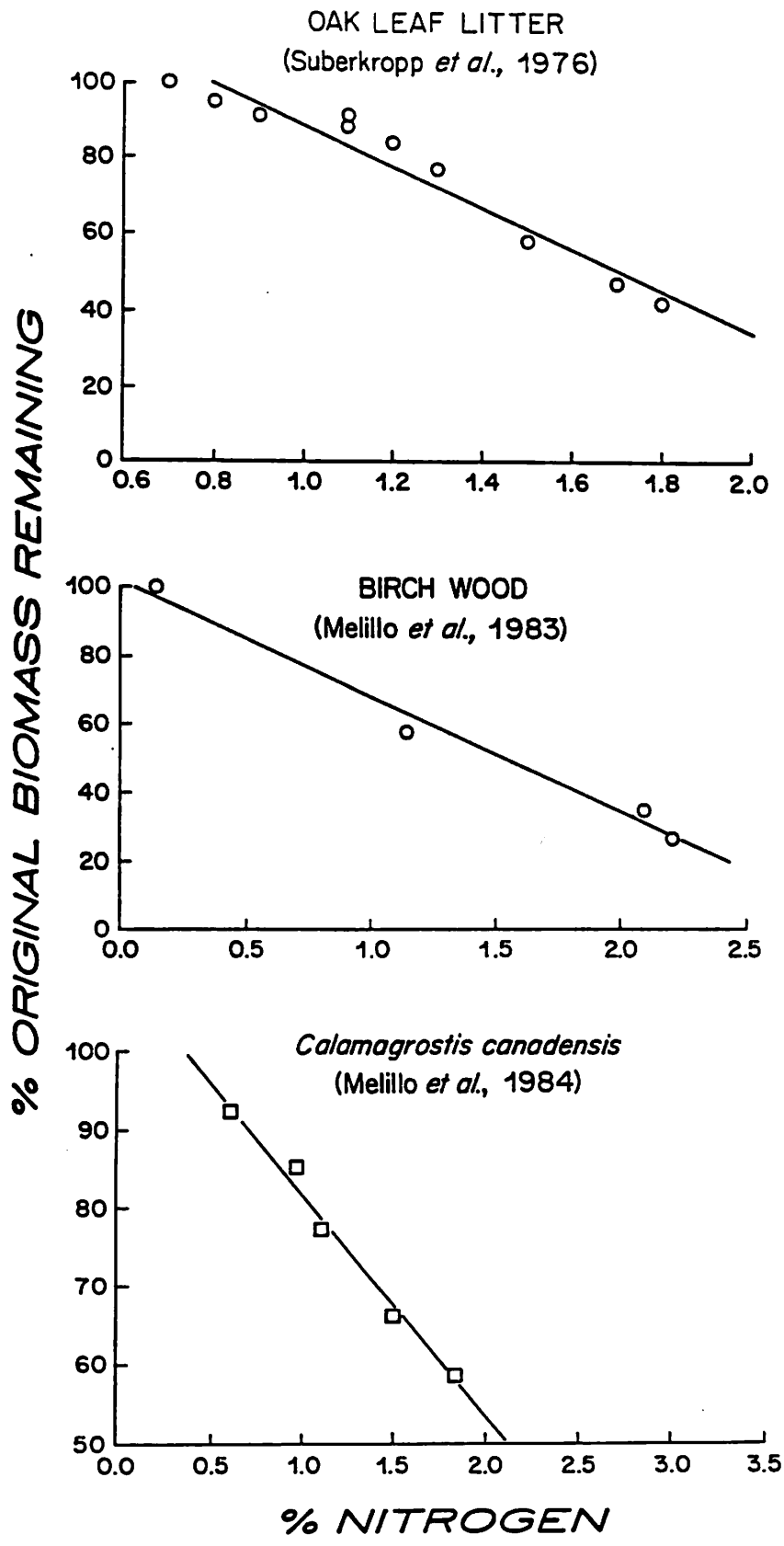

OAK LEAF LITTER
(Suberkropp et al., 1976)
BIRCH WOOD
(Melillo et al., 1983)
Calamagrostis canadensis
(Melillo et al., 1984)
% ORIGINAL BIOMASS REMAINING
% NITROGEN

Fig. 6

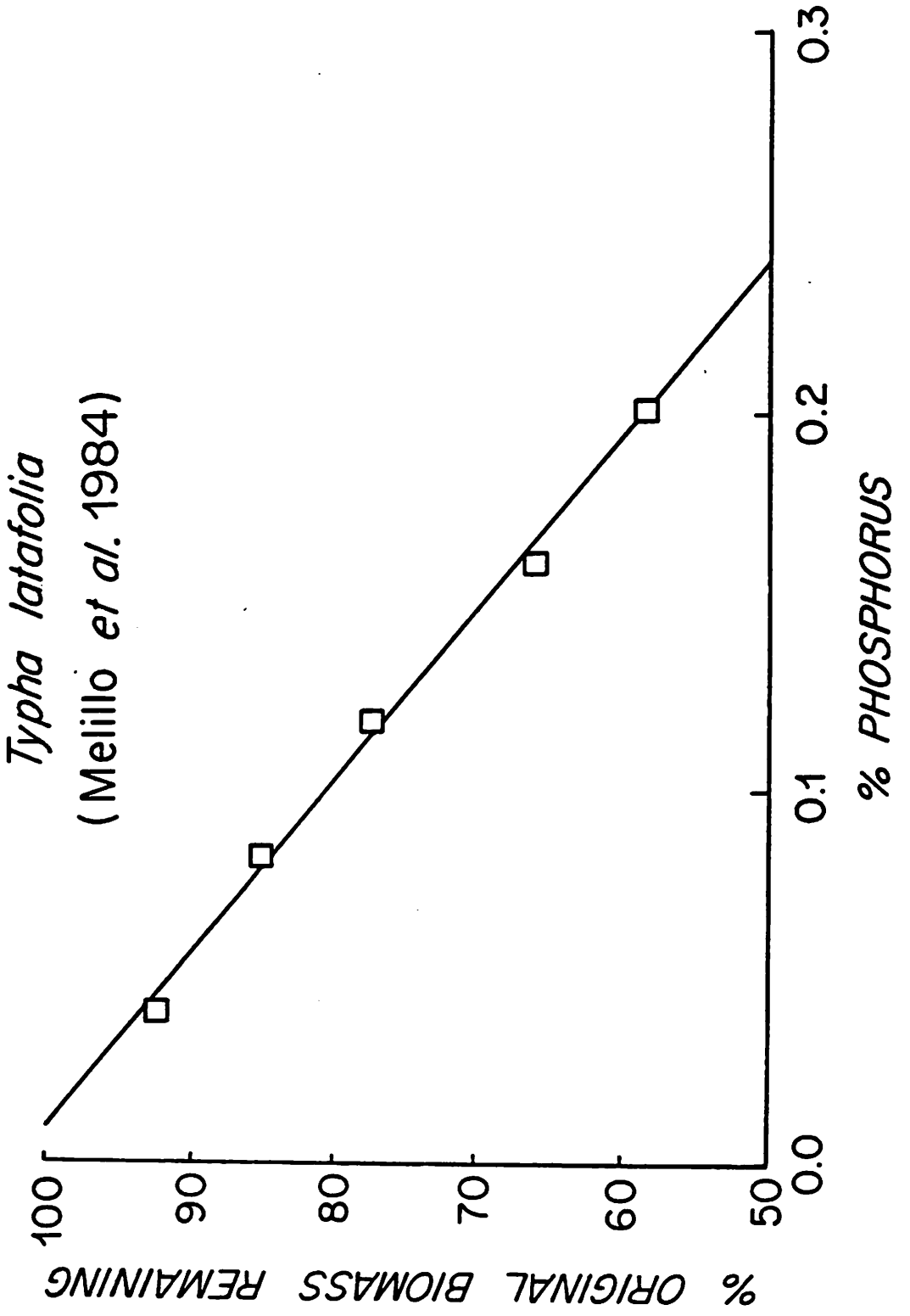

Typha latafolia
(Melillo et al. 1984)
% ORIGINAL BIOMASS REMAINING
100
90
80
70
60
50
0.0
0.1
0.2
0.3
% PHOSPHORUS

Fig. 7

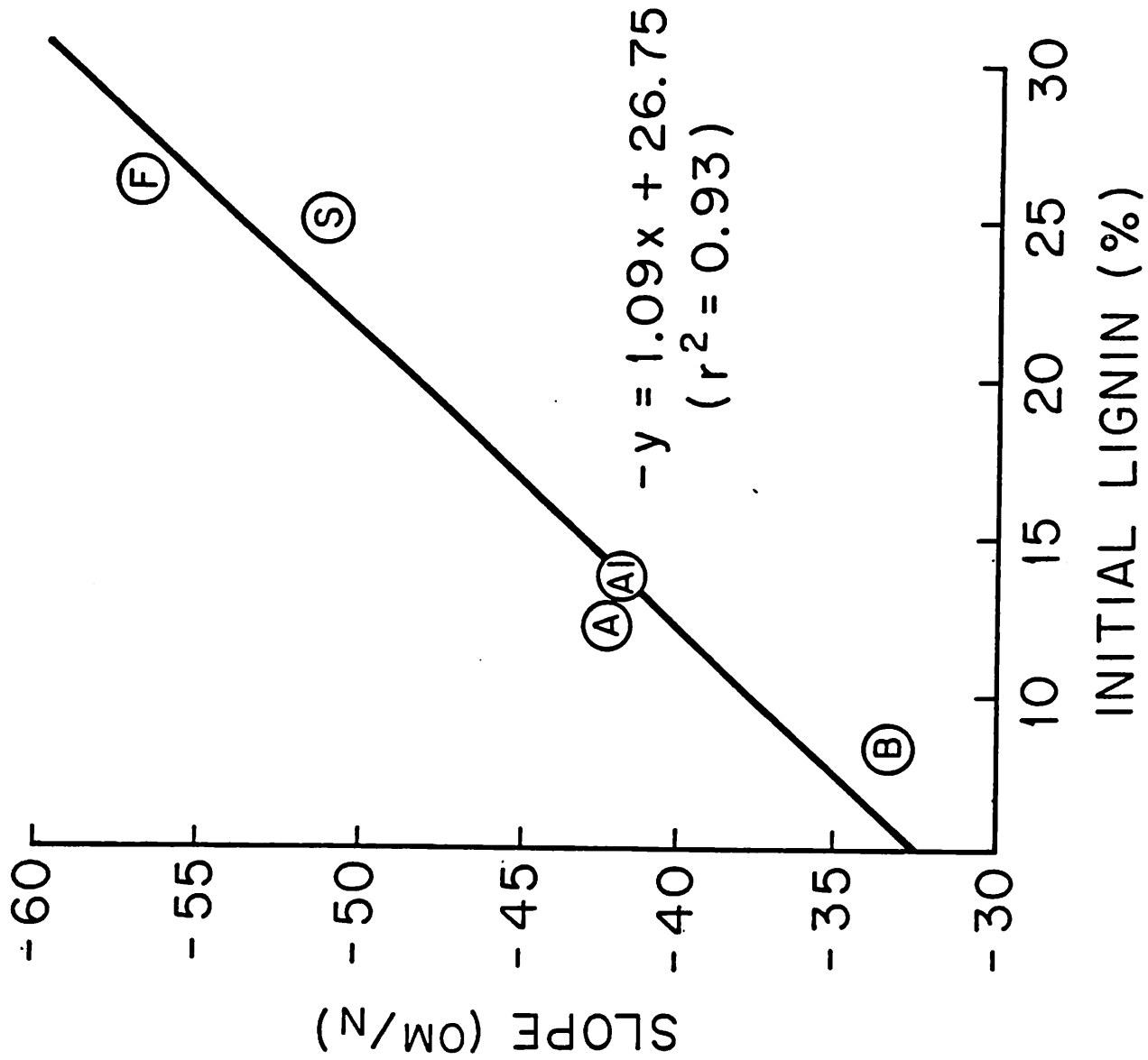

-y = 1.09x + 26.75
(r^2 = 0.93)
F
S
A
AI
B
-60
-55
-50
-45
-40
-35
-30
SLOPE (OM/N)
10
15
20
25
30
INITIAL LIGNIN (%)

Fig. 8

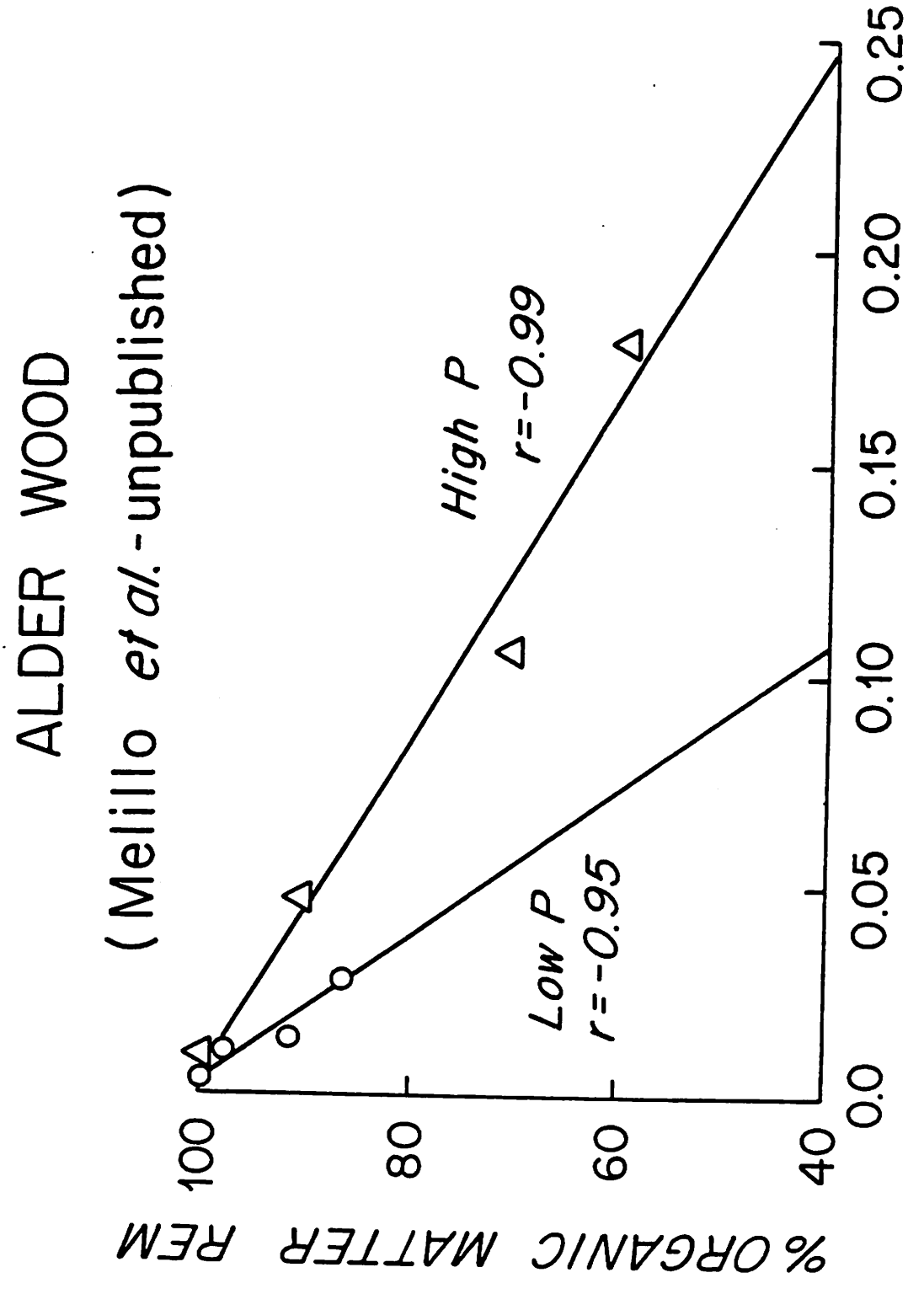

ALDER WOOD
(Melillo et al.-unpublished)
High P
r=-0.99
Low P
r=-0.95
% ORGANIC MATTER REM
100
80
60
40
0.0
0.05
0.10
0.15
0.20
0.25
% PHOSPHORUS IN REM

Fig. 9

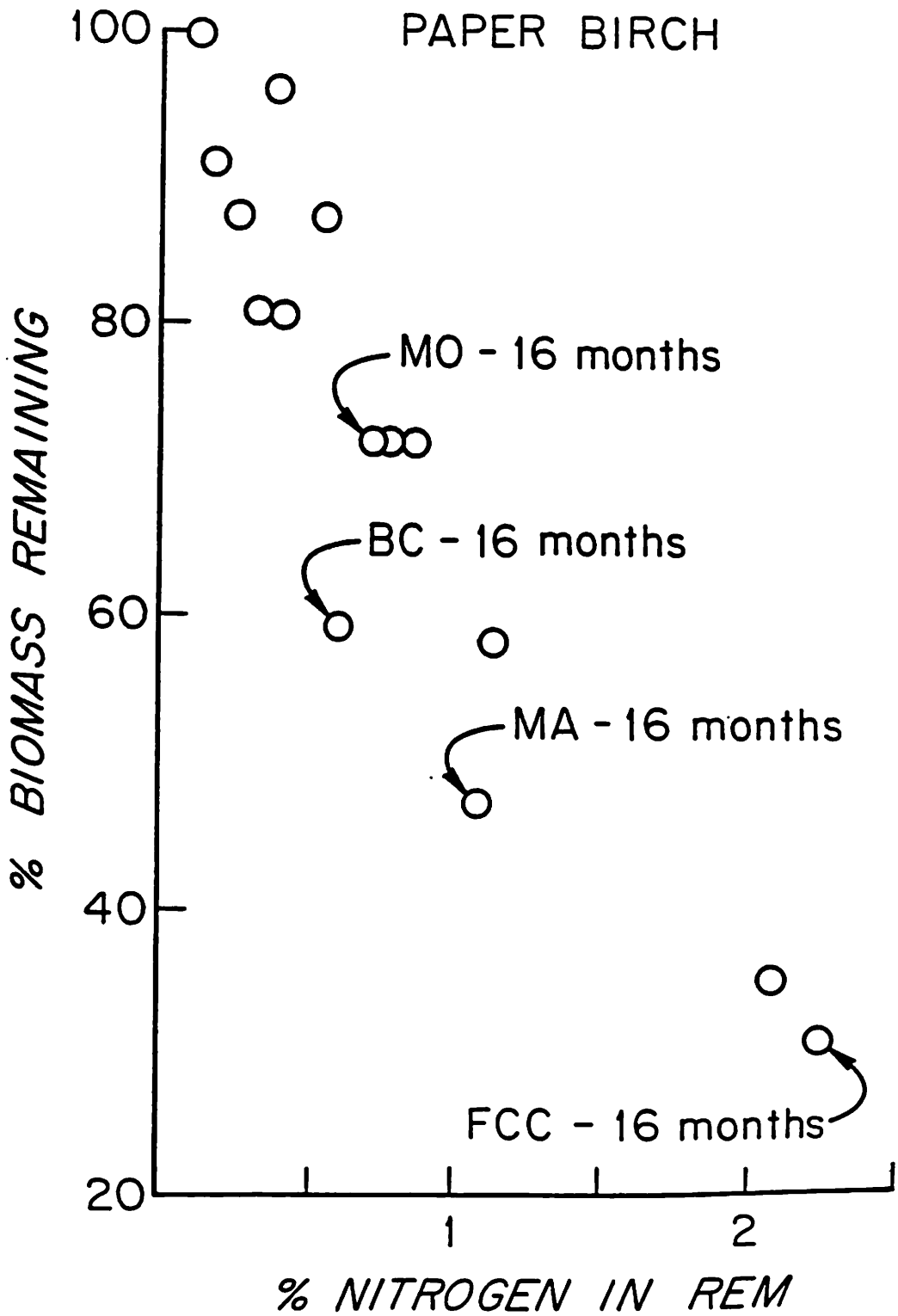

PAPER BIRCH
100
80
60
40
20
% BIOMASS REMAINING
MO - 16 months
BC - 16 months
MA - 16 months
FCC - 16 months
1
2
% NITROGEN IN REM

Fig. 10

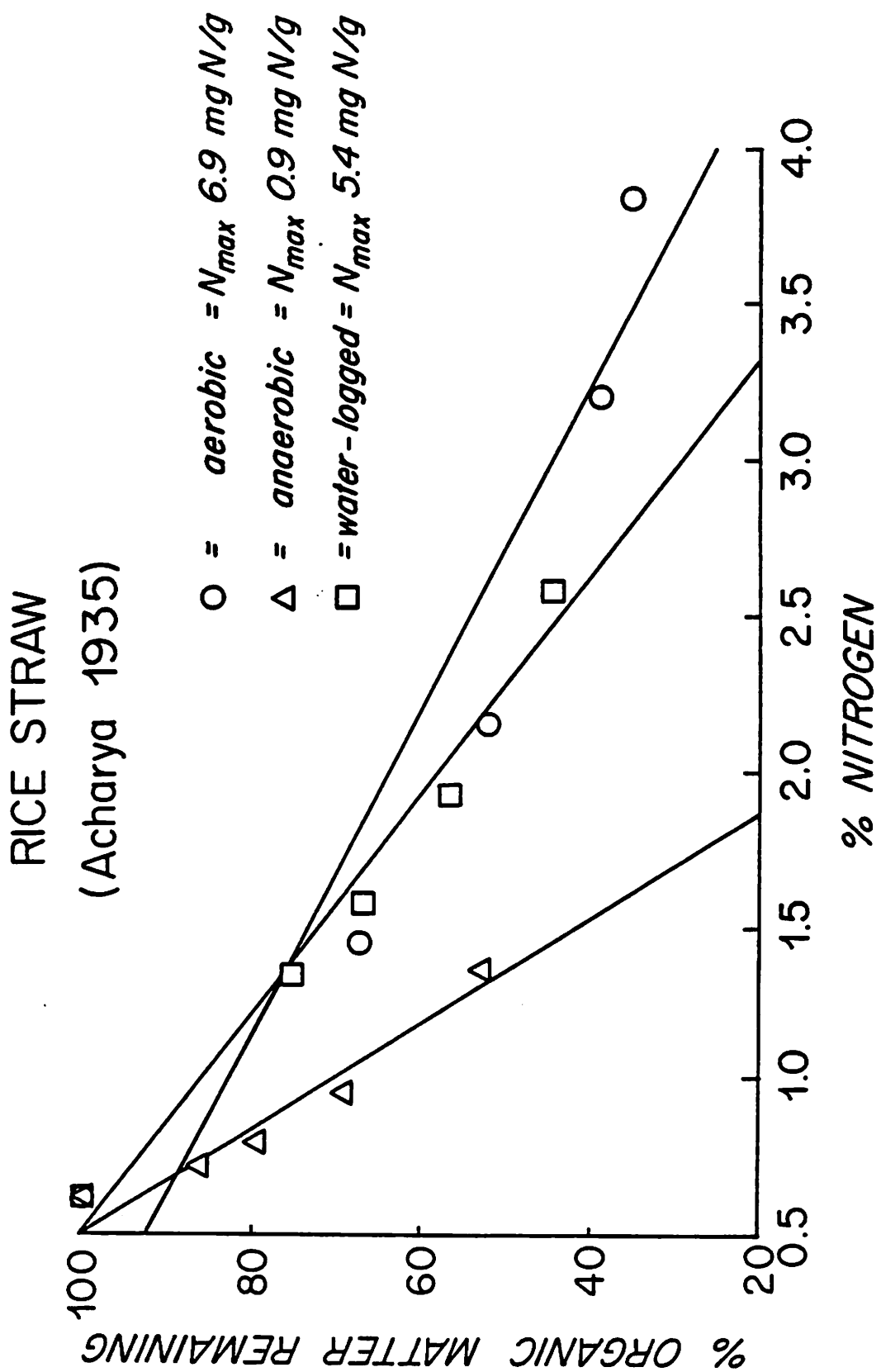

RICE STRAW
(Acharya 1935)
O = aerobic = N_{max} 6.9 mg N/g
Δ = anaerobic = N_{max} 0.9 mg N/g
□ = water-logged = N_{max} 5.4 mg N/g
% ORGANIC MATTER REMAINING
100
80
60
40
20
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
% NITROGEN

Fig. 11

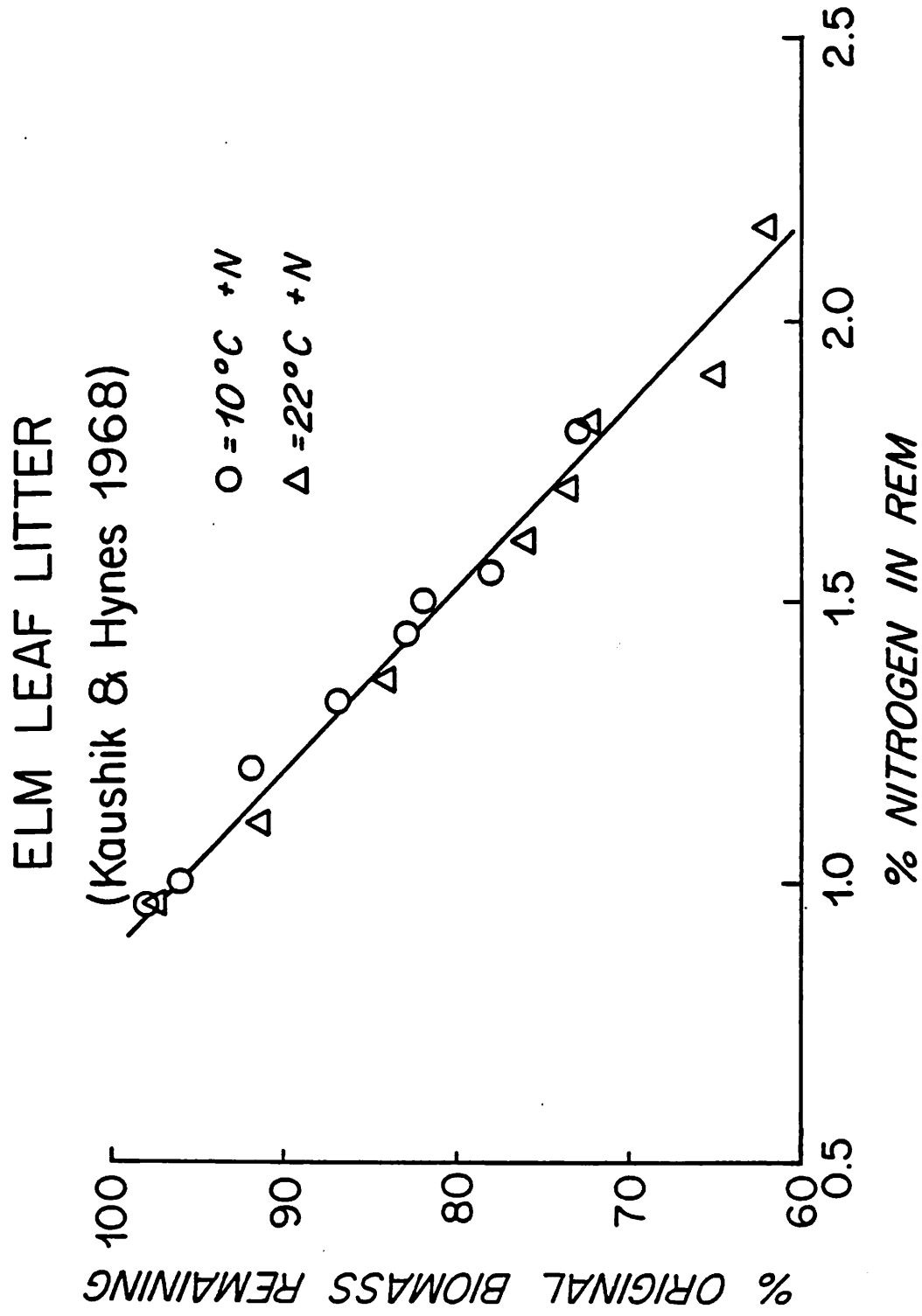

ELM LEAF LITTER
(Kaushik & Hynes 1968)
O = 10°C +N
Δ = 22°C +N
% ORIGINAL BIOMASS REMAINING
100
90
80
70
60
0.5
1.0
1.5
2.0
2.5
% NITROGEN IN REM

Fig. 12

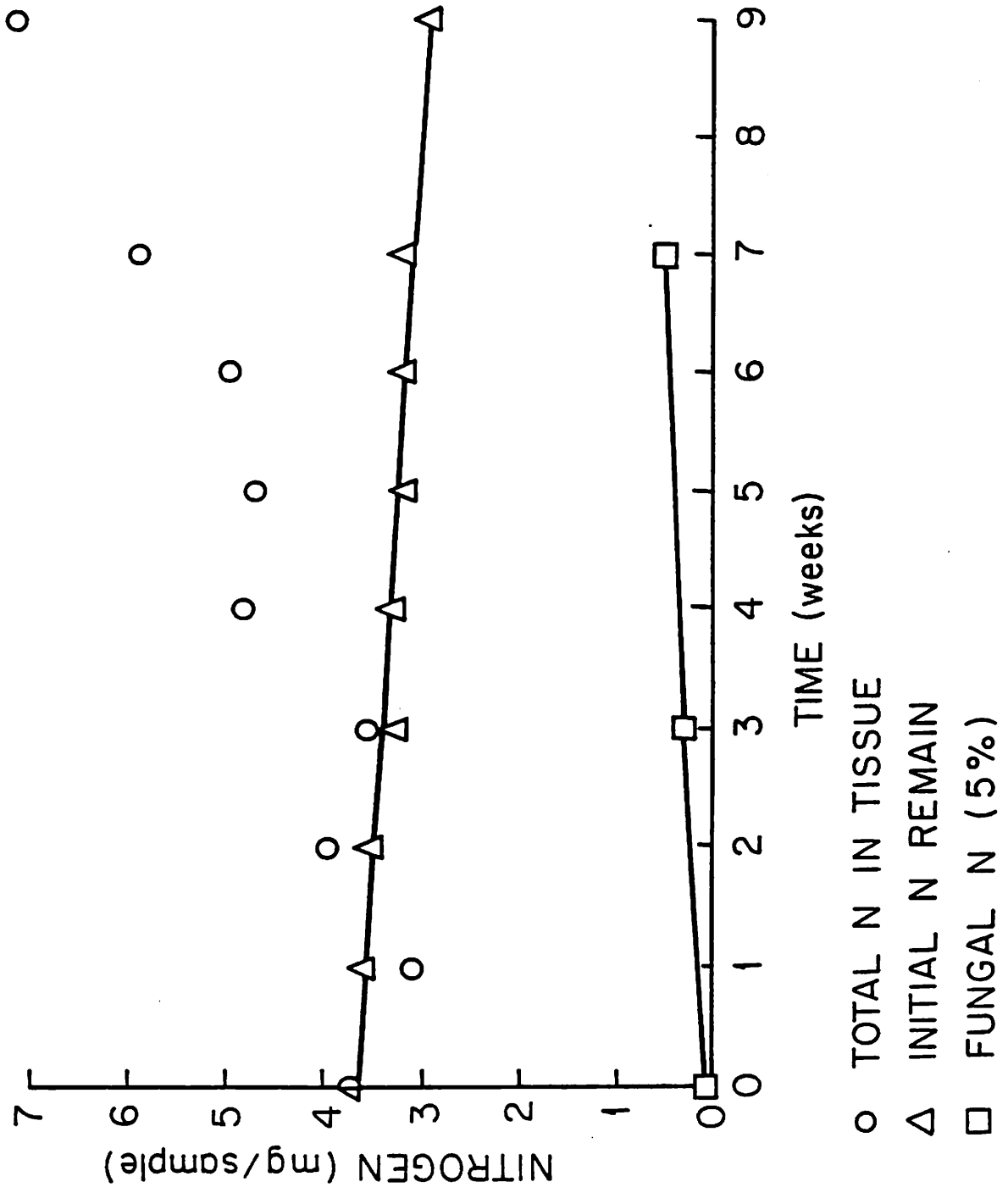

NITROGEN (mg/sample)
0
1
2
3
4
5
6
7
TIME (weeks)
0
1
2
3
4
5
6
7
8
9
o TOTAL N IN TISSUE
Δ INITIAL N REMAIN
□ FUNGAL N (5%)

Fig. 13

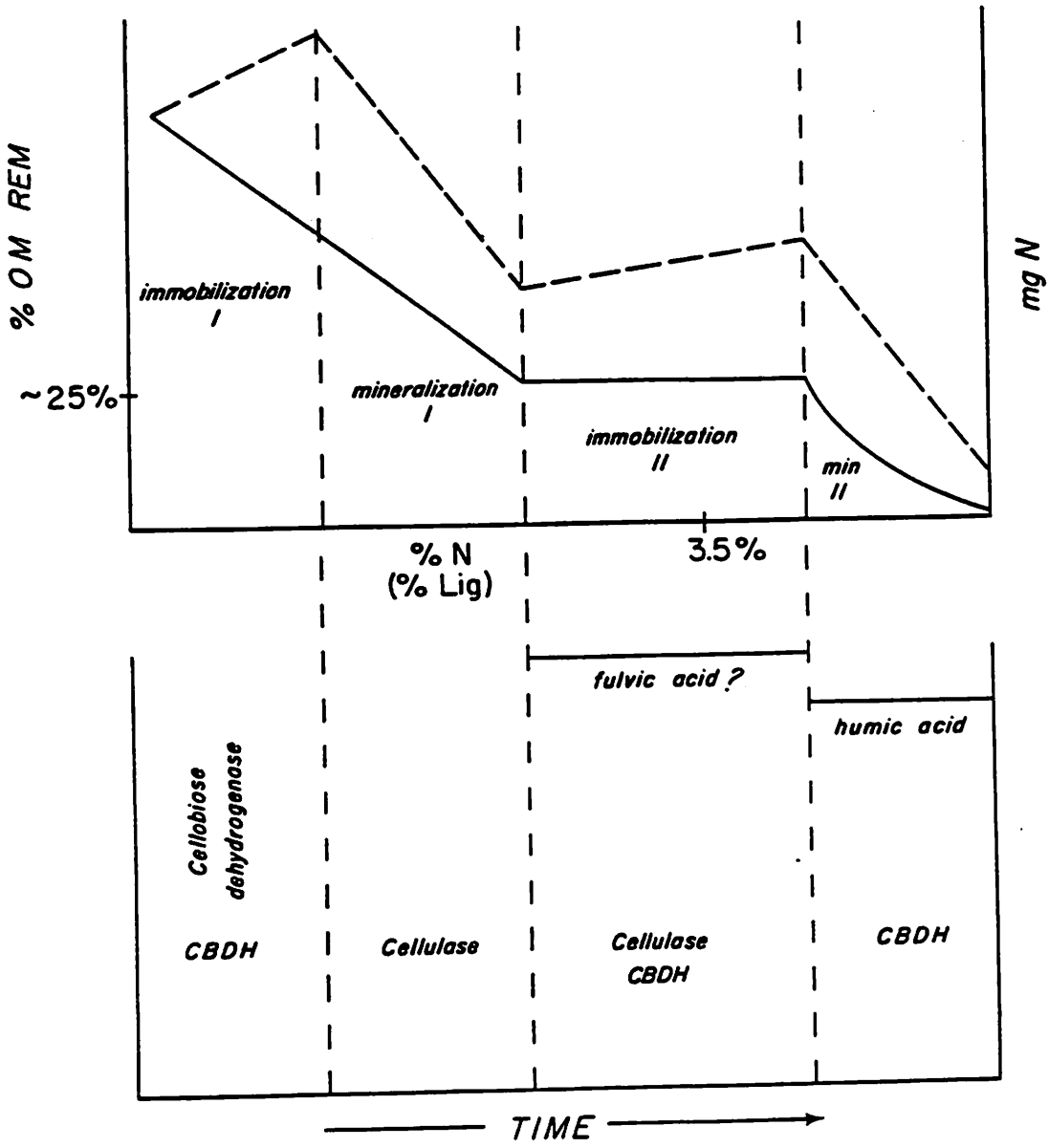

% OM REM
mg N
~25%
immobilization I
mineralization I
immobilization II
min II
% N
(% Lig)
3.5%
fulvic acid ?
humic acid
Cellobiose dehydrogenose
CBDH
Cellulase
Cellulase
CBDH
CBDH
TIME

Fig. 14

THE INFLUENCE OF BEAVER (Castor canadensis) ON THE PRODUCTION DYNAMICS OF AQUATIC INSECTS

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Biology Department
Woods Hole Oceanographic Institution

INTRODUCTION

In North America, beaver (Castor canadensis) act to significantly influence the structure and dynamics of aquatic ecosystems through their feeding and dam building activities. Some important effects are: (1) modification of channel geomorphology and hydrology through the retention of sediment, organic matter, and water, (2) creation and maintenance of wetlands, (3) modification of nutrient cycling and decomposition dynamics through the wetting of soils and the creation of anaerobic zones, and (4) modification of the riparian zone, including its composition, form, quality (lignin, nitrogen, etc.), and quantity of allochthonous inputs. This habitat modification ultimately influences the dynamics of other organisms, such as the aquatic biota, migratory birds and large mammals. Despite these apparent effects, few studies have addressed directly the environmental alterations of lotic ecosystems by beaver (see major literature reviews by Yeager and Hay 1955, Jenkins and Busher 1979, Hodgdon and Larson 1980).

The retention of sediment and organic matter by beaver dams alter the character of the substrate and, supposedly, the nature and dynamics of the invertebrate community (Sprules 1940; Hodkinson 1975). Rocky substrate is covered by fine particulate matter as the water current is reduced, with community composition shifting towards a larger proportion of invertebrates adapted to soft bottom. However, it is not known if annual production dynamics are changed, even though the community composition is altered.

The principle objective of our research is to evaluate the role of beaver as agents influencing the dynamics of aquatic ecosystems (Naiman et al. 1983 MS). The purpose of this paper is to present preliminary data on how beaver influence the diversity and production dynamics of aquatic insects emerging from beaver ponds, and to compare these data to those from unmodified sections of the same streams and larger rivers.

STUDY AREAS

The study sites are situated near Sept-Iles, Québec, on the North Shore of the Gulf of St. Lawrence, Canada. This region is Precambrian Shield with streams characterized by low nutrient concentrations (<0.3 mg N/L as nitrate and <0.003 mg P/L as orthophosphate), 5-15 mg C/L of dissolved organic carbon, about 2100 degree days annually (°C/yr), and

generally acidic brown waters (pH: 4.8-7.2). Five sites were used (Table 1): three small streams (Last Chance Creek, Beaver Creek, and Cran Carré Creek) and two rivers (the Muskrat and Matamek). All sites are situated in a pristine boreal forest of predominantly black spruce (Picea mariana) and balsam fir (Abies balsamea). Various biological and physiochemical aspects of these streams have been described by Naiman (1982, 1983a, b, c), Melillo et al. (1983), Conners and Naiman (1983), Naiman and Sedell (1981), and Power et al. (1973).

Last Chance Creek, a small second order stream draining 2.4 km^2, has a large beaver pond as its source. The stream flows through four secondary dams before entering a typical forested section. The mean annual discharge is ~0.145 m^3/s. All secondary dams are in good repair and actively maintained.

Beaver Creek, a second order stream draining 1.8 km^2, also has a large beaver pond in its headwaters. Over its 0.9 km length there are 12 abandoned or recolonized dams separated by short riffles. Mean annual discharge is ~0.113 m^3/s.

Cran Carré Creek is a third order stream draining 20.7 km^2. Thirteen dams, most of which are situated in the upper stream reaches where the forest opens into meadows, are separated by low-gradient riffles. Mean annual discharge is ~0.944 m^3/s.

The Muskrat River is a fifth order stream draining 207 km^2. In the lower reaches there are a few beaver dams which are destroyed annually by the spring freshet and rebuilt again during summer. Typical river morphology is that of a deep and narrow channel meandering between widely spaced waterfalls. Mean annual discharge is 8.4 m^3/s.

The Matamek River is a sixth order stream draining 673 km^2. There are no dams in the lower reaches, although beaver are active along the banks of slower flowing sections (e.g., tree cutting, lodges). Mean annual discharge is 13.7 m^3/s.

METHODS AND MATERIALS

Insects were collected weekly (Table 1), from May to mid-October, 1982, using emergence traps placed on the center of the water surface at each site. Traps were constructed with a wooden frame on styrofoam floats, nitex netting (200 μm), a mason jar at the apex to concentrate insects, and sampled a surface area of 0.25 m^2 (Mundie 1971). The traps were anchored in the center of the stream with ropes.

Insects were preserved in the field with 70% ethanol. In the laboratory they were sorted and identified to genus using the following keys: Ephemeroptera (Edmunds et al. 1976); Plecoptera, Trichoptera, Coleoptera, Hemiptera, and Hymenoptera (Usinger 1956), Collembola (Christiansen 1978), Diptera (McAlpine et al. 1981), and Neuroptera (Evans 1978).

Biomass of individual genera in each collection was estimated by drying representative samples at 60°C for 24 h, weighing the specimens on a Cahn 25 electrobalance, and then multiplying the unit dry weight by the number of individuals in that collection. Annual emergence was calculated by summing the biomass for each weekly collection over the ice-free season.

Generic diversity (H) was calculated for each collection using the equation:

$$H = -\sum_{i=1}^{G} (P_i)(\log_2 P_i) \qquad \text{where,}$$

P_i = proportion of total sample belonging to ith genus and G = number of genera (Krebs 1978).

Generic equitability (E) was calculated for each collection using the equation:

$$H_{max} = \log_2 G \qquad \text{and,}$$

$$E = \frac{H}{H_{max}} \qquad \text{(Krebs 1978).}$$

Analysis of variance (ANOVA) procedures were used to test for differences total numbers, emerging biomass, diversity, and equitability between sites (Sokal and Rohlf 1969). In cases where the Bartlett Test indicated a non-homogeneity of variances, the data were log-transformed to approximate a normal distribution. Student-Newman-Keuls (SNK) and least significant difference (LSD) procedures were used to compare means from individual sites when significant differences (P = 0.05) were found by ANOVA techniques.

RESULTS

Emergence

During the study 242 genera were identified from the 12 sites, with the Chironomidae being the best represented. The number of insects emerging annually ranged from 3296/m^2 in Last Chance Creek to 31,144/m^2 from an eroding beaver pond on Cran Carré Creek (Table 2). All sites, except one, were statistically similar in the total number of insects emerging each week; the only exception was the eroding pond on Cran Carré Creek which had significantly higher emergence (Table 3).

By habitat (e.g., riffle vs. pool), there was no consistent pattern for the annual biomass of emerging adults. In Last Chance Creek and

Beaver Creek there was no significant difference between beaver ponds, or between ponds and a riffle (Table 2). However, in Cran Carré Creek, where the beaver ponds had annual emergences similar to those for ponds on Last Chance Creek and Beaver Creek, annual emergence from a riffle and an eroding beaver pond were 2-6 times greater. In the Muskrat River, emergence from a riffle was twice that from a pool, but in the Matamek River emergence from a pool was nearly twice that of a riffle. Only the eroding pond and riffle on Cran Carré Creek showed a significant difference from the other sites in the biomass emerging annually (Table 3).

Beaver impoundments increase the percentage of the annual biomass composed of Chironomidae (Table 2). On Last Chance Creek, Beaver Creek, and Cran Carré Creek 19-74% ($x = 53\%$) of the total biomass from beaver ponds was Chironomidae, whereas the percentage for riffles and eroding ponds was only 30-33% ($x = 32\%$). The river sites had lower percentages than the stream sites (12-27%; $x = 21\%$), with no consistent difference between riffles and pools.

For all sites, Simuliidae formed only a few percent (0-9%; $x = 3\%$) of the annual biomass (Table 2). There were no significant differences between riffles and beaver ponds, or between any site.

The pattern of total emergence over the season was similar between sites within the same stream (Fig. 1). Beaver Creek was the only exception. There, peak emergence from a beaver pond preceeded that from a riffle by about two months. There were considerable differences in emergence pattern between streams, however. For most streams peak emergence was in July and August. For Last Chance Creek, and some sites on Beaver Creek and Cran Carré Creek, peak emergence occurred in May and June (Fig. 1). Nevertheless, none of these differences could be attributed directly to beaver activity.

To better visualize community changes, insects from four major orders (e.g., Diptera, Plecoptera, Trichoptera, and Ephemeroptera) were grouped, and the percentage contribution of each to total number and biomass calculated (Fig. 2). In terms of numbers, Diptera comprised 60.2-94.2% ($x = 83.1\%$) of all emerging insects, with no significant difference between sites (Table 3), and 33 to 71 ($x = 48$) of the genera collected at a site. As biomass, Diptera contributed 12.1 to 87.3% ($x = 43.6\%$) of the total, with the two dam sites in Last Chance Creek significantly greater than all the others (Table 3).

There were significantly greater numbers of Plecoptera emerging from the Matamek River and one site on the Muskrat River, and significantly greater biomass from both sites on the Matamek River (Table 3). For the Ephemeroptera, the pond on Beaver Creek had significantly greater numbers of emerging adults, while several sites on Cran Carré Creek and Beaver Creek showed a significantly greater biomass (Table 3). For Trichoptera, only the eroding pond on Cran Carré Creek and a beaver pond exhibited significantly greater numbers of emerging adults; there was no significant

difference between any site with regards to biomass (Table 3). In general, these analyses demonstrate the direct effect of beaver on the percentage composition of Diptera, and possibly Ephemeroptera, but fail to demonstrate any direct effect on Plecoptera and Trichoptera, either in terms of total numbers or biomass.

Diversity

Diversity was generally highest from June through August while equitability remained nearly constant from May to late-September (Fig. 3). Mean generic diversity ranged from 1.77 to 3.00 and mean equitability from 0.57 to 0.82, with no coherent patterns (Table 2) that could be directly attributed to beaver activity. Diversity was greatest at the eroding pond on Cran Carré Creek; but a pond on Cran Carré Creek and a pond on the Muskrat River were also significantly higher than the other sites (Table 3). There was no significant difference in equitability between any site (Table 3).

DISCUSSION

Our results are similar to those described by Clifford (1978) and Hodkinson (1975) for streams and beaver ponds in Alberta, Canada. In those studies the biomass of emerging adults are not reported but the timing and duration of emergence, the number of genera involved, and the dominance of Chironomidae are nearly identical to what we have reported here.

The fact that we could not demonstrate a direct effect of beaver on the number or biomass of emerging insects may be due, in part, to the placement of our traps. Originally, it was felt that emergence traps set in the center of a stream would provide a reliable index of secondary production that could be compared from site to site. However, in many cases, a large proportion of stream insects require physical structures on the stream margins for emergence and, thus, our estimates are an underestimate of the total (Merritt and Cummings 1978). On the other hand, the traps may provide the physical structure necessary for emergence and hence give an overestimate for those insects that emerge through the water column, such as the Chironomidae. The results would be seriously biased if a larger proportion of the community consistently emerged from the stream margin in either riffles or beaver ponds, or used the traps as physical structures for emergence, and would assist in explaining why differences in annual production could not be demonstrated between these two very different habitats.

Nevertheless, there are changes taking place within the stream community over both the short and long term. Dams slow water currents and store substantial organic matter. As Cummins and Lauff (1969), Hodkinson (1975), and Reice (1980) have shown, substrate type has a strong influence on the character of the benthic community and the particular species of

which it is composed. One consequence of shifting to a soft bottom substrate is a proportional increase in Chironomidae as we have reported here but there are undoubtably many other adjustments made at the generic and species levels we have not yet been able to examine.

One consequence of beaver ponding streams, less well appreciated, is the "reservoir effect" (Baxter 1977, Duthie and Ostrofsky 1982). When impoundments are created and flood adjacent terrestrial terrain, nitrogen and phosphorus are leached, resulting in increased aquatic production for one or two years. This trophic upsurge reappears when impoundments are drained and refilled as nutrients, previously trapped in sediments, are released. We believe this phenomenon to be responsible for the significantly higher production rate measured at the eroding beaver dam on Cran Carré Creek (T-2). It has long been known among fish culturists that the productivity of fish ponds may be increased by draining and allowing a pond to remain dry for a period of time. In this application, which is not unlike the long-term effects of beaver ponds, the periodic drawdown and desiccation of sediments enhances ecosystem productivity (Duthie and Ostrofsky 1982).

Finally, beaver act to increase total system production by increasing the aquatic surface area and the extent of the productive ecotone between the terrestrial and aquatic environments. The water surface area is increased 10 to 20-fold, with a corresponding increase in total aquatic productivity (Naiman, unpublished data). Most of this newly created habitat can be classified as highly productive wetlands. When a new pond is formed, shoreline development (i.e., the ratio of shoreline length to the circumference of a circle of the same area as the pond) is almost always higher than for natural ponds (Baxter 1977). Where littoral zone processes are important, the total mass of aquatic insects emerging each year will be significantly augmented by beaver activity.

Ponds formed by beaver dams also differ from natural ponds in their longitudinal profiles, which can influence community dynamics. Most natural ponds are deepest near the middle, whereas beaver ponds are almost always deepest just upstream of the dam. One consequence of this is that surface currents passing down the pond will not dissipate themselves in shallow water as they do in natural ponds, but may be deflected downward or reflected backward at the dam. The influence of this phenomenon on benthic organisms is through alteration of the temperature and oxygen regimes, which acts to keep the pond well mixed throughout the year.

Some results of this study have been difficult to explain at the level of examination attempted so far (i.e., generic) but are only one facet of a multidisciplinary project investigating how beaver influence the dynamics of stream ecosystems. It is expected, when analyses of the invertebrate community are completed, these data in combination with results of concurrent investigations on channel geomorphology, allochthonous inputs, nutrient cycling, and decomposition, will aid in quantifying the direct influence of beaver on stream ecosystem dynamics.

ACKNOWLEDGEMENTS

This research was supported by the National Science Foundation (DEB-8105677). We thank Gilles Lebel for assistance in the field and J. Stanford, R. Morin and W. L. Montgomery for constructive comments on the manuscript. Contribution No. 5479 of the Woods Hole Oceanographic Institution and No. 74 of the Institution's Matamek Research Station.

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Table 1. Characterization of sites used in 1982 to examine insect emergence in Québec.

SITE/TRAP NO.	DESCRIPTOR	TEMPERATURE RANGE (°C)	ANNUAL DEGREE DAYS (°C/yr)	pH RANGE	RANGE OF WATER DEPTH (cm)	RANGE OF WATER VELOCITY (cm/s)	SUBSTRATE
Last Chance Creek		0.1-22.0	2217	5.1-5.3			
T-11	old dam				21- 62	0.0- 14.9	FPOM, fine sand
T-12	new dam				22-110	0.0- 5.2	FPOM, fine sand
Beaver Creek		0.1-21.0	2069	6.0-7.0			
T-5	old dam				5-114	0.0- 20.0	FPOM, silt
T-6	riffle				21- 49	2.5- 55.5	Coarse sand, rock
Cran Carré Creek		0.1-22.0	1939	5.8-6.5			
T-1	medium-aged				60-114	1.0- 43.5	FPOM
T-2	eroding dam				5- 89	2.1- 62.5	CPOM
T-3	riffle				11- 57	7.6-111.1	Cobble
T-4	medium-aged				14-120	3.2- 62.5	Sand
Muskrat River		0.1-20.1	2157	4.9-6.1			
T-7	pool				73-155	3.5- 45.5	Fine sand
T-8	riffle				50-152	0.0-100.0	FPOM
Matamek River		0.1-21.0	2225	4.8-6.0			
T-9	riffle				5-190	15.9- 83.3	Cobble, pebbles
T-10	pool				61-210	15.4- 55.5	Sand, pebble

Table 2. Emergence of adult insects, composition, generic diversity, and generic equitability.

SITE/TRAP NO.	TOTAL EMERGENCE NUMBERS (No./m^2/yr)	TOTAL EMERGENCE BIOMASS (mg DW/m^2/yr)	BIOMASS COMPOSITION PERCENT CHIRONOMIDAE	BIOMASS COMPOSITION PERCENT SIMULIIDAE	BIOMASS COMPOSITION PERCENT OTHERS	NUMBER OF GENERA CHIRONOMIDAE	NUMBER OF GENERA SIMULIIDAE	NUMBER OF GENERA OTHERS	DIVERSITY x	DIVERSITY SE	EQUITABILITY x	EQUITABILITY SE
Last Chance Creek												
T-11	4,716	832.2	74	2	24	47	3	14	2.31	0.18	0.77	0.03
T-12	3,296	522.2	54	9	37	25	2	15	2.08	0.26	0.69	0.06
Beaver Creek												
T-5	9,604	760.5	64	1	35	42	1	45	1.77	0.21	0.57	0.06
T-6	8,280	684.4	30	6	64	44	2	43	2.37	0.24	0.65	0.06
Cran Carré Creek												
T-1	5,552	524.6	54	1	45	49	1	30	2.75	0.18	0.82	0.03
T-2	31,144	3835.0	33	5	62	59	4	56	3.00	0.15	0.77	0.05
T-3	23,772	1599.1	33	4	63	36	4	50	2.35	0.19	0.74	0.05
T-4	6,152	717.6	19	4	77	39	2	31	2.23	0.18	0.73	0.05
Muskrat River												
T-7	4,748	656.0	27	1	72	34	2	32	2.44	0.23	0.77	0.02
T-8	5,084	1161.3	24	3	73	36	2	38	3.00	0.33	0.79	0.04
Matamek River												
T-9	8,596	1302.7	20	1	79	33	2	44	2.28	0.28	0.65	0.08
T-10	10,048	2058.5	12	0	88	35	2	23	2.09	0.26	0.68	0.07

Table 3. Summary of statistical analyses performed on the data. For each insect order the percentage of total emergence is given for numbers and biomass.

Parameter	x + SE[2]	ANOVA Significance (p)	Sites Showing a Significant (P= 0.05) Difference[1]	Multiple Range Test Used
No/m^2/wk	571 ± 68.7	<0.001	T-2	LSD
Biomass mg DW/m^2/wk	70 ± 7.6	0.013	T-2; T-3	LSD, Log Transform
Diversity	2.4 ± 0.07	0.008	T-2; T-1, T-7	LSD
Equitability	0.70 ± 0.232	0.138	None	-
Diptera				
% No./m^2/wk	72.8 ± 29.3	0.367	None	-
% Biomass/m^2/wk	47.1 ± 35.7	0.001	T-11, T-12	LSD
Plecoptera				
% No./m^2/wk	6.9 ± 17.7	<0.001	T-8, T-9, T-10	SNK, Log Transform
% Biomass/m^2/wk	11.9 ± 25.9	<0.001	T-9, T-10	SNK
Ephemeroptera				
% No./m^2/wk	3.9 ± 11.6	<0.001	T-5	SNK
% Biomass/m^2/wk	14.3 ± 27.4	<0.001	T-5, T-4, T-1; T-2 T-6	LSD
Trichoptera				
% No./M^2/wk	4.9 ± 11.9	0.025	T-2, T-4	SNK, Log Transform
% Biomass/M^2/wk	19.9 ± 29.6	0.497	None	-

1) Sampling sites with significantly higher values. Semicolons separate subgroups that are significantly different from other sites.

2) Mean ± standard error.

FIGURE CAPTIONS

Fig. 1. The annual pattern of emergence and total biomass of aquatic insects captured by surface traps for each site in 1982; total biomass (——), Chironomidae (----), all others (— — —).

Fig. 2. The percentage composition (e.g., numbers and biomass), by insect order, of adults emerging at the water surface for each site in 1982.

Fig. 3. The pattern of generic diversity and equitability for adult insects emerging at the water surface during the 1982 growing season. Refer to Table 1 for explanation of codes.

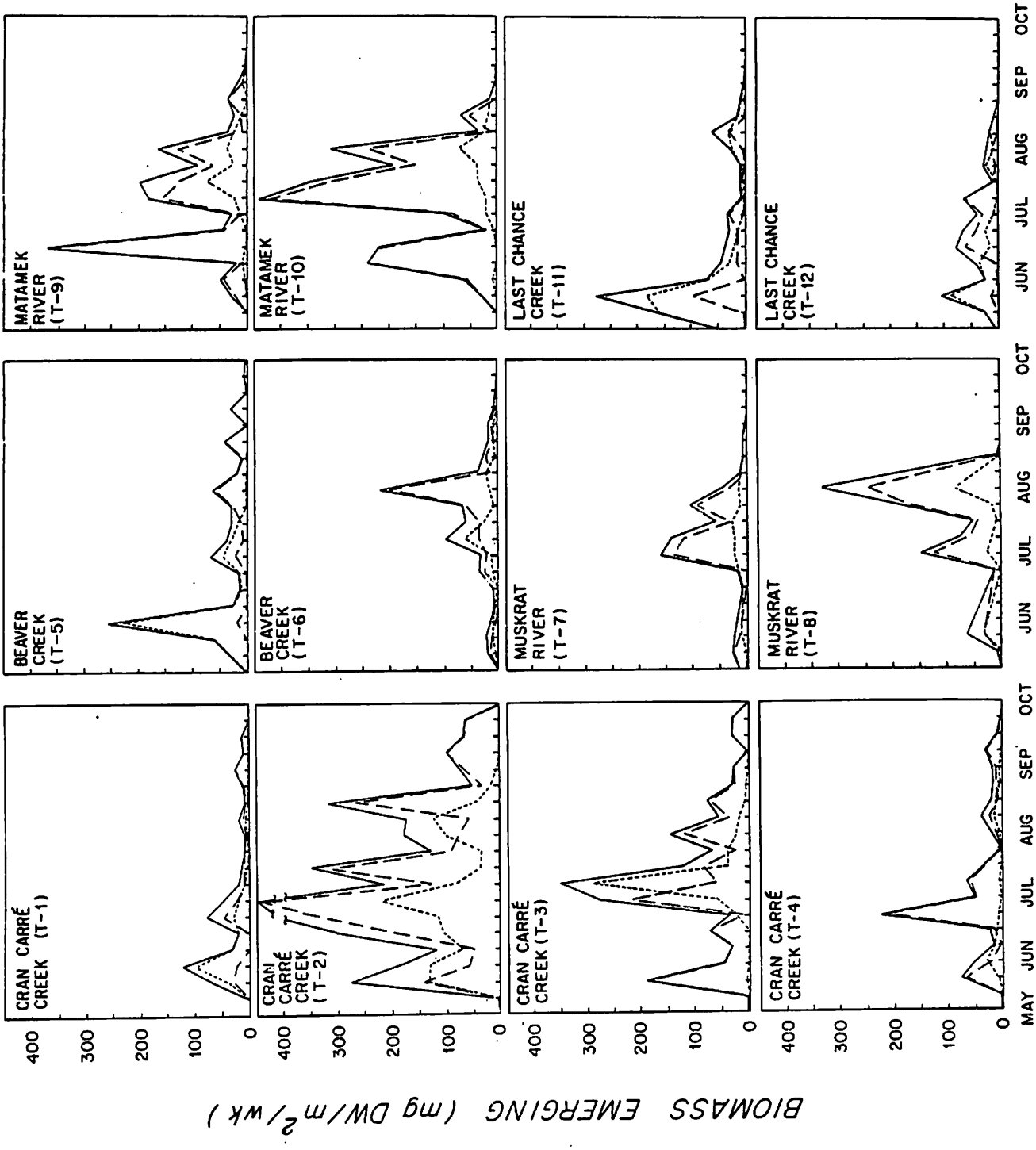
CRAN CARRÉ CREEK (T-1)
CRAN CARRÉ CREEK (T-2)
CRAN CARRÉ CREEK (T-3)
CRAN CARRÉ CREEK (T-4)
BEAVER CREEK (T-5)
BEAVER CREEK (T-6)
MUSKRAT RIVER (T-7)
MUSKRAT RIVER (T-8)
MATAMEK RIVER (T-9)
MATAMEK RIVER (T-10)
LAST CHANCE CREEK (T-11)
LAST CHANCE CREEK (T-12)
0
100
200
300
400
MAY JUN JUL AUG SEP OCT
BIOMASS EMERGING (mg DW/m²/wk)
1982

Fig. 1

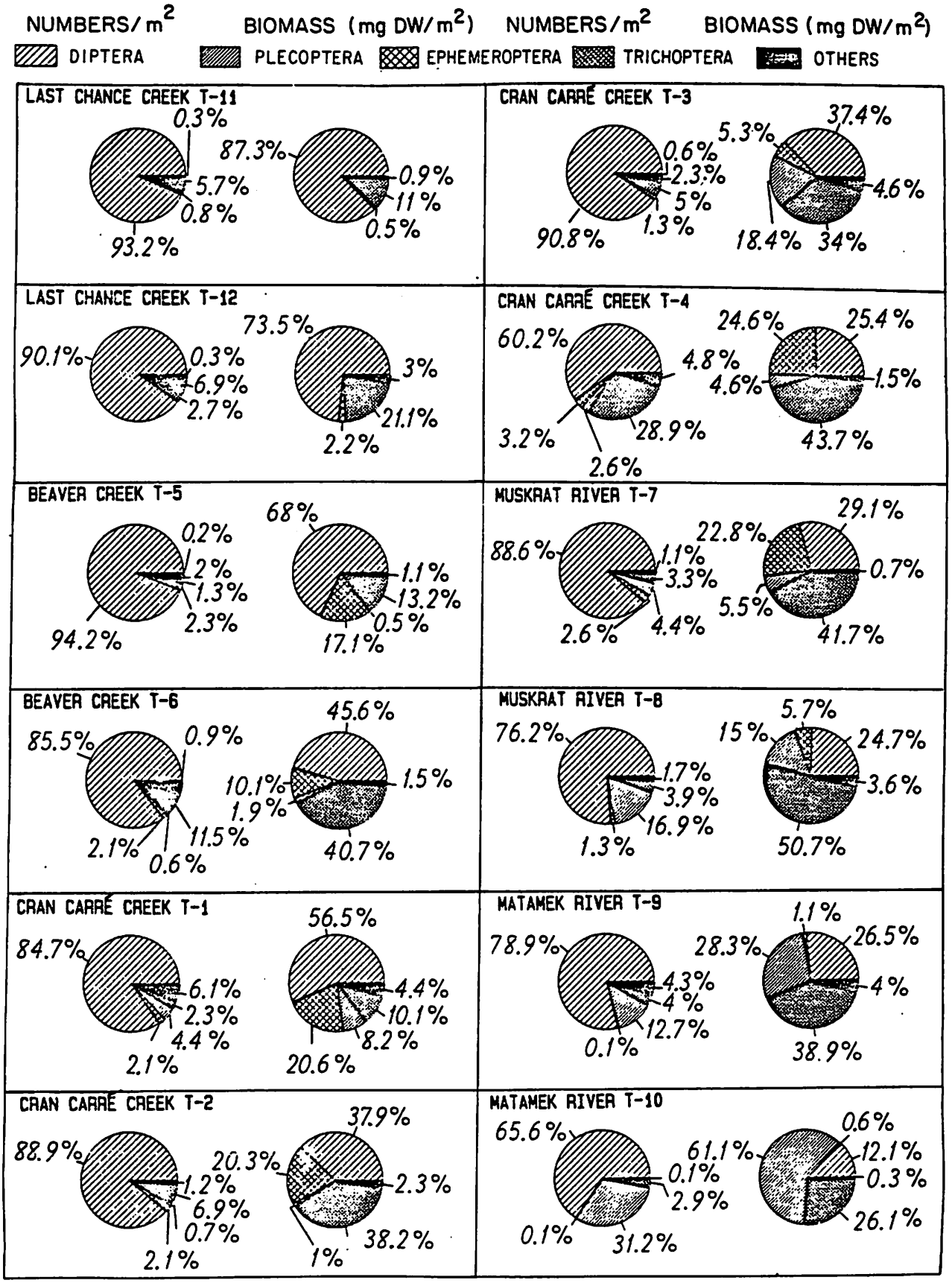
NUMBERS/m²
BIOMASS (mg DW/m²)
NUMBERS/m²
BIOMASS (mg DW/m²)
DIPTERA
PLECOPTERA
EPHEMEROPTERA
TRICHOPTERA
OTHERS
LAST CHANCE CREEK T-11
0.3%
87.3%
5.7%
0.9%
11%
0.8%
0.5%
93.2%
CRAN CARRÉ CREEK T-3
37.4%
5.3%
0.6%
2.3%
4.6%
5%
1.3%
90.8%
18.4%
34%
LAST CHANCE CREEK T-12
73.5%
90.1%
0.3%
3%
6.9%
21.1%
2.7%
2.2%
CRAN CARRÉ CREEK T-4
24.6%
25.4%
60.2%
4.8%
4.6%
1.5%
3.2%
28.9%
43.7%
2.6%
BEAVER CREEK T-5
68%
0.2%
2%
1.1%
1.3%
13.2%
2.3%
0.5%
94.2%
17.1%
MUSKRAT RIVER T-7
29.1%
22.8%
88.6%
1.1%
3.3%
0.7%
5.5%
2.6%
4.4%
41.7%
BEAVER CREEK T-6
45.6%
85.5%
0.9%
10.1%
1.5%
1.9%
11.5%
2.1%
0.6%
40.7%
MUSKRAT RIVER T-8
5.7%
76.2%
15%
24.7%
1.7%
3.9%
3.6%
16.9%
1.3%
50.7%
CRAN CARRÉ CREEK T-1
56.5%
84.7%
6.1%
4.4%
2.3%
10.1%
4.4%
8.2%
2.1%
20.6%
MATAMEK RIVER T-9
1.1%
78.9%
28.3%
26.5%
4.3%
4%
4%
12.7%
0.1%
38.9%
CRAN CARRÉ CREEK T-2
37.9%
88.9%
20.3%
2.3%
1.2%
6.9%
0.7%
38.2%
2.1%
1%
MATAMEK RIVER T-10
0.6%
65.6%
61.1%
12.1%
0.1%
0.3%
2.9%
26.1%
0.1%
31.2%

Fig. 2

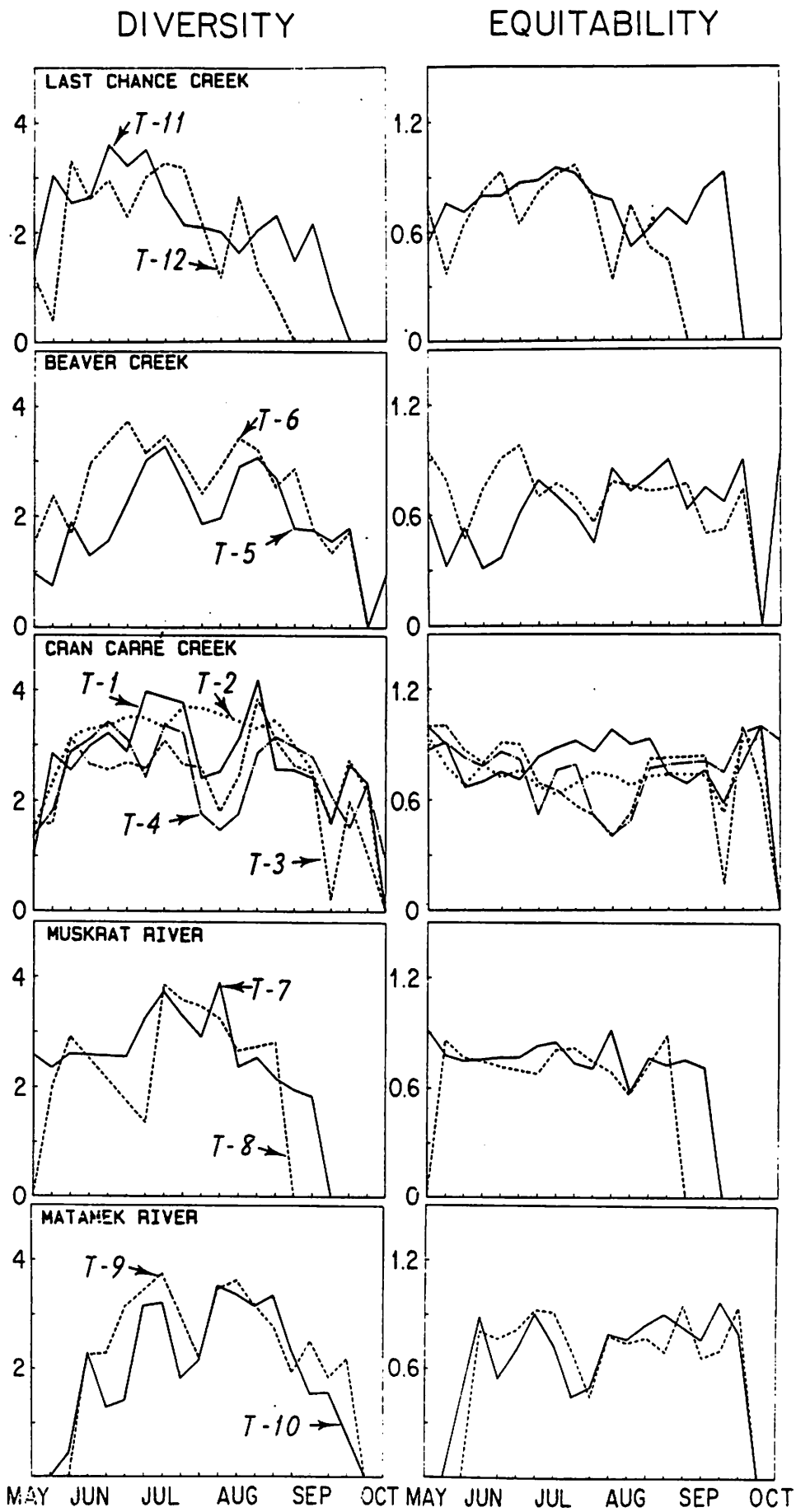
DIVERSITY
EQUITABILITY
LAST CHANCE CREEK
T-11
T-12
BEAVER CREEK
T-6
T-5
CRAN CARRÉ CREEK
T-1
T-2
T-4
T-3
MUSKRAT RIVER
T-7
T-8
MATANEK RIVER
T-9
T-10
0
2
4
0.6
1.2
MAY
JUN
JUL
AUG
SEP
OCT

Fig. 2

THE EFFECTS OF VERTEBRATE PREDATION ON MACROBENTHIC COMMUNITIES IN STREAMS WITH AND WITHOUT INDIGENOUS FISH POPULATIONS

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INTRODUCTION

The issue of the role of predators in regulation of community structure has been a major one in ecology since Paine's landmark paper of 1966. Predation has been demonstrated to be a major determinant of community structure in many aquatic ecosystems including the rocky intertidal zone, planktic and benthic communities in lakes, and freshwater microcosms. Recent studies in ponds have shown the importance of fish predators to the benthic community (Gilinsky 1984; Crowder and Cooper 1982; Hall, Cooper and Werner 1969). In ponds the bluegill sunfish, Leopomis macrochirus, functions as a structuring agent by size-selective and habitat specific predation. Changes in fish density (Gilinsky 1984) or habitat complexity (Crowder and Cooper 1982) have major effects on the benthic community.

When similar questions about the role of vertebrate predation in streams are posed, the answers are quite different. Reice (1983) manipulated patches of substrate in New Hope Creek, NC, U.S.A., to either permit or restrict access of fish. The two substrate types [cobbles with mean length ($\pm$ SE) = 12.4 $\pm$ 0.346 cm and pebbles with mean length ($\pm$ SE) = 4.0 $\pm$ 0.07 cm] produced radically different communities. However, the communities on the same type of substrate, with and without fish, were nearly replicates of one another. Allen (1982) removed trout from a 1200 m reach of a Colorado, U.S.A. mountain stream and compared the structure of the benthic community to control reaches upstream and downstream. He could find no significant differences in the communities due to the presence or absence of trout. In an 18 month long study of the role of fish predation in second order streams (S.R. Reice, unpublished MS) only minor species specific responses were detected, but no broad community changes. So, the only published experimental tests of the role of fish on lotic community structure show that fish predation causes no significant effects.

It was our goal to expand these few experiments into the pristine streams of the Côte Nord. By manipulating the presence or absence of vertebrate predators in benthic cages we can pinpoint the role of the predator in determining community structure in the stream. We conducted a set of two experiments in each of two streams. The streams had a normal fish fauna or no fish at all. These experiments focus on experienced and "naive" faunas with respect to fish. The experiments we conducted at Matamek this summer sought to improve our understanding of the role of fish and other vertebrate predators in Québec streams.

Hypothesis: The effect of vertebrate predation will differ between streams with and without resident fish populations.

METHODS

Study Sites:

Two 3rd order streams were studied. Cran Carré Creek flows directly into the St. Lawrence River. Low Hope Creek flows into Lac Mechant. Both streams have beaver ponds upstream of our study sites. The physical data from Summer 1983 is summarized in Table 1. The main biological difference between them is that Cran Carré Creek has salamanders (Eurycea bislinata) and three species of fish (Table 1), while Low Hope Creek has salamanders but no indigenous fish populations.

Experimental Design:

Two predator manipulation experiments were conducted in each stream. These manipulations are summarized in Table 2. The experiments were carried out in benthic cages of similar design to those of Peckarsky (1979). The cages are 20 x 30 cm by 10 cm deep. The cages had 3 mm mesh side panels (30 x 10 cm) to permit migration of aquatic invertebrates. The tops, bottoms, and end panels were 0.8 mm mesh.

The experimental protocol was as follows. Twenty cages were filled with cobble sized rocks and left open (i.e., top removed) for colonization. They were left open for 2 1/2 weeks. Then five cages were sampled and designated I for Initial Community. All vertebrate predators were removed from all the remaining 15 cages. Then one predator was stocked in each of five P (for predator cages). The tops were then attached to create the vertebrate predator inclusion treatment. In five other cages, the tops were affixed to exclude vertebrate predators. These were the NP (for No predator) cages. The final five cages were left open (and designated 0) to allow free movement of predators and other species. After 9-10 days all cages were removed.

Samples were washed in the field through a #60 Tyler Series sieve (250 m). All predators from P cages were recovered live. All species were preserved in 95% ethyl alcohol. All taxa were keyed to the lowest feasible taxonomic level (usually to genus). Statistical analysis was by one way ANOVA (Tukey's Honestly Significant Difference Test (HSD)). All four treatments were compared for total number of individuals (N), species richness (S), species diversity (H^1 and e^{H1}) and the abundances of the common taxa. All analyses of taxa were done following a ln (N+1) transformation to homogenize variances. Each experiment was analyzed separately.

RESULTS

I. Low Hope Creek - Round 1

In this experiment the indigenous salamanders, Eurycea bislineata, were manipulated. The results are shown in Table 3 (A and B). Both number of individuals and number of species showed no significant effect of the predation manipulation. The fact of increased individuals in the 0 treatment shows that immigration via drift continued. All closed cages (P + NP) had significantly fewer individuals (approximately 1/2 of 0 levels). Two measures of diversity show that P cages had lower diversity than all others. These data combined with a nonsignificant difference in species richness show that the reduction in H^1 diversity in P cages was due to increased dominance (lower evenness). In the five taxa which showed a significant treatment effect none had a difference between P and NP cages. Salamander presence or absence had little overall effect on any parameter except diversity.

II. Cran Carré Creek, Round I

Trout fry were rare at the time the experiment was started (early Spring). Therefore three Pungitius pungitius (nine-spined sticklebacks) and two Salvelinus fontinalis (brook trout) were used as predators in the five P cages.

None of the community parameters (Table 4A) responded to the treatment. Variations in N, S, H^1 and e^H were minor and insignificant. Of the seven taxa common enough for statistical analysis, only Simulium had different abundances based on the predation treatment (Table 4B). There were significantly fewer Simulium when fish were absent than in all other treatments. In no case did fish predation significantly reduce the numbers of individuals in a taxon below the levels in fish exclusion cages.

III. Low Hope Creek - Round 2

We introduced brook trout fry (Salvelinus fontinalis) into the predator cages. Presence of absence of trout had no significant impact on any community parameter or individual taxon (Table 5). The mean number of large invertebrate predators (excluding chironomids) was 18.60 in the no fish cages. It was only 7.60 in the fish cages. This may account for the observed numbers of chironomids in the fish addition treatments. The statistical difference in number of chironomids is obscured due to high variances. Even in the putatively "naive" community, fish had no significant effect on any taxon (out of 78 taxa) considered or on any community parameters measured.

Again, brook trout fry were manipulated. This experiment parallels the previous experiment (LHC-2) precisely. Trout had no effect on any measured community parameter. Out of 72 taxa, only 1 taxon, the

Leptephlebildae, responded to the predator manipulation. NP cages average 2-48 leptephlebilds per cage, while predator cages had only 0.64. No other taxon responded.

Prey Item Analysis of Predator Gut Contents

Methods

Predators from P cages were preserved in 95% ethyl alcohol. Guts were dissected out and all identifiable prey keyed out.

Results

The results of both rounds of experiments in the two streams are presented in Table 7. There were only a few common prey items.

In Cran Carré Creek in Round 1 both Salvelinus fontinalis and Pungitius pungitius consumed principally Chironomidae, Simulium and Hydracarina. P. pungitius also consumed Taeniopterygidae commonly, which S. fontinalis did not.

In Round 1, in Low Hope Creek, the salamander Eurycea bislineata had mostly empty guts. This reflects either of two possibilities. First, they did not feed while they were in the cages. Alternatively, their gut clearance raes were sufficiently high, that prey taken nocturnally were completely digested by the time they were collected (midday).

In Round 2, only S. fontinalis fry were used in both streams. In Cran Carré Creek, Chironomidae and Hydracarina were common prey. This was also true in Low Hope Creek. However, in LHC, Chydoridae were also taken commonly. In Cran Carré Creek, there were 10 rare prey tax, but only three in Low Hope Creek.

DISCUSSION

These experiments confirm the earlier findings of Reice (1983) and Allen (1982). Fish do not exert significant regulatory pressure on aquatic invertebrate populations or communities in streams.

The salamander manipulation had no major effect on numbers or species richness in low Hope Creek. There was a difference in diversity with cages with salamanders have lower H' than all other treatments. Since the variation in species richness is minor (1 species) this effect must be due to reduced dominance in the cages with salamanders. This probably comes about through behavioral effects rather than direct feeding. Since the salamanders were adults, they may not feed in the water. They normally inhabit the creek margin. Their empty guts (4/5) are strong evidence that they were not feeding. Their presence may have been sufficient to alter the distribution of aquatic insects (see Peckarsky and Dodson (1980) for

examples of stonefly predator effects on prey distribution even when predation was excluded).

These experiments stacked the deck in favor of finding an effect of fish. We introduced fish into enclosures in a stream without natural fish populations, hence a "naive fauna" refish. If fish have a real effect it should have been found here. It was not.

We must conclude that fish predation is an insignificant factor in benthic distribution and abundance in these Quebec streams.

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Table 1. Physical and biological characteristics of study streams.

	Cran Carré	Low Hope Creek
Temperature	10.6 - 20°C	14.4 -23°C
Current	0.07 - 0.80 m/sec	0.09- 0.58 m/sec
Width (m)	X = 3.8 ± 0.87	X = 3.9 ± 0.14
Cage Depth		
Low	1-10 cm	4-14 cm
High	20-30 cm	14-24 cm
Vertebrate Predators		
	Eurycea bislineata Salvelinus fontinalis Pungitius pungitius Lutra canadensis	E. bislineata

Table 2. Predator manipulation experiments in Summer 1983.

	Cran Carré	Low Hope Creek
	Fish:	Salamander:
Round 1 June-July	Salvelinus fontinalis Pungitius pungitius	Eurycea bislineata
Round 2 July-August	Salvelinus fontinalis	Salvelinus fontinalis

Table 3. Low Hope Creek, Round 1

A. COMMUNITY PATTERNS

	I	NP	P	O
Number of Individuals (x)	1144.4	1288.8	1516.6	2852.2

	P	NP	O	I
Species Richness	29	30	34	36

	P	NP	O	I
H'Diversity	0.499	0.717	0.745	1.110

	P	NP	O	I
$e^{H'}$	1.648	2.049	2.106	3.035

B. SPECIES PATTERNS (x)

	I	P	NP	O
Oligochaeta	0.04	4.40	25.60	180.40

	I	P	NP	O
Chironomid pupae	0.0	20.4	21.8	37.4

	NP	P	O	I
Leuctra	26.0	28.0	68.0	120.0

	P	NP	I	O
Hydracarina	37.20	40.80	105.20	109.80

	I	P	NP	O
Nematoda	1.0	1.80	3.60	17.40

Tukey's HSD Test (P=0.5). All means not underlined by the same line are significantly different.

Table 4. Cran Carré Creek, Round 1 (Mixed Fish in P)

A. COMMUNITY PATTERNS				
Number of Individuals (x)	I 905.8	O 998.2	NP 1075.2	P 1185.6
Species Richness	NP 21.0	O 21.0	P 21.6	I 24.6
Species Diversity (H') - mean value	NP 1.194	P 1.311	O 1.402	I 1.559
Equivalent Species ($e^{H'}$)	NP 3.302	P 3.710	O 4.063	I 4.754
B. SIGNIFICANT SPECIES PATTERNS (x)				
Simulium spp.	NP 9.80	I 29.80	P 40.60	O 52.00
Eurylophella sp.	O 1.60	P 2.00	NP 6.00	I 9.20
Oligochaeta	I 1.20	P 4.60	NP 6.20	O 15.40
Isotommidae	P 0.80	NP 1.40	I 4.00	O 5.80
Heleidae	O 4.40	P 5.00	NP 6.20	I 9.00
Promoresia sp.	I 6.80	O 12.20	P 17.20	NP 23.6
Chironomidae	I 617.60	O 681.60	NP 695.40	P 866.00

Means not underlined by same line are significantly different at $P \leq 0.05$ (Tukey's HSD).

Table 5. Low Hope Creek, Round 2 (Salvelinus fontinalis in P)

A. COMMUNITY PATTERNS				
Number of Individuals (x)	P 1253.40	O 1280.20	NP 1780.40	I 3089.40
Species Richness (x)	P 18.30	I 20.11	O 20.98	NP 22.34
Species Diversity (H')	I 0.847	NP 1.129	O 1.325	P 1.382
Equivalent Species ($e^{H'}$)	I 2.333	NP 3.087	O 3.765	P 3.983
B. TAXONOMIC PATTERNS (x)				
Chironomid larvae	P 677.65	O 753.53	NP 1167.18	I 2407.40
Stenonema sp.	I 0.43	P 1.35	NP 1.61	O 5.25

Means not underlined by the same line are significantly different at $P \leq 0.05$ (Tukey's HSD).

Table 6. Cran Carré Creek, Round 2 (Salvelinus fontinalis in P)

A. COMMUNITY PATTERNS				
Number of Individuals (x)	P 409.60	I 524.50	O 647.00	NP 708.40
Species Richness	I 26.66	P 27.19	O 29.17	NP 31.10
Species Diversity (H')	I 2.049	NP 2.107	P 2.224	O 2.350
Equivalent Species ($e^{H'}$)	I 7.765	NP 8.225	P 9.246	O 10.487
B. TAXONOMIC PATTERNS (x)				
Sphaerium sp.	P .56	O 2.10	NP 2.44	I 4.18
Heptageniidae	NP 0.20	P 0.820	I 1.83	NP 4.30
Leptophlebiidae	I 0.19	O 0.32	P 0.64	NP 2.48
Phyacophila sp.	I 3.30	NP 5.35	P 10.40	O 38.08

Means not underlined by the same line are significantly different at $P \leq 0.05$ (Tukey's HSD).

Table 7A. Invertebrate prey in Guts (Round 1)

Cran Carré	Low Hope Creek
Salvelinus fontinalis	*Eurycea bislineata*
Ephemeroptera (1)	Ephemeroptera (1)
Chironomidae (C)	4 guts empty (out of 5)
Simulium (C)	
Hydracarina (C)	
Promoresia (3)	
Dytiscidae (1)	
Pungitius pungitius	
Chironomidae (C)	
Taeniopterygidae (C)	
Simulium (C)	
Heliidae (1)	
Hydracarina (C)	

Table 7B. Invertebrate prey in guts of *Salvelinus fontinalis* (Round 2)

Cran Carré	Low Hope Creek
Chironomidae (C)	Chironomidae (C)
Hydracarina (C)	Hydracarina (C)
Isotomidae (1)	Chydoridae (C)
Megaloptera (1)	Hydropsychidae (1)
Trichoptera (2)	Triaenodes (1)
Hydropsychidae (1)	Homoptera (1)
Ryacophila (1)	
Simulium (1)	
Tipulidae (1)	
Lepidoptera (1)	
Aphididae (1)	(#) = number eaten
Perlidae (1)	(C) = common item

APPARENT MOLECULAR WEIGHT CHARACTERIZATION OF COLLOIDAL/DISSOLVED ORGANIC CARBON IN THE STREAMS AND RIVERS OF THE MATAMEK REGION

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In order to further our understanding of colloidal/dissolved organic carbon (C/DOC) dynamics in running water ecosystems it is necessary to begin to characterize this material. Some attempts have been made to do this through analysis for major groups of compounds but two rigorous studies have only accounted for 20-25% of the organic carbon present (Larson, 1978; Telang, 1981). Thus, we have adopted a very pragmatic approach to this problem, namely the characterization of C/DOC by apparent molecular weight. Although this is an extremely gross characterization procedure it has two particular advantages: (a) it accounts for the full spectrum of C/DOC, and (b) apparent molecular weight fractions are amenable to a direct testing of their utility to microorganisms through a microcalorimetric approach (see Lock and Ford, page 82).

Because of the pristine nature of the watersheds in the Matamek region we wished to test two hypotheses concerning potential longitudinal changes in C/DOC from 1st order streams through to the largest accessible river in the region, the 9th order Moisie river. The hypotheses were:

(a) As water moves from the headwaters to the estuary, there will be a progressive depletion of low molecular weight (microbially labile) compounds through their incorporation into microbial biomass.

(b) Conversely, there will be a proportional and/or absolute increase in high molecular weight (>1000 compounds (microbially "recalcitrant") from the headwaters to the estuary.

Study sites and timing

Water samples were collected on a seasonal basis from the standard study sites on First Choice Creek (first order), Beaver Creek (second order), Muskrat River (fifth order), Matamek River (sixth order) and Moisie River (ninth order), (Naiman 1983) plus an additional first order stream, Second Choice Creek, a tributory to the Matamek river entering just below the first falls. Samples were taken on 19-21 May, 28-30 June, 17-19 August, 22-24 September and 9-12 December. A survey was also carried out on 12 other first order streams during June and October and these were all tributory to Matamek lake with one exception, which was tributory to Beaver Creek (Fig. 2).

METHODS

All water samples were collected in chromic acid washed 500 ml glass stoppered bottles and returned to the laboratory for ultrafiltration. Initially the waters were filtered through a combusted Whatman GF/F fiberglass filter (0.7 μm porosity) and then sequentially through the following Amicon Diaflo Membranes (90 mm):

XM 300	300K apparent molecular weight cut-off
XM 50	50K " " " "
YM 10	10K " " " "
YM 2	1K " " " "

The filtration took place in two Amicon TCF 10A spiral flow cells with an elaborate protocol of pre-soaking of membranes in 10% sodium chloride solution followed by extensive washing of the cells and membranes with organic matter "free" water (Milli-Q Organex Q water purification). Contamination checks were made on the wash waters from all the membranes and these were generally below the detection limit of the organic carbon analysis. Fractions were collected in 50 ml combusted test tubes and acidified with two drops of phosphoric acid. DOC analysis was performed using a Dohrman 54 Carbon Analyser.

Statistical analysis

To compare any variation in amounts of carbon between rivers and between fractions, the total data set was transformed $\log_e (\chi + 0.5)$ to approach normality and a two way analysis of variance was performed with data points through time considered as replicates. This analysis was performed using Genstat (Alvey, 1977) on a Dec-system 10 computer. The proportions of AMW fractions (as a % of C/DOC) were transformed arc $\sin\sqrt{\chi}$ to approach normality. A 2-way analysis of variance was then performed using Genstat to produce a total error mean square term from which the standard error term in the Student Newman Keuls (SNK) multiple range test could be calculated. The SNK test was then used to determine which AMW fractions (as proportions of C/DOC) were significantly different from each other.

RESULTS AND DISCUSSION

Seasonal study on six rivers and streams

The findings from this study are presented in Fig. 1. An analysis of variance shows that the concentrations are significantly different between fractions (F=17.11) and between rivers (F=12.05), however these differences have no consistent pattern with increasing stream order. In four out of the six rivers, the dominant component in absolute terms was the 0.7 μm-300K fraction (colloidal and very high molecular weight organic carbon), where First Choice Creek and Second Choice Creek had

statistically less of this fraction than the other rivers which in turn were not significantly different from each other. For the other AMW fractions there was no significant differences ($\rho < 0.05$) between the rivers except First Choice Creek had less of the 300-50K fraction than Beaver Creek and Matamek. Thus, these data do not support the hypotheses that low molecular weight organic compounds are depleted and high molecular weight compounds progressively accumulate in river water as it traverse from the headwaters to the sea.

The expression of each AMW fraction as a % of C/DOC normalized the data for total C/DOC content of each stream (Fig. 1). However, once again we find no evidence of a progressive increase in the high molecular weight components. There was a significant increase in the proportional contribution of the 0.7 μm - 300K fraction between First Choice Creek/Second Choice Creek and Beaver Creek/Matamek but not between the remaining two rivers. While no significant difference was found between the proportional contributions of the <1K fractions for any of the rivers thus the hypothesis of low molecular weight fractions being depleted with increasing stream order is again rejected. The only other statistically significant proportional difference occurred in the 50-10K fraction where the proportion in First Choice Creek was statistically higher than that of the Matamek River and Beaver Creek.

The clear rejection of both hypotheses concerning longitudinal changes in colloidal/dissolved organic carbon composition require a reappraisal of both the routes of allochthonous C/DOC input on a longitudinal basis and the internal genesis of C/DOC in rivers.

Season specific findings on AMW fractions

Of the five seasonal samplings, early August stands out as being different from the others (Fig. 1). An extremely dry July had resulted in discharges which were approaching base flow conditions. This probably meant that many of the first order streams would have dried-up and drainage from the surficial organic deposits (Muskegs, litter, etc.) markedly reduced. Thus one would anticipate a reduction in the 0.7 μm-300K fraction and this indeed is what was observed, being most marked in the Muskrat and Matamek rivers. On the basis of these findings one would also predict that a similar event should take place during freeze-up in winter and decreases in the 0.7 μm-300K fraction were observed in the two rivers which had begun to freeze, Beaver Creek and Muskrat River. Thus these findings provide circumstantial evidence that the dominant molecular fraction (0.7 μm-300K) originates from surficial drainage.

The August sample (Fig. 1) also had greatly elevated concentrations of low molecular weight material (<1K). It is suggested that this was due to a combination of low flow and high levels of autochthonous production where exudates and lytic products of primary producers, (low molecular weight compounds) were leaching into a relatively small flux of water.

First order stream study

In the course of the 1983 field season it quickly became apparent that the two first order streams sampled in the seasonal study of six rivers were not only different in terms of the C/DOC concentration but were also different in their apparent molecular weight spectra. Specifically they were depleted in the 0.7 μm-300K fraction, being particularly so in First Choice Creek. These findings prompted us to survey 12 first order streams feeding Lake Matamek (for logistic reasons) which drained both the escarpment of the Canadian Shield and the Muskeg of the St. Lawrence plain plus one other stream tributory to Beaver Creek.

Samples were collected as before on the 16th of June and the 9th of September but on these occasions they were fractionated with only one ultrafilter, the XM300, in order to determine the size of the 0.7 μm-300K fraction the dominant component in rivers > first order. Subsequent organic carbon analysis was as before.

RESULTS AND DISCUSSION

The streams samples (Fig. 2) fell into two natural geomorphological groups, those draining the escarpment of the Canadian Shield (A-G) and those draining low gradient muskeg (H-M). The C/DOC concentrations were on average 6.5 (range 3.5-7.5) mg C ℓ^{-1} for escarpment streams A-G and 10.6 (range 5.7-15.1) mg C ℓ^{-1} for muskeg streams H-M during June. In October they were 10.2 (range 3.4-15.5) mg C ℓ^{-1} and 19.3 (12.3-26.8) mg C ℓ^{-1} respectively. These findings are in marked contrast to those in either First or Second Choice Creek which averaged 1.6 and 2.7 mg C ℓ^{-1} respectively. The proportional contribution of the 0.7 μm-300K fraction to C/DOC content was 10.2% (range 0-36%) for th escarpment streams and 40.3% (range of 21-63%) for the muskeg streams. The findings for Second Choice Creek fall into the upper range for the muskeg streams with an average for June and September of 49% while First Choice Creek has an average of 29.6%. However, this latter figure may be anomalous since the previous seasonal study indicated that this fraction was less than 15% in 4 out of 5 samples.

Implications for interpretation of longitudinal C/DOC dynamics in rivers

There are two curious aspects of the data base on seasonal/river variation in C/DOC (Fig. 1). If we propose that these rivers approximate a "continuum" (Vannote et al. 1980) then we have to account for (a) the massive increase in C/DOC between the first order and second order streams and (b) a substantial decrease between the second order streams through to the ninth order river. Although mineralization and immobilization (incorporation into microbial biomass) of C/DOC can be proposed as an explanation for the latter the suddent "massive appearance" of C/DOC in second order streams is much more problematic (i.e., a massive increase in primary production seems unlikely).

Both of these problems are substantially eased if the anticipated inputs of C/DOC are reconsidered in the light of the findings from the first order stream survey. It seems likely that the majority of the tributaries of Beaver Creek and Muskrat River which had the highest C/DOC concentrations and proportion of 0.7 μm-300K fraction, would be of the muskeg draining type found on the south side of Lake Matamek (streams H-M) with similarly high C/DOC concentrations and proportions of the 0.7 μm-300K fraction. Therefore, we suggest that the extremely high concentrations of C/DOC begin in the first order streams and no increase occurs in the transition to second order streams.

The second problem of the massive decrease in C/DOC concentration with increasing stream order may be amenable to a similar explanation. The Matamek River and to a much greater extent the Moisie River are probably fed by first order streams of the type found draining the escarpment. Thus, in the Moisie river the 1st order streams tributary to it may have a C/DOC concentration in the ~ 6-10 mg C ℓ^{-1} range which is much closer to the observed range of ~ 5-8 mg C ℓ^{-1}. The first order stream input to the Matamek River and possibly the Muskrat River is likely to be a combination of "escarpment" and "muskeg" draining streams with the balance being reflected in the observed intermediate C/DOC concentration in these rivers.

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FIGURE CAPTIONS

Figure 1. Apparent molecular weight spectra of six streams and rivers in the Matamek region through time. The sampling periods were 19-21 May, 28 June - 1 July, 17-19 August, 22-24 September and 9-12 December. * 10K (1K fraction contaminated).

Figure 2. A survey of C/DOC and organic carbon 0.7 μm-300K in first order streams in the Matamek region. FCC = First Choice Creek, SCC = Second Choice Creek.

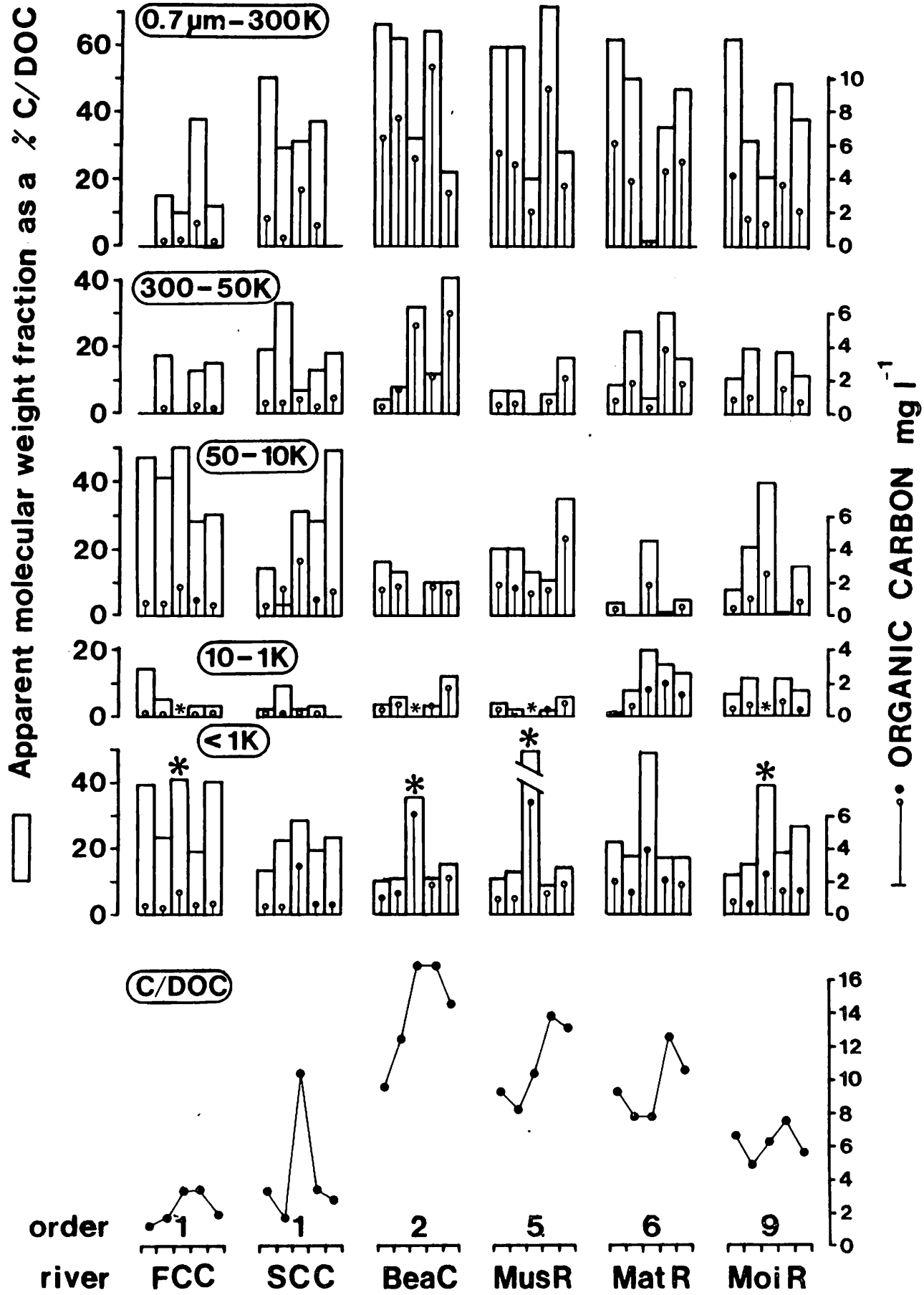
Apparent molecular weight fraction as a % C/DOC
ORGANIC CARBON mg l-1
0.7µm-300K
300-50K
50-10K
10-1K
<1K
C/DOC
order
river
1
1
2
5
6
9
FCC
SCC
BeaC
MusR
MatR
MoiR

Fig. 1

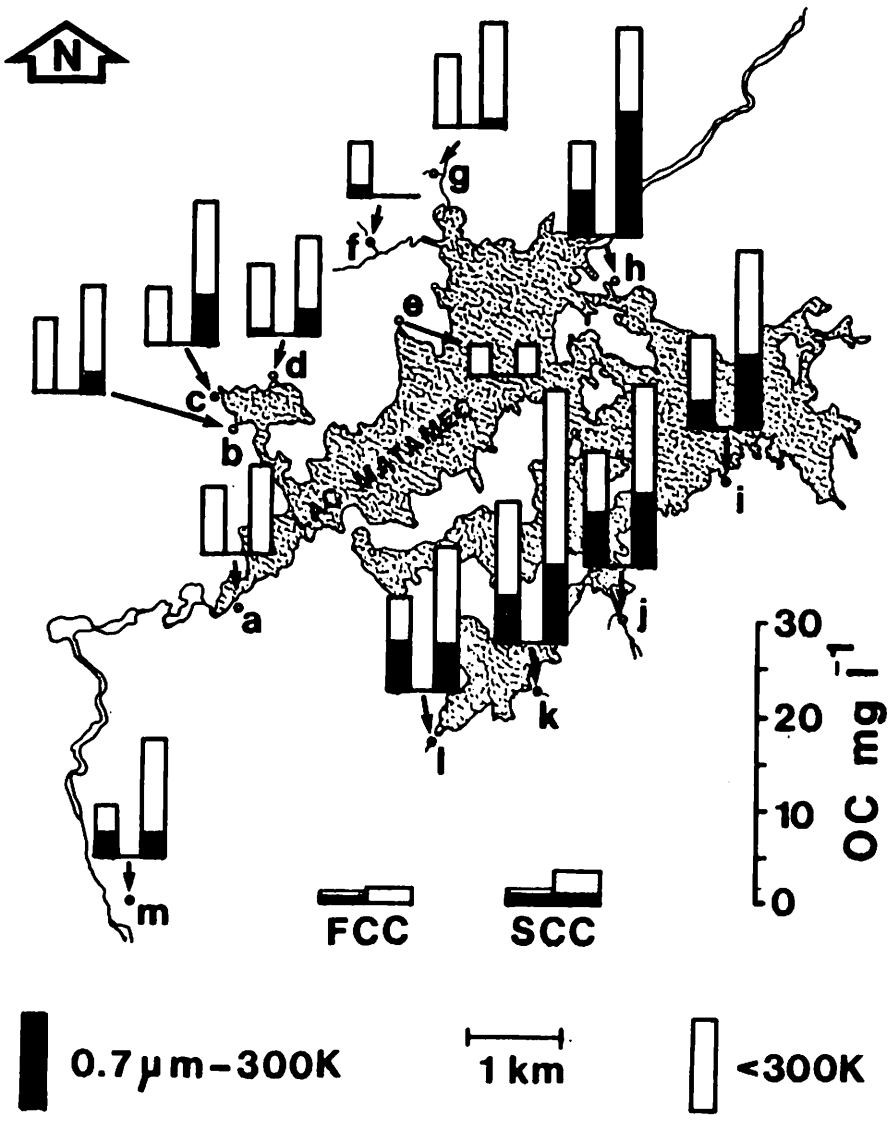

Fig. 2

HEAT OUTPUT STUDIES ON EPILITHON FROM RIVERS AND STREAMS IN THE MATAMEK REGION

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The studies on the fractionation of colloidal/dissolved organic carbon were conceived as an initial step in the investigation of the relative utility of various apparent molecular weight (AMW) fractions of organic carbon to epilithic metabolism. This was to be determined through the use of flow microcalorimetry, where the heat output of epilithon perfused with unfractionated river water would be compared with that of river water from which an AMW fraction had been removed. Thus the contribution of an AMW fraction was to be obtained by difference. Studies in the UK had indicated that the C/DOC content of river water was a major supplier of organic energy to the epilithon. However, short term manipulation (~ 1-2 hours) of the apparent molecular weight spectral composition of the water produced small (~ 20%) or non-existant changes in heat output (Lock and Ford, submitted). We therefore wished to repeat these studies across a wide range of stream orders and to specifically examine the heat output responses of both heterotrophic (dark-growth) and autotrophic/ heterotrophic (light-growth) epilithon.

METHODS

The study was carried out at four sites; First Choice Creek, Beaver Creek, Muskrat River and Moisie River. Epilithon was grown on 1.6 mm black glass beads threaded onto nylon monofilament line. The bead strings were attached to plexiglas plates which were inserted into 3 m long, 15 cm diameter tubes which were either submerged in the rivers attached to a floating pontoon or plumbed directly into the stream via a small dam in the case of First Choice Creek. At each site there was one opague tube (dark-growth) and one with a clear plexiglas window (light-growth). In addition Z-bend light traps were fitted to both the dark and light growth tubes to keep the same hydraulic conditions between the two light regimes.

After a period of 2-4 weeks growth the beads were removed from the flow-tubes and placed into a flow microcalorimeter (Lock and Ford, 1983). The epilithon was then perfused to an equilibrium heat output with GF/F filtered river water and then the perfusion regime was switched to river water with everything >1K AMW removed by ultrafiltration (1-2 hours) and finally an organic matter free medium with an inorganic composition approximating that of the rivers. In this way it was possible to determine respectively the proportion of heat-output due to (a) organic matter >1K; (b) organic matter <1K; and (c) the "residual" heat output which was apparently independent of short term changes in the organic energy supply.

RESULTS AND DISCUSSION

All of the incubation systems suffered greatly from silting and foaming inside the tube (this was not encountered in our UK or Arctic work) which meant the epilithon from each site had to be disturbed at varying intervals throughout its growth period to remove debris. This problem was most extreme in Beaver Creek where the system had to be "rinsed" every 48 hours and in the end it was necessary to incubate the beads upside down. Thus it was not possible to make any meaningful comparisons of seasonal heat-outputs between rivers (one of the original objectives of the study) and any between river comparison could only be extremely tentative.

Most striking were the very low levels of heat output, generally less than 1.0 $\mu W\ cm^{-2}$ and often undetectable. This finding contrasts sharply to the temperate stream of North Wales where heat outputs generally in excess of 0.8 $\mu W\ cm^{-2}$ and up to 6.8 $\mu W\ cm^{-2}$ have been recorded. Out of a total of 31 determinations 12 were below the detection limit of 0.05 $\mu W\ cm^{-2}$ and 6 were less than 0.2 $\mu W\ cm^{-2}$ and thus below the limit for the construction of a heat budget. These very low/non measurable heat outputs are probably due in a major part to the extreme problems encountered in their culture but are also probably indicative of the low metabolic activity of these boreal rivers.

Heterotrophic epilithon (dark-grown)

Only two out of the five detectable heat-outputs were large enough to partition between the AMW fractions, however these two were of a reasonable magnitude, 0.34 $\mu W\ cm^{-2}$ in First Choice Creek and 0.67 $\mu W\ cm^{-2}$ in Muskrat River. In First Choice Creek there was no detectable response to AMW manipulation or to the total removal of organic matter (OMF) while in Muskrat River 18% of the heat output was attributed to the organic matter >1K while 16% was attributed to the organic matter <1K.

There are two major conclusions to be drawn from these results. Firstly, in these rivers water borne organic energy matter is capable of supporting an active epilithon in the absence of epilithic primary production. Secondly, in the Muskrat River, there is a clear immediate response to the removal of organic matter >1K, suggesting that the higher molecular weight organic matter has a substantial role in the organic energy dynamics of this river. This latter finding is contrast to those in the U.K. where no immediate responses to manipulation of the >1K fraction was detected.

Autotrophic and heterotrophic epilithon (light-grown)

There were 14 detectable heat-outputs from the light grown epilithon of which 11 were of sufficient magnitude to enable a heat budget to be constructed (Fig. 3). Of this 11, 5 of these showed no response to a manipulation of the organic content of the perfusion medium (i.e., removal of >1K fraction or perfusion with an organic matter free medium). This

type of response was typical of epilithon from rivers studied in the U.K. (Lock and Ford, submitted).

However, there were six epilithon which did respond to an alteration of the organic matter composition and were spread across the four rivers studied. Two out of the six were apparently processing higher molecular weight material at a substantial rate, where its removal resulted in an 18-30% decrease in heat output. While, all six of these rivers had a moderate to high dependence upon the organic matter <1K where its removal resulted in a 9-30% decrease in heat output.

As yet, information of this type is extremely limited and in comparison with the only other study on U.K. rivers, it is interesting to note that although the total heat output (metabolic rate) is lower in these boreal rivers they exhibit much greater immediate responses to manipulations of the organic matter composition. In the U.K. rivers there is generally no immediate response and only reaching a total response (removal of all organic matter) of ~ 20% in a few cases.

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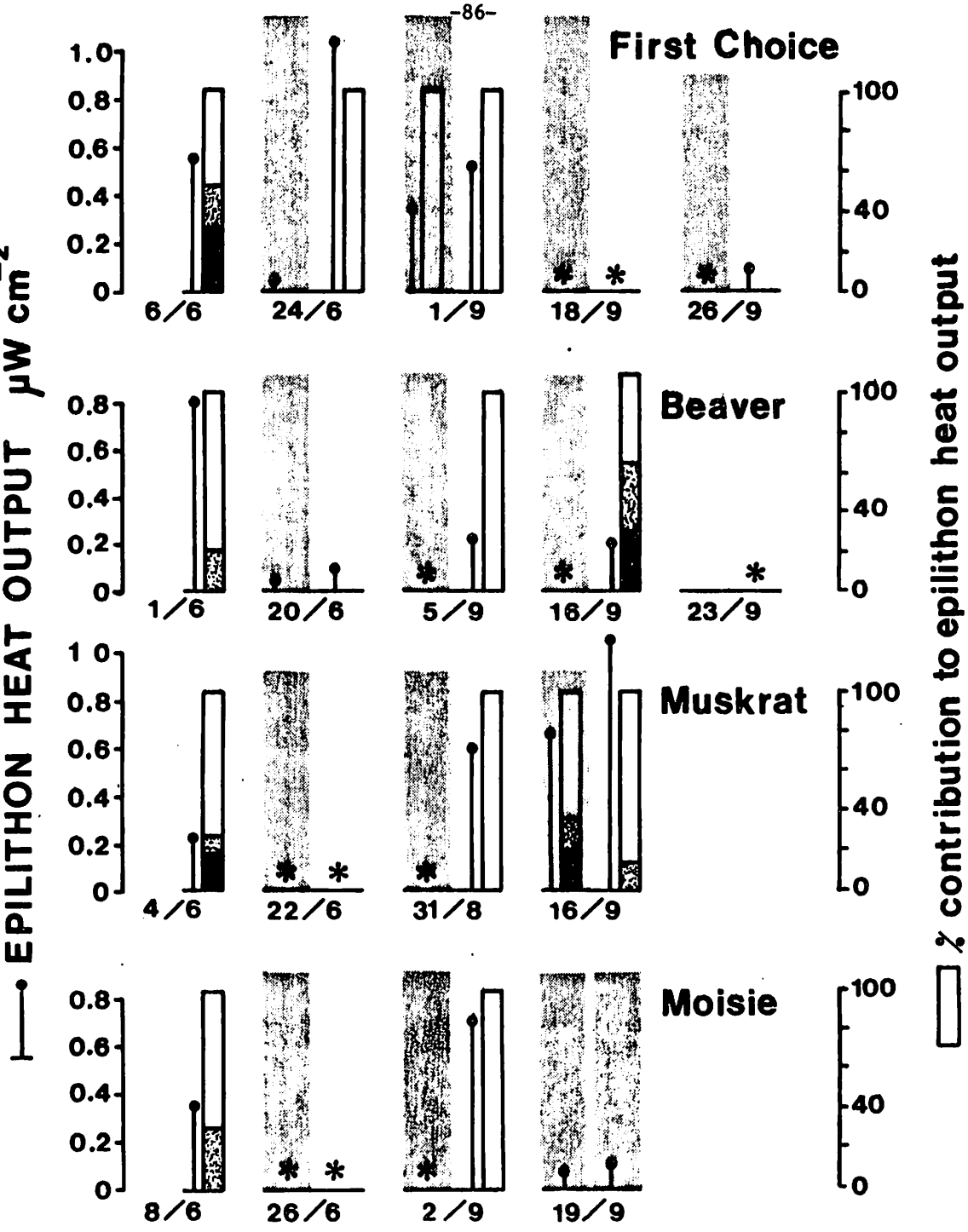
FIGURE CAPTIONS

Figure 1. Epilithon heat output through time with the proportional contribution of organic carbon >1000 apparent molecular weight and <1000 apparent molecular weight to this. The "residual-heat" is the portion of the heat output which does not change in response to short term manipulations of the perfusion medium.



organic carbon >1000 AMW

organic carbon <1000 AMW

'residual'

dark

* <0.05 µW cm⁻²

Fig. 1

SEDIMENTARY DIATOM ANALYSIS OF TWENTY LAKES IN THE MATAMEK AND NEIGHBOURING WATERSHEDS

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ABSTRACT

Twenty lakes in the Matamek and the neighbouring watersheds (Fig. 1) were accessed by floatplane and sampled in summer 1983 for water chemistry and surficial sediments. Thirty-two physical and chemical variables, including pH, alkalinity, cations and metals concentrations were measured on water samples from the epilimnion and hypolimnion of each lake. Surficial sediment diatom flora was sampled using a K-B gravity corer. In three lakes, two to four replicate cores were collected and analyzed to estimate spatial variability of the sediment flora.

Result from water analyses show the acidic nature (pH 5.80 to 4.59) of these highly coloured, little buffered, soft waters. Aluminum and magnesium concentrations reached 494 and 70 $\mu g \cdot l^{-1}$, respectively (Table 1). Comparison of our pH measurements with 1970 values from Pope (1973) showed a consistent decrease over time (Table 2). The influence of marine aerosols was shown to produce a gradient of Na and Cl concentration inversely proportional to the distance to the shoreline. Applications of empirical chemical models such as alkalinity/sulfate ratio and regression of pH on log calcium also indicated that these lakes are undergoing acidification.

Analyses of the surficial sediment diatom flora showed the strong dominance of six species found together with an important number of rare species. Two hundred and twenty nine diatom taxa were found, varying between 40 and 88 per lake (Table 3). True cell density ranged from 0.90 to 82.01 x 10^6 valves per gram of dry sediment. Replicate core variability within a lake proved to be as high as among lakes. Calculation of alpha index (Nygaard 1956) for each core and regression of its log transformed value against measured surface pH produced the following equation (Fig. 2).

$$\text{Surface pH} = 5.914 - 0.194 \log (\text{alpha})$$

This equation proved to be significantly different from the ones calculated by previous workers (Del Prete and Schofield 1981, Norton et al. 1981) and was applied to down core analyses of flora from sediments collected in summer 1982 in Key Lake and Lake C-22 (Ditner and Duthie 1983). Although the wide confidence interval of pH values predicted from this equation obscured any evidence of change with depth, a significant increase in numbers of acidophilous species and a decline in number of circumneutral species were observed in Key Lake's core, thus suggesting that a change in the flora is taking place.

With respect to multi-lakes comparison, the surficial sediment flora does not provide clear evidence of a relationship with decreasing surface pH. It would therefore appear that indices related to surficial sediment flora are not sensitive enough to account for the narrow pH range and the strong chemical resemblance of the lakes investigated in this study. The inadequate representation of species' relative frequency by a single core certainly contributes to this result. Examination of alpha index and of the arithmetic procedures surrounding its calculation pinpoint the critical effect of the inclusion of outliers on the observed results. The currently accepted model of progressive linear change in the community may not be an adequate way to quantify acidification processes, and other models, inspired from the theory of catastrophy (Zeeman 1976), may prove more fruitful. A more extensive discussion of these concepts can be found in Hudon et al. (1984). Further analyses of this data set using multivariate statistics, are going to be carried out in the near future, to explore the potential of other methods to synthesize the response of the flora to changes in their growth conditions.

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Table 1. Summary of physical and chemical variables recorded for hypolimnetic and epilimnetic water samples collected in 20 Matamek lakes. Method number refers to: 1 = field measurements, 2 = Environment Canada (1979), 3 = Ontario Ministry of Environment (1981), 4 = Kramer 1980. * Detection Limit.

Variables Name	Symbol	Units	Minimum	Maximum	Range	Method
pH		log $[H^+]$	4.50	6.45	1.95	1
Alkalinity		µEg/l	0.00*	104.90	104.90	1,4
Conductivity (at 25°C)		µMhos/cm	7.8	24.0	16.2	1
Temperature		°C	6.0	22.0	16.0	1
Transparency (Secchi)		m	1.0	5.2	4.2	1
Distance from sea		km	3.0	49.7	46.7	1
Aluminum	(Al)	µg/l	66.0	560.0	494.0	2
Barium	(Ba)	µg/l	< 1.0*	8.0	7.0	2
Beryllium	(Be)	µg/l	< 1.0*	2.0	1.0	2
Cadmium	(Cd)	µg/l	< 0.2*	0.3	0.1	2
Calcium	(Ca)	µg/l	280.0	3000.0	2720.0	2
Chromium	(Cr)	µg/l	< 1.0*	1.0	0.0	2
Chlorine	(Cl)	µg/l	< 100.0*	2900.0	2800.0	2
Cobalt	(Co)	µg/l	< 1.0*	1.0	0.0	2
Copper	(Cu)	µg/l	< 1.0*	9.0	8.0	2
Iron	(Fe)	µg/l	36.0	1100.0	1064.0	2
Lead	(Pb)	µg/l	< 3.0*	6.0	3.0	2
Magnesium	(Mg)	µg/l	70.0	600.0	530.0	2
Manganese	(Mn)	µg/l	10.0	100.0	90.0	2
Molybdenum	(Mo)	µg/l	< 1.0*	1.0	0.0	2
Nickel	(Ni)	µg/l	< 1.0	2.0	1.0	2
Potassium	(K)	µg/l	60.0	560.0	500.0	2
Sodium	(Na)	µg/l	250.0	2140.0	1890.0	2
Strontium	(Sr)	µg/l	2.0	20.0	18.0	2
Titanium	(Ti)	µg/l	< 1.0*	23.0	22.0	2
Vanadium	(Vd)	µg/l	1.0	2.0	2.0	2
Zinc	(Zn)	µg/l	2.0	17.0	15.0	2
Sulfate	(SO_4)	µg/l	< 200.0*	5800.0	5600.0	3
Silicon	(SiO_2)	µg/l	< 20.0*	4300.0	4280.0	3
Nitrate	(NO_3-NO_2-N)	µg/l	< 10.0*	61.0	51.0	3
Ammonium	(NH_3-N)	µg/l	< 5.00*	56.0	51.0	3
Total Kjeldahl	(N)	µg/l	62.0	273.00	211.0	3
Total Phosphorus	(P)	µg/l	< 0.2*	14.2	14.0	3

Table 2. Chemical characteristics of eleven Matamek watershed lakes during the summers of 1970 and 1983. The 1970 data are from Pope (1973).

Lake	pH	
	1970	1983
Bill	6.5	5.60
Muskrat	6.3	5.65
Matamek	5.9	5.76
à la Croix	5.3	4.90
Key	5.7	5.50
Ross	6.2	5.30
Gallienne	5.6	5.30
Méchant	5.8	5.20
Tchinicaman	6.4	5.10
Claveau	6.7	5.70
X	6.1	5.20

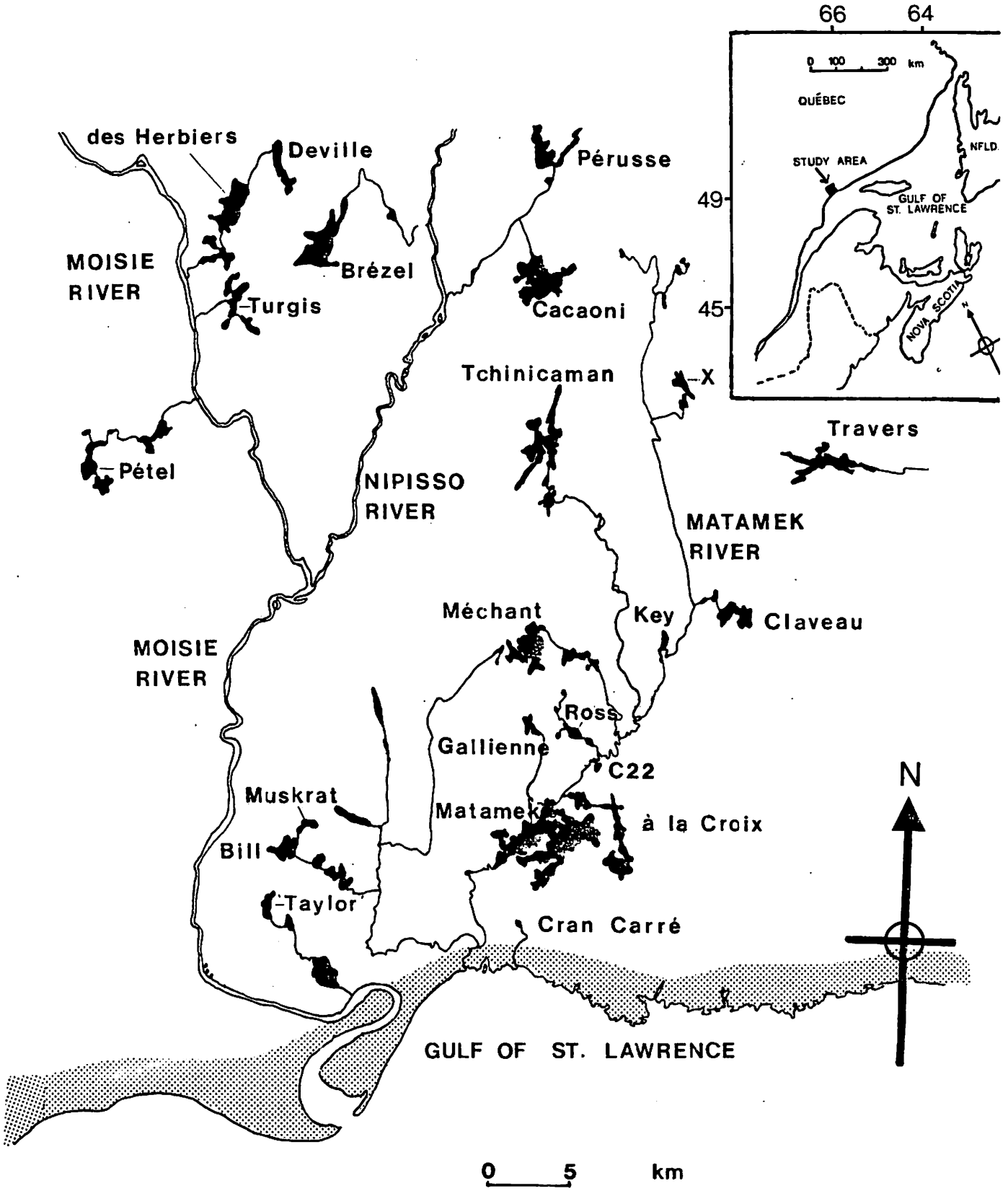
Table 3 List of the diatom species found in the Matamek and surrounding watersheds. Hustedt's grouping: (-5), alkalibiontic; (-1), alkaliphilous, (0), indifferent; (+1), acidophilous, (+1), acidobiontic; Frequency: (a), present in all lakes; (c) present in more than 50% of the lakes; (o), present in more than 10% but less than 50% of the lakes; (r), present in less than 10% of the lakes; (x), present in down-core analyses only.

Species	Hustedt's Grouping	Frequency
Achnanthes		
austriaca Hust.	-1	x
bioreti Germain	0	o
clevei Grun.	-1	x
conspicua A. Mayer	0	x
levanderi Hust.	+1	c
linearis (W.Sm.)Grun.	0	c
linearis f.curta H.L.Sm.	0	c
marginulata(Kütz.)Grun.	+1	c
microcephala(Kütz.)Grun.	0	c
minutissima (Kütz.)	0	c
saxonica Krasske	+1	c
stewartii v. stewartii Patr.	0	x
sublaevis v. crassa Reim.	0	o
spp.	0	x
Actinella		
punctata Lewis	+5	c
Anomoeoneis		
serians v. serians (Bréb. ex Kütz.) Cl.	+5	o
v. acuta Hust	+1	c
v. brachysira (Bréb. Kütz) Hust.	+1	a
styriaca (Grun.) Hust.	+1	x
vitrea (Grun.) Ross	+1	o
Asterionella		
formosa Hass.	-1	c
ralfsii W. Sm.	+5	c
Caloneis		
bacillum (Grun.) Cl.	-1	o
Cocconeis		
pediculus Ehr.	-1	r
placentula Ehr.	-1	x
Cyclotella		
bodanica Eulenst.	-1	x
meneghiniana Kütz.	-1	x
stelligera (Grun.)Cl.	-1	c
Cymbella		
amphicephala Naegeli	0	c
cesatii (Rabh.) Grun.	0	o
delicatula Kütz	0	x
hauckii V. H.	-1	x
helvetica Kütz	0	x
heteropleura Ehr.	0	r
lunata W. Sm.	+1	o
microcephala Grun.	-1	c
minuta v. minuta Hilse ex Rabh.	0	c
v. pseudogracilis (Choln.) Reim.	-1	c
naviculaformis Auerswald	0	x
Diatoma		
anceps (Ehr.) Kirchn.	+1	x
Diploneis		
elliptica (Kütz.) Cl.	0	x
marginestriata Hust.	+1	r
ovalis (Hilse) Cl.	-1	r
Eunotia		
arcus v. arcus Ehr.	+1	c
v. fallax Hust.	+1	x
bactriana Ehr.	+1	r
bidentula W.Sm.	+5	c
bigibba Kütz.	+5	x
curvata (Kütz.)Lagerst.	+1	c
diodon Ehr.	+1	o
elegans Ostr.	+1	o
exigua (Bréb. ex Kütz.) Rabh.	+5	c
fallax A. Cl.	+5	c
flexuosa v. flexuosa Bréb. ex Kütz.	+5	c
v. eurycephala Grun.	+5	o
hexaglyphis Ehr.	0	o
incisa W. Sm. ex Greg.	+1	c
maior (W. Sm.) Rabh.	+1	o
meisteri Hust.	+5	c
microcephala Krasske ex Hust.	+5	c
monodon Ehr.	+5	o
naegelii Migula	+1	c
parallela Ehr.	0	x
pectinalis v. pectinalis	+1	a

(O.F. Müll.?) Rabh.		
v. minor (Kütz.) Rabh.	1	a
v. recta A. Mayer ex Patr.	+1	c
v. rostrata Germain	+1	c
v. undulata (Ralfs) Rabh.	+1	r
v. ventricosa Grun.	+1	r
perpusilla Grun.	+1	c
praerupta v. praerupta Ehr.	+5	c
v. bidens (Ehr.) Grun.	+5	r
praerupta-monos Ehr.	+5	x
rostellata Hust. ex Patr.	+1	x
septentrionalis Ostr.	+1	x
serra v. serra Ehr.	+1	c
v. diadema (Ehr.) Patr.	+1	o
sudetica v.sudetica O.F. Müll.	+1	a
v. unknown	+1	x
suecica A. Cl.	+1	x
tautoniensis Hust ex Patr.	+1	o
tenella (Grun.) Cl.	+1	c
tridentula W. Sm.	+1	o
trinacria Krasske	+5	x
vanheurckii	+1	c
v. vanheurckii Patr.	+1	c
v. intermedia (Krasske ex Hust.) Patr.	+1	c
spp.	+1	-
Fragilaria		
brevistriata Grun.	+1	o
capucina Desm.	-1	x
constricta		
v. constricta Ehr.	+1	c
f. stricta (A.Cl.) Hust.	0	c
construens	-1	c
v. construens (Ehr.) Grun.		
v. pumila Grun.	+1	x
v. venter (Ehr.) Grun.	-1	c
lapponica Grun.	0	x
leptostauron		
v. leptostauron (Ehr.) Hust.	-1	x
v. dubia (Grun.) Hust.	-1	x
pinnata & var. Ehr.	-1	c
vaucheriae (Kütz.) Peters.	-1	x
virescens v. virescens Ralfs	+1	c
v. capitata Ostr.	+1	o
spp.	0	-
Frustulia		
rhomboides	+1	a
v. rhomboides (Ehr.) De T.		
v. amphipleuroides (Grun.) Cl.	+1	x
v. capitata (A. Mayer) Hust.	+1	c
v. saxonica (Rabh.) De T.	+1	a
vulgaris Thwaites	+1	r
Gomphonema		
acuminatum Ehr.	-1	x
angustatum & var. (Kütz.) Rabh.	-1	o
gracile Ehr.	-1	r
parvulum (Kütz.) Grun.	-1	r
Gyrosigma spp	-1	x
Melosira		
ambigua O. Müll.	-1	x
distans v. distans (Ehr.) Kütz.	+1	a
v. lirata (Ehr.) Bethge	+1	x
italica (Ehr.) Kütz.	-1	x
Meridion		
circulare (Grev.) Ag.	-1	o
v. constricta (Ralfs) V.H.	-1	r
Navicula		
arvensis Hust.	+1	o
bryophila Ostr.	+1	o
contenta Grun.	0	x
cocconeiformis Greg. ex Grev.	+5	c
globulifera Hust.	0	r
gysingensis Foged	0	c
latelongitudinalis	0	x
minima Grun.	-1	r
monmouthiana-stodderi Yerm.	0	x
placentula (Ehr.) Kütz.	-1	x
pseudonivalis Bock	0	x
pseudoscutiformis Hust.	0	x
pupula v. pupula Kütz.	-1	r
v. capitata Skv. & Meyer	-1	x

v. rectangularis (Greg.) Grun.	0	o
radiosa v. radiosa Kütz.	0	c
v. parva Wallace	0	o
v. tenella (Bréb. ex Kütz.) Grun.	0	r
rhynchocephala Kütz.	0	x
seminulum Grun.	0	c
sohrensis Krasske	0	c
subtilissima Cl.	+1	c
Neidium		
affine v. affine (Ehr.) Pfitz.	+1	c
v. amphirhynchus (Ehr.) Cl.	+1	c
v. ceylonicum (Skv.) Reim	0	x
v. hankense (Skv.) Reim.	+1	x
v. humerus Reim.	+1	x
v. longiceps (Greg.) Cl.	+1	x
bisulcatum (Lagerst.) Cl.	+1	r
dubium (Ehr.) Cl.	+1	o
hitchcockii (Ehr.) Cl.	+1	x
iridis v. iridis (Ehr.) Cl.	+1	c
v. amphigomphus (Ehr.) V.H.	+1	c
v. ampliatum (Ehr.) Cl.	0	x
v. subundulatum (A. Cl.) Reim.	0	x
v. unknown	0	-
ladogense v. ladogense (Cl.) Foged. Hust.	+1	o
v. densestriatum (Ostr.) Foged	+1	o
spp.	0	-
Nitzschia		
acuta Hust.	0	x
denticula Grun.	-5	x
dissipata (Kütz.) Grun.	-1	x
gracilis Hantzsch	-1	x
hantzschiana Rabh.	-1	x
palea (Kütz.) W. Sm.	-1	c
recta Hantzsch	-1	x
sigma (Kütz.) W. Sm.	-1	r
sigmoidea Hust.	-1	x
spp.	-1	-
Peronia		
fibula (Bréb. ex Kütz.) Ross	0	o
heribaudii Brun et Peragallo	0	x
spp.	0	x
Pinnularia		
abaujensis		
v. abaujensis (Pant.) Ross	+1	c
v. linearis (Hust.) Patr.	+1	c
v. rostrata (Patr.) Patr.	+1	r
v. subundulata (A. Mayer ex Hust.) Patr.	+1	x
acrosphaeria W. Sm.	0	x
acuminata W. Sm.	0	x
appendiculata (Ag.) Cl.	0	o
biceps v. biceps Greg.	0	o
f. petersonii Ross	0	x
borealis Ehr.	+1	x
braunii v. braunii (Grun.) Cl.	+1	x
v. amphicephala (A. Mayer) Hust.	0	x
brebissonii (Kütz.) Rabh.	+1	r
caudata (Boyer) Patr.	0	x
divergens W. Sm.	+1	x
divergentissima (Grun.) Cl.	+1	x
fontellii A. Cl.	0	x
globiceps Greg.	-1	x
intermedia (Largest.) Cl.	0	x
leptosomoides Grun.	0	x
maior (Kütz.) Rabh.	0	o
mesolepta (Ehr.) W. Sm.	+1	x
microstauron Ehr. Cl.	0	o
nodosa Ehr.	0	r
stauroptera Rabh.	0	x
stomatophora Grun.	+5	x
streptoraphe Cl.	+1	x
subcapitata Greg.	+1	x
substomatophora Hust.	+1	c
sudetica Hilse	+1	x
undulata v. undulata Greg.	0	x
v. stauroneiformis (Hust.) A.Cl.	+1	x
viridis v. viridis (Nitz.) Ehr.	+1	r
v. commutata (Grun.) Cl.	-5	r

Semiorbis		
hemicyclus (Ehr.) Patr.	+5	c
Stauroneis		
anceps v. anceps Ehr.	0	r
f. gracilis Rabh.	0	o
f. linearis (Ehr.) Hust.	0	r
kriegeri Patr.	+1	x
livingstonii Reim.	+1	o
obtusa Lagerst.	+1	x
phoenicenteron (Nitz.) Ehr.	0	r
B. gracilis (Ehr.) Hust.	0	x
Stenopterbia		
intermedia Lewis	+1	c
pelagica Hust.	+1	x
Surirella		
arctissima Schmidt	0	o
delicatissima Lewis	+5	c
lapponica A.Cl.	+1	x
linearis	+1	c
v. linearis W. Sm.		
v. constricta (Ehr.) Grun.	+1	x
Synedra		
delicatissima W. Sm.	-1	c
radians Kütz.	-1	x
rumpens Kütz.	+1	o
tenera W. Sm.	0	o
spp.	0	x
Tabellaria		
fenestrata (Lyngb.) Kütz.	+1	a
flocculosa (Roth) Kütz.	+1	a
quadriseptata Knuds.	+5	c


66
64
0 100 300 km
QUÉBEC
STUDY AREA
NFLD.
GULF OF ST. LAWRENCE
NOVA SCOTIA
49
45
des Herbiers
Deville
Pérusse
MOISIE RIVER
Brézel
Turgis
Cacaoni
Tchinicaman
X
Travers
Pétel
NIPISSO RIVER
MATAMEK RIVER
Méchant
Key
Claveau
MOISIE RIVER
Ross
Gallienne
C22
Muskrat
Matamek
à la Croix
Bill
Taylor
Cran Carré
N
GULF OF ST. LAWRENCE
0 5 km

ANALYSES OF MATAMEK ACID RAIN DATA
REGRESSION OF SURFACE PH • LOG ALPHA

REGRESSION OF SURFACE PH • LOG ALPHA (-CRAN CARRE)

PLOT OF SURFACE PH • LOG10 ALPHA
UPPER ('U') AND LOWER ('L') LIMITS OF THE 95% CONFIDENCE INTERVAL
PREDICTED VALUES FOR THE RESULTING EQUATION = 'P'
PREDICTED VALUES FOR THE EQUATION OF DEL PRETE AND SCHOFIELD = 'D'
PREDICTED VALUE FOR THE EQUATION OF NORTON ET AL = 'N'

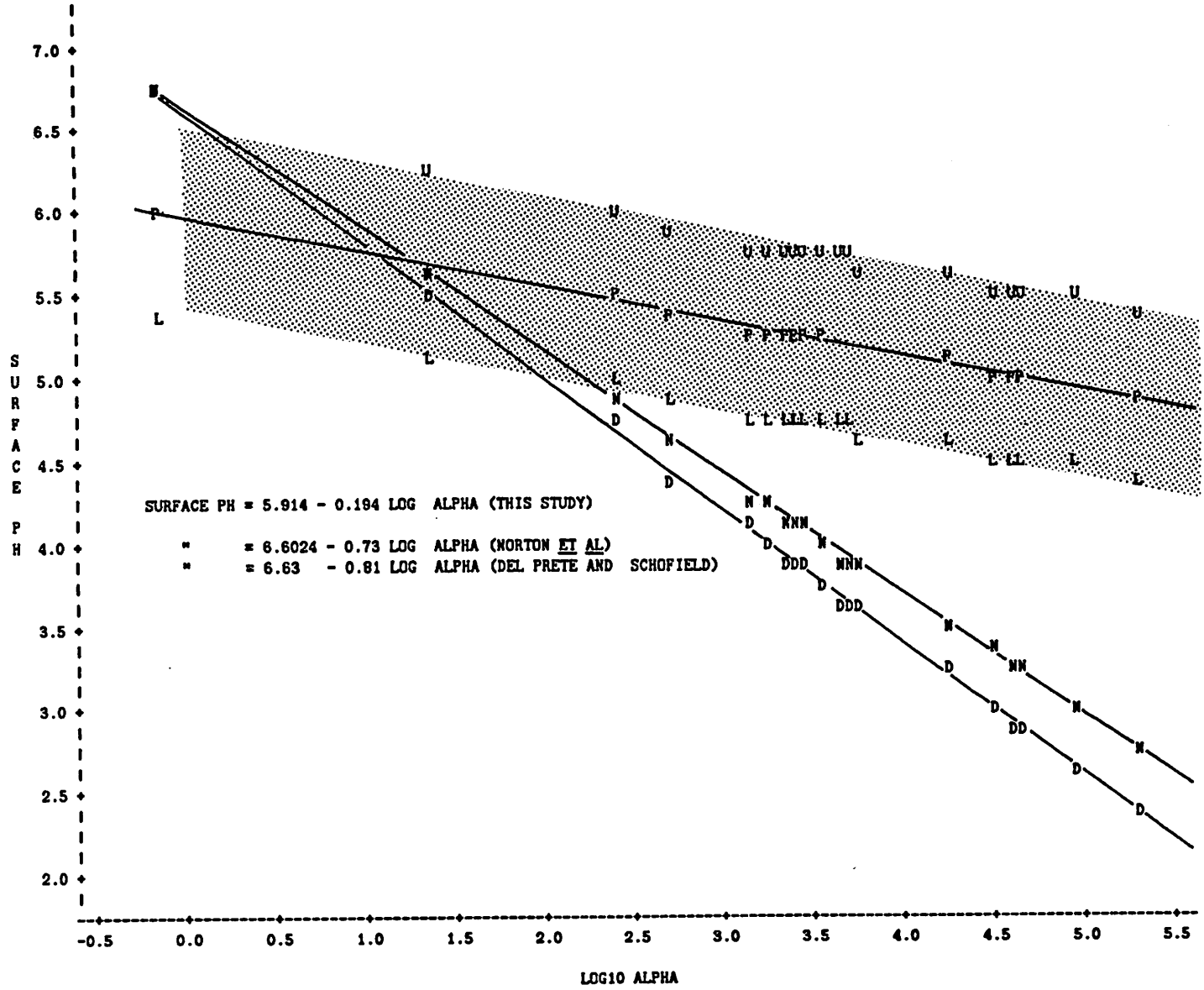


Fig. 2

PHYSIOLOGICAL ADAPTATION OF PERIPHYTIC ASSEMBLAGES OF INCREASING DENSITIES: METHODS AND PRELIMINARY RESULTS

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INTRODUCTION

The microscopic community colonizing solid surfaces in aquatic environment is strongly dominated by diatomaceous algae. This fast-growing community provides an ideal miniature ecosystem to investigate the physiological changes occurring during colonization. The concepts of community maturity and succession, previously elaborated for macroscopic plant communities (Odum 1969) would lead us to expect that cells colonizing a surface would respond to biotically induced changes by modifying their metabolism. For instance, an increase in cell density is likely to increase shading, current obstruction and detritus accumulation, and could exert an indirect impact on pigment concentration, excretion products, and/or ability to assimilate and store different molecular compounds. Due to vertical cell stratification on the surface (Hudon and Bourget 1981, 1983), these factors should more affect the cells closely adherent to the surface than the cells found in the superficial layer, closer to the free-moving water mass.

The objective of this study was therefore to determine the extent of physiological changes taking place during colonization of three different types of substrata, while taking into account the natural layering of the community. Mature (high density) and immature (low density) assemblages were compared with regard to total biomass, pigments, carbohydrate content, species diversity and primary production under light (using ^{14}C-Bicarbonate) and dark (using ^{14}C-Glucose) conditions.

MATERIAL AND METHODS

In the Matamek region, the periphyton communities have recently been studied by Ditner (1981), Naiman (1983), Duthie and Hamilton (1983), and Hamilton (1983). Preliminary experiments on heterotrophic assimilation of ^{14}C-Glucose by phytoplankton were persued by Jordan (1977).

Glass slides and concrete balls were immersed in 10 cm of water at the second fall's stream tanks on the Matamek River, on two separate occasions (23 June and 8 July) so as to obtain assemblages of different cell densities on each substratum by the end of July when the experiments were to take place.

a) Monitoring during colonization

Water quality (conductivity, alkalinity, pH, °C), flow regime, light intensity and nutrient content were monitored throughout the colonization period. Colonization of glass slides by diatoms was monitored by directly counting the number of cells and filaments of the major species fixed after a known immersion period, using light microscope. Observations of living assemblages on rock were carried out with a dissecting microscope. At the end of the colonization period, rocks supporting visibly high or low periphyton density were also taken from a nearby pool, and were analyzed simultaneously with the other substrata for algal physiology, taxonomic composition and primary production.

b) Taxonomic composition and physiological characteristics

Each substratum (glass slide, concrete ball or rock) supporting low or high periphyton density was brought to the laboratory, where the periphyton flora was separated into top and bottom layers. It was assumed that the top layer comprised mostly the loosely adherent cells removed by the jet of a washbottle. The bottom layer, comprising the more adherent cells, was scrubbed off in a separate container using a plastic vegetable brush. Total volume of each portion was adjusted according to the apparent periphyton density. Total surface area scrubbed was estimated by covering the surface with aluminum foil and converting the obtained weight to surface area by density conversion. Replicate aliquotes were taken for the different analyses while each sample was agitated with a magnetic stirrer. A summary of sampling design is presented in Figure 1.

Samples for diatom identification and enumeration were acid cleaned, spread on coverslips using Battarbee (1973) chambers and permanently mounted in Naphrax. At least 300 valves were counted per sample. Shannon's diversity index H (1948) was then calculated. Measurements of ATP, pigment concentration, carbohydrate concentration and ash free dry weight were made on replicate aliquotes following procedures modified from Strickland and Parsons (1972).

c) Primary production

After the end of the colonization period, each type of substratum supporting low or high density of periphyton was put into an 18-litre recirculating plexiglass incubation chamber divided into clear and dark compartments. Twenty-five uCi of ^{14}C-glucose or ^{14}C-bicarbonate were added to the chamber and incubated in the stream for four hours. At the end of the incubation period, the substrata were emersed and taken to the laboratory where the periphytic community was separated into top and bottom layers as described above. Replicate aliquotes were taken from each sample for measurement of total community production using scintillation counting (Modified from Strickland and Parsons 1972) and for measurement of individual species' production using track autoradiography (Hamilton 1983, modified from Knoechel and Kalff 1976).

RESULTS AND DISCUSSION

a) Monitoring during colonization period

Stream water quality measurements showed the Matamek stream tanks to be relatively variable on a short temporal basis (Fig. 2-3-4). Temperature ranged from 17 to 22°C (Fig. 2a). The dryness of the 1983 summer season is shown by the steady increase of cumulative light intensity (Fig. 2b) and the very drastic decrease in discharge in early July, dropping below measurable levels in the stream tank by mid July (Fig. 2c). Conductivity, pH and alkalinity values reflected the soft, acidic nature of these little buffered waters (Fig. 3a-b-c). Nutrient concentration showed total phosphorus, silicon and total nitrogen to be constant through time, phosphorus concentration being at the detection level and presumably in limiting amounts for algal growth (Fig. 4).

Monitoring algal settlement on glass slides (Table 1) showed the early flora to be dominated heavily by Tabellaria flocculosa, settling initially in short filamentous strands. Within six days, the length of the filaments had doubled, accounting for the major part of the increase in biomass. These results indicate that, once the space on the substratum itself has been used, growth of the primary colonizers is a more important contribution to biomass increase than immigration. The process of horizontal, two dimensional space occupation preceeds the vertical expansion of the community. Live observation on rocks covered with a thick (5 cm) periphyton growth showed it to be composed of a loose filamentous matrix trapping gas bubbles, sand grains and detrital particles. The filaments were mainly of Tabellaria flocculosa and Eunotia pectinalis v. pectinalis, suggesting the replacement of the former (pioneer form) by the latter in denser communities. (This hypothesis will be verified when results of nuclear track autoradiography are available.) The dense community growing on rocks also supported an important fauna of grazers, composed mainly of chironomids and oligochaetes. These grazers were increasing the heterogeneity of the algal mass by tangling filaments into tubes and possibly contributed to water movements and nutrient inputs in interstitial waters.

b) Taxonomic composition

Sixty four species of diatoms, belonging to 23 genera were identified (Table 2). The comparison of results between the different densities of the different substrata shows the existence of considerable variations of species richness and diversity, without apparent relation to cell density (Table 3). Although immersed for up to six weeks prior to the analyses, cell densities on glass slides and concrete balls remained well below those found on rocks. The development appeared slower on glass slides, but the community composition was otherwise similar to that of the other two substrata, Tabellaria flocculosa and Eunotia spp. were always the dominant groups.

Due to the complex stratification of factors (substratum, development, layer) and the possibility of interactions, further analysis of the data requires that three-way ANOVA be used.

c) Physiological characteristics and primary production

Data analysis and treatment are incomplete, and will be presented later.

CONCLUSION

The data analyzed so far show that, although structural complexity obviously increases with cell density, taxonomic composition and species abundance are of little use to describe the changes taking place in the periphytic community. The faster development of diatom assemblage on concrete ball indicates that substratum roughness may improve initial cell adherence. However, despite the differences in cell density, the three substrata supported a very similar flora. These results should facilitate the interpretation of physiological and primary production data.

ACKNOWLEDGEMENTS

We wish to thank Ms. Sandra Ditner for her invaluable help during field work. The cooperation of the personnel of the Matamek Research Station also vastly facilitated field work. This research was supported by a grant from the Natural Sciences and Engingeering Research Council of Canada to H.C.D.

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Table 1. Summary of the results of the observations and counts of live *Tabellaria flocculosa* cells on slides immersed in the Matamek river on June 23, 1983.

	Days	#of cells per field $\bar{x}$ (s.d.)	#of filaments per field $\bar{x}$ (s.d.)	#of cells per filament $\bar{x}$ (s.d.)	#of single cell per field $\bar{x}$ (s.d.)	# of fields
New Slides	5 (28/6)	117.29 (75.59)	15.91 (10.45)	7.74 (5.00)	8.09 (9.90)	31
Old Slides	11 (4/7)	231.63 (120.62)	16.49 (6.05)	13.49 (5.52)	5.60 (6.04)	35

Table 2. Species of diatoms found in Matamek river periphyton.

Achnanthes	levanderi Hust.
	marginulata Grun.
	microcephala (Kütz.) Grun.
	minutissima (Kütz.)
	saxonica Krasske
	spp.
Actinella	punctata Lewis
Anomoeoneis	serians (Bréb. ex Kütz.) Cl.
	vitrea (Grun.) Ross
*Caloneis	bacillum (Grun.) Cl.
	ladogensis v.densistriata (ϕst.) Foged
*Coscinodiscus	spp.
Cymbella	microcephala Grun.
	minuta Hilse ex Rabh.
	minuta v. silesiaca (Bleisch. ex Rabh.) Reim.
Diatoma	anceps (Ehr.) Kirchn.
Eunotia	arcus Ehr.
	curvata (Kütz.) Lagerst.
	exigua (Bréb. ex Kütz.) Rabh.
	incisa W. Sm. ex Greg.
	microcephala Krasske ex Hust.
	pectinalis (O.F. Müll. ?) Rabh.
	pectinalis v. minor (Kütz.) Rabh.
	perpusilla Grun.
	praerupta Ehr.
	serra Ehr.
	sudetica O.F. Müll.
	tenella (Grun.) Cl.
	spp.
Fragilaria	brevistriata Grun.
	construens (Ehr.) Grun.
	pinnata Ehr.
	virescens Ralfs
	spp.
Frustulia	rhomboides (Ehr.) De T.
	v. saxonica (Rabh.) De T.
Gomphonema	acuminatum Ehr.
	angustatum (Kütz.) Rabh.
	gracile Ehr.
	spp.
Melosira	distans (Ehr.) Kütz.
Navicula	atomus (Kütz.) Grun.
	bacillum Ehr.
	cocconeiformis Greg. ex Grev.
	* minima Grun.
	* protracta Grun.
	radiosa v. parva Wallace
	seminulum Grun.
	sohrensis (Krasske)
	spp.
Neidium	affine (Ehr.) Pfitz.
	v. amphirhyncus (Ehr.) Cl.
	ladogense v. densestriatum (ϕstr.) Foged
*Nitzschia	palea (Kütz.) W. Sm.
Peronia	heribaudii Brun et Peragallo
Pinnularia	abaujensis (Pant.) Ross
	biceps Greg.
	mesolepta (Ehr.) W. Sm.
Stauroneis	anceps Ehr.
Stenopterbia	intermedia Lewis
Surirella	delicatissima Lewis
	linearis W. Sm.
	ovalis de Brébisson
Synedra	delicatissima W. Sm.
	rumpens Kütz.
Tabellaria	fenestrata (Lyngb.) Kütz.
	flocculosa (Roth.) Kütz.

* species found in brackish or hard waters.

SUBSTRATA	SLIDES			CONCRETE BALLS				ROCKS			
DENSITY	LOW	HIGH		LOW		HIGH		LOW		HIGH	
LAYER	TOTAL*	TOP	BOTTOM	TOP	BOTTOM	TOP	BOTTOM	TOP	BOTTOM	TOP	BOTT.
								n = 2		n = 4	
Number of species	16	16	20	21	16	14	16	16-32	23-24	16-26	16-19
Diversity	0.651	0.652	0.698	0.714	0.560	0.543	0.579	0.574-0.635	0.763-0.853	0.203-0.671	0.482-0.804
Total cell density $x10^5/cm^2$	0.22	0.27	0.48	1.89	0.40	8.97	0.21	7.74-9.96	5.07-7.52	34.69-129.24	14.15-19.21
% *Tabellaria flocculosa*	60.6	56.6	51.1	55.2	68.4	66.1	66.9	46.7-59.3	42.7-50.5	60.8-91.1	18.5-75.4
% *Eunotia* spp.	20.3	17.1	31.1	31.8	18.1	24.7	24.1	23.7-24.9	34.0-34.4	4.8-25.2	17.0-65.4

Table 3. Summary of taxonomic composition, cell density and dominance in the top and bottom layers of three different substrata supporting different cell densities. n = number of measurements, when n > 1, the range is indicated. *Due to low cell density, the two layers were analyzed together.

FIGURE CAPTIONS

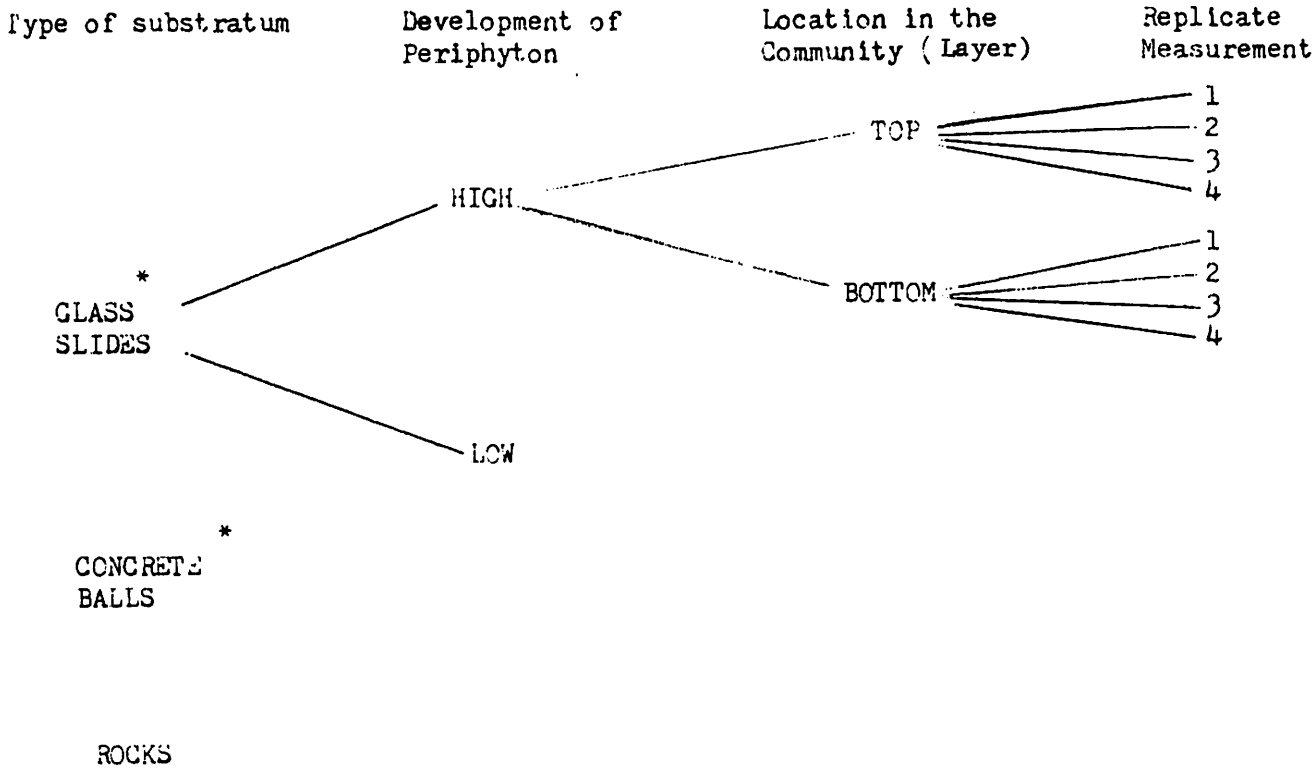
Figure 1. Schematic design of the Matamek Stream Tanks' experiment in summer 1983.

Figure 2. Monitoring of physical variables in the Matamek stream tanks in June-July 1983.
A. Water temperature (°C)
B. Cumulative light intensity (x 10^5 $\mu E \cdot m^{-2} \cdot S^{-1}$)
C. Water discharge ($L \cdot S^{-1}$)

Figure 3. Monitoring of chemical variables in the Matamek Stream tanks in June-July 1983.
A. Conductivity (μ mhos)
B. pH (log $[H^+]$)
C. Alkalinity (10^{-3} mg$\cdot$ 1^{-1})

Figure 4. Monitoring of nutrient concentration (ppm) in the Matamek Stream tanks in June-July 1983.

EXPERIMENTAL DESIGN IN THE MATAMEK RIVER--SUMMER 1983



* Substrata colonized under controlled conditions for a known period of time.

Fig. 1

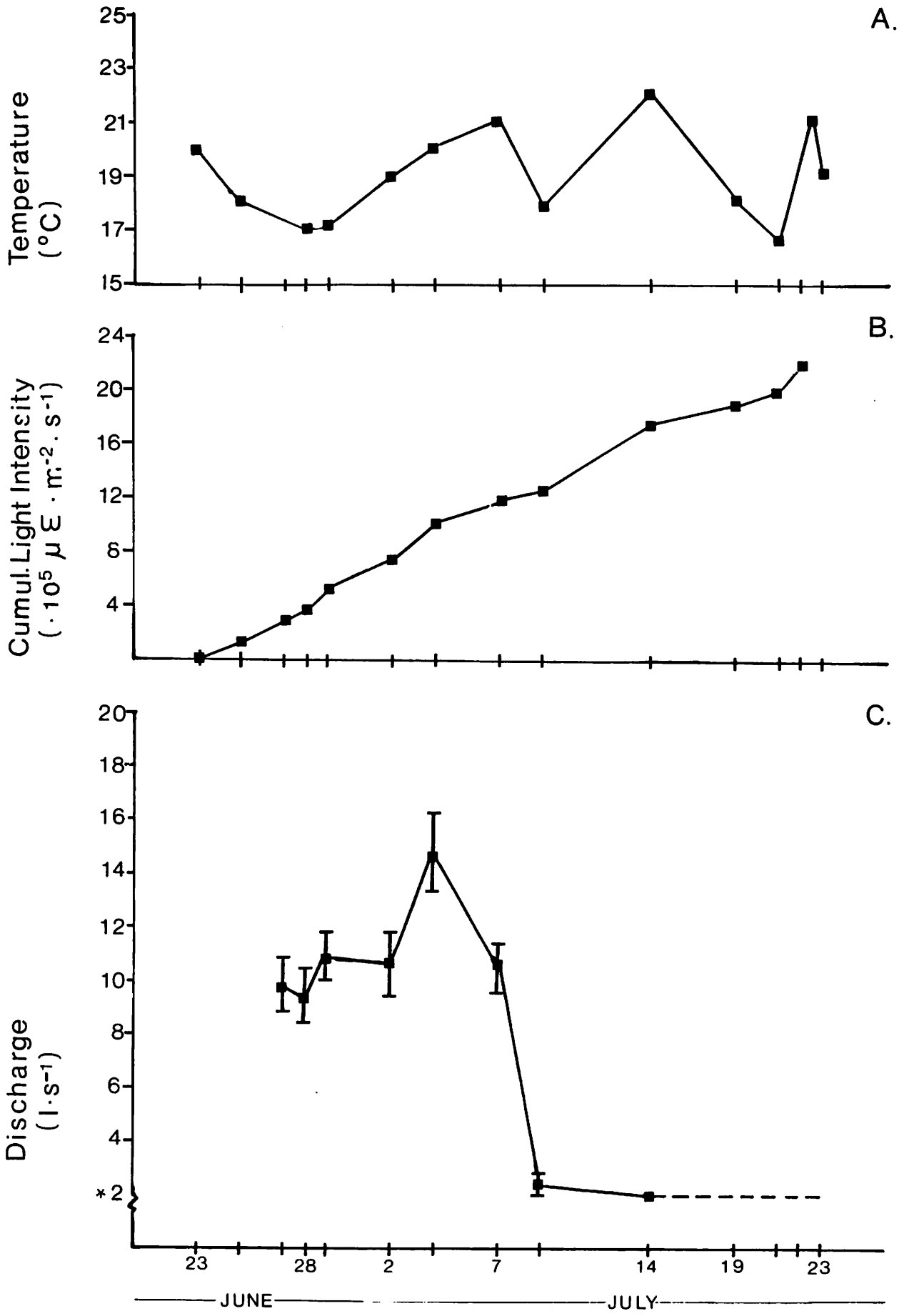

A.
Temperature (°C)
25
23
21
19
17
15
B.
Cumul. Light Intensity (·10⁵ μE · m⁻². s⁻¹)
24
20
16
12
8
4
C.
Discharge (l·s⁻¹)
20
18
16
14
12
10
8
6
4
*2
23
28
2
7
14
19
23
JUNE
JULY

Fig. 2

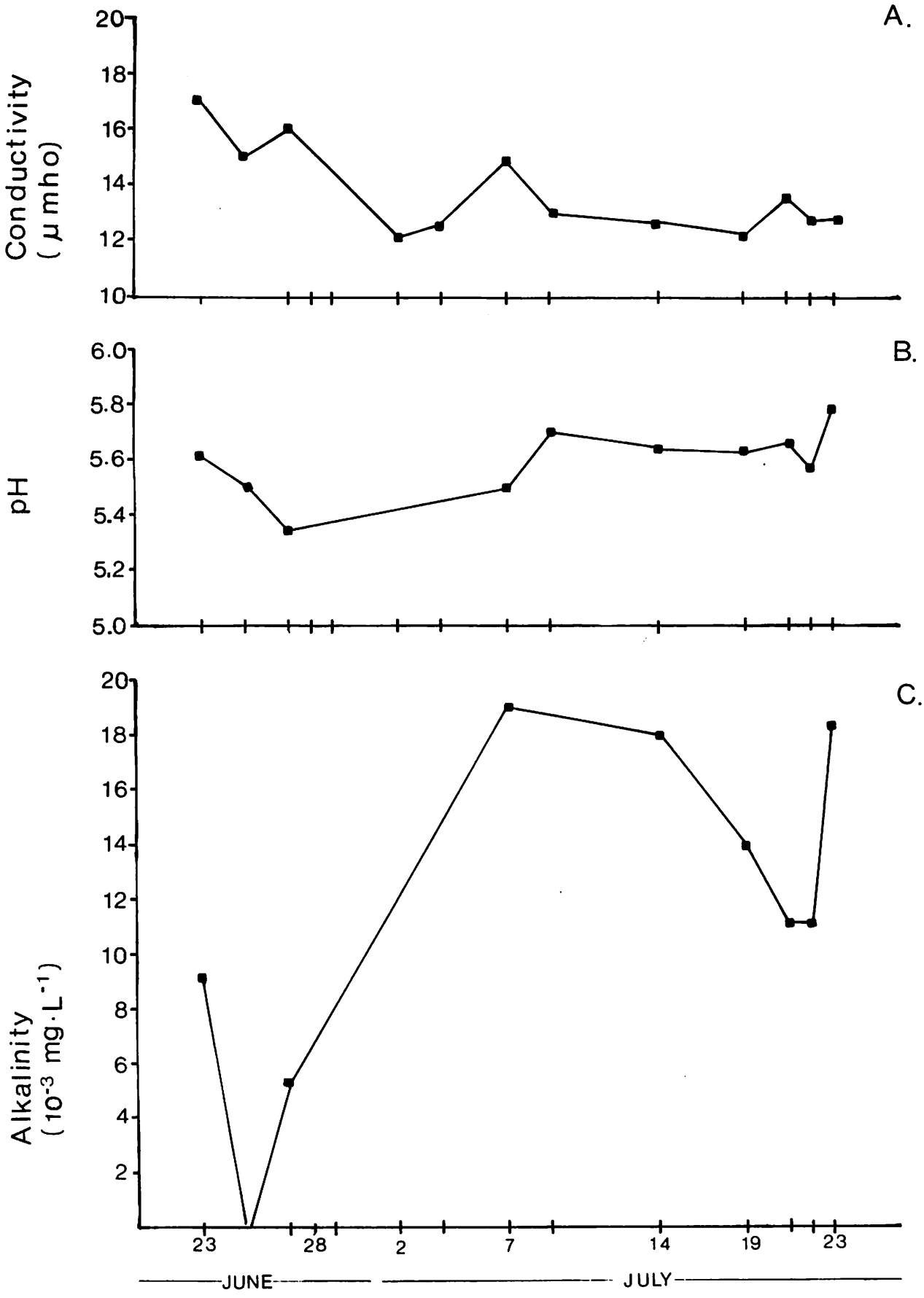

A.
Conductivity
(μmho)
20
18
16
14
12
10
B.
pH
6.0
5.8
5.6
5.4
5.2
5.0
C.
Alkalinity
(10^{-3} mg·L^{-1})
20
18
16
14
12
10
8
6
4
2
23
28
2
7
14
19
23
JUNE
JULY

Fig. 3

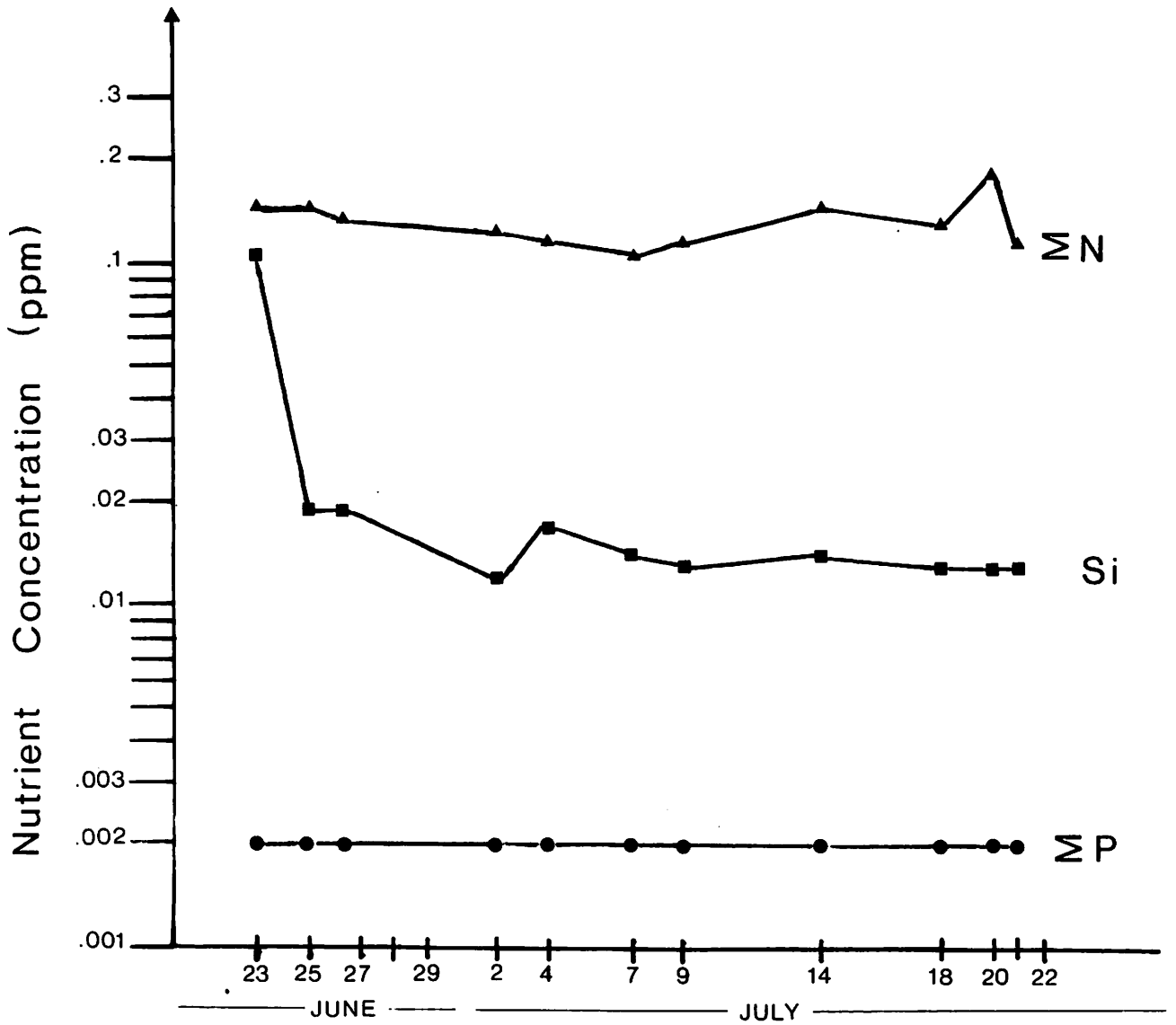

Nutrient Concentration (ppm)
.3
.2
.1
.03
.02
.01
.003
.002
.001
≤N
Si
≤P
23
25
27
29
2
4
7
9
14
18
20
22
JUNE
JULY

Fig. 4

STREAM ORDER OF SOME LOWER NORTH SHORE RIVERS

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INTRODUCTION

The stream orders of five Lower North Shore rivers were determined using the standard geomorphological techniques as outlined by Naiman and Critchley (1980). One order was added to that calculated in each case to account for first order streams not shown on the 1:50,000 Canadian Geological Survey topographic maps used for the study. Field checking for accuracy was not undertaken, but Naiman (pers. comm.) found this approach reasonably accurate for the Moisie and Matamek watersheds where some field checking was possible. The logarithm of drainage basin area was regressed against stream order (Figure 1) for the rivers listed below as well as the Moisie (9th order, 19,871 km sq), Matamek (6th order, 673 km sq), and Muskrat (5th order, 207 km sq): (data after Naiman and Critchley, 1980).

RESULTS

RIVER	STREAM ORDER	DRAINAGE BASIN (km sq)
Grand Watchichou	6	1064
Nabisipi	7	2062
Natashquan	8	16110
Olomane	7	5439
Etamamiou	8*	3030

*Note: The order of the Etamamiou River should probably be classed one lower, since a seventh order stream branches just above Lac Manet and re-joins at Lac Foucher, thus creating an eighth order stream. This lower classification was used for the regression analysis.

DISCUSSION

As expected the variables are very highly correlated (r=0.964), though some caution should be exercised in interpretation of order when dealing with complex river systems such as the Etamamiou.

REFERENCES

Naiman, R. J. and J. Critchley. 1980. River ecosystem studies. Watershed analysis. Matamek Annual Report for 1979: 8-17.

Gouvernement du Quebec. 1970. Superficies des bassins versants du Quebec, Troisieme Partie. Ministere des Richesses Naturelles, Direction generale des eaux: Service del l'hydrographie. 55 pp.

Plot of Log Basin Drainage Area vs Stream Order

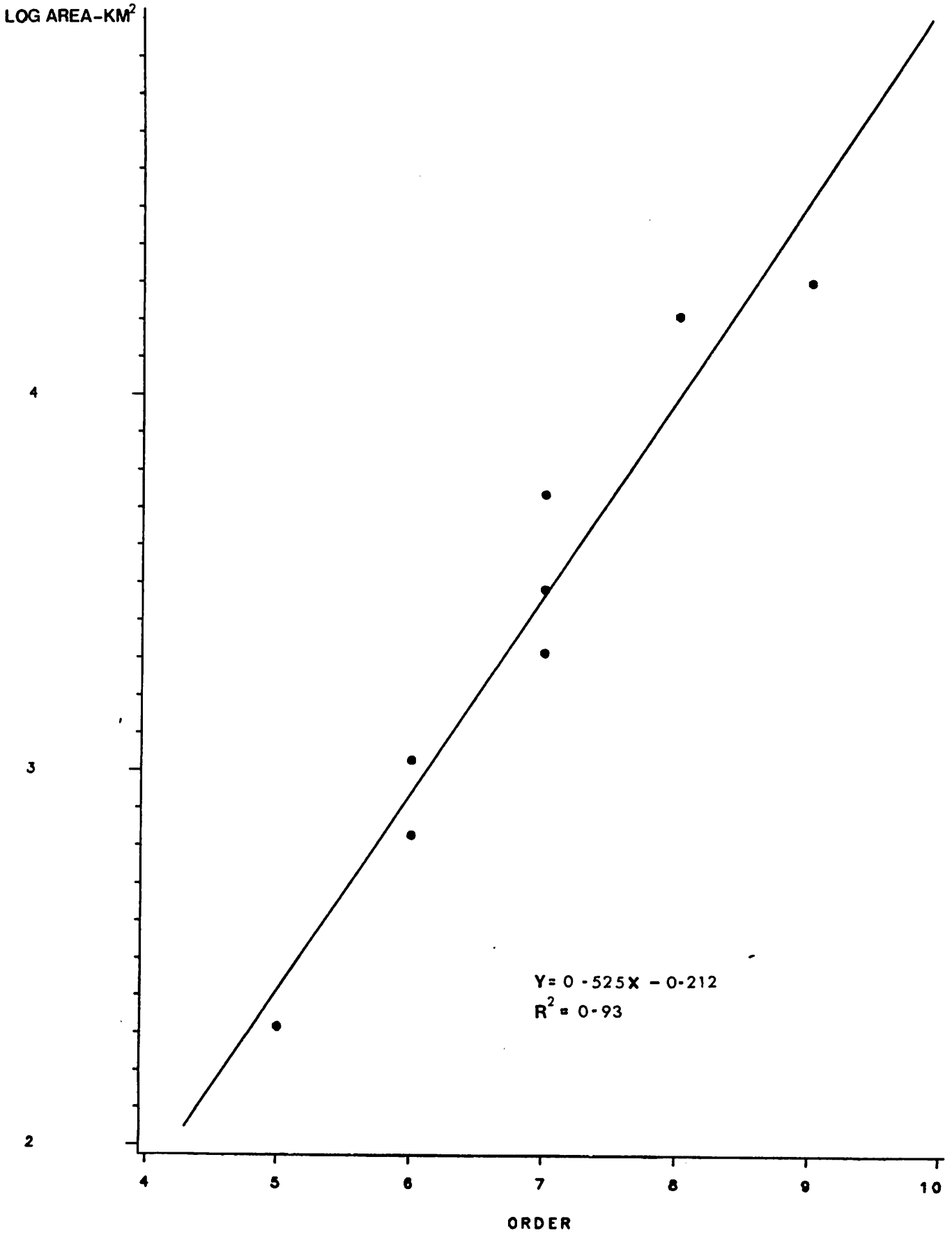

Fig. 1

FISH PROGRAMS 1983

Roderick Morin, Alain Cloutier and Alan McNeil
Woods Hole Oceanographic Institution and
Matamek Research Station

The broad research objectives during 1983 were to synthesize our knowledge of fish ecology for the Matamek region and to relate fish production to physical and biotic characteristics of streams. These objectives will enable us to describe and quantify the trophic pathways leading to fish production, enhancing considerably our knowledge of the trophic basis for salmonid production. This ecosystem approach to fish production was initiated in 1983. The results of field work in 1983 are being analyzed and will be incorporated with data from literature and field studies in 1984. We present here an outline of the main programs, the questions asked, and the approaches we have taken.

Fish production dynamics

The principal question addressed in this study is whether total fish community production can be related to stream order. Stream order is a unit of stream classification that has enabled us to characterize numerous ecosystem-level processes throughout the Matamek watershed (Naiman 1983). Secondly, we would like to know, as an alternative to the stream order classification system, what combinations of habitat variables regulate total fish community production. Lastly, we want to know how fish communities change along the length of rivers. We expect that the number of fish species and their feeding guilds will increase as streams become larger and stream habitat is more diverse.

During 1983 we measured total fish production in two fourth-order streams, Thom and St. Charles creeks, and one sixth-order stream, the Matamek River between the third and fourth falls. Fish production was determined for the major fish species using Allen's graphical method (Chapman 1978).

The role of habitat in relation to fish biomass was studied by sectioning off areas in each stream. In each section the biomass of each fish species was estimated and habitat was assessed by transects at 5 m intervals. Twenty-six habitat variables were recorded in all. A sampling was made of each species in each stream to determine age structure, growth rates, age of maturity and fecundity. An analysis of diet by stream order will be made from collected specimens and previous studies.

This study is the first synthesis of fish species composition and community structure for North Shore rivers. During 1983 we conducted a study of diet movements and activity patterns in brook trout, salmon parr and longnose suckers (Catastomus catastomus). We examined the spatial structure of fish communities in our study sites and how major stream configurations; i.e, pools and riffles, are utilized by fish.

Population trends in Matamek brook trout

Brook trout have been extensively studied in the lower Matamek River, from the top of the First Falls to the base of the Fifth Falls. Population estimates of parr and brook trout have been made at the base of the Second Falls yearly since 1971 and analyses have been made of growth, maturity and feeding throughout the lower river since 1967. Brook trout is the dominant fish species of the Matamek River. In spite of this, no single study has integrated this information as it is found presently in articles, theses and manuscript reports. Since fish are protected in the Matamek River, scientific sampling is the probable main source of human influence. Records of the number of trout removed are available for all years.

In 1983 we undertook an analysis of population trends in brook trout of the Matamek River. This study describes the ecology of brook trout in the Matamek River, compares their life history in areas with and without exploitation, and describes their life history responses to known levels of exploitation. In general, the brook trout population located below the Second Falls has declined since 1971. Exploitation was strongest in 1967, 1974, 1978 and 1979. The age of maturity has decreased noticeably since 1967. Growth and fecundity appear to have increased; however, it has not been determined whether these changes are statistically significant. Analysis will be completed in 1984.

REFERENCES

Chapman, D. W. 1978. Production in fish populations, p. 5-25. In: S. D. Gerking (ed.) Ecology of Freshwater Fish Production. Blackwell Scientific Publications, London. 520 pp.

Naiman, R. J. 1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. Ecol. Monog. 53: 73-94.

SALMON MONITORING

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Woods Hole Oceanographic Institution

During 1983 we monitored the size, age composition and number of migrating smolts and adult salmon in the Matamek River. Adult salmon were captured in the fishway located at the First Falls. The fishway was operated from June 15 to August 28. Smolts were seined at the Matamek River estuary from May 25 to July 23. In addition to sampling migrant populations, population estimates of brook trout and salmon parr were made below the second and fourth falls during August.

The adult Atlantic salmon population of the Matamek River reached a critically low level during 1983. The migration of adults in the fishway occurred from July 6 to August 13, but the number captured was not sufficient for a reliable population estimate. Only 11 salmon passed through the fishway, the lowest number recorded since the fishway was first operated in 1975. Four salmon were captured in the trapnet set below the Third Falls. Of these four, two were recaptures of salmon tagged in the fishway. To our knowledge, both the fishway and trapnet functioned at full potential throughout the salmon migration. We are presently unable to attribute their low catches to any unique river conditions that may have reduced their catch efficiency.

Smolts were captured in the Matamek estuary from May 28 to July 7. Due to a reduction in smolts during 1982, sampling was conducted less frequently in 1983 than in previous years and smolt tagging was discontinued. These measures were undertaken to reduce potential mortality to smolts resulting from intense sampling. Seining catches were generally low during 1983, usually <5 smolts per seine haul; however, on June 23 approximately 50 smolts were captured in a single haul. This was the largest concentration recorded over the past three years of sampling. The peak of the smolt run, based on our seine catches in the estuary, occurred between June 18 and July 7.

Gibson and Coté (1982) reported the results of intensive smolt tagging in the Matamek River during the 1970's. They evaluated data on the movement patterns of smolts at sea, the rate of return, and the exploitation at sea. Gibson and Porter (1983) have more recently expressed reservations on the application of these results to other rivers in part because the results were based on a limited number of tag returns. It is of interest now to update the data to improve this weakness and also since it is unlikely at the present population level that smolt tagging will be resumed for many years to come.

Table 1 presents data on tag returns since 1975. These are the results of smolts tagged in the Matamek River from 1974 to 1980. In all, 36 returns were made, 30% of which were adults taken in the Matamek River,

the remaining 70% taken in fisheries at sea. Of the 36 returns, 20 (55%) were taken in Newfoundland fisheries, 1 (3%) off Nova Scotia, 1 off the coast of Labrador, 1 in Norway and 2 (6%) in the local Sept-Iles fishery. Based on the date and location of captures, it appears that over 90% of the salmon taken in commercial fisheries would have returned to the Matamek River as 2-sea-winter salmon.

In recent years, tag returns from commercial fishermen have included salmon that were tagged in the fishway. These salmon presumably spawned and returned to sea before being captured. This is of interest since repeat spawners are rare in the Matamek River. Table 2 presents data on these returns.

REFERENCES

Gibson, J. R. and Y. Côté. 1982. Production de saumonneaux et recaptures de saumons adultes étiquetes à la rivière Matamec, Côte-Nord, Golfe du Saint-Laurent, Québec. Naturaliste Can. 109: 13-25.

Gibson, J. R. and T. R. Porter. 1983. Perspective. Atlantic Salmon Journal, Spring 1983. pg. 37.

Table 1. Mark and recapture data on salmon smolts marked and released from the Matamek River.

Tagging date	Recapture data	Recapture location	Tag No.
June 21-74	July 17-75	Matamek River	23071
June 26-74	June 18-76	Old Bonaventure, Nfld.	23011
June 29-74	July 10-75	Harbour Le Cou, Nfld.	23584
June 29-74	July 18-76	Matamek River	23559
June 14-75	Sept. 1-76	Hopedale, Labrador	23112
June 17-75	July 15-76	Burgeo, Nfld.	24254
June 17-75	Aug. 23-76	Matamek River	24295
June 18-75	June 2-77	Fogo district, Nfld.	23796
June 19-75	Sept. -79	Norway	23761
June 21-75	Aug. 15-76	Matamek River	23732
June 12-76	May 31-78	Burgeo, Nfld.	24378
June 19-76	June -78	Port-aux-Basques, Nfld.	24625
June 19-76	June 13-78	Burnt Island, Nfld.	24655
June 13-77	July 24-78	Harbour Deep, Nfld	24842
June 13-77	July 17-78	Matamek River	24840
June 15-77	July 25-78	Snooks Head, Green Bay, Nfld.	24882
June 16-77	Sept. 13-78	Matamek River	24894
June 16-77	July 10-78	S. Head Seals Isl., Trinity Bay, Nfld.	24898
June 16-77	July 10-78	Goose Berry Cove, Nfld.	
June 17-77	July 19-78	Matamek River	24772
June 2-78	June -80	Sept-Iles, Qué	
June 3-78	June 23-79	Boot Harbour, Nfld.	23312
June 13-78	July 28-80	Cape Edgemot, N. Scotia	23346
June 15-78	Aug. 25-79	Matamek River	
June 16-78	June 29-79	Englee, 4 mi S.E., Nfld.	24048
June 16-78	July 10-79	Matamek River	
June 21-78	July 2-79	Red Island, Nfld.	24080
June 28-78	July 18-79	Crouse Conche, Nfld.	24142
July -78	June 2-80	East of des Cailles, Moisie, Qué	23310
June -79	June 27-80	Caugt La Scie, Nfld.	23874
June -79	July 1-80	Burnside Bay, Nfld.	22401
June -79	July 4-80	Salvage, Nfld.	22330
June -79	June 20-80	Conche, Nfld.	22377
July 14-79	Aug. 1-80	White Bay, Nfld.	00583
-80	June 23-81	Matamek River	22986
-80	July 23-81	Matamek River	22600

Table 2. Data on adult salmon tagged in the Matamek River fishway and subsequently recaptured at sea.

Tagging			Recapture			
Date	F. length (cm)	Age	Date	Location	Weight (lb)	Tag No.
July 7-79	76.3	3, 2+	Sept. 1-80	Sacred Islands, Nfld.	17	583
July 24-80	58.0	3, 1+	July 17-81	Blanc Sablon, Qué	7	485
Aug. 11-81	43.0	3, 1+	June 14-82	Douglastown, Gaspé Bay, Qué	-	194

OSMOREGULATION IN THE BROOK TROUT, Salvelinus fontinalis. I. DIEL, PHOTOPERIOD AND GROWTH RELATED PHYSIOLOGICAL CHANGES IN FRESHWATER

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Biology Department
Woods Hole Oceanographic Institution

ABSTRACT

1. Brook trout (Salvelinus fontinalis) raised from eggs under two photoperiod and two feeding regimes were tested for physiological changes preparatory for transition from freshwater to seawater. Size, age, growth rate, photoperiod, and diel rhythms were examined for possible influences on plasma osmolarity, $[Na^+]$, $[Cl^-]$, $[K^+]$, $[Mg^{2+}]$, thyroxine concentration, hematocrit, and gill Na^+,K^+-ATPase activity of brook trout in freshwater.

2. Significant diel cycles were found in plasma osmolarity, $[Na^+]$ and thyroxine concentration.

3. Significant size and/or age related changes occurred for plasma osmolarity, $[Na^+]$, $[K^+]$ and hematocrit, but could explain little of their total variation ($0.02 < r^2 < 0.18$).

4. A sexually dimorphic response to photoperiod was observed in hematocrit for both mature and immature fish, with hematocrit of mature females declining in autumn and hematocrit of immature males increasing in autumn.

5. Gill Na^+,K^+-ATPase activity did not respond to photoperiod or feeding treatment and showed no change with size or age.

6. Plasma thyroxine levels responded to feeding and photoperiod treatment. There was a significant correlation between the percent mean difference in plasma thyroxine and the mean difference in growth rate between high and low feed fish ($r^2 = 0.51$), suggesting a relationship between thyroxine and growth.

Table 1. Size, age, photoperiod and feeding effects on plasma parameters and gill Na^+,K^+-ATPase. Sample size (N), range, mean, standard deviation (S.D.), and slope (b), y-intercept (y-int.), coefficient of determination (r^2), and significance of regression slope (p), are given for each physiological variable and their regression on length and age. Brook trout were 6.0 and 30.5 cm fork length and 180 to 700 d old. Feeding and photoperiod effect were determined using two-way ANOVA (Yes, $p < 0.05$; No, $p > 0.05$). Yes(H) indicates that photoperiod effect was only significant in high(H) feeding group.

					LINEAR REGRESSION						
	N	Range	Mean	S.D.	Independent Variable	b	y-int.	r^2	p	Feeding Effect	Photoperiod Effect
Osmolarity	793	272-362	307	12.4	Length	0.64	296	0.12	<0.01	YES	NO
					Age	0.022	298	0.07	<0.01		
$[Na^+]$	535	126-186	152	8.0	Length	0.33	146	0.06	<0.01	NO	NO
					Age	0.013	147	0.06	<0.01		
$[K^+]$	607	0.10-7.12	1.99	1.24	Length	-0.037	2.68	0.03	<0.01	YES	NO
					Age	0.0009	2.42	0.01	<0.01		
$[Mg^+]$	605	0.64-2.23	1.04	0.22	Length	-	-	-	0.47	NO	YES(H)
					Age	-	-	-	0.12		
$[Cl^-]$ (100 l)	352	96-133	108	5.5	Length	0.13	105	0.02	0.02	-	-
					Age	0.012	102	0.08	<0.01		
$[Cl^-]$ (1,000 l)	311	103-142	124	6.6	Length	-0.15	127	0.02	0.02	-	-
					Age	-0.008	128	0.03	<0.01		
Hematocrit	940	30-72	48	7.2	Length	0.47	40	0.18	<0.01	-	-
					Age	0.01	44	0.04	<0.01		
Na^+,K^+-ATPase	687	1.3-21.2	7.9	3.4	Length	-	-	-	0.52	NO	NO
					Age	-	-	-	0.60		
Thyroxine	728	0.0-10.1	3.01	1.87	Length	0.14	0.48	0.20	<0.01	YES	YES(H)
					Age	0.0045	1.05	0.10	<0.01		

FIGURE CAPTIONS

Figure 1. Experimental design and fish culture conditions consisting of two photoperiod regimes (one normal, one 3-mo delayed) and two feeding regimens (high feed and low feed).

Figure 2. Effect of feeding treatment on size and growth rate. (A) Length and (B) weight of normal photoperiod fish in high feed (squares) and low feed (circles) groups as a function of time. Mean value of 40-75 fish per sampling date. (C) Log_e specific growth rate (G_w) as a function of the natural logarithm of fish weight (g) in high and low feed groups. Regression line is for high feed fish only ($Log_e G_w = 1.97 + -0.49 Log_e W_t$). (D) Log_e of specific growth rate of fish of unit size (a comparative measure of growth rate which is independent of body size, see text for explanation), as a function of time for high and low feed groups under normal photoperiod conditions.

Figure 3. Diel cycles of plasma thyroxine, osmotic and ionic concentrations, and hematocrit (mean $\pm$ 1 standard error of the mean) over a 20 hr period. Only plasma thyroxine, osmolarity and $[Na^+]$ had significant diel cycles ($p < 0.05$, one-way ANOVA). Experiment was conducted on February 12 under normal photoperiod conditions (10.4 hr daylight, 13.6 hr darkness). The clear horizontal bar indicates daylight period, darkened bar indicates darkness. Sample size was 6 fish for each time interval, except for the 1200 and 0200 intervals when only 4 samples for $[Na^+]$, $[K^+]$ and $[Mg^{2+}]$ were used.

Figure 4. Annual variation in hematocrit (°/o red blood cells) for males (open diamonds) and females (closed diamonds) under normal photoperiod conditions. Mean value of 6-10 fish per sample $\pm$ 1 standard error of the mean. Daylength (•) and spawning time (horizontal bar) are also shown. Fish in this experiment were from high feed group, all of which became mature at age 1+ yr in their second autumn (November 1982). Mean female hematocrit in autumn in significantly lower than the non-autumn mean ($p < 0.05$, student's t-test).

Figure 5. Annual cycles of plasma thyroxine in high feed (squares) and low feed (circles) groups in normal photoperiod (A, solid symbols) and 3 month delayed photoperiod (B, open symbols), as a function of calendar date of sampling. Mean value of 5-16 fish per sample $\pm$ standard error of the mean. An asterisk (*) next to mean of high feed group indicates a significantly ($p < 0.05$, student's t-test) higher mean plasma thyroxine levels than the low feed group at that sampling period. Each point represents samples taken on a single day except for three instances (June, July and August 1981) when samples taken within 2-4 days were combined. Daylength (•) and time of spawning (horizontal bar) are shown for each photoperiod. Feeding treatment had a significant effect on thyroxine levels in both photoperiods ($p < 0.01$, two-way ANOVA). Photoperiod treatment significantly affected thyroxine levels in the high feed group ($p < 0.01$, two-way ANOVA), but not the low feed group ($p = 0.43$).

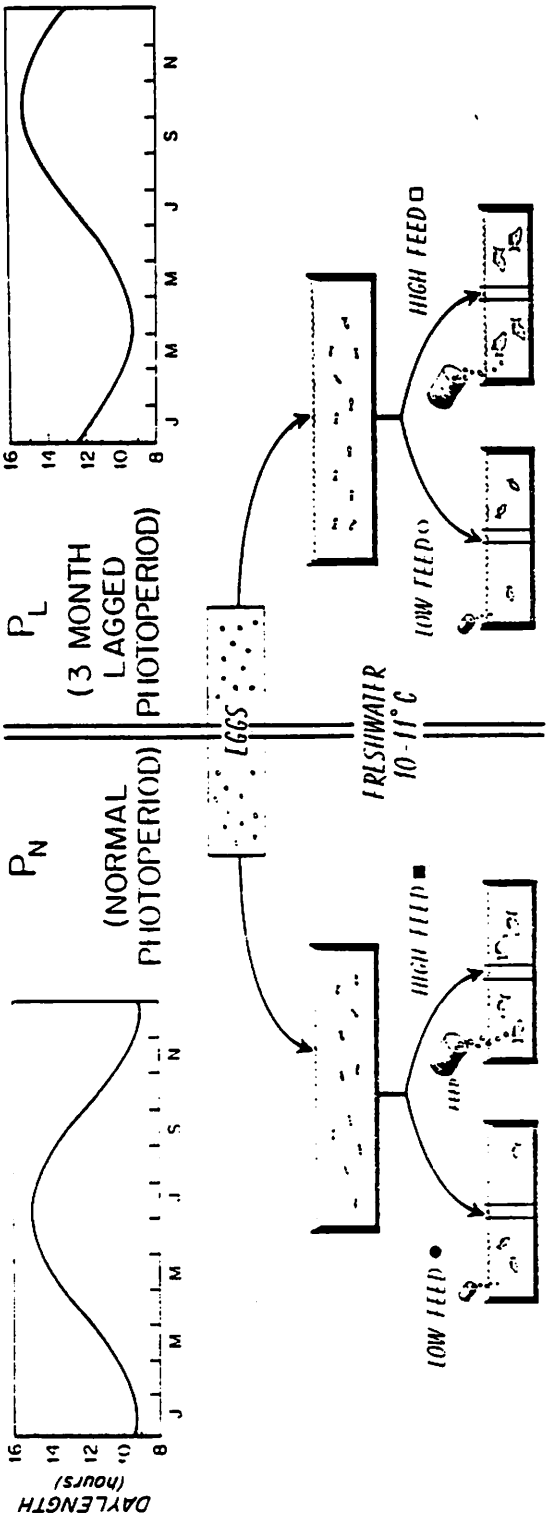
DAYLENGTH (hours)
16
14
12
10
8
J
M
J
S
N
P_N
(NORMAL PHOTOPERIOD)
P_L
(3 MONTH LAGGED PHOTOPERIOD)
EGGS
FRESHWATER 10-11°C
HIGH FEED ■
LOW FEED ●
HIGH FEED □
LOW FEED ○

Fig. 1

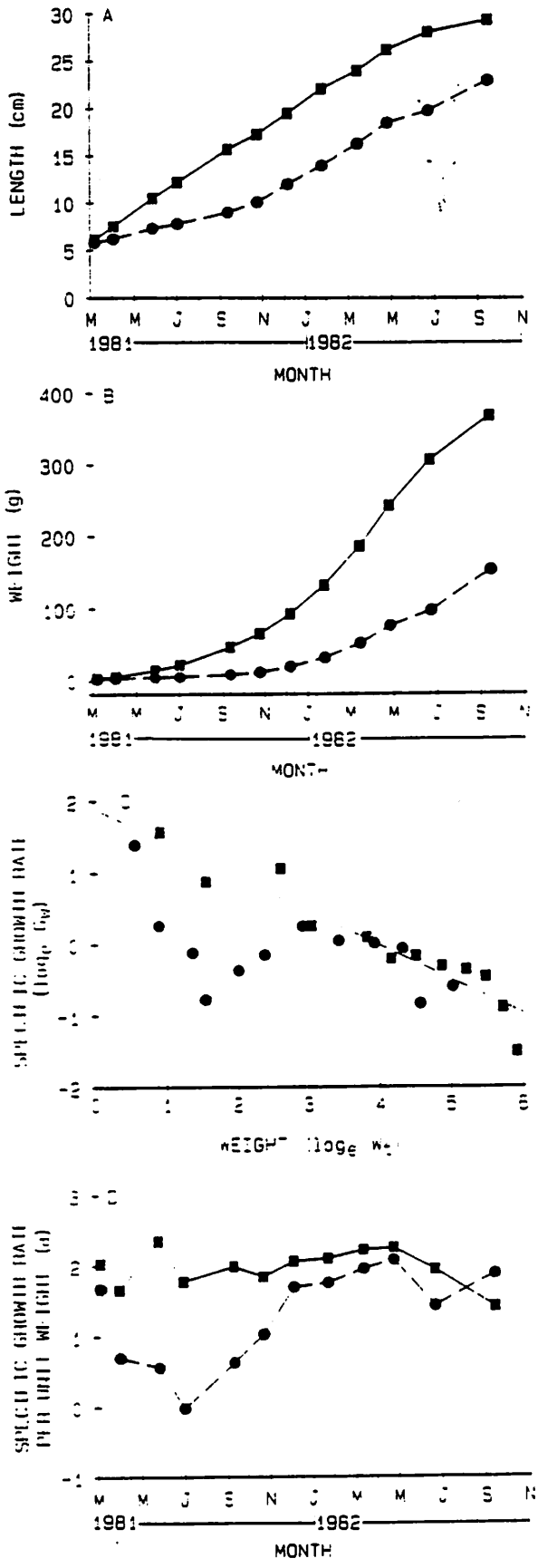
A
LENGTH (cm)
30
25
20
15
10
5
0
M M J S N J M M J S N
1981
1982
MONTH
B
WEIGHT (g)
400
300
200
100
0
1981
1982
MONTH
C
SPECIFIC GROWTH RATE
(loge cm)
2
1
0
-1
-2
0 1 2 3 4 5 6
WEIGHT loge wt
D
SPECIFIC GROWTH RATE
PER UNIT WEIGHT (g)
3
2
1
0
-1
M M J S N J M M J S N
1981
1982
MONTH

Fig. 2

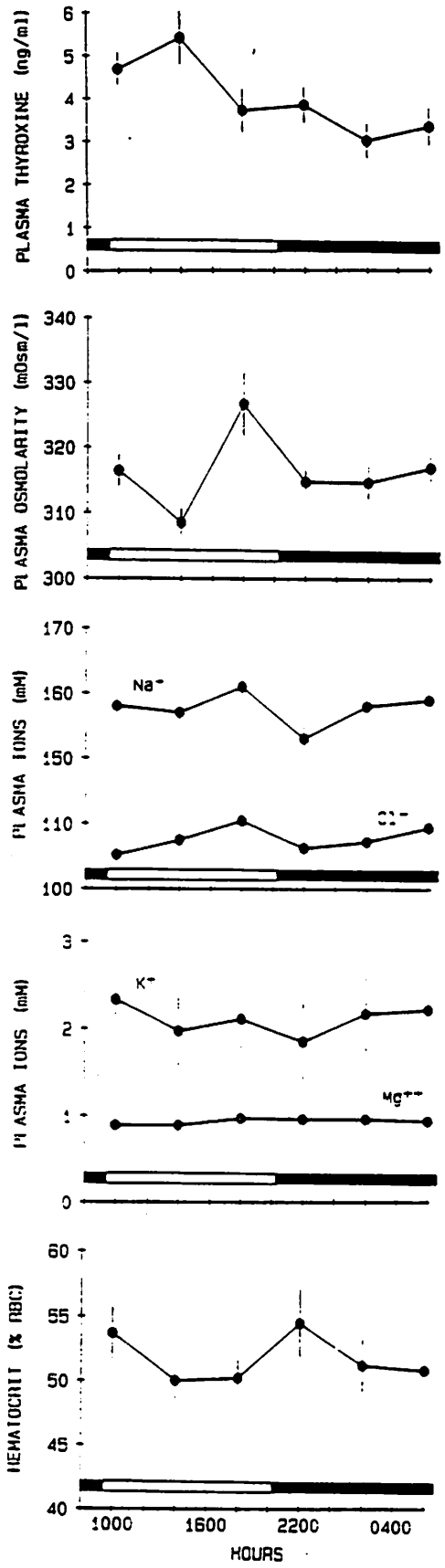
PLASMA THYROXINE (ng/ml)
6
5
4
3
2
1
0
PLASMA OSMOLARITY (mOsm/l)
340
330
320
310
300
PLASMA IONS (mM)
170
160
150
110
100
Na+
Cl-
PLASMA IONS (mM)
3
2
1
0
K+
Mg++
HEMATOCRIT (% RBC)
60
55
50
45
40
1000
1600
2200
0400
HOURS

Fig. 3

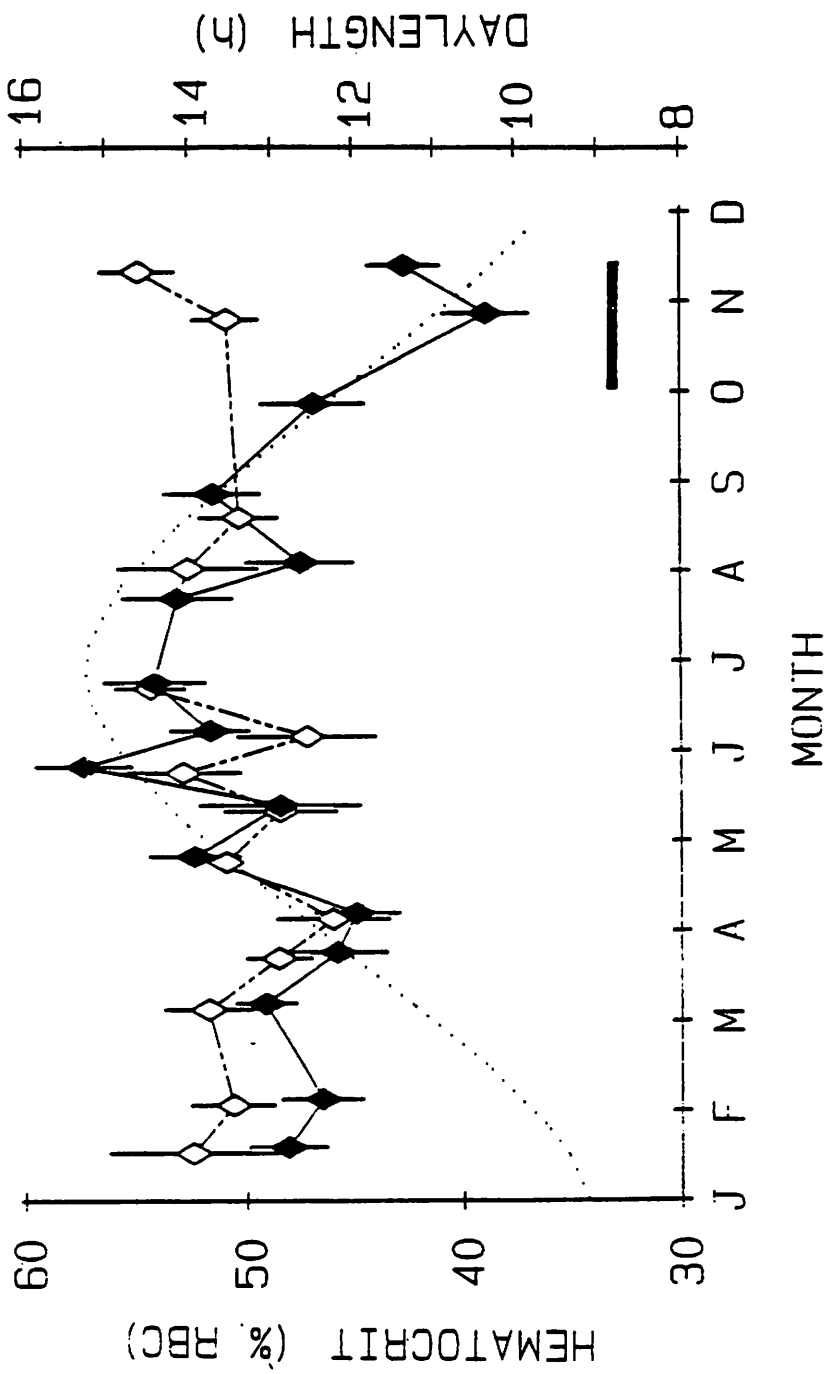
DAYLENGTH (h)
16
14
12
10
8
HEMATOCRIT (% RBC)
60
50
40
30
J F M A M J J A S O N D
MONTH

Fig. 4

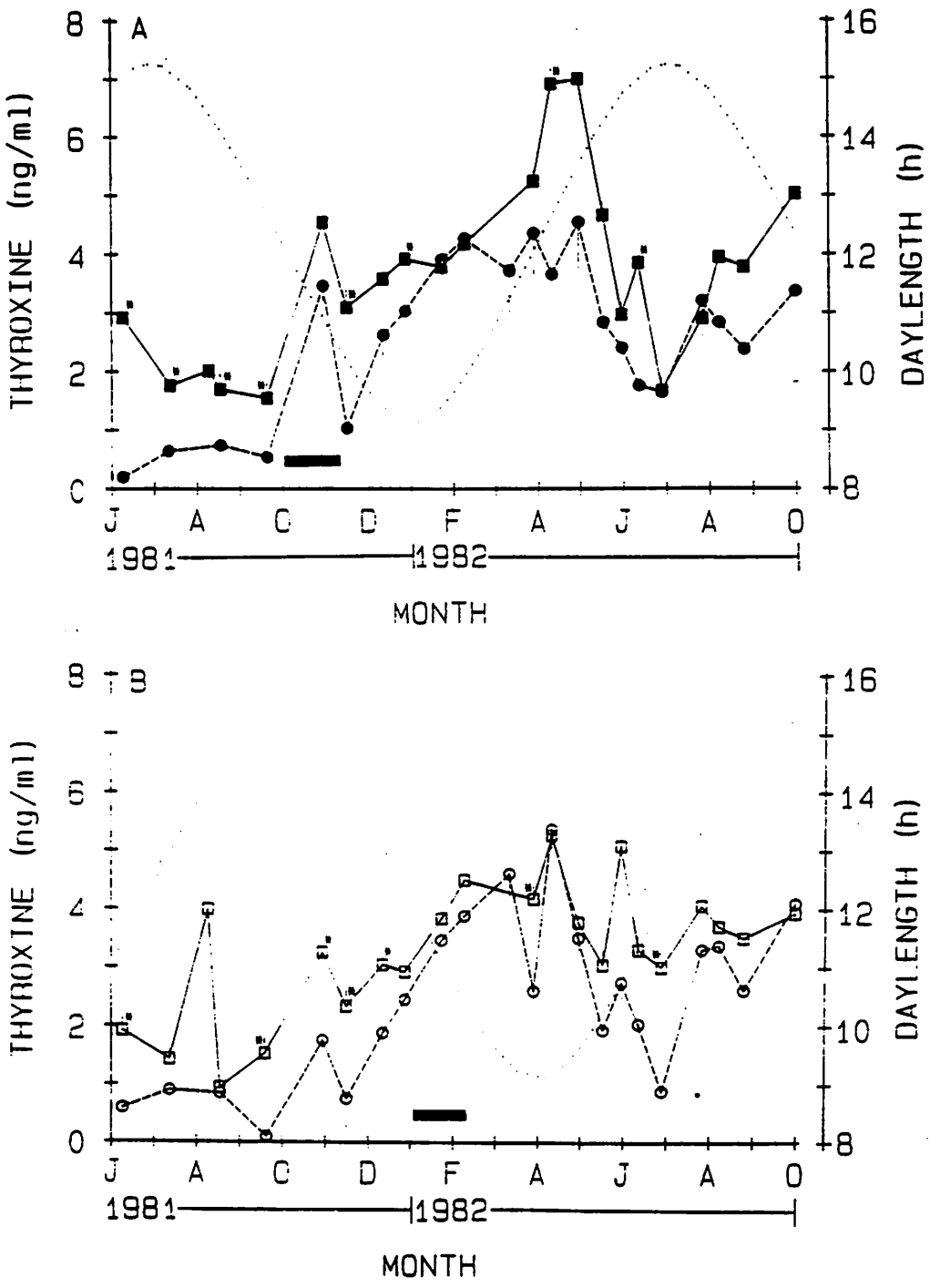
A
B
THYROXINE (ng/ml)
DAYLENGTH (h)
8
6
4
2
0
16
14
12
10
8
J
A
O
D
F
A
J
A
O
1981
1982
MONTH

Fig. 5

OSMOREGULATION IN THE BROOK TROUT, Salvelinus fontinalis. II. EFFECTS OF SIZE, AGE AND PHOTOPERIOD ON SEAWATER SURVIVAL AND IONIC REGULATION

Stephen D. McCormick and Robert J. Naiman
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Woods Hole Oceanographic Institution

ABSTRACT

1. Brook trout (Salvelinus fontinalis) of a single genetic stock, and hatched at the same time, were raised under two photoperiod and two feeding regimes to obtain fish of the same age but with different sizes and photoperiod experiences. In 11 experiments over 1.5 yrs, fish were gradually exposed to 32 ppt seawater for 20 d to investigate the ontogeny of salinity tolerance.

2. Daily changes in plasma osmolarity, $[Na^+]$, $[Cl^-]$, $[K^+]$, $[Mg^{2+}]$, thyroxine, hematocrit and gill Na^+,K^+-ATPase during adaptation to 10, 20 and 32 ppt were examined in one experiment.

3. Size was the primary determinant of seawater survival ($r^2 = 0.77$); the effect of size on seawater survival slowed after fish reached a fork length of 14 cm. The effect of age on seawater survival ($r^2 = 0.65$) was through its covariance with size.

4. Photoperiod affected seawater survival only through its influence on the timing of male maturation, which decreased salinity tolerance.

5. Regulation of plasma osmolarity, $[Na^+]$, $[Cl^-]$, $[K^+]$, $[Mg^{2+}]$ and hematocrit in sea water increased linearly with size over the entire range of sizes (6-32 cm).

6. Gill Na^+,K^+-ATPase activity after 20 d in seawater decreased with increasing size of brook trout, possibly reflecting decreased demand for active ion transport in larger fish.

7. Plasma thyroxine concentrations declined in seawater, but no definitive role of this hormone in seawater adaptation was found.

8. Size dependent survival and osmoregulatory ability of brook trout is compared to other salmonids and a conceptual model is developed.

Table 1. Dichotomous log-linear regression of length, age and male maturity on survial in 32 ppt seawater for 12 d. B is the slope of the regression line. Index of male maturity for an experiment was determined by multiplying the percent mature males in an experiment by their mean gonadosomatic index. The odds ratio was calculated for the range of values in our experiments and represents the change in probability of survival for that range. Odds ratio greater than one indicates increasing chance of survival (e.g. an odds ratio of 100 for size indicates the probability of survival increases 100 times when brook trout go from 6 to 32 cm). An asterisk indicates the odds ratio is significantly different from 0 ($p < 0.05$). Chi-square for this model was 377.4 with 5 degrees of freedom ($p < 0.001$).

Independent Variables	B	Standard Error, B	Odds Ratio
Interval			
1	-.61	.06	-
2	.73	.09	-
3	.52	.13	-
Length	-2.90	.33	106.6 *
Age	-0.89	0.28	1.1
Male Maturity	.006	.002	.169 *

Table 2. Physiological variables after 4 d in seawater regressed on length, and log hazard as a function of physiological variables. Linear regression statistics include correlation coefficient (r), y-intercept (y-int), slope (b), standard error of the slope (S_b), probability of rejecting the null hypothesis that the slope of the regression line is 0 (p), and the number of experiments (N). Each experiment is the mean of 6-8 individuals. All listed correlation coefficients are significant ($p < 0.05$).

	LENGTH					
Dependent variable	r	y-int.	b	S_b	p	N
Osmolarity	-.80	465.7	-3.27	0.37	0.001	44
$[Cl^-]$	-.40	188.9	-0.77	0.27	0.010	38
$[Na^+]$	-.46	215.2	-1.15	0.38	0.004	38
$[K^+]$	-.70	5.42	-0.129	0.022	0.001	38
$[Mg^{2+}]$	-.64	4.45	-0.081	0.016	0.001	38
Hematocrit	.44	42.9	0.285	0.095	0.005	40
Na^+,K^+-ATPase	-	-	-	-	0.101	40
Thyroxine	.48	0.98	0.083	0.026	0.003	36

	LOG SEAWATER HAZARD RATE					
Independent variable	r	y-int.	b	S_b	p	N
Osmolarity	.70	-5.04	.009	.001	0.001	44
$[Cl^-]$	.42	-3.47	.012	.004	0.008	38
$[Na^+]$	.49	-3.24	.009	.003	0.002	38
$[K^+]$	.53	-1.87	.141	.037	0.001	38
$[Mg^{2+}]$	.65	-2.18	.251	.048	0.001	38
Hematocrit	-.39	-0.05	-.030	.012	0.013	40
Na^+,K^+-ATPase	-	-	-	-	0.219	40
Thyroxine	-.46	-1.03	-.140	.047	0.003	36

Table 3. Physiological variables after 20 d in seawater regressed on length. Linear regression statistics include correlation coefficient (r), y-intercept (y-int), slope (b), standard error of the slope (S_b), probability of rejecting the null hypothesis that the slope of the regression line is 0 (p), and the number of experiments (N). Each experiment is the mean of 3-8 individuals. All listed correlation coefficients are significant ($p < 0.05$).

	LENGTH					
Dependent variable	r	y-int.	b	S_b	p	N
Osmolarity	-.57	445.5	-2.48	0.69	0.001	29
$[Cl^-]$	-	-	-	-	0.076	29
$[Na^+]$	-	-	-	-	0.190	20
$[K^+]$	-	-	-	-	0.345	28
$[Mg^{2+}]$	-.49	4.51	-0.079	0.028	0.008	28
Hematocrit	-	-	-	-	0.160	29
Na^+,K^+-ATPase	-.55	42.1	-0.687	0.190	0.002	29
Thyroxine	-	-	-	-	0.776	24

Table 4. Phylogenic comparison of size dependent salinity tolerance and seaward migration in salmonids.

Species	Salinity Tolerance: Salinity (ppt)	Salinity Tolerance: Method of Acclimation	Salinity Tolerance: Duration (d)	Size at 75°/o Survival (cm)	Size at Seaward Migration(cm)	References
Oncorhynchus						
Pink Salmon	32	direct	> 14	< 6.0	2.5 4.0	(Weisbart, 1968; Scott and Crossman, 1973)
Chum Salmon	32	direct	> 14	< 6.0	3.2-7.0	(Weisbart, 1968; Scott and Crossman, 1973)
Chinook Salmon	30	direct	30	6.5	6.0-10.0	(Wagner et al., 1969; Healy, 1980)
	30	gradual	30	4.2		
Coho Salmon	30	direct	30	7.0	10.0 11.0	(Conte et al., 1966; Healy, 1980)
Salmo						
Atlantic Salmon	29	direct	44	13.8	12.7-15.2	(Johnston and Saunders, 1981; Scott and Crossman, 1973)
Steelhead Trout	30	direct	30	16.0	15.0 20.0	(Conte and Wagner, 1965; Wagner et al., 1963)
Salvelinus						
Brook Trout	32	gradual	20	19.0	15.0 18.0	(present study; Montgomery et al., unpublished manuscript)

FIGURE CAPTIONS

Figure 1. Time course of changes in plasma and gill physiological parameters after exposure to 10 ppt, 20 ppt and 32 ppt. Arrows indicate the day of salinity change, which was gradual and took 3.5-4 hr. Each physiological variables had significant differences among means during seawater exposure ($p < 0.05$, oneway ANOVA).

Figure 2. Size (fork length) at time of seawater exposure, mean survival time in seawater, and plasma osmotic concentration after 4 d in seawater as a function of time of year of seawater exposure. Experiments were conducted under normal photoperiod conditions. Closed squares represent high feed (fast growing) fish, closed circles represent low feed (slow growing) fish.

Figure 3. Seawater survival as a function of size and age. Log of seawater hazard rate versus (A) log of fork length and (B) log of age for fish in high feed (squares) and low feed (circles) fish in normal photoperiod (closed figures) and 3-month delayed photoperiod (open figures). 11 experiments (4 groups per experiment) were conducted over 17 mos. Points encircled with dashed lines represent experiments with mature males exposed to seawater during autumn photoperiod. Linear regression of log hazard on log size had r^2 of 0.64 and 0.77 for experiments with and without fully mature males, respectively. Regression lines do not include experiments with fully mature males. Linear regression of log hazard on log age had r^2 of 0.58 and 0.65 for experiments with and without fully mature males, respectively.

Figure 4. Standardized residuals of the regression of log hazard rate on log length, as a function of season for (A) immature brook trout, (B) mature brook trout and (C) brook trout greater than 14.0 cm. Season corresponds to the photoperiod conditions fish experienced just prior to and during seawater exposure.

Figure 5. Plasma osmolarity and gill Na^+,K^+-ATPase in seawater as a function of brook trout size. (A) Plasma osmolarity after 4 d in seawater, (B) plasma osmolarity after 20 d in seawater, and (C) gill Na^+,K^+-ATPase activity after 4 d (open triangles) and 20 d (closed triangles) in seawater, versus fork length of brook trout. Regression lines, where drawn, have slopes which are significantly different from zero ($p < 0.05$, see Tables 2 and 3).

Figure 6. Salmonid phylogeny of size dependent ion transport ability and resulting size dependent seawater survival. Lines A, B and C may represent Salvelinus, Salmo and Oncorhynchus, respectively, and X_A, X_B and X_C the size (or size range) at which seawater survival occurs. The horizontal dashed line represents tissue tolerance of high plasma osmolarity. Tissue tolerance may also differ among genera and species, and will affect the size at which seawater survival occurs.

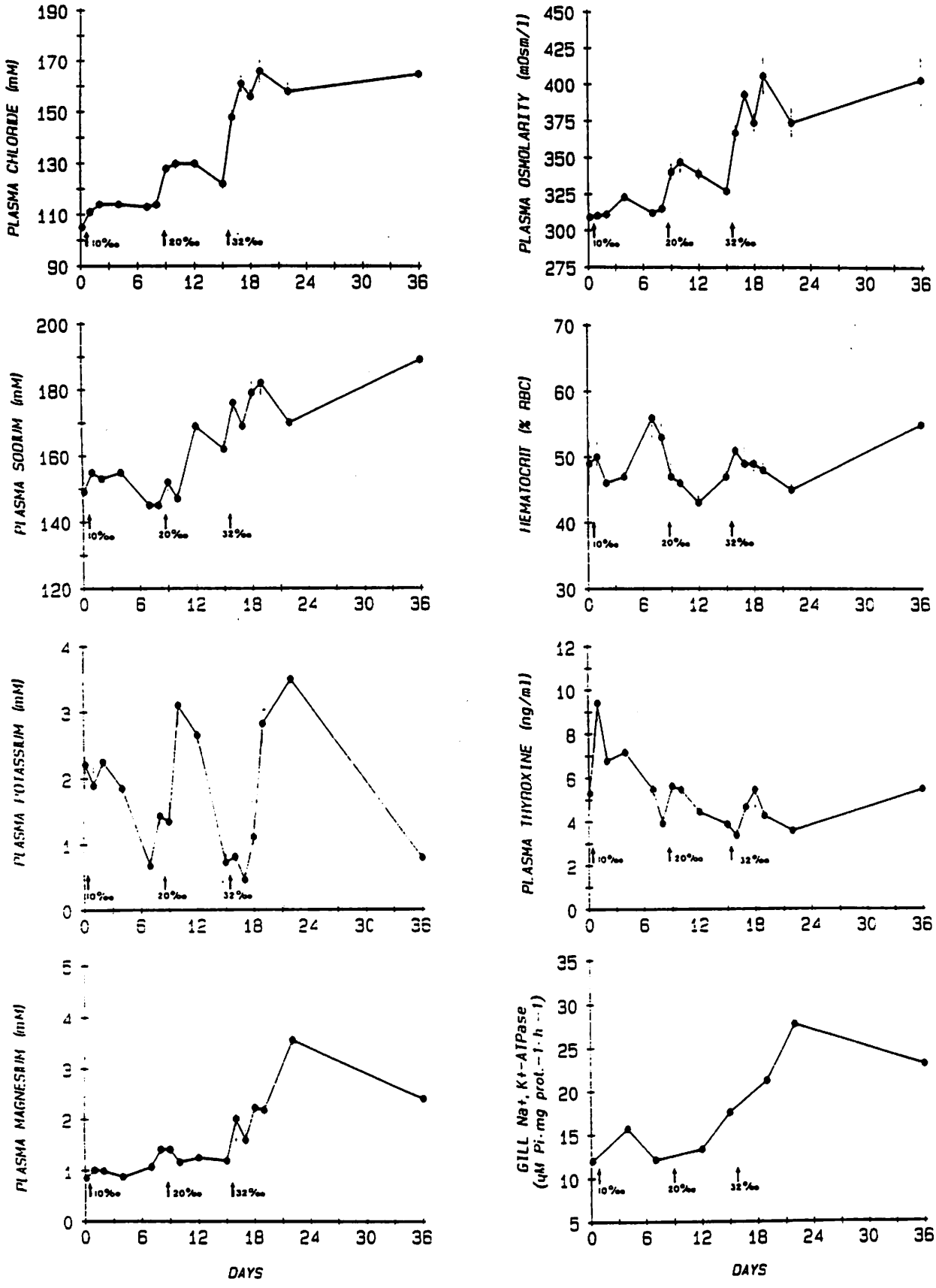
PLASMA CHLORIDE (mM)
PLASMA OSMOLARITY (mOsm/l)
PLASMA SODIUM (mM)
HEMATOCRIT (% RBC)
PLASMA POTASSIUM (mM)
PLASMA THYROXINE (ng/ml)
PLASMA MAGNESIUM (mM)
GILL Na+, K+-ATPase (µM Pi·mg prot.⁻¹·h⁻¹)
10‰
20‰
32‰
DAYS

Fig. 1

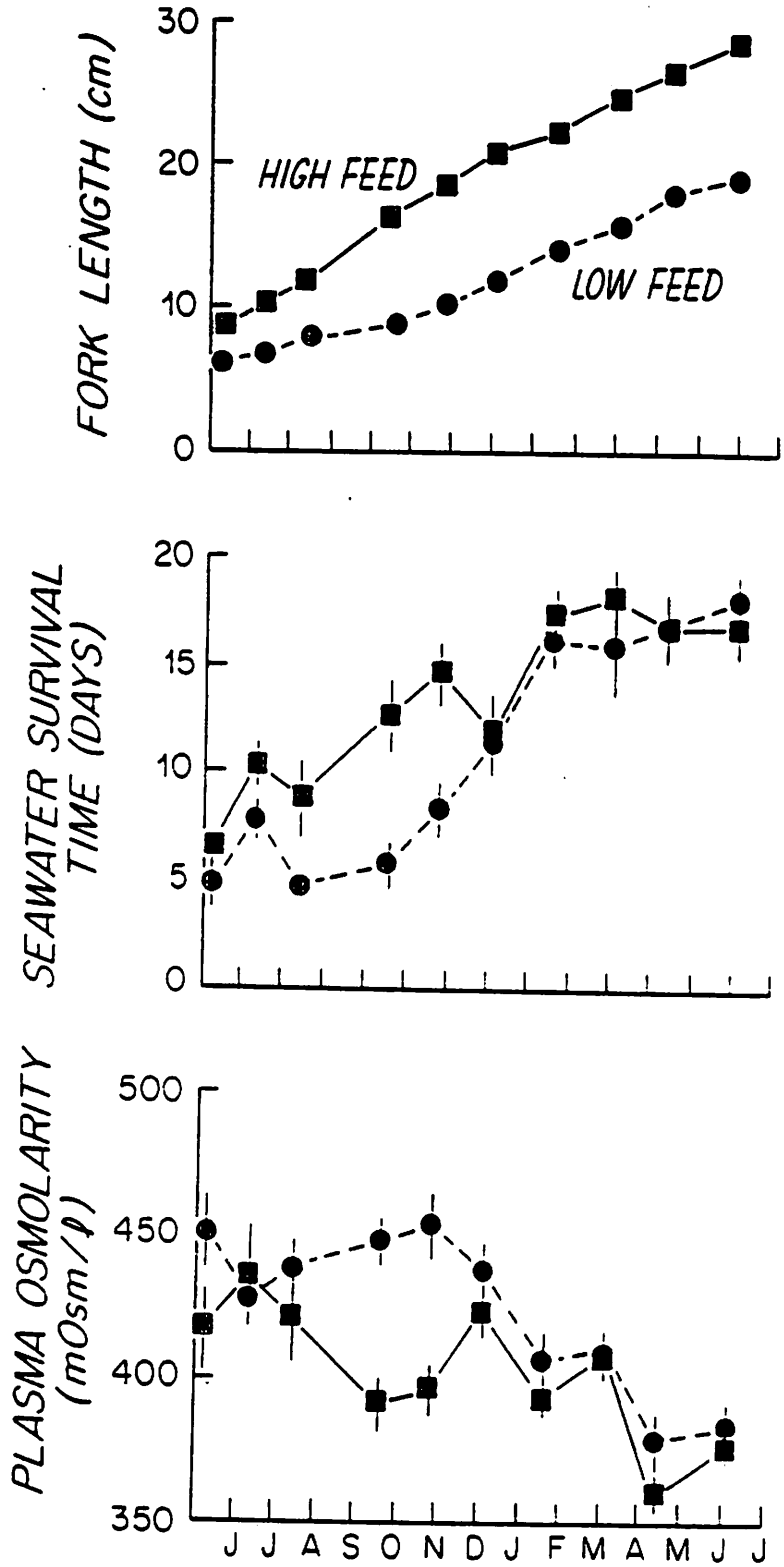
FORK LENGTH (cm)
30
20
10
0
HIGH FEED
LOW FEED
SEAWATER SURVIVAL TIME (DAYS)
20
15
10
5
0
PLASMA OSMOLARITY (mOsm/ℓ)
500
450
400
350
J J A S O N D J F M A M J J

Fig. 2

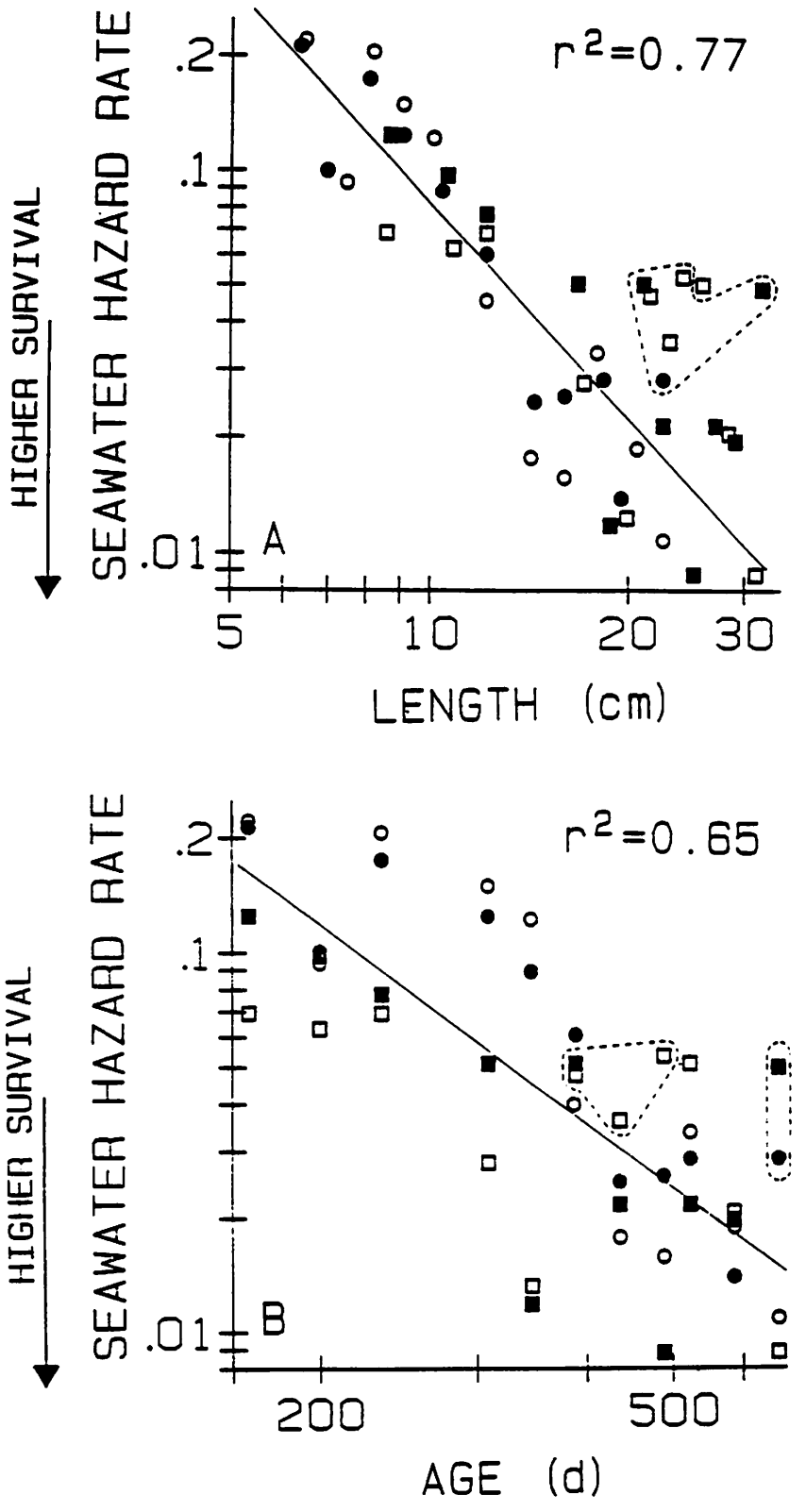
HIGHER SURVIVAL
SEAWATER HAZARD RATE
.2
.1
.01
A
r^2=0.77
5
10
20
30
LENGTH (cm)
HIGHER SURVIVAL
SEAWATER HAZARD RATE
.2
.1
.01
B
r^2=0.65
200
500
AGE (d)

Fig. 3

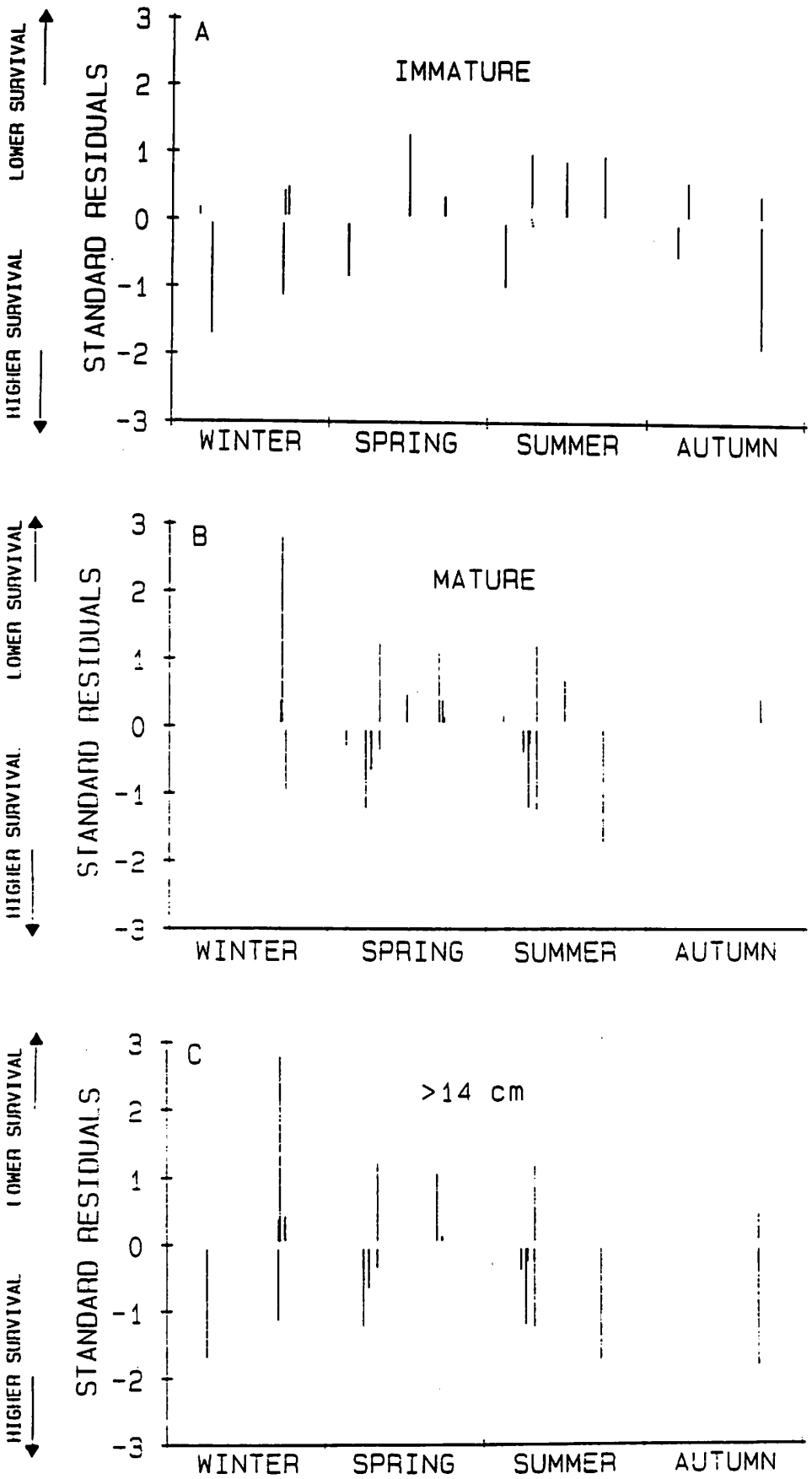
A
IMMATURE
B
MATURE
C
>14 cm
STANDARD RESIDUALS
LOWER SURVIVAL
HIGHER SURVIVAL
3
2
1
0
-1
-2
-3
WINTER
SPRING
SUMMER
AUTUMN

Fig. 4

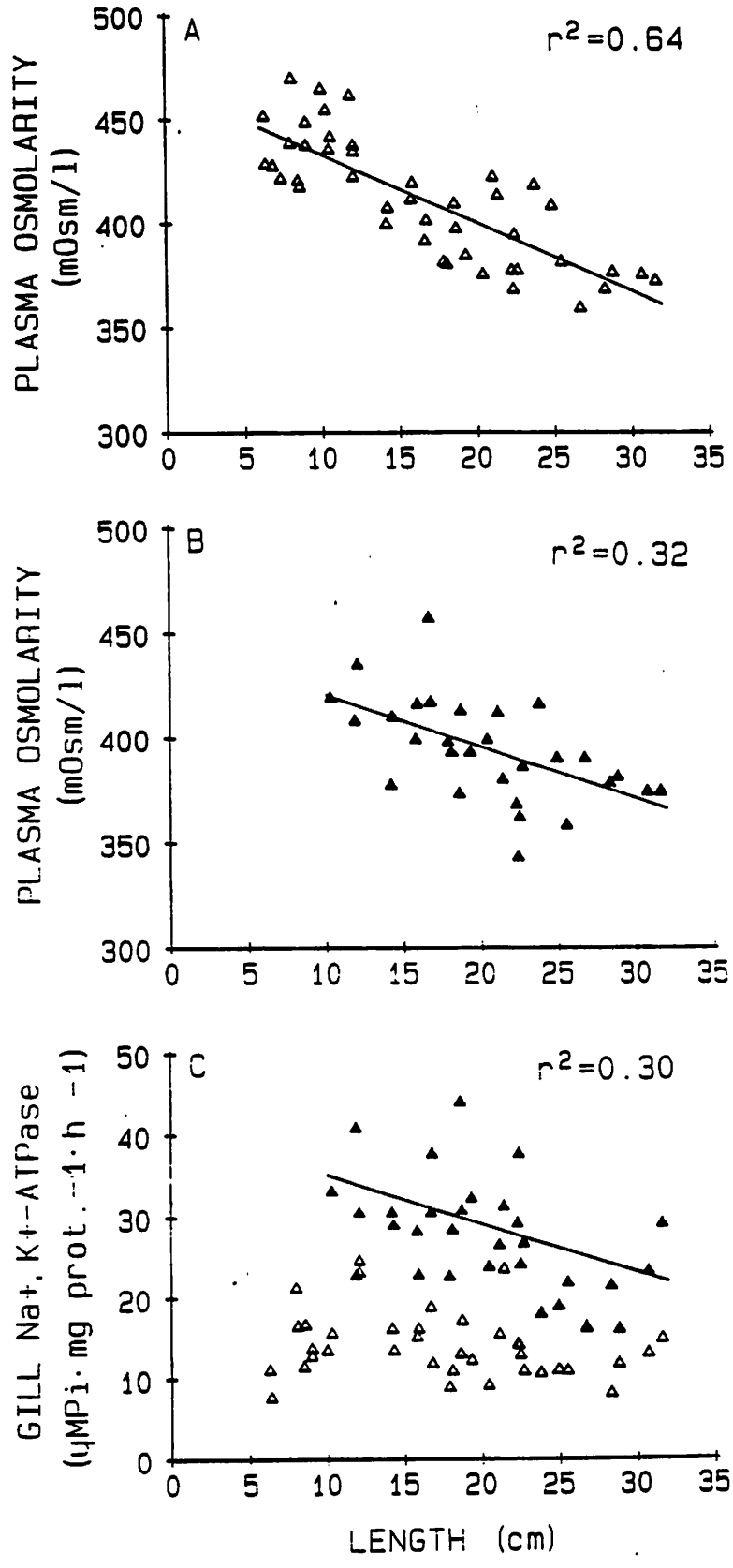
A
r^2=0.64
PLASMA OSMOLARITY (mOsm/l)
500
450
400
350
300
0
5
10
15
20
25
30
35
B
r^2=0.32
PLASMA OSMOLARITY (mOsm/l)
C
r^2=0.30
GILL Na+, K+-ATPase (µMPi·mg prot.⁻¹·h⁻¹)
50
40
30
20
10
0
LENGTH (cm)

Fig. 5

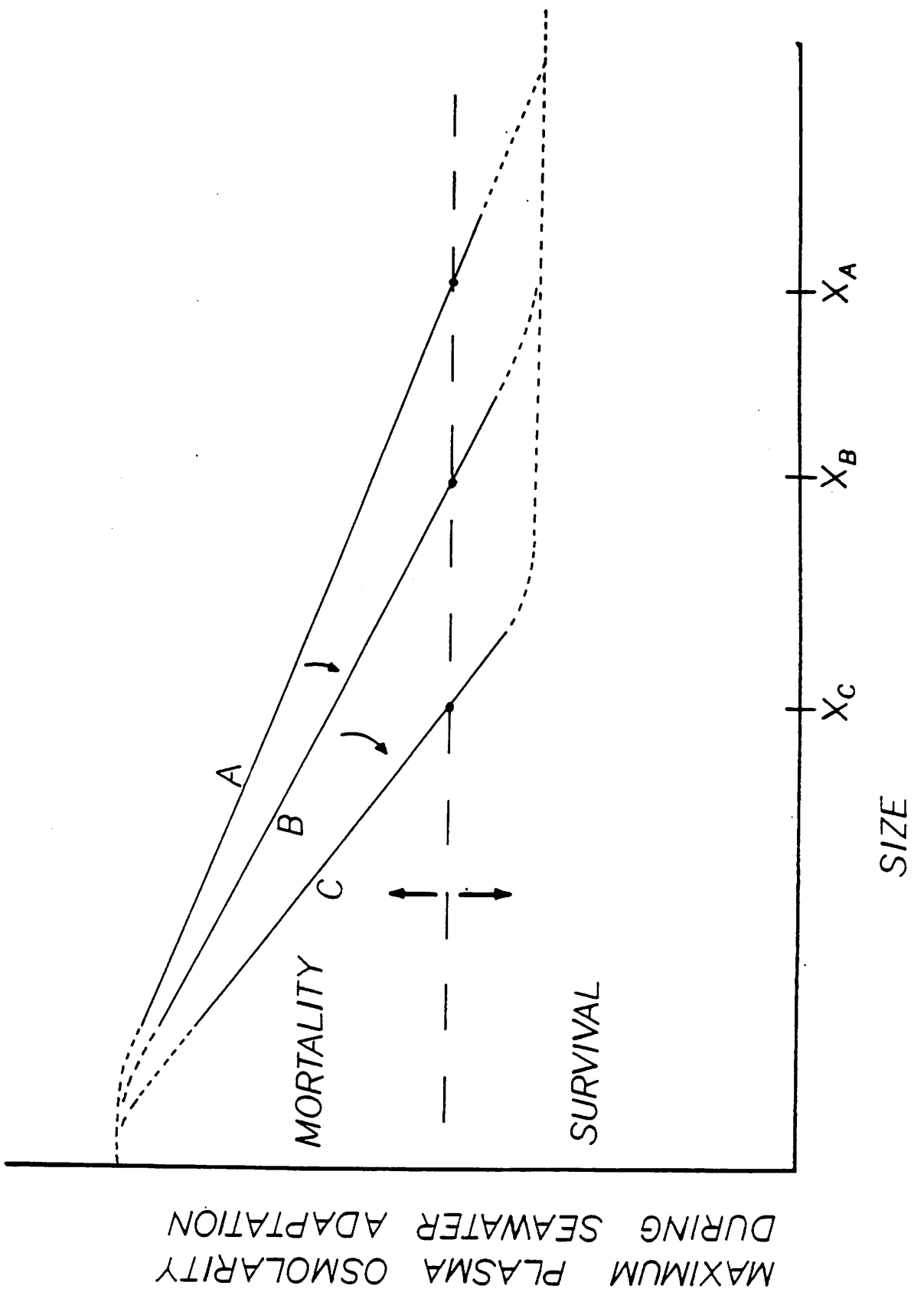
MAXIMUM PLASMA OSMOLARITY
DURING SEAWATER ADAPTATION
MORTALITY
SURVIVAL
A
B
C
X_A
X_B
X_C
SIZE

Fig. 6

SOME DETERMINANTS OF MATURATION IN BROOK TROUT, Salvelinus fontinalis

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Biology Department
Woods Hole Oceanographic Institution

ABSTRACT

Size, age, growth rate and photoperiod were examined for their effects on the timing of maturation and the proportion of mature male and female brook trout (Salvelinus fontinalis). Photoperiod completely entrained the gonadosomatic index and the timing of functional maturation (spermiation and ovulation). High feed and delayed photoperiod conditions resulted in a greater proportion of mature individuals of each sex in their first year, though the percent maturation in each experimental group was higher for males. Size by itself can explain almost all of the variation in the percent maturation across all experimental groups (r^2= 0.99 and 0.97 formales and females, respectively). The results indicate that 1) given a positive growth rate, age and growth rate are less important than size in determining maturation of brook trout and 2) the maturation response to size is sexually divergent. Size dependent maturation has important implications for the control of maturation in domestic stocks, our understanding of brook trout demography, and for future investigations of the physiological and hormonal control of salmonid maturation. A conceptual model depicting the effects of environmental factors on size and the initiation of maturation is presented.

INTRODUCTION

Although age at first maturity is most commonly reported in studies of natural populations, Alm (1959) concluded that size and growth rate were more important determinants of salmonid maturation. An understanding of salmonid demography depends, in part, on our ability to differentiate between size, age and growth rate as determinants of maturity. In addition, management of domestic salmonids can be facilitated through manipulation of maturation. Since feeding rate and diet influence both size and growth rate, but not age, maturation may to some degree be controlled by culture methods (Alm, 1959). Photoperiod may also be used to control the timing of maturation of domestic salmonids (Billard et al., 1978).

While investigating the effect of size, age and photoperiod on osmoregulation in brook trout, Salvelinus fontinalis (McCormick and Naiman, 1984a,b), we found feeding and photoperiod influenced the timing and degree of maturation. Knowledge of the determinants of brook trout maturation may offer substantial insight into salmonid reproduction. Since brook trout most often complete their life cycle in freshwater

(Power, 1980), their reproductive physiology will be uncomplicated by complex physiological changes associated with oceanic migrations. Furthermore, Hoar (1976) has suggested that the genus Salvelinus is most similar to the earliest salmoninae, a 'primitive archetype' upon which greater specializations were made by Salmo and Oncorhynchus. The objective of this paper, therefore, is to investigate the effects of size, age, growth rate and photoperiod on maturation in brook trout, a representative of the genus Salvelinus.

MATERIALS AND METHODS

20,000 brook trout eggs from the Massachusetts State Fish Hatchery at Sandwich were fertilized on October 28, 1980. Fertilized eggs were transported to the Woods Hole Oceanographic Institution's Shore Lab facility and supplied with 10-11 C well water. Eggs were randomly divided into two annually cycling photoperiods corresponding to a latitude of 42°N; one photoperiod cycle corresponded to the normal calendar date (longest day June 21, shortest day December 21), while the other was 3 mo delayed from the norm (longest day September 21, shortest day March 21, Fig. 1). Daylength was changed every 5 d. Sunrise and sunset were simulated each day by a 15 min period of gradual illumination or dimming of incandescent bulbs. Beginning and end of daylight period were delayed 2 hr from Eastern Standard Time. Vita-Lite spiralux fluorescent bulbs and incandescent bulbs were used to simulate daylight.

After first feeding fish were transferred to 1,000 l flow-through tanks which received supplemental aeration. Within one wk after feeding fish were divided randomly, within each photoperiod treatment, into two feeding groups. For 4 wk after first feeding, fish in each group were fed equal amounts. Afterward, one group was fed commercial fish pellets ad libitum following common hatchery procedures (Leitritz and Lewis, 1976). The low feed group was fed approximately half the amount, per unit body weight, fed the high feed group. Every 6-8 wk at least 25% of the fish from a 1,000 l tank in each feeding group in the normal photoperiod were weighed. Only 10% of the fish in each feeding group in the delayed photoperiod were weighed. Fish were dip-netted, anesthetized, blot-dried on a moist chamois cloth, fork length was measured to the nearest mm and fish were weighed to the nearest 0.01 g.

Specific growth rates (G_w) were calculated using the following formula:

$$G_w = ((\ln W_t - \ln W_o)/t) \cdot 100$$

where W_t is the weight at time t, W_o is the weight at time 0 (the time at which weight was last measured), and t is time in days. In order to compare growth rates of animals of different sizes, the $\ln G_w$ of a fish of unit size ($\ln G_w'$) was calculated (Jobling, 1983) using the following equation:

$$\ln G_w' = \ln G_w - b \ln W_t,$$

where b is the slope of the linear relationship between ln G_w and ln W_t. An experimentally derived value of b = -0.47 was used in all calculations of ln G_w' (b is the slope of the regression between ln G_w and ln W_t in high feed fish, 0.06-367.9 g; normal photoperiod b = 0.47 (r = 0.96), delayed photoperiod b = 0.48 (r = 0.90). A generalized value of b = -0.41 for salmonids was reported by Brett (1979).

Gonads of fish which were periodically sacrificed were weighed to the nearest 0.01 g and gonadosomatic index (GSI) calculated [(gonad weight/ body weight) • 100]. Determinations of the state of maturation of individual fish (i.e., mature or immature) were made between the longest and shortest daylengths in each photoperiod (e.g., June 21 to December 21 in normal photoperiod). Males were determined to be mature when gonads were wider than 3 mm (Jones, 1959). Females were determined to be mature when egg diameter was greater than 1.0 mm and the ovary took up more than 1/2 the length of the body cavity (Vladykov, 1956). Condition factor was calculated as (weight/length^3) • 100.

Contingency tables and 3- and 4-way log-linear contingency tables were used to determine significant differences among the proportion of mature individuals in experimental groups (Dixon, 1981).

RESULTS AND DISCUSSION

Photoperiod Entrainment of Maturation

Relative to the normal photoperiod, gonadal development (Gonadosomatic index) in mature males and females was shifted by approximately 3-mo in the delayed photoperiod (Fig. 1). Under normal photoperiod conditions the period in which milt could be easily exuded from mature males (spermiation) corresponded to the normal spawning time of brook trout at 42°N (latitude of Woods Hole; Power, 1980). The mid-point of spermiation in the delayed photoperiod was slightly more than 3 mo after that of the normal photoperiod.

Previous investigations have shown photoperiod to be an effective Zeitgeber of several physiological and hormonal cycles of teleosts, including maturation (Henderson, 1963; Billard et al., 1978; Clarke et al., 1978). Eriksson and Lundqvist (1980) found that the rate of change in daylength, rather than daylength per se, was responsible for entraining maturation in precocious Atlantic salmon (Salmo salar). Despite the ability of photoperiod to entrain maturation in our experiments, the 3-mo delayed photoperiod failed to shift the plasma thyroxine cycle that occurred under normal photoperiod conditions (McCormick and Naiman, 1984a), even though several lines of evidence suggest that the thyroid plays a role in teleost maturation (see Leatherland, 1982, for review). Nevertheless, these results indicate that a seasonal cycle of plasma thyroxine (characterized by high 'spring' levels) is not required for gonadal development in brook trout.

Growth

The weight and specific growth rate per unit weight ($\ln G_w'$) of fish in high and low feed groups in each photoperiod is shown in Fig. 2. Wet weight is used to represent body size with the knowledge that length is an equally valid measurement highly correlated with weight. Reduced rations in low feed groups resulted in smaller body size for a given age and lower growth rates in the first year. Similar growth rates for high and low feed groups in 1982 possibly reflect a growth-ration relationship that changes with body size, though little is known of this process (Ricker, 1979). Growth as a function of feeding treatment was similar between photoperiods. Since the delayed photoperiod shifted developmental timing, fish in this group were larger at every point in the maturation cycle, including the time at which the 'decision' to initiate maturation was made. For instance, high feed fish in the delayed photoperiod were 36.3 g heavier than normal photoperiod fish on the equivalent photoperiod day 3 mo earlier in 1981 (Table 1).

Since diet composition was constant and growth rate was positive for all experimental groups throughout the study, we assume the nutritional state was satisfactory for all groups. Mean condition factor was always greater than 0.96 (low feed groups, 0.96-1.36; high feed groups; 1.09-1.41).

Determinants of Maturation

Year 1- Feeding in combination with photoperiod treatment had a significant effect on the proportion of mature individuals in both sexes in their first year ($p < 0.01$, 3-way log-linear contingency tables; Table 1). Within each photoperiod there was a significantly greater ($p < 0.01$) percentage of mature males in the high feed group than in the low feed group. Size and growth rate, but not age, differed between these two groups (Table 1). In the high feed treatments, the 3-mo delayed photoperiod produced a greater proportion of mature males than the normal photoperiod (72% and 44%, respectively), and were 36.3 g heavier and 90 d older on the longest photoperiod day. Since growth rate was similar for high feed fish in each photoperiod (Table 1), size or age must be responsible for the difference in the proportion of mature individuals in the normal and delayed photoperiods. Because size or growth rate is responsible for differences between feeding groups, and size or age is responsible for differences between normal and delayed photoperiods, only size can explain all of the results.

The pattern of maturation of females in their first year was similar to that of males with a significantly greater proportion of females becoming mature under high feed, delayed photoperiod conditions (38%) than under low feed or normal photoperiod conditions ($\leq$ 5%; $p < 0.01$, 3-way log-linear contingency table; Table 1). As with male maturation, size most easily explains these results. The proportion of mature females, however, was significantly lower than that for males ($p < 0.01$, 4-way log-

linear contingency table). This is particularly evident in the high feed groups where the percentage of mature females was one-fifteenth and one-half that of mature males in the normal and delayed photoperiods, respectively. If, as hypothesized, size is of overiding importance in determining maturation in brook trout, a sexually divergent response to size is a logical extension of this hypothesis that explains male-female differences in maturation. A larger size at first maturation for females may reflect the greater limitations imposed by size on egg production relative to sperm production (Darwin, 1871).

Year 2- In year 2 the proportion of mature individuals varied between 86% and 100% and did not differ by sex, feeding level or photoperiod treatment ($p > 0.10$, 4-way log-linear contingency table; Table 1). In accordance with our interpretation of the importance of size, it would appear that a minimum size (97 g on the longest photoperiod day; Table 1) has been reached by all experimental groups in their 2^{nd} year.

The relationship of size to the proportion of mature individuals across all experimental groups for both sexes is shown in Fig. 3. Regression of percent maturation on log wet weight on the longest photoperiod day had values of $r^2 = 0.99$ and 0.97 for males and females, respectively (Fig. 3). The area between the curves represents the degree of sexual divergence in the response of maturation to size. For example, in order to achieve 50% maturation under the present experimental conditions, males must be 21.9 g and females 45.8 g by the longest photoperiod day.

The importance of size in maturation of brook trout is in substantial agreement with Alm (1959), who found a greater number of mature individuals among larger, faster growing brook trout and several other salmonid species. There is growing evidence that size determined developmental events (maturation included) occur in many teleosts (Policarsky, 1983). The results presented here and shown schematically in Fig. 4 indicate that at high growth rates, size alone can increase the proportion of mature brook trout. Factors other than feeding levels, such as temperature, also influence size and have the potential to affect maturation. Furthermore, temperature, and perhaps other environmental factors may have a direct effect on salmonid maturation (Saunders et al., 1983).

Although these results indicate that size is an important determinant of maturation in brook trout, certain levels of growth rate, nutrition and health are probably required for maturation to occur (Fig. 4). It may be necessary to achieve several physiological thresholds before maturation is initiated. Furthermore, the biological property triggering the maturation process may not be size per se, but a factor (or factors) strongly correlated with size, such as energy reserves or lipid storage. Minimum lipid: body mass ratios have been hypothesized to be responsible for variations in the onset of puberty in human and primate females (Reiter and Grumbach, 1982). Such a threshold mechanism would account for the importance of size in brook trout maturation, and would explain variations in spawning schedules which, for example, occur every other year in northern, food-limited populations (Vladykov, 1956).

ACKNOWLEDGEMENTS

We thank the Massachusetts Division of Fisheries and Wildlife for providing brook trout eggs. E. Rosa-Molinar, R. Rheault and E. Montgomery ably provided technical assistance. J. M. Capuzzo and two anonymous reviewers made several helpful comments on the manuscript. This project was supported by the U.S. Department of Commerce, NOAA, Office of Sea Grant NA80-AA-D-00077 (R/A-14) and the Matamek Research Program of the Woods Hole Oceanographic Institution. S. D. McC. was supported by a Tai-Ping Predoctoral Fellowship in Marine Biology and the Woods Hole Oceanographic Institution's Education Office. This is contribution No. 5537 of the Woods Hole Oceanographic Institution and No. 83 of the Woods Hole Oceanographic Institution's Matamek Research Station.

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Table 1. Percentage of individuals of each sex which became mature in their first and second year as a result of feeding and photoperiod treatments. Mean wet weight, age and growth rate shown in each treatment are those which occurred on the sampling date closest (± 14 d) to the longest photoperiod day (e.g., 1st day of summer in normal photoperiod). Numbers in brackets are the sample size for males and females, respectively. Parenthetical growth rates are those calculated frm the first weighing period (86 d old, mean weight 0.53-0.60 g).

Feed Regime	% Mature Males	% Mature Females	Size (g)	Age (d)	Growth Rate ln Gw'	
YEAR 1						
Normal Photoperiod						
Low [21,23]	0	0	4.0	196	0.53	(1.26)
High [70,34]	44	3	13.7	196	1.91	(2.28)
3-Mo Delayed Photoperiod						
Low [41,41]	7	5	7.3	301	0.15	(1.13)
High [75,60]	72	38	50.0	292	2.11	(2.56)
YEAR 2						
Normal Photoperiod						
Low [20,23]	86	92	96.7	582	1.30	(2.19)
High [17,31]	96	100	306.3	582	1.94	(2.91)
3-Mo Delayed Photoperiod						
Low [41,41]	95	100	157.7	665	1.67	(2.36)
High [75,60]	100	100	367.2	665	1.78	2.88

FIGURE CAPTIONS

Figure 1. Gonadosomatic index of males (closed triangles) and females (open triangles) in the high feed group as a function of time. Values are the mean ($\pm$ 1 standard error) of 4 - 12 fish per sampling period. Horizontal bars correspond to the period of spermiation under each photoperiod treatment. Period of final maturation in females (when eggs could be extracted by pressing the body walls) occurred within the same period but usually began 1-2 wk later. GSI of females is shown only in 1982 because of the low number of mature females in 1981.

Figure 2. Effect of feeding treatment on wet weight and growth rate. High feed (squares) and low feed (circles) fish in normal (solid) and 3-mo delayed (open) photoperiods as a function of time. Weights are the mean value of 40 - 125 fish.

Figure 3. Percent maturation of males (closed triangles) and females (open triangles) as a function of wet weight (g) on the longest photoperiod day. Curves were fitted using 3rd order polynomial regressions (r^2 = 0.99 and 0.97 for males and females, respectively). Shaded area represents sexual differences in the response of maturation to size.

Figure 4. Schematic representation of the environmental effectors and biological determinants of maturation. Thick lines emphasize size dependent maturation found for brook trout.

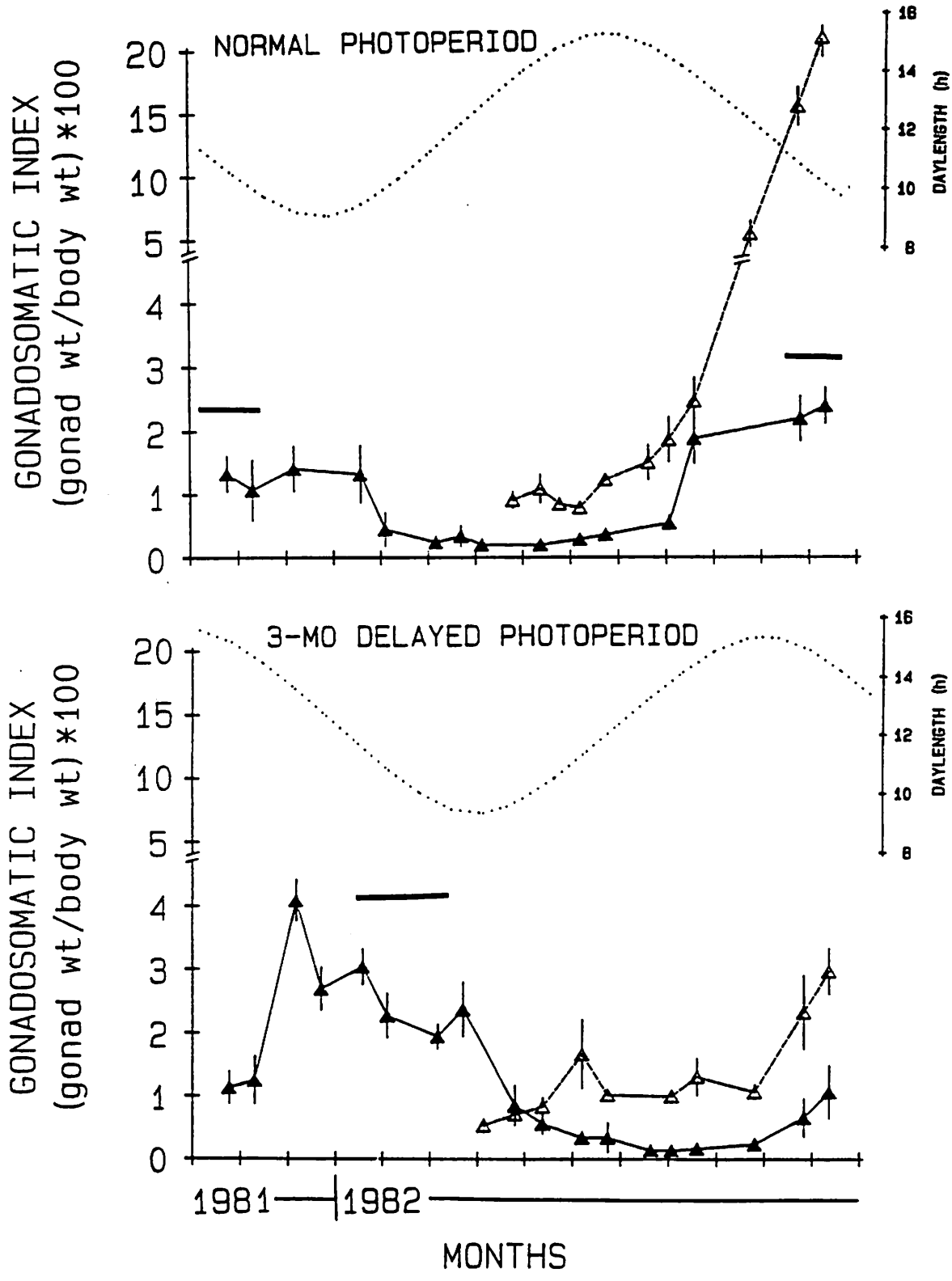
NORMAL PHOTOPERIOD
3-MO DELAYED PHOTOPERIOD
GONADOSOMATIC INDEX
(gonad wt/body wt)*100
DAYLENGTH (h)
1981
1982
MONTHS

Fig. 1

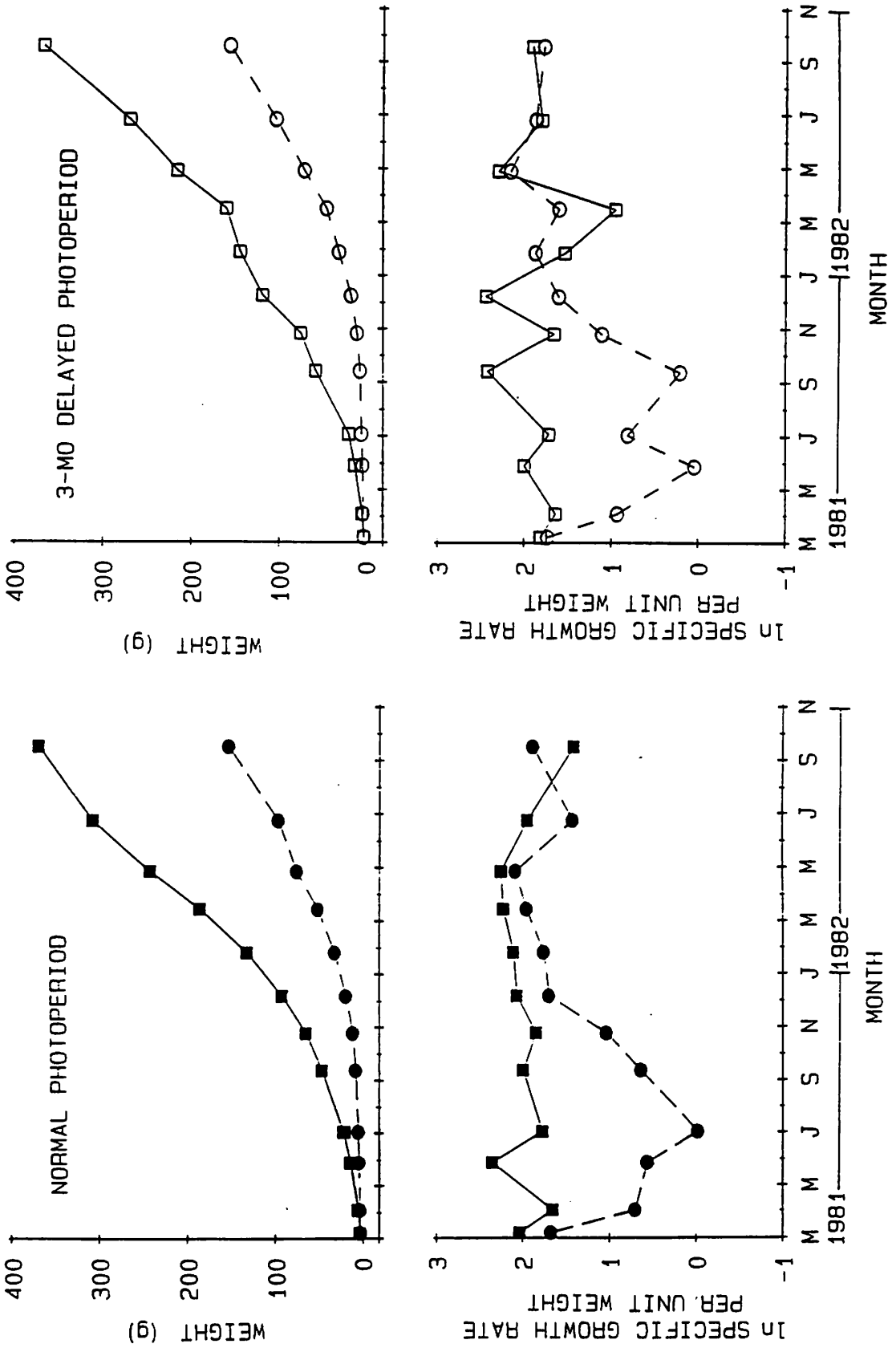
3-MO DELAYED PHOTOPERIOD
NORMAL PHOTOPERIOD
WEIGHT (g)
400
300
200
100
0
ln SPECIFIC GROWTH RATE PER UNIT WEIGHT
3
2
1
0
-1
M M J S N J M M J S N
1981
1982
MONTH

Fig. 2

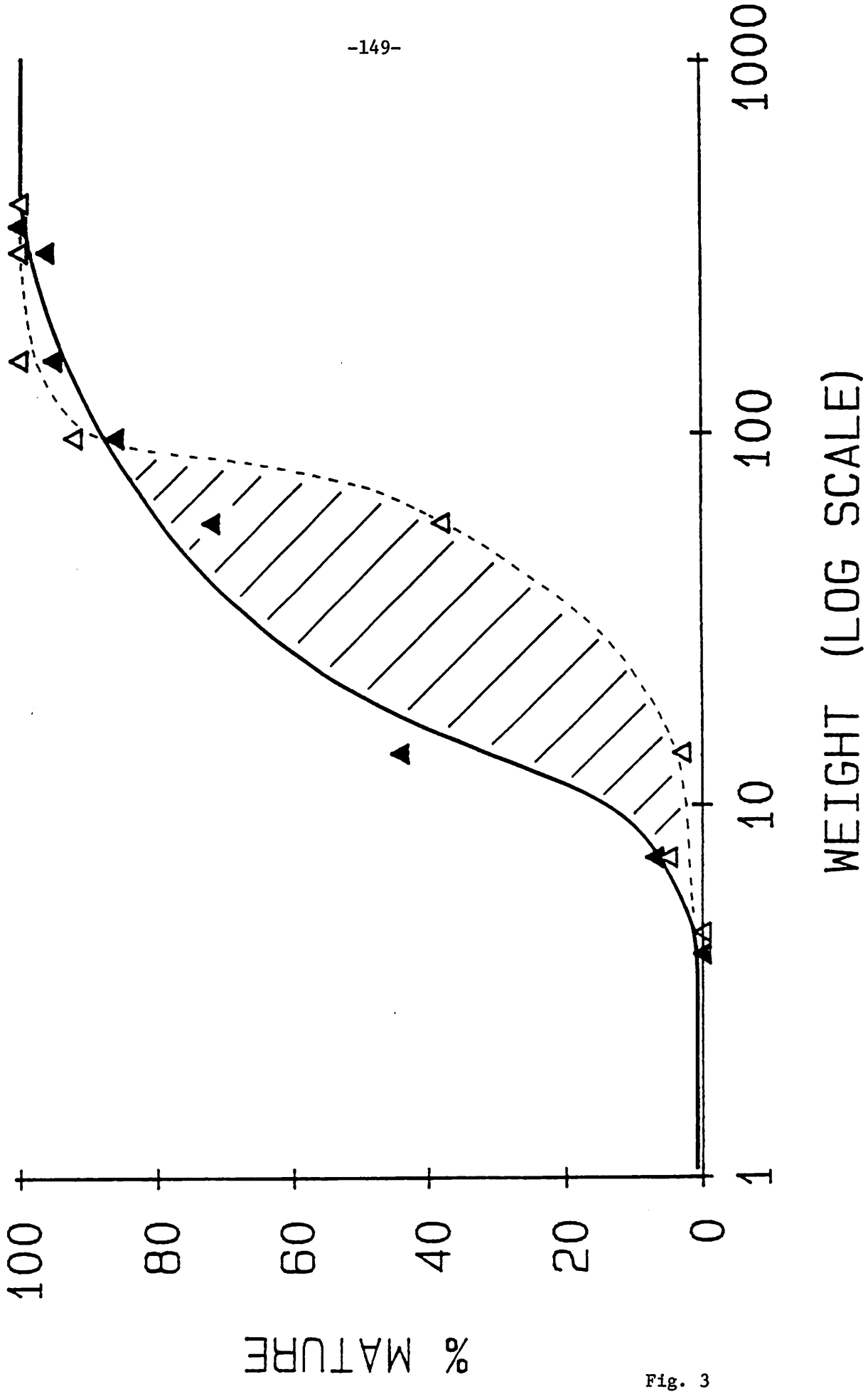

Fig. 3

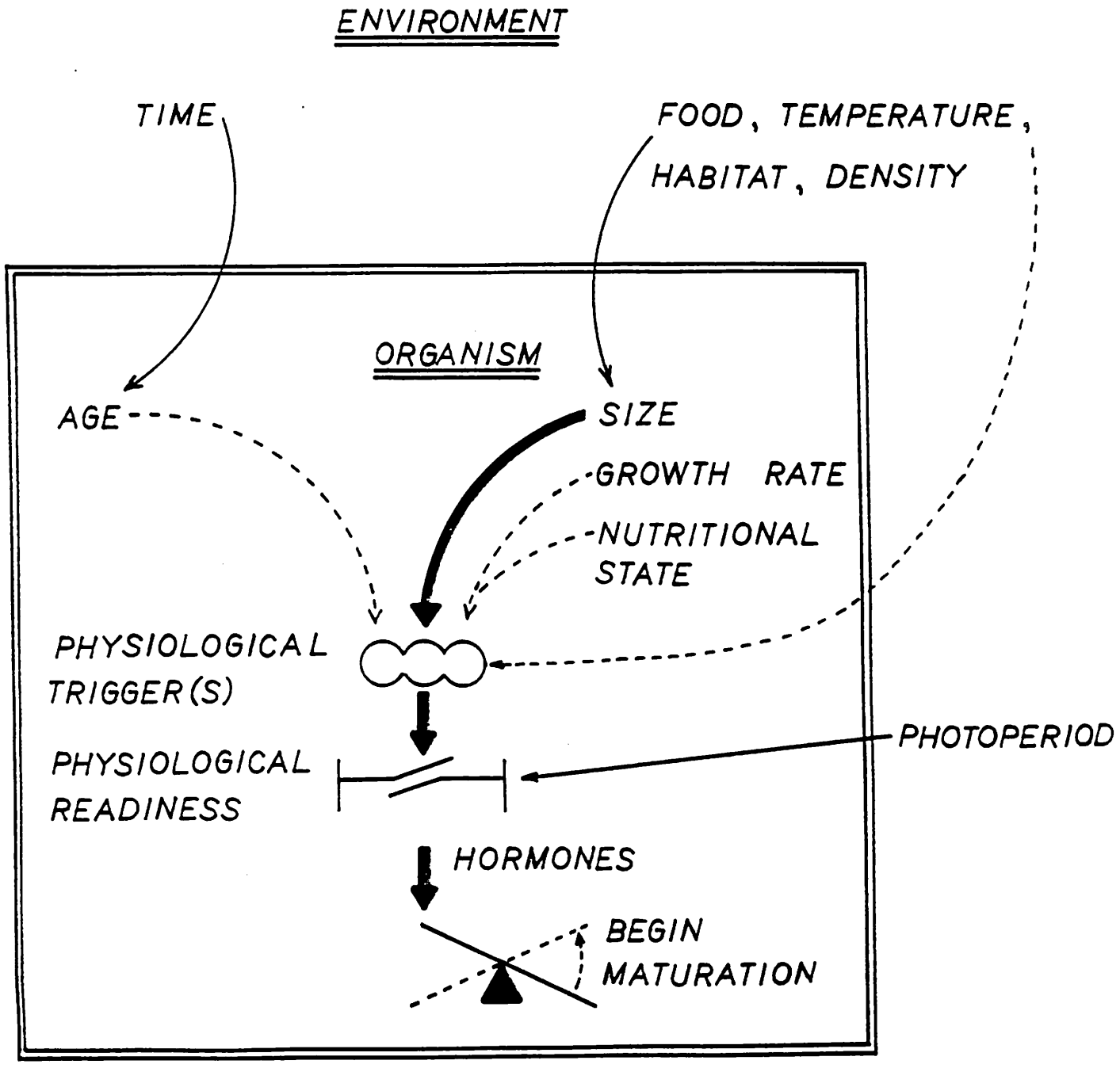
ENVIRONMENT
TIME
FOOD, TEMPERATURE,
HABITAT, DENSITY
ORGANISM
AGE
SIZE
GROWTH RATE
NUTRITIONAL STATE
PHYSIOLOGICAL TRIGGER(S)
PHOTOPERIOD
PHYSIOLOGICAL READINESS
HORMONES
BEGIN MATURATION

Fig. 4

50272-101

REPORT DOCUMENTATION PAGE	1. REPORT NO. WHOI-84-29	2.	3. Recipient's Accession No.

4. Title and Subtitle

The Matamek Research Program: Annual Report for 1983

5. Report Date July 1984

6.

7. Author(s)

Robert J. Naiman

8. Performing Organization Rept. No. WHOI-84-29

9. Performing Organization Name and Address

Matamek and Education Programs of
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts 02543

10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.

(C) NA 80AA-D-00077
(G) DEB-81-05677

12. Sponsoring Organization Name and Address

NOAA, Office of Sea Grant; National Science Foundation; the Tai Ping Foundation, the National Scientific and Engineering Research Council of Canada, the Atlantic Salmon Association; the Department of Recreation, Fish and Game Province of Quebec; the University of Waterloo, Ontario; Natural Environment Research Council, United Kingdom.

13. Type of Report & Period Covered

Technical

14.

15. Supplementary Notes

This report should be cited as: Woods Hole Oceanog. Inst. Tech Rept. WHOI-84-29.

16. Abstract (Limit: 200 words)

This report summarizes activities associated with the Institution's Matamek Research Station during 1983. Research was conducted on the biological, chemical and physical environment of streams and rivers, principally in the Moisie and Matamek River watersheds, on the effects of beaver in shaping the dynamics of aquatic ecosystems, on salmonid ecology, on decomposition dynamics, on invertebrate community dynamics, on sedimentary diatom responses to acid precipitation, and on microbial production. Canadian universities, American universities, the University College of North Wales, the Quebec government, and the Woods Hole Oceanographic Institution cooperated in this program.

17. Document Analysis a. Descriptors

1. Streams
2. Rivers
3. Salmonids

b. Identifiers/Open-Ended Terms

c. COSATI Field/Group

18. Availability Statement:

Approved for publication; distribution unlimited.

19. Security Class (This Report)	21. No. of Pages
UNCLASSIFIED	150
20. Security Class (This Page)	**22. Price**

(See ANSI-Z39.18) *See Instructions on Reverse*

OPTIONAL FORM 272 (4-77)
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