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**The Matamek Research Program:
Annual Report for 1982**

by

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Technical Report

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ABSTRACT

This report summarizes activities associated with the Institution's Matamek Research Station during 1982. 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, and on interactions between riparian vegetation and juvenile salmonids. Canadian universities, the Quebec government, and the Woods Hole Oceanographic Institution cooperated in this program.

In December, 1982, the Matamek Research Station received a new laboratory from the Ministère du Loisir, de la Chasse et de la Pêche. It is expected to be functional for the 1983 field season and will be used for on-site studies of fish physiology and biochemistry.

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INTRODUCTION

The 1982 scientific program at the Matamek Research Station can best be characterized as a time of changeover where new projects were successfully instigated and old projects successfully completed. 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, the Atlantic Salmon Association, the Ministère du Loisir, de la Chasse, et de la Pêche du Québec, the Woods Hole Oceanographic Institution, and the University of Waterloo all combined to produce a program of broad scope and high quality. As established in 1979, the 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 (see frontispiece; to be operational in 1983), the quality of our programs will be vastly improved. In 1982 the full time research group consisted of 23 persons, with 12-16 additional researchers utilizing the station for various periods. These personnel represent a diverse array of interests 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, thermal equilibria of aquatic insects, insect emergence, nitrogen fixation, 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 were extensions of studies mostly completed during the 1981 field season (e.g., leaf decomposition, allochthonous inputs). The watershed analysis is continuing in the other areas, especially on the role of beaver, 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 total data base being used to construct a 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.

Canadian graduate student projects include a comparative life history study of Atlantic salmon in response to river harshness (jointly funded with the Atlantic Salmon Association), competitive interactions between brook trout fry and sticklebacks, the parasites of sticklebacks, and the ecology of landlocked Atlantic salmon. Student interns investigated growth and habitat of brook trout fry and osmoregulatory physiology in migrating brook trout.

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 scientists at Canadian universities 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
Coordinator,
Matamek Research Program

10 June 1983

INTRODUCTION

En 1982, le programme scientifique de la Station de Recherche Matamek se caractérisait par une période où les nouveaux projets furent initiés et les anciens complétés avec succès. L'aide financière du National Science Foundation, NOAA (Office of Sea Grant), Tai-Ping Foundation, North Atlantic Treaty Organisation, du Conseil de recherches en sciences naturelles et en génie du Canada, du Ministère du Loisir, de la Chasse et de la Pêche, Woods Hole Oceanographic Institution et de l'Université de Waterloo a été regroupée pour produire un programme de grande qualité et d'envergure considérable. Depuis 1979, ce programme met son emphase sur la dynamique des écosystèmes riverains en vue de caractériser l'écologie des bassins de drainage et les populations de salmonidés. L'addition d'un nouveau laboratoire offert par la Province de Québec (qui sera en opération dès 1983) permettra d'améliorer la qualité de nos programmes. En 1982, le groupe de recherche, travaillant à plein temps, était au nombre d'environ 20 personnes; de plus, 12-16 chercheurs sont venus se joindre à l'équipe pour des périodes variables et ce tout au long de l'été. Ces personnes représentent un ensemble d'intérêts variés et ont contribué à l'élaboration du programme de recherche.

L'analyse intégrée des écosystèmes fluviaux comprenaient cette année:

- l'histoire des eaux acides déterminée par la composition des diatoms dans les sédiments des lacs;
- l'adaptation des insectes aquatiques aux conditions thermiques;
- l'émergence des insectes;
- la fixation d'azote;
- la dynamique de la décomposition du bois, des feuilles et des plantes;
- la nature et la qualité des apports provenant des sources allochtones;
- le rôle des castors dans les écosystèmes aquatiques;
- l'analyse chimique des pluies;
- la composition chimique des cours d'eau.

Dans l'ensemble, ces études explorent la base trophique pour la production des salmonidés et sont maintenant utilisées pour édifier un modèle conceptuel décrivant la base environnementale pour la production du poisson dans les rivières boréales. Plusieurs de ces études ont été prolongées à partir de projets complétés en 1981 (ex: la décomposition des feuilles, l'apport des sources allochtones). Cependant, l'analyse du bassin fluvial se poursuit dans d'autres domaines, en autre celui du rôle du castor, lequel occupe la majeure partie du programme actuel.

Le programme sur l'écologie des salmonidés poursuit le recensement annuel des populations de salmonidés ainsi que les caractéristiques biologiques du saumon adulte et juvénile. Ceci fournit une certaine continuité aux études déjà entreprises dans le passé et ce avec l'ensemble des données utilisées pour élaborer un modèle des systèmes complexes de reproduction. Nous avons poursuivi notre étude sur l'importance de la taille, de l'âge et de la photopériode en déterminant la capacité osmorégulatoire de l'omble fontaine autant en laboratoire qu'au niveau du

terrain. En outre, vous avons étudié l'influence de la végétation riveraine sur l'écologie des alevins de l'omble fontaine.

Les projets des étudiants gradués canadiens portaient 1) sur l'étude comparative des populations du saumon Atlantique en fonction des conditions d'écoulement des rivières (avec l'aide financière de l'Atlantic Salmon Association); 2) sur l'interaction entre les alevins de l'omble fontaine et les épinoches; 3) sur les parasites des épinoches et 4) sur l'écologie de l'ouananiche (Salmo salar). Les étudiants internes ont analysé la croissance et l'habitat des alevins de l'omble fontaine et la physiologie osmorégulatoire de l'omble fontaine en migration.

Le programme de recherche de Matamek offre aux scientifiques de l'Amérique du Nord ainsi qu'aux étudiants une occasion unique de collaborer à un effort scientifique commun. L'emplacement de la Station de Recherche de Matamek, à proximité d'une variété de lacs et rivières à l'état vierge, et en plus son caractère largement subventionné offrent la possibilité de multiples études qui peuvent se poursuivre indéfiniment. L'aide apportée par les scientifiques de différentes universités canadiennes et aussi par le Ministère du Loisir, de la Chasse et de la Pêche a été exceptionnelle. Vous sommes très reconnaissants envers le Gouvernement du Québec et nos collègues canadiens pour leur support continu.

Robert J. Naiman
Coordinateur

10 juin 1983

1982 PROGRAM PERSONNEL

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MATAMEK CANADIAN AWARDS - 1982

Principal Investigator	Affiliation	Title of Project	Award \$C
Geoff Power	University of Waterloo	Interactive and selective segregation of North Shore, Gulf of St. Lawrence, ouananiche	\$4,000
Geoff Power	University of Waterloo	Adaptive life history strategies in North Shore Gulf of St. Lawrence stocks of Atlantic salmon	\$8,600
Gerard FitzGerald	Université Laval	Interspecific competition between brook charr (<i>Salvelinus fontinalis</i>) alevins and sticklebacks <i>Gasterosteidae</i>	\$3,400
Hamish Duthie	University of Waterloo	Determination of pH changes in the Matamek watershed based on sedimentary diatom analysis	\$9,000

Publications - 1982
Scientific Papers

Matamek Contribution

No.

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MONITORING ATLANTIC SALMON IN THE MATAMEK RIVER, 1982

Roderick Morin, Robert J. Naiman, Alan McNeil,
Francine Lafontaine, and Gordon Walsh
Woods Hole Oceanographic Institution
and The Matamek Research Station

Yearly monitoring of Atlantic salmon continued in 1982, including estimates of the adult salmon run, tagging smolts, and population estimates of salmon parr and brook trout below the Second to Fifth Falls of the lower Matamek River. Biological data, including size, age, sex and reproductive condition, were taken whenever possible. A central objective of the salmonid program is to maintain the absence of human impact on Matamek salmon in freshwater. No adult salmon are sampled, other than by length measurement and scale sampling. Removals of smolt and parr are minimal and are not sustained on a yearly basis when it is determined that sampling may significantly influence population survival.

Modification was made to the salmon ladder in 1982 by the addition of a removable cage. The ladder became operational on June 15 and the first adult salmon entered on July 15. Only 23 grilse and 6 two-sea-winter salmon entered the ladder. The peak run occurred between July 26 and 29, later than in the previous three years (Whoriskey et al. 1981; Morin et al. 1982). The upstream trapnet was installed on July 29. High water in August significantly reduced the number of salmon entering the trapnet by delaying the river migration of salmon or, more likely, by reducing the efficiency of the trapnet. Nine salmon (all grilse) entered the trapnet, only one of which displayed the characteristic jaw formation of maturing males.

The adult salmon population was estimated at 76 (Peterson/Chapman estimate, Ricker 1975). Due in part to a small number of recaptures, the estimate is less accurate than most previous years and has wide ranging confidence limits (95% c.l.: 30; 301). Grilse formed 83% of all adult salmon captured. Summaries of the age and size composition of grilse and 2SW salmon are provided in Tables 1 and 2.

Sampling for smolt began on May 18 in the Matamek estuary. As in 1981, fyke nets and angling upriver were ineffective for the purpose of a smolt population estimate. Seine hauls in the Matamek estuary were similarly poor. Figure 1 compares smolt catch per seine haul in the Matamek estuary for 1976 and 1982. The reduced smolt catches of 1981 and 1982 appear to reflect a recent decline in smolt production. Gibson and Côté (1982) reported that between 218 and 440 smolt were tagged and released annually from the Matamek River between 1974 and 1978. Without any reduction in sampling effort, only 89 and 95 smolt were captured during 1981 and 1982, respectively.

The age and sex composition of smolt captured in the Matamek estuary indicated a sharp reversal in 1982 from previous trends (Figure 2). Mean

age and female/male sex ratio declined due to a prominent 2-year-old component of the run and an increase in migrating males. Fork length continued to show no significant difference between years.

In 1981 the salmonid program was extended to include yearly estimates of parr and trout populations at each set of falls on the lower Matamek River. Due to high water in late summer, these estimates could not be obtained for all locations in 1982. Table 3 presents the results of 1982 estimates. We note that estimates made in August may be positively biased, particularly for brook trout, because of low recapture rates brought on by the combined effects of handling and high river discharge. The difference between spring and late summer population estimates of brook trout below the Second Falls has been observed before (Gibson 1973) and is attributed to seasonal movements of trout at that site.

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Table 1. Age composition of Atlantic salmon sampled in the Matamek River, 1982. Column numbers indicate total fish sampled for given ages of smoltification. Grilse spend one further year at sea; 2-sea-winter (2SW) salmon spend two years at sea.

	Age of smoltification			
	2	3	4	6
Grilse	8	20	1	1
2SW salmon	4	2		
Smolt	22	30	10	

Table 2. Fork lengths (cm) of Atlantic salmon sampled in the Matamek River, 1982.

	Mean	s	n
Grilse	52.6	4.24	30
2SW salmon	74.8	2.23	6
Smolt	15.8	1.78	88

Table 3. Population estimates for salmon parr, brook trout and longnose sucker at the bases of the second and fifth falls of the Matamek River, 1982.

Location	Species	Date	Method	Estimate (95% confidence limits)
2nd Falls	trout	May 21-June 28	Schnabel	626 (471; 852)
	trout	August 16-20	Peterson/Chapman	360 (206; 697)
	parr	August 16-20	Peterson/Chapman	377 (283; 516)
	sucker	August 16-20	Peterson/Chapman	1250 (608; 3124)
5th Falls	trout	August 23-28	Peterson/Chapman	1725 (1209; 2561)

FIGURE CAPTIONS

Figure 1. Comparison of smolt abundance determined by seine hauls in the Matamek River estuary, between 1976 (open columns) and 1982 (closed columns). 1976 data are taken from WHOI Tech. Rep. 77-28 (Gibson, 1977).

Comparaison de l'abondance des saumonnetaux dans l'estuaire de la rivière Matamek en 1976 (colonnes ouvertes) et en 1982 (colonnes noires). Abondance relatif est exprimé par le nombre de saumonnetaux capturé par coup de seine. Données de 1976 tirées de WHOI Tech. Rep. 77-28 (Gibson, 1977).

Figure 2. Characteristics of the Atlantic salmon smolts determined by year.

Valeurs observées de l'âge moyen, rapport de sexe et longueur à la fourche moyenne des saumonnetaux de la rivière Matamek depuis 1967.

	n	a	Mean
1976	30	4.34	8.38
1982	88	1.78	12.8

Table 1. Regulation estimates for salmon part, brook trout and longnose sucker at the head of the second and fifth falls of the Matamek River, 1982.

Location	Species	Date	Method	Estimate (95% confidence limits)
2nd Falls	trout	May 21-June 25	Sechnale	455 (411, 532)
	trout	August 18-20	Peterson/Chapman	766 (508, 937)
	part	August 18-20	Peterson/Chapman	377 (187, 516)
	sucker	August 18-20	Peterson/Chapman	1250 (608, 3124)
5th Falls	trout	August 13-25	Peterson/Chapman	1725 (1209, 2581)

APPLICATION OF STAGE-CLASSIFIED DEMOGRAPHIC MODELS
TO ATLANTIC SALMON POPULATIONS

Hal Caswell, Robert Naiman, and Roderick Morin

Woods Hole Oceanographic Institution

Understanding the population consequences of diverse and simultaneous changes in rates of birth, growth, and survival is the task of the science of demography. Population ecologists have traditionally relied on techniques derived from human population studies to analyze populations of plants and animals. Unfortunately, these techniques assume that the life history of the species involved is isomorphic to that of man. While this is a reasonably valid assumption for many organisms, for most it is not.

In practice, this assumption amounts to assuming that a classification of the organisms by age provides an accurate picture of their demographic potential, and that there is only a single pathway to reproduction.

The Atlantic salmon is a good example of a species whose life cycle violates these assumptions. Individuals of the same age may differ in size, maturity, and habitat, with important implications for their probabilities of survival and reproduction. The possibility of precocious maturation and of spawning after different numbers of sea years provide multiple pathways to reproduction. In addition, as the life cycles of the male and female salmon have diverged over recent years, sexual differences have assumed an increasingly important role in determining population dynamics.

These aspects of the salmon life cycle require modifications of classical demographic techniques. Many of these modifications have been worked out on a theoretical basis; in this project we are attempting to apply them to the Atlantic salmon, using the data accumulated on the Matamek population. The dramatic life cycle changes exhibited by the Atlantic salmon in general, and the Matamek population in particular, make it an especially interesting application. We hope to be able to shed light on the results which may be expected if recent trends continue as well as on the possible evolutionary causes of such trends.

The first step in such an analysis is the construction of a life cycle graph for the population. This graph shows the demographically relevant stages in the population and the transitions open to individuals over a single time unit (in this case, one year). Figure 1 shows one of the graphs being considered for salmon. From this graph, a population projection matrix is derived, and from that matrix we can obtain estimates of such parameters as population growth rate, eventual population structure, stage-specific reproductive values, and the sensitivity of population growth to modifications in any of the life cycle parameters (Caswell 1978, 1982).

During the past year, our efforts have focused on collecting, compiling, and computerizing the accumulated Matamek population data. Although these data have been collected since 1967, they have never been compiled in one place in a unified format. Work on this stage of the project is nearly complete, and when finished will provide a valuable resource for workers interested in studying various aspects of Atlantic salmon populations.

ACKNOWLEDGEMENTS

This research is supported by the NOAA Office of Sea Grant.

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FIGURE LEGEND

Figure 1. A graphical description of the life cycle of the Atlantic Salmon. The numbered circles indicate the stages in the life cycle, the arrows the transitions possible over a one year time step. P's denote survival probabilities, M's maturation probabilities, and F's fecundities.

Figure 1. A graphical description of the life cycle of the Atlantic Salmon. The numbered circles indicate the stages in the life cycle, the arrows the transitions possible over a one year time step. P's denote survival probabilities, M's maturation probabilities, and F's fecundities.

NORTH SHORE SALMON STUDY: THE CONCEPT OF RIVER HARSHNESS

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INTRODUCTION

A study of Atlantic salmon from various Quebec North Shore rivers is now in its final stages. Data collection is substantially complete, and a good information base has been established for both adult and juvenile stocks. These data are presently being analysed to develop the concept of river harshness suggested by Schaffer and Elson (1975).

REVIEW

Schaffer and Elson (1975) stated that according to life history theory "environmental factors increasing reproductive success per unit reproductive effort will select for greater reproductive effort at all ages, and at the same time an earlier age of first reproduction... conversely, increased post-breeding survival favours reduced effort at all ages and a later age of first reproduction." They predicted that, for Atlantic salmon, long fast rivers, with their (presumably) greater demands on migrating fish in terms of effort required to reach spawning grounds, would induce delayed age at first reproduction. A longer time spent at sea, and thus larger fish would result. 'Easy' rivers should be typified by reproduction at an earlier age and therefore smaller mean size of individuals.

Until their study, evidence of such a relationship could be considered almost anecdotal or in the realms of salmon 'lore.' They, however, reported correlations between river length and mean weight of angled salmon for several regions including the North Shore. Their simple index of difficulty of upstream migration was the distance fish ascended into freshwater, largely as estimated from the Atlantic Salmon Association's 1967 map. Other studies of relevance to the problem are few and far between, and then only touch on it in a peripheral manner; they are, however, generally supportive of the basic thesis. For example, Power (1981) showed an inverse relationship between the proportion of grilse and river discharge for Quebec and Newfoundland rivers, whilst Fontenelle et al. (1980) suggested a relationship, related to the river harshness concept, between age at first maturity and length of river used by spawners in Brittany, France. A recent study of Icelandic salmon provides further support for the idea (Schaffer pers. comm.).

Critique/Rationale for proposed analysis

The scope of Schaffer and Elson's seminal paper posed inevitable limitations in terms of the depth of their analysis. We perceive certain problems with their approach which can be addressed in the present study.

Not the least of these is the fact that river lengths used in their calculations do not correspond to the ranges of salmon as established/confirmed by ourselves. We have noted substantial under-estimation of actual penetration by salmon into several river systems. Table 1 shows Accessible River Length (ARL: defined as length of main trunk historically frequented by anadromous salmon), and values as used by Schaffer and Elson, for various North Shore rivers. ARL has been calculated from 1:250,000 maps, based on information obtained during this project. Where best estimates; e.g., from local knowledge have been made, this is indicated.

The use of mean weight of angled salmon in plots against river length is potentially a coarse measure of stock characteristics. It should prove fruitful to also examine individual age classes by sex, in order to eliminate effects attributable to sampling bias and sexual differences. Similarly, mean length data may be more useful than mean weight, in that time/location of capture, trauma induced changes in feeding, reporting bias and state of maturity are somewhat less liable to influence length than weight. Data collected over the past three years will allow such detailed analysis. Indeed, preliminary analysis of results indicates that a positive and significant correlation between ARL and fork length of two sea-winter salmon may exist.

The primary index of difficulty of upstream migration used by Schaffer and Elson was limited to consideration of a single factor; i.e., river length. It is logical that the difficulty of ascent of a particular river will be mitigated by a variety of other factors, as well as length of riverine migration. For instance, whilst a long river might necessitate high energy reserves for fish to reach suitable spawning areas, occurrence along the way of turbulent, severe rapids might put a premium on greater agility and smaller body size. It is reasonable to speculate that a river with high waterfalls will impose different demands or constraints on fish conformation than one without. Consistent with life history theory, such demands ultimately influence optimum size at first reproduction. Similarly, the effects of the physical environment on spent fish will be an important determinant of optimal strategy. Where there is little chance of survival, one would predict different mean size at first maturity than for a case where post-spawning survival is high.

Figure 1 demonstrates the central role of the geo-physical environment in determining, at an ultimate level, optimum age at maturity/size at first reproduction of salmon, in a relatively undisturbed environment such as the North Shore.

Physical data (from 1:50,000 maps) for the study rivers are currently being gathered. These include ARL, length of tributaries used by salmon, drainage basin area, river order, gradient and frequency and severity of falls/rapids. Whilst it is obviously difficult to assign importance to dimensions or qualities which are themselves difficult to measure or define (e.g., severity), some degree of logical ranking can be achieved by the technique of paired comparisons (Ross 1976). Eventually it may prove

TABLE 1.

River	ARL (km)	Length (km) used by Schaffer & Elson (1975)
Corneille	23.5*	22.4
Gt. Watchichou	54.5*	32.0
Romaine	51.3	64.0
Godbout	68.5*	72.0
St. Marguerite	73.5	68.8
Mingan	84.5*	52.8
Moisie	147.0	129.6
Etamamiou	173.0*	48.0
St. Jean	160.0	84.8
Natashquan	310.0	100.8

*estimate

GENERALISED A.SALMON LIFE CYCLE FOR QUEBEC NORTH SHORE RIVERS

Figure 1.

possible to calculate an index of river harshness, related to mean age/size at first reproduction, and to account for the biological variability due to different physical characteristics of various rivers.

ACKNOWLEDGEMENTS

We would like to express our thanks to Pierre Bourque, Steve Riley and Fiona Heyesen for their assistance, both in the field, and the laboratory. The comments of Dr. Noel Hynes, Dr. Paul Elson and Dr. William Shaffer have been most useful in stimulating thoughts on the concept of harshness. Feedback from participants at the N.E. Atlantic Salmon Workshop in New Brunswick (November 1982) was helpful in development of the generalized salmon life-cycle.

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VARIATION IN BODY MORPHOLOGY OF JUVENILE
ATLANTIC SALMON (*Salmo salar*): PART 2.
STREAM TANK EXPERIMENT

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INTRODUCTION

Studies of Matamek River juvenile (age 2+) Atlantic salmon showed that parr from slow-moving water had wider bodies and a larger snout to anterior insertion of pectoral fin than parr from fast-moving water (Brzeski and Bielak 1982). Longer heads and longer anal fin bases were characteristic of the "fast-flow" sample. Differences evident between parr from two distinct habitats in the Matamek suggested environmental influence on morphological development of those fish. Traits shown by "fast-flow" parr were considered to allow greater control and maneuverability in turbulent water.

An experiment was designed to show whether such differences would be evident in fry (age 0+) by the end of a growing season.

METHODS

In July 1981, salmon fry obtained from the provincial fish hatchery at Tadoussac were introduced into two flumes at the Matamek streamtanks (0.2 fish/m²). Hatchery fish of unknown parentage, but probably of mixed North Shore stock, were used instead of Matamek fry which could not be collected in sufficient numbers. The flumes (0.93 x 6.0 m) exposed the fish to near-identical natural conditions in all respects except flow-regime. At the beginning of the experiment, flumes 1 and 2 had flow rates of 54.4 and 6.1 cm/s respectively. These fell to 1.25 and 0 cm/s by the conclusion of the experiment 47 days later. After two weeks flume 1 was at less than 10.0 cm/s.

Fry were fed to satiation daily (0.6 gm/fry/day of dried fish meal, supplemented occasionally with blended shrimp), and at the end of the experiment, were sacrificed, measured, and the results statistically treated as previously described (Brzeski and Bielak 1982). Thirty fish were similarly sampled, as a control, at the beginning of the experiment. To determine whether variance of morphological traits differed (initial sample, flume 1, flume 2), F-tests on coefficients of variation were carried out.

RESULTS

All means of morphological characteristics were significantly different ($p < 0.05$), except for body depth (Table 1). Fry from flume 1 were, overall, significantly larger at the end of the experiment than those from

flume 2. As well as exhibiting faster development, fast-water fry showed less variance in morphometric traits than those in flume 2 (Table 2).

All the variables were highly correlated and initially included in the discriminant function analysis. A classification success of 86.2% was possible based on six variables: FL, PEC, DOR, BD, HW, and SNAPE (Table 3). BD and HW were classified as larger in the fish from flume 2, and FL, PEC, DOR, and SNAPE were larger in the fish from flume 1 (Table 4).

DISCUSSION

It is evident from the results that all fry morphometric characters (except body depth) differed significantly between the two treatments, and that fry reared in the fast-water flume were larger in all respects than those in flume 2. This size difference reflects faster growth of juveniles in flume 1. The discrimination achieved (Table 3) was due to growth and overall size differences rather than to individual morphological variation. As well as showing faster development, flume 1 fry showed less variance in 10 out of 12 morphological traits than flume 2 fry.

The rapid growth of parr in the fast-water tank suggests that juvenile salmon thrive better under higher-flow conditions. In the wild, they are then subjected to more food (drifting insects), but under these controlled conditions where they were fed to satiation, food should not induce such variation. However, Rimmer (1978) observed that motion of prey is necessary for salmon alevins to be stimulated into feeding; alevins will ignore stationary prey and dart only at moving prey near them, whether the prey itself is moving or whether the water is transporting it. It is possible that fry in the slow-water flume only consumed the dried fish meal as it was thrown into the tank; not subject to as great a volume of flow as fry in the fast water tank, they may not have benefitted to as great an extent from drifting food in the stream water itself.

Potential low dissolved oxygen conditions in flume 2 may similarly have affected growth and indeed, survival; while loss of fry in flume 1 was due to escape, in flume 2, loss was due to mortality.

It is difficult to draw any firm conclusions regarding the morphology of salmon fry raised under the two different flow regimes. However, it can be inferred, from their lower variances of morphological measurements, that fry in flume 1 more rapidly develop those characteristics important with respect to hydrodynamics, than those in the slow-water flume. The experiment also indicated that higher flow conditions favour growth and survival of Atlantic salmon fry.

The experiment bears repetition with fry from a single stock tested under more rigorously controlled conditions and distinct, sustained differential flow regimes.

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Table 1. Means (x) and standard errors (S.E.) of the 12 morphological characteristics measured (mm) for salmon parr (age 0+) raised in tanks of fast flowing (N = 61) and slow flowing (N = 69) water.

Morphological characteristics	Flume 1: fast water		Flume 2: slow water	
	x	S.E.	x	S.E.
FL (fork length)	53.80	.82	47.39	.84
PEC (pectoral fin length)	11.75	.16	10.69	.16
PEL (pelvic fin length)	7.57	.12	6.99	.12
DOR (length of dorsal fin base)	6.78	.13	5.98	.10
ANAL (length of anal fin base)	4.30	.08	3.78	.07
BD (body depth)	10.22 ^a	.19	9.73 ^a	.21
BW (body width)	4.93	.10	4.63	.09
HL (head length)	12.86	.19	11.76	.17
HD (head depth)	7.95	.15	7.30	.11
HW (head width)	5.75	.08	5.47	.08
SNAP (snout to anterior insertion of pectoral fin)	12.14	.21	10.83	.20
SNAPE (snout to anterior insertion of pelvic fin)	27.25	.43	23.97	.47

^ano significant difference $p > 0.05$

Table 2. Coefficients of variation (c.v.) of the logarithms of 12 morphological characteristics measured for Salmon parr (age 0+) on Day 1 (N = 30) and Day 47 of the experiment (flume 1: N = 61, flume 2: N = 69).

Morphological characteristics	Day 1 (control)	Day 47		Decreasing order of C.V.
		flume 1	flume 2	
FL	2.5	3.2	4.2	S F C
PEC	5.22	4.7	5.25	S C F
PEL	7.1	6.5	7.4	S C F
DOR	5.8	8.5	8.2	F S C
ANAL	11.8	10.1	11.6	C S F
BD	6.2	6.9	8.3	S F C
BW	8.4	10.7	10.8	S F C
HL	3.2	4.5	5.5	S F C
HD	4.6	7.2	6.6	F S C
HW	11.4	6.7	7.4	C S F
SNAP	5.0 ^a	5.4 ^b	10.1 ^{a, b}	S F C
SNAPE	4.7	4.0	6.0	S C F

^asignificant difference $p < 0.05$

^bsignificant difference $p < 0.05$

Table 3. Results of the multivariate discriminant function analysis based on six variables of salmon parr (age 0+) from fast-water (flume 1) and slow-water (flume 2).

	Flume 1 fast water (N = 61)	Flume 2 slow water (N = 69)
Discriminant function score; group centroid in reduced space	1.00	-0.89
Difference in fast and slow centroids	1.89	
Number of cases correctly classified	51 (83.6%)	61 (88.4%)
Classification success for the population	86.15%	

Table 4. Standardized coefficients associated with each of six variables comprising the function used to discriminate between salmon parr (0+) from the fast-water and the slow-water tanks.

Variable	Standardized discriminant function coefficient
FL	0.92
PEC	0.90
DOR	0.52
BD	-2.15
HW	-0.48
SNAPE	0.73

OSMOREGULATION IN THE BROOK TROUT, SALVELINUS FONTINALIS

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Brook trout (Salvelinus fontinalis) often migrate from freshwater to seawater when given free access to the ocean. Movement into comparatively rich marine systems can result in growth rates that are four to five times that of cohorts remaining in freshwater. This fact, in combination with high return rates of brook trout to their parent stream, makes this a potentially valuable species for sea ranching, fish farming and enhancement programs. However, several questions concerning the migratory tendency of brook trout remain unanswered. One important question is the osmoregulatory ability of brook trout, specifically the roles of size, age and photoperiod in determining their ability to osmoregulate in seawater. Current work in our laboratory is designed to answer this and other questions related to salmonid osmoregulation and smoltification.

In order to determine whether size, age and/or photoperiod are important in the osmoregulatory ability of brook trout, we separated several thousand fry of a controlled genetic stock into fast and slow growing groups using feeding rate to control growth. We further divided the fish into two photoperiods; one is "normal" daylength, decreasing in fall and increasing in the spring, while the second is 3 months out of phase with the normal photoperiod. Every 6 weeks fish from each group are acclimated to seawater using a gradual procedure of one week at 10 o/oo, another week at 20 o/oo and then exposure to 30-31 o/oo seawater. Growth and survival of brook trout in seawater is monitored for a least 20 days. To determine the osmoregulatory ability of these fish, plasma levels of Na^+ , Cl^- , K^+ , Mg^{++} and total osmotic concentration are measured at discrete intervals. Gill Na^+-K^+ ATPase, an enzyme responsible for blood ion homeostasis, is measured in animals exposed to seawater and in a freshwater control group. The circulating levels of the hormone thyroxine is also being measured to determine its effect on osmoregulatory ability and seawater survival.

Experiments conducted over the past year and a half have shown a strong dependence of seawater survival and hypoosmoregulatory ability on body size. Larger, faster growing fish show greater salinity tolerance than smaller, slower growing fish (Fig. 1). Body size can explain up to 79% of the variation in seawater survival time of brook trout.

Photoperiod exerts its strongest influence on hypoosmoregulatory ability through the maturation cycle. During declining photoperiod a period of normal spawning for brook trout, mature males exhibit poor salinity tolerance relative to immature males and mature and immature females (Fig. 3). Mature males also demonstrate poorer abilities to regulate plasma chloride, magnesium and total osmotic concentration.

In smolting salmonids, increasing photoperiods result in a myriad of physiological changes, perhaps mediated by thyroxine, which facilitate hypoosmoregulation. No dramatic increases in salinity tolerance occur in brook trout under increasing photoperiods. However, Figure 3 demonstrates that a photoperiod controlled annual cycle in thyroxine does occur, declining in the falling and rising to a springtime maximum in March. The magnitude of springtime increases in thyroxine levels in the brook trout do not equal those shown to occur in smolting salmonids. An increase in gill $\text{Na}^+ - \text{K}^+$ ATPase activity, which might indicate preparation for seawater entry mediated by thyroxine, did not occur and thus the physiological significance of the thyroxine cycle remains unclear.

In the coming months we will be defining our model of hypoosmoregulation in brook trout to include variables such as gonadosomatic index, growth rates and condition factors. With this added information we should obtain even greater accuracy in predicting salinity tolerance and discerning the underlying physiological mechanisms that allow brook trout to osmoregulate in seawater.

Physiological constraints discovered under laboratory conditions may be important in nature to varying degrees. In 1982 we examined natural populations of brook trout in order to determine whether physiological constraints affect anadromy and hypoosmoregulation. Field studies were conducted between naturally anadromous (Rivière à la Truite) and non-anadromous (Matamek River) populations of brook trout so as to determine temporal, spatial, size and age related changes in thyroxine, gill $\text{Na}^+ - \text{K}^+$ ATPase and hypoosmoregulatory ability. Three fyke nets were set in Rivière à la Truite and checked daily from early June to mid-September. In the Matamek River two fyke nets were set between the 2nd and 3rd Falls and checked three times a week throughout the summer. Some trout were seined from the Matamek Estuary during June, in a cooperative effort with the smolt project. The mouth of the Moisie River was seined twice monthly at two sites; one at the mouth of the river and one approximately 1 km upstream.

Upon capture, all fish except lamprey and eel were anesthetized and fork lengths were measured to the nearest cm. All fish, except lamprey and eel, were given a fin clip and released downstream of the capture net. A small representative sample of brook trout, salmon parr, and lake chub were taken and either were sacrificed immediately, or taken back to the station and placed in 32 o/oo sea water for 24 hours (e.g., seawater challenge), then sacrificed. From all sacrificed fish, fork length, weight, and silvering were recorded; blood was taken for subsequent analysis of thyroxine and osmolarity, and three to four gill arches were removed from each fish and frozen for determination of gill $\text{Na}^+ - \text{K}^+$ ATPase activity.

Brook trout, salmon, longnose sucker, white sucker, lake chub and lamprey all left Rivière à la Truite in significant numbers just after peak water levels (Fig. 4). Emigration of all species was protracted

over a two month period until late July. Several peaks in brook trout movements occurred, often coinciding with increased water levels due to rainfall. The first half of the migratory period contained a significantly ($P < 0.05$), 2x2 contingency table) greater proportion of larger (>16 cm) brook trout than the latter half.

Seawater challenge experiments indicate that both size and location (i.e., proximity to saline waters) are important in determining hypoosmoregulatory ability under natural conditions. Fish taken from Rivière à la Truite showed moderate ability to maintain blood ion concentration after 24 hours in seawater (Table 1) with slight increases in ability with increased size. Brook trout from the downstream site at the Moisie River estuary performed better than brook trout from the upstream estuary site and Rivière à la Truite (Table 1). Similarly, brook trout from the Matamek River estuary performed better under hypersaline conditions than fish from the Matamek River.

Thyroxine and gill $\text{Na}^+ - \text{K}^+$ ATPase determinations are complete and await further analysis. Preliminary results indicate that gill $\text{Na}^+ - \text{K}^+$ ATPase in estuarine brook trout show elevated activity (Table 1). These results support our observations of increased hypoosmoregulatory ability of estuarine fish, and suggest that behavioral changes act in concert with physiological constraints of size to determine hypoosmoregulatory ability.

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Table 1. Size, plasma osmolarity and gill $\text{Na}^+\text{-K}^+$ ATPase of brook trout after 24 hours in seawater. Fish from Rivière à la Truite were sampled June 9 and 25 during peak emigration. Fish from the estuary were captured on several occasions from July 2 to August 31.

	N	Size (cm)		Osmolarity (Osm/L)	Gill $\text{Na}^+\text{-K}^+$ ATPase ($\mu\text{ MPi mg Prot}^{-1}\cdot\text{hr}^{-1}$)	
		Range	Mean		Mean (+ sem)	Mean (+ sem)
Rivière à la Truite	9	9.5-19.5	13.2	454 (11.5)	-	-
Moisie River Estuary (upstream)	10	12.3-18.4	14.1	496 (5.2)	5.9 (0.8)	5.9 (0.8)
Moisie River Estuary (downstream)	9	15.2-20.5	18.1	395 (6.7)	9.4 (0.9)	9.4 (0.9)

Figure Legends

Figure 1. Mean seawater survival time versus mean fork length of brook trout exposed to 32 ppt seawater. Open circles represent experiment performed in autumn and winter, and which contained significant numbers of mature males.

Figure 2. Mean seawater survival time of mature males, immature males and females. Normal photoperiod (P_N) experiment was conducted under autumn day length conditions when normal spawning occurred. Lagged photoperiod (P_L) experiment occurred under summer day length conditions.

Figure 3. Plasma thyroxine levels and day length as a function of time.

Figure 4. Daily capture of fishes in upstream facing net at mouth of Rivière à la Truite in 1982.

TROUT FRY STUDIES IN 1982 - RESULTS OF HABITAT STUDIES

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In response questions raised during studies of brook trout fry ecology during 1980 and 1981, an expanded program was conducted in 1982 with the following objectives:

- 1) to determine whether the results of experimental habitat manipulations from 1981 could be replicated;
- 2) to examine the role of social behavior in relation to habitat utilization by brook trout fry;
- 3) to describe diel movement patterns and feeding activity of trout fry;
- 4) to determine the nature of interactions between trout fry and ninespine stickleback (Pungitius pungitius).

In this paper, we report on preliminary results from studies based on the first two objectives. Observations and collections of trout fry in the Matamek River were conducted biweekly as in 1981 (Morin et al. 1982). Samples were taken concurrently at Rivière à la Truite (Fig. 1) to compare treatment effects between territorial and non-territorial fry. Observations and marking experiments in 1981 confirmed that trout fry in the Rivière à la Truite study site commonly occupy territories. Habitats were selected in Rivière à la Truite that corresponded to experimental manipulations of riparian vegetation and woody debris in the Matamek River. Trout fry were removed every two weeks from each habitat type for analysis of growth and feeding. Collection sites in Rivière à la Truite were changed periodically to avoid influences on territory formation caused by fry removals. In both rivers, invertebrate collections were made by benthic Surber sampler, from wood samples, by drift nets and by surface insect traps. The purpose of this was to compare dominant food organisms in the trout fry diet with major organisms available at the substrate, on submerged woody debris, in the water column and at the water surface.

Matamek River

Results from 1982 studies on the ecological role of riparian vegetation and woody debris appear generally to replicate the results of similar analyses from 1981. In both years, trout fry were most abundant in denuded areas during June and early July, preferring sites with riparian cover in late July and August (Fig. 2). Trout fry distribution in 1982 showed similar patterns of increasing depth and distance from water surface from mid July on (Fig. 3); however, in 1982 no significant difference

could be found in spatial distribution when compared between treatments and reference areas. Trout fry in all treatments occupied deeper water further from shore during June and early July 1982 than at corresponding periods in 1981. The growth of trout fry was not significantly different both between treatments and years.

The analysis of feeding data is presently incomplete; however, preliminary results indicate that, as in 1981, habitat manipulations do not have a predictable effect on trout fry feeding. This is mainly due to the mobility of trout fry between treatment sites. In both years, fry fed predominantly on surface organisms and were observed close to the water surface. However, two key differences were noted between years. First, fry did not consume the same surface organisms in both years. For example, winged Thysanoptera were dominant in 1981 and rare in 1982. Secondly, in June of 1982 zooplankton were more prominent in fry diets than at the same period in 1981. The consumption of zooplankton was replaced by midsummer with winged Diptera and other surface organisms in all treatments (Fig. 4). The zooplankton of both drift samples and stomachs during June 1982 comprised mainly Diaptomus minutus (Copepoda) and Bosmina longirostris (Cladocera) in similar proportions (78-90% of all zooplankton in drift; 88-100% in stomachs). It is likely that trout fry in June 1982 occupied deeper water further from the surface (Fig. 3) in order to exploit drifting zooplankton. It therefore appears that some year-to-year variations in the availability of invertebrate prey may occur, potentially influencing fish distribution.

Habitat Utilization

Comparative analyses of growth and feeding were conducted in the Matamek River and Rivière à la Truite to determine whether territory formation has a marked influence on habitat utilization. We predicted that in Rivière à la Truite, riparian vegetation and woody debris would influence the availability of invertebrates and favor the growth of trout fry. This relationship would, predictably, not hold for the Matamek River where trout fry distribution was not defined by territories and was less stable over time.

Preliminary results support these predictions. Trout fry in denuded areas of Rivière à la Truite were significantly smaller than fry in areas with a woody substrate and riparian cover (paired t-tests, $P < 0.05$). Trout fry in denuded areas also consumed fewer invertebrates associated with the water surface than fry in areas with riparian cover. Chironomid larvae (Diptera) were a major component of diet in all treatments, but were more prominent in the diet of trout fry in open areas (Fig. 5). Winged aquatic and terrestrial organisms made up between 41 and 45% of all organisms consumed in areas with riparian vegetation and woody debris during July. They made up 24-33% of the diet in denuded areas at the same time. The diversity of organisms consumed (Shannon-Wiener diversity based on families) was generally greatest in areas with riparian vegetation and woody debris and smallest in denuded areas (Table 1), providing further

evidence in support of the view that riparian vegetation and woody debris contribute significantly to fish diets. The same relation does not hold for the Matamek River, although in most cases feeding diversity was greater in Matamek fry.

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Table 1. Feeding diversity (Shannon-Wiener index) of brook trout fry in Rivière à la Truite (a) and the Matamek River (b) based on the identification of prey to family. Column headings refer to stream sections where riparian vegetation or both riparian vegetation and woody debris are absent. Reference areas have both riparian vegetation and woody debris present.

	Vegetation + Debris	Vegetation	Reference
^a June 15	0.6762	2.8164	2.1321
June 29	0.2734	0.8664	1.0581
July 13	1.8976	2.0773	2.7334
^b June 11	2.1273	1.5765	1.5167
June 25	2.7827	1.5357	2.1839
July 10	2.5481	2.4510	2.0930

Figure Captions

- Figure 1. Map of North Shore of St. Lawrence River showing location of study sites, Matamek River and Rivière à la Truite. Inset at right shows design of habitat manipulations in the Matamek River. Arrows indicate locations on the Matamek River where duplicate sets of manipulations were made. At the upper location, observations of trout fry were made weekly in 1981 and biweekly in 1982 by snorkeling; at the downstream location observations were made along with biweekly removals of trout fry in both years.
- Figure 2. Relative abundance of trout fry in treatments and reference sections during 1981 (solid bars) and 1982 (hatched bars), Matamek River study. Abundance is expressed as the percent occurrence of fry in treatment or reference section relative to all treatments and references for each sampling period. Stippled lines show expected percent occurrence if trout fry were distributed equally throughout all treatments and references.
- Figure 3. Comparison of 1981 and 1982 data for mean depth of water column where trout fry were sighted and the mean distance of trout fry from water surface over time. Similar relationships were found in 1982 for all treatments. 1981 data are based on weekly mean values smoothed by a running average of three.
- Figure 4. Relative importance (RI) of zooplankton (solid bars) and winged adult Diptera (hatched bars) in the diet of brook trout fry, Matamek River 1982. RI was calculated on the combined basis of % frequency of occurrence, % abundance and the % weight contribution of each taxon in the diet of trout fry. Similar results were found in all treatments.
- Figure 5. Relative importance of chironomid larvae and grouped taxa in the diet of brook trout fry, Rivière à la Truite 1982. Surface insects include winged aquatic insects and terrestrial insects and Arachnidae. Results are shown for reference areas (riparian vegetation and woody debris present) and open areas (riparian vegetation and woody debris absent).

DIEL MOVEMENTS OF BROOK TROUT FRY

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Brook trout fry in the Matamek River move considerably between habitats but display seasonal patterns in habitat selection and spatial distribution (Morin et al. 1982, this report). It has not been determined whether trout fry select different habitats according to the time of the day, or whether their spatial distribution changes over a 24 h period. This study was undertaken in conjunction with studies of the diel feeding activity and daily rations of brook trout fry (Walsh, this report).

Trout fry were observed from the stream edge every three hours over 24 h in Rivière à la Truite and at two locations in the Matamek River. At night, fry were observed by flashlight. Trout fry were counted and their position in the water column was determined by measuring the depth of the water column, their distance from the water surface and their distance from the stream edge. The results were log-transformed and analyzed by one-way ANOVA followed by Student-Neuman-Keuls (SNK) tests when significant differences were found. Data on mean distance from shore in the Matamek River were tested by a non-parametric Kruskal-Wallis one-way ANOVA due to unequal variances. Rejection levels were set at $P = 0.05$. We also present the results of invertebrate drift studies from Rivière à la Truite. Fifteen minute drift samples were taken from the surface and bottom of the water column every three hours. Drift was taken in order to relate the activity and distribution of fry to the availability of prey.

Trout fry exhibited diel patterns of spatial distribution at all sites. Differences in mean distance of fry from the shore and the mean water depth were highly significant for all tests. At night, trout fry moved closer to shore into more shallow water than during daytime (Fig. 1, 2). The night hours, 2200 to 300 h, generally corresponded to the significantly smaller mean distance and depth (SNK tests).

Trout fry were quiescent at night, invariably located at the stream bottom. Observation by flashlight disturbed the fry, causing them to dart about erratically, probably accounting for the variation in the number of fry observed in treatment sites in the Matamek River (Table 1). Trout fry did not display a clear pattern of habitat selection at night. In all of our observations, fry were dispersed during the daytime and were crowded along stream edges at night.

These observations concur with the results of feeding studies (Walsh, this report) that indicate that trout fry are inactive at night. The activity cycle of trout fry, however, does not appear to be directly related to the availability of invertebrate prey. Chironomid larvae composed a major part of both drift (Table 2 and 3) and trout fry diets. However, the peak abundance of chironomid larvae occurred at night while fry were inactive.

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FIGURE CAPTIONS

- Figure 1. Mean distance of trout fry from the shoreline, observed over 24 h, at Rivière à la Truite (July 8-9, dashed line) and below Fifth Falls of the Matamek River (July 21-22, solid line). Mean distance was significantly different for each set (Rivière à la Truite: ANOVA, $F = 22.55$, d.f. = 6; Matamek: Kruskal-Wallis, $H = 46.22$, d.f. = 6). Mean distances at 2200 and 0100 h, Rivière à la Truite, were significantly less than other means (Student-Neuman-Keuls test). Horizontal bar indicates night period.
- Figure 2. Mean depth of water column where trout fry were located, observed over 24 h, at Rivière à la Truite (July 8-9, dashed line) and below Matamek River Fifth Falls (July 21-22, solid line). Mean depth was significantly different for each set (Rivière à la Truite: ANOVA, $F = 48.59$, d.f. = 6; Matamek: ANOVA, $F = 22.42$, d.f. = 6). Mean distances between 2200 and 0300 h for both rivers were significantly less than other means (Student-Neuman-Keuls tests). Horizontal bar indicates night period.

Table 1. The number of brook trout fry sighted in habitat treatment and reference sections of the Matamek River. Observations were made on August 6-7.

Time	Vegetation and Debris Removal	Reference	Debris Removal	Reference	Vegetation Removal	Total
1200	0	1	1	1	0	3
1500	0	1	0	0	0	1
1800	0	0	0	0	0	0
2100	4	6	7	1	0	18
2400	8	4	6	0	1	19
0300	8	8	4	0	1	21
0600	0	0	1	0	0	1
0900	0	0	1	0	0	1

Table 2. Diel pattern of invertebrate drift (number of organisms/m³) on July 8-9, Rivière à la Truite. Each sample was taken at the water surface over a 15-minute period.

Taxa	1200	1500	1800	2100	2400	0300	0600	0900
Rotifera	48.5	22.6	46.0	36.1	29.5	27.4	93.9	36.5
Cladocera								
<u>Bosmina</u>	7.1	13.5	15.6	48.6	27.8	10.9	51.8	26.9
<u>Alona</u>		0.2		0.3		0.3	0.6	0.3
Chydorinae			0.4	0.7	2.5	0.3	1.6	0.3
<u>Daphnia</u>		0.2	0.1	0.1	0.3			
<u>Polyphenius</u>			0.4	1.0	0.2	0.2	0.4	
Copepoda								
Harpacticoida	1.9	1.0	1.6	4.3	3.2	3.9	2.5	1.3
<u>Cyclops</u>	1.6	9.7	9.2	7.8	8.4	13.5	20.7	27.9
<u>Ergasilus</u>			0.1	0.3	0.3	0.5	0.2	0.3
<u>Epischura</u>			0.3				1.4	
Nematoda	0.7	0.6	0.6	0.7	0.7	0.8	1.0	0.2
Oligochaeta								
Naididae	0.2		0.4		1.2	0.2	0.4	0.2
Arachnida	1.6	0.6	0.1	0.1				
Hydracarina adult	1.0	4.8	3.5	2.7	2.5	1.7	2.1	3.4
larva	5.2	14.8	11.5	13.0	7.9	6.4	18.3	8.2
Collembola	11.3	19.8	6.6	6.4	3.4	1.0	2.1	2.7
Plecoptera								
Unknown nymph	0.9			3.0	2.9	2.5		1.0
Nemouridae nymph	0.7	0.2	1.9					
Ephemeroptera								
Unknown nymph	0.9	2.6	0.7	1.4	3.7	4.4	1.0	0.5
Bactidae nymph	0.3							
Trichoptera								
Unknown larva		0.4			0.2			
Odonata		0.2						
Hymenoptera								
Scelionidae	0.2		0.1					
Braconidae		0.2						
Diapriidae		0.2						

Table 2. (continued)

Taxa	1200	1500	1800	2100	2400	0300	0600	0900
Thysanoptera adult		0.2						
larva	2.1	6.8	3.8	3.8	1.0	1.7	0.4	0.7
Coleoptera								
Chrysomelidae larva		0.2						
Homoptera	0.2		0.3					0.2
Diptera								
Chironomidae adult	0.3	0.4	0.7	0.1	0.2			
pupa					2.7	0.2		0.3
larva	10.4	15.0	8.7	44.3	84.8	36.7	8.0	5.7
pupal case	5.2	10.0						
Simuliidae larva		0.4	0.1	0.3	2.0	0.7		
larval head		13.7	1.4	1.2	0.5	3.4	5.1	2.2
pupal case		0.4						
Nymphomyidae adult			0.1		0.2			
pupa	0.5			0.1				
larva					0.2			
Sciaridae adult			0.1					
Empididae larva					0.2			
Culicidae larva		0.2						
<hr/>								
Total	100.8	138.9	113.4	176.5	186.5	116.8	211.5	118.8

Table 3. Diel pattern of invertebrate drift (number of organisms/m³) on July 8-9, Rivière à Truite. Each sample was taken at stream bottom over a 15-minute period.

Taxa	1200	1500	1800	2100	2400	0300	0600	0900
Rotifera	30.6	28.4	44.7	14.8	41.7	29.0	72.3	38.1
Cladocera								
<u>Bosmina</u>	20.0	13.5	23.9	26.8	40.9	44.4	43.8	26.9
<u>Alona</u>	0.5	0.3	0.1	0.4	0.3	0.6	2.1	0.2
Chydorinae	0.5		0.6	0.5	1.6	0.7	1.3	0.5
<u>Daphnia</u>	0.1				0.1			
<u>Polyphenius</u>			0.1	0.1	0.1	0.3	0.4	1.0
Ostracoda						0.8	0.9	
Copepoda								
Harpacticoida	2.9	3.2	2.9	1.8	3.5	2.4	3.6	2.9
<u>Cyclops</u>	5.4	8.5	13.0	5.4	6.1	12.6	23.0	22.0
<u>Ergasilus</u>	0.1		0.6	0.2	0.7	0.8	0.9	
<u>Epischura</u>		0.1					0.2	0.3
Nematoda	1.0	0.4	0.6	0.4	0.7	0.3	0.3	0.4
Oligochaeta								
Naididae	0.3	0.1	0.8	0.2	1.0	0.3	0.6	0.4
Archnida	0.4	0.6		0.1	0.6		0.1	0.3
Hydracarina adult	4.8	3.6	4.9	1.3	2.1	1.9	1.9	2.8
larva	10.2	13.0	13.7	9.1	9.6	13.0	15.3	13.8
Collembola	18.4	7.6	3.1	2.2	1.6	1.2	1.5	1.8
Plecoptera								
Unknown nymph	1.0	1.0	1.2		3.1	1.7	1.6	0.8
Nemouridae nymph				2.2				
Leuctridae nymph						0.1		
Ephemeroptera								
Unknown nymph	2.1	2.4	0.9	0.3	4.6	4.3	1.1	1.5
Baetidae nymph		0.3						
Leptophlebiae nymph				0.1				
Trichoptera								
Unknown larva	0.1	0.4	0.1	0.1	0.3		0.1	
Isoptera larva		0.1						

Table 3. (continued)

Taxa	1200	1500	1800	2100	2400	300	600	900
Hymenoptera								
Scelionidae		0.2						
Thysanoptera adult				0.1	0.1			
larva	1.9	5.2	4.3	1.5	2.0	0.7	1.6	1.3
Homoptera	0.1							
Diptera								
Chironomidae adult	0.1	0.2		0.1	0.1		0.4	0.1
pupa	1.9	0.8	0.4	0.4		0.2	0.4	0.3
larva	12.8	15.7	9.7	18.4	90.9	51.9	14.1	10.4
pupal case		2.6			1.1			
Simuliidae larva			0.4	0.1	1.9	1.6	0.2	0.2
larval head	0.4	11.2	3.0	3.4	0.9	4.4	2.9	4.0
pupal case		0.1						
Tipulidae pupal case		0.2						
Nymphomyidae adult					0.1			
pupa			0.1	0.1	0.1		0.1	
larva			0.1		0.2			0.1
Sciaridae adult				0.1				
Empididae larva	0.3		0.1	0.1	0.1			0.2
Total	115.9	119.7	129.3	90.3	214.5	173.2	190.7	130.3

DAILY PATTERNS OF FEEDING BEHAVIOR, DAILY RATIONS, AND GROWTH OF
JUVENILE BROOK CHARR (SALVELINUS FONTINALIS) IN TWO DIFFERENT HABITATS

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The feeding ecology of brook charr fry was investigated in order to: 1) describe diel feeding patterns and daily rations; 2) examine seasonal variations in feeding activity and rations; 3) evaluate the effects of environmental factors; 4) establish the relation between growth rates and rations and 5) calculate the ration required by the fry. To attain these objectives, samples were taken several times in the season to examine temporal effects, and in two different habitats (Fig. 1) to examine environmental effects. Since this study evaluates the performance of fry using resources of the environment, it is relevant to other studies at Matamek on brook charr diet, habitat selection and inter- and intra-specific interactions.

Stomach content analysis showed that brook charr fry fed mainly during the day in Matamek River and Rivière à la Truite (Fig. 2). The weight of fry stomach contents from Rivière à la Truite were maximum at the end of the daylight period while those of fry from the Matamek River were maximum during most of the daytime, except in August when high water temperatures seem to have reduced the food intake (Fig. 2, Table 1).

Feeding pattern and daily ration differed between habitats. The fry in the Matamek River were able to maintain a high stomach content weight for more hours during June and July than did fry in Rivière à la Truite during July and August (Fig. 2). Daily rations were estimated at 5.09 and 4.09% of body weight for fry from Rivière à la Truite in July and August, respectively. In the Matamek River, the estimates were 7.12, 9.75 and 1.27% in June, July and August, respectively.

Fry from the Matamek River had a greater instantaneous growth rate than those from Rivière à la Truite (3.96% vs 2.72% per day, Fig. 3) and were significantly heavier in August (Table 1). Further data is presented in Table 2. Differences in water temperature may account for observed differences in daily rations and growth rates between habitats (Fig. 4). Further analysis of drift abundance in both habitats will be required to account for differences in feeding patterns, since water temperature did not vary during daylight hours.

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Table 1. Daily food rations of brook charr fry in the Matamek River and Rivière à la Truite. Daily ration, expressed as % dry body weight, was calculated by the method of Elliott and Persson (1978). All values, except evacuation gastric rate (R) and daily ration, are means ($\pm$ S.D.). In Rivière à la Truite, open and closed areas denote habitat without or with riparian vegetation, respectively.

Location	Fish			Daily fry food ration			Water Temperature °C
	N	Fork length mm	Wet weight g	Dry weight mg	R	N	
Matamek River							
June 19-20	114	25.6 (1.7)	0.14 (0.04)	17.47 (4.72)	0.0863	84	7.12
July 12-13	130	33.1 (4.5)	0.39 (0.14)	53.00 (21.19)	0.1120	103	9.75
August 16-17	120	47.0 (11.7)	1.41 (0.49)	272.60 (111.81)	0.0509 ^a	97	1.27
Rivière à la Truite							
July 8-9							
Open	129	29.8 (3.0)	0.26 (0.10)	34.41 (13.94)	0.0569 ^b	103	5.09
Closed	25	28.8 (2.6)	0.28 (0.09)	39.38 (13.66)		-	
August 12-13	99	36.9 (5.5)	0.67 (0.33)	103.45 (61.61)	0.0435 ^{a, b}	99	4.09
							12.5 - 14.5
							10 - 11

^a regression not significant ($P > 0.05$).

^b R estimated assuming that fry did not feed during night.

Table 2. Instantaneous growth rates (G, in % of body weight per day) of juvenile brook charr. Numbers in brackets represent the number of days.

Rivière à la Truite			Matamek River		
Date	N	G	Date	N	G
June 15	16		June 19-20	113	
		1.48 (14)			4.42 (23)
June 29	17		July 12-13	130	
		4.60 (10)			3.70 (35)
July 8-9	129		August 16-17	120	
		3.73 (18)			
July 27	18				
		1.36 (17)			
August 12-13	99				

FIGURE CAPTIONS

- Figure 1. Map of North Shore of St. Lawrence River showing location of study sites at the base of Fifth Falls of the Matamek River and in the lower Rivière à la Truite.
- Figure 2. Variations in mean (+ 95% confidence limits) relative stomach content dry weight of juvenile brook charr collected in the Matamek River and Rivière à la Truite, with time of day. Sample sizes and water temperatures are indicated. Solid and hatched horizontal bars represent times of night and twilight.
- Figure 3. Growth of juvenile brook charr in the Matamek River (----) and Rivière à la Truite (—). Regression lines are of the form $y = 4.17 + 0.0396x$ ($r^2 = 0.99$) for the Matamek River and $y = 4.44 + 0.0272x$ ($r^2 = 0.98$) for Rivière à la Truite, where y represents in wet weight (mg) and x represents the number of days since June 1. The regression coefficients of the two lines are significantly different (ANCOVA, $P < 0.001$). Sample sizes are indicated above the 95% confidence limits of observed mean wet weights.
- Figure 4. Relationship between the instantaneous growth rates and water temperatures. In upper panel, observed daytime temperature for the Matamek River and maximum and minimum temperatures for Rivière à la Truite are shown. Hatched horizontal lines indicate temperature limits for maximum growth according to McCormick et al. (1972). In lower panel, observed instantaneous growth rates for Matamek River and Rivière à la Truite brook charr are shown. The hatched horizontal line indicates the maximum growth rate of charr fry fed ad libitum (McCormick et al. 1972).

MATAMEK

RIVIERE A LA TRUITE

TIME OF DAY

THE INTERACTIONS OF BROOK TROUT FRY (Salvelinus fontinalis)
AND NINE-SPINE STICKLEBACKS (Pungitius pungitius)
IN THE MATAMEK RIVER, QUEBEC

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INTRODUCTION

Although there are a number of resource partitioning and competition studies using salmonid fish, most of these studies concern interactions among closely related species (Dickson and MacCrimmon 1982; Gibson 1978; Stein 1972; Keenleyside 1962; Kalleberg 1958). In general, these studies demonstrate that dominant species have faster growth rates than subordinate species, because the former monopolize preferred habitat, food or both.

There are few studies concerning interspecific interactions between salmonids and non-salmonids (e.g., Magnan and FitzGerald 1982; Johannes and Larkin 1961). These studies have shown that non-salmonids may have considerable impact on the feeding biology of salmonids. A preliminary study conducted in 1981 by Miller and Montgomery (1982) revealed intense interspecific aggression between brook trout (Salvelinus fontinalis) fry and nine-spine sticklebacks (Pungitius pungitius). They observed that mortality in brook trout fry was the direct result of agonistic interactions and concluded that interspecific aggression may be an important factor in determining the productivity and distribution of salmonid fish. For example, territorial sticklebacks may displace territorial fry from preferred feeding areas.

This report presents data collected as a follow-up to the Miller and Montgomery study. Our objectives were to examine the feeding habits of the two species when in sympatry with a view to determining the importance of interspecific competition for food in the relatively unproductive waters of the Matamek River. Second, to investigate the role of interspecific aggression in determining the spatial distribution of the two species.

MATERIALS AND METHODS

Food habits

Ninety-eight trout fry and 82 sticklebacks (57% males and 43% females) were captured on June 20, July 12 and August 7 below the Fifth Falls of the Matamek River and were immediately placed in 10% formaldehyde. Five to 10 minutes were required to capture and preserve each sample. There was no evidence of food regurgitation. Food items in the stomach were identified to the lowest taxonomic level feasible, counted, and analysed using the composition method (Hyslop 1980).

The food habits of trout fry and sticklebacks, were compared using a contingency table analysis (Legendre et Legendre 1979). Diversity indices were calculated using $(1/P_i^2) \times 10^4$ (MacArthur 1972), where P_i is the percent numerical composition of the i th taxon found in the diet. Unfortunately, there are no appropriate statistical tests available for this index.

Growth

Fork lengths of the 98 trout fry and total lengths of the 82 sticklebacks were measured on preserved specimens, in the laboratory.

Behavior

Observations of the aggressive interactions between sticklebacks and trout fry were conducted in one flume of the stream tank at the Second Falls of the Matamek River. For details of this apparatus see Dickson and MacCrimmon (1982). Fish of both species used for the behavioral observations were obtained by seining from the Matamek River from June 28 to August 5, 1982. The mean fork length of trout fry used in the experiments was $4.0 \text{ cm} \pm .26$ and that of sticklebacks was $5.3 \text{ cm} \pm .49$. Although male and female sticklebacks are territorial (Morris 1958) only females were used.

Test populations consisted of trout fry and/or sticklebacks studied in allopatry and in sympatry. To replicate and extend the results of Miller and Montgomery (1982), densities of 2, 6, 8 and 12 fish per m^2 were used. Food was introduced into the stream tank each evening and consisted of zooplankton, collected in a nearby pool.

In the stream tank, individual fish were identified by coloration pattern and were chosen at random for observation. The frequency and duration of each behavior pattern was recorded for five minutes using a Datamyte Model 801 event recorder. For sticklebacks, the quantified behavioral patterns were chase, charge, approach, lateral display and bite. The same patterns, except lateral display, were quantified for the trout fry. Wootton (1976) provides detailed descriptions for the aggressive behavior of sticklebacks.

Field observations

Observations of aggressive interactions between the two species were made below the Fifth Falls of the Matamek River to examine if the interactions observed in the stream tank were also present in the field. The habitat was an open area without aquatic vegetation and an average water depth of 20 cm. The same behaviors followed in the stream tank were recorded from the shore for five minute periods. The total observation time was two hours from July 7 to July 28, 1982.

To compare the daily activity of sticklebacks and trout fry in sympatry, observations were made every three hours for five minutes on five individual fish of both species during a 24 h cycle.

Different agonistic acts, as previously described, were pooled to give a single measure of aggression. Behavioral data were analysed with Kruskal-Wallis and STP tests (Sokal and Rohlf 1981). As equal samples were required, the number of observations for each species was reduced to equal numbers with the aid of a random number table.

RESULTS

Food habits

In June trout fry fed principally on simuliid larvae whereas chironomid, simuliid pupae and chironomid adults were the most important components in the diet of the sticklebacks (contingency table analysis, chi square, $p \leq 0.05$; Fig. 1). Diversity indices were similar for the two species.

In July, trout fry consumed mainly Simuliidae (larvae and adults), while sticklebacks ate mainly chironomid larvae and pupae, and cladocerans (contingency table analysis, chi square, $p \leq 0.05$). Sticklebacks had a more diverse diet than that of trout fry.

In August chironomid larvae were the most abundant items in the diet of both species (contingency table analysis, chi square, $p \leq 0.05$). Trout fry had a slightly more diverse diet than that of the sticklebacks.

Behavior

In allopatric stickleback populations, total intraspecific aggression was directly related to the density of sticklebacks (Fig. 3), while in allopatric trout fry populations, total intraspecific aggression increased with the density of trout fry up to density 8 and decreased at density 12 (Fig. 4).

Interspecific aggression by sticklebacks toward trout fry increased with increasing densities up to 8 and decreased at density 12 (Fig. 2). Interspecific aggression by trout fry toward sticklebacks was directly related to density (Fig. 2).

The only significant difference in intraspecific aggression between allopatric and sympatric populations occurred for sticklebacks at density 12. Intraspecific aggression was significantly higher than in allopatric population (Kruskal-Wallis and STP, $p \leq 0.05$).

In the field, we observed important interspecific aggression by sticklebacks toward trout fry, with a maximum peak at 18h00 (Kruskal-Wallis and STP, $p \leq 0.05$; Table 3 and Fig. 5).

If we compare the daily activity of sticklebacks and trout fry in sympatry in the field, we find that sticklebacks are active longer than trout fry (Fig. 6).

DISCUSSION

Seining in the Matamek River has shown that the two species occur in different places in June; sticklebacks are, on average, further offshore in areas of flooded grass while the trout fry are mostly in inshore areas.

Thus, differences in diet in early summer may be due to spatial separation rather than differences in dietary preference, suggesting a niche shift of trout fry caused by competition with sticklebacks.

In July and August, however, the trout fry have moved into the deeper offshore areas occupied by the sticklebacks. When this occurs there is greater overlap of diet between the two species.

In general, intraspecific aggression by trout fry increases with density in both allopatric and sympatric populations. Often there is a formation of a dominance hierarchy at "intermediate" or "high" densities because certain individuals start to form territories (Noakes 1978). Thus, intraspecific aggression observed in the stream tank may explain, in part, the dispersion of trout fry in the Matamek River about the middle of July suggested by Kalleberg (1958) and Mason (1976) for trout in other rivers.

For the sticklebacks, we observed decreasing aggression at density 12, except for the intraspecific aggression in allopatry. This decrease in stickleback aggression could be related to a break-down of territoriality at high densities similar to that observed by several other authors (e.g., Kawanabe 1969; Cole 1976). However, McNicoll (1979) did not observe the territorial break-down at high densities (20 fish/1.2 m²) in a brook trout population held in a laboratory stream tank.

In the field the high frequency of stickleback aggression toward trout fry is because sticklebacks are highly territorial.

In summary, there is intense aggression between nine-spine sticklebacks (Pungitius pungitius) and brook trout fry (Salvelinus fontinalis) in the stream tank and in the field at Matamek. Analysis of the diet of brook trout fry and nine-spine sticklebacks showed considerable overlap especially in July and August. These results show strong evidence of competition for food and space between these two species and suggest the need for a detailed study in the use of resources (habitat and diet) in the field.

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Table 1. Mean length (cm) $\pm$ one S.E. of brook trout fry and sticklebacks caught below the Fifth Falls of the Matamek River.

	N	MEAN	S.E.
TROUT FRY (June 20)	36	2.6	0.16
TROUT FRY (July 12)	32	3.4	0.35
TROUT FRY (August 7)	30	4.3	0.38
STICKLEBACKS (June 20)	22	4.6	0.05
STICKLEBACKS (July 12)	30	4.7	0.19
STICKLEBACKS (August 7)	30	5.1	0.39

Table 2. Particulars of each experiment completed at the stream tank at the 2nd falls of the Matamek River, 1982.

DENSITY (FISH/M ²)	DATE OF EXPERIMENT		T(°C)		NUMBER OF 5 MIN OBSERVATION PERIODS
	START	FINISH	MAX	MIN	
2	28 June 82	05 July 82	13°	10°	36
6	06 July 82	11 July 82	16°	14°	36
8	13 July 82	28 July 82	23°	16°	36
12	29 June 82	05 August 82	21°	14°	36

Table 3. Summary of interspecific aggression by nine-spine sticklebacks toward brook trout fry in the Matamek River (1982). Data are the total frequency of each behavior pattern.

Date	Number of 5 min. period	Approach	Charge	Chase	Nips	Lateral display
07 July 82	9	1	0	15	47	16
14 July 82	8	3	0	39	18	14
28 July 82	6	2	0	12	7	5

Fig. 1. Numerical composition (percent) of different food items in fish stomachs from Matamek River (1982); A, Chironomidae larvae; B, Chironomidae pupae; C, Chironomidae adults; D, Simuliidae, larvae; E, Simuliidae pupae; F, Simuliidae adult; G, Diptera; H, Trichoptera; I, cladocerans; J, others. Underlined letters indicate that the frequency at which a taxon was eaten is higher than if the taxon was randomly eaten (contingency table analysis). n, number of stomachs examined and di, diversity index (MacArthur 1972).

	<u>91</u>	<u>74</u>	<u>21</u>	0	1	2	28 July 82
	<u>41</u>	<u>31</u>	<u>21</u>	0	1	3	14 July 82
	<u>4</u>	<u>7</u>	<u>21</u>	0	2	3	28 July 82

trout fry

june

sticklebacks

july

august

FIG. 2. INTERSPECIFIC AGGRESSION, FROM MATAMEK STREAM TANK, 1982.

FIG. 3. INTRASPECIFIC AGGRESSION BY STICKLEBACKS, FROM MATAMEK STREAM TANK, 1982.

o significantly different (Kruskal-Wallis and STP, $p \leq .05$).

FIG. 4. INTRASPECIFIC AGGRESSION BY TROUT FRY, FROM MATAMEK
STREAM TANK, 1982.

FIG. 5. INTERSPECIFIC AGGRESSION BY STICKLEBACKS, IN MATAMEK RIVER, 1982. N=5

o significantly different (Kruskal-Wallis and STP, $p \leq .05$).

FIG. 6. RESTING BEHAVIOR, IN MATAMEK RIVER, 1982.

INTERACTIONS OF OUANANICHE (Salmo salar ouananiche) AND
BROOK CHARR (Salvelinus fontinalis) IN
LAC VICTOR, QUEBEC.

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The Landlocked salmon, or ouananiche, are widely distributed along Quebec's North Shore. Colonization by salmon of these northern lakes and rivers, once accessible from the coast, presumably followed the retreat of the ice sheets during the decline of the Pleistocene glaciation (Power 1958). Since that period "races" have evolved whose natural anadromous lifestyles have been replaced with lifelong residency in the freshwater environment. Faced with new demands, particularly increased competition from coexisting species, life history strategies have been modified. Through more efficient utilization of already limited resources, complex communities have developed in these northern ecosystems.

The object of this investigation is to better understand the interactions of ouananiche and brook charr in lac Victor. Since these two species are ecologically similar, one would expect to find, through competitive interactions, behavioral differences resulting in efficient allocation of the available food resources. This type of segregation, along with some more basic characteristics of these populations, are outlined in this preliminary report.

METHODS

Vertical distribution of ouananiche, brook charr and arctic charr (Salvelinus alpinus) were examined by setting gill nets (stretch mesh sizes ranging from 25 mm to 102 mm) at three different stations every two weeks, at depths of 0-2 m, 5-10 m, and 20-30 m. For the first two levels, the nets were set from the shore and extended out at right angles. Deep sets were executed at the bottom of the nearest basin.

For each specimen captured, fork length, fresh wet weight, sex, stage of gonad development of females, numbers of Diphyllbothrium sp. cysts on the stomachs, and morphological measurements were recorded. All stomachs were analysed immediately. Food items were identified to order and counted. To determine percent contribution to total volume by each taxa, mean volumes of individual belonging to each of the orders were determined and multiplied by the numbers found in each stomach.

For growth analysis, fish were aged by scales for ouananiche and otoliths for the charrs. Age determinations were repeated two to three times for each specimen. Where no consensus was reached between readings, scale or otolith data were discarded.

RESULTS AND DISCUSSION

The slow growth rates of ouananiche and brook charr in lac Victor are illustrated in Fig. 1 and 2. Although north temperate lakes are typically low in productivity, growth of lac Victor fish is surprisingly low presumably due to the added effect of unfavorable morphometry. The fact that ouananiche in Astray Lake (54° 34' north latitude, Power 1958) are considerably larger than in lac Victor, as are other more northerly populations, suggests that the expected latitudinal gradients in growth rates are masked by other factors. Although morphometry may indirectly account for much of this variation, restrictions caused by competitive interactions merits further investigation as a possible contributor to these major differences.

A distinct difference in growth rate of brook charr exists between lac Victor and neighboring lac Chavary, a deep oligotrophic lake within the same watershed. Unlike the former, lac Chavary has no resident ouananiche or forage fish populations. Superior growth rates of lac Chavary brook charr suggests that interspecific interactions in lac Victor have reduced the availability of prey items to each species. While the greater number of species in lac Victor may have resulted in resources being more efficiently utilized, relative availability appears to be reduced.

Figure 3 shows how the mean condition factor of ouananiche decreases with age. It appears there is a relationship between degree of infestation by Diphyllbothrium sp. and condition of the fish. As the ouananiche move out of the river into the lake, consumption of fish increases and, consequently, parasites accumulate through ingestion. After age 5+, the mean condition factor remains below 0.9. The poor condition of older fish may be the result of higher exploitation of parasite infested intermediate hosts. Sexual differences in condition factor could be indicative of the additional burden of egg production in females.

Preliminary analysis of data from experimental gill nets (Fig. 3) suggests that there is no significant difference in the vertical distribution of ouananiche and brook charr in lac Victor. This apparent lack of distinct segregation within the water column implies that although food use may be segregated to some degree, both species maintain a degree of plasticity and feed opportunistically. Consequently, these fish cannot afford to adopt a strict spatial regime.

Stomach content analyses (Figs. 5 and 6) illustrate the basic trends of food resource partitioning between ouananiche and brook charr. River dwelling brook charr, consisting of mostly 0+ to 3+ fish, appear to be largely planktivorous. During night sampling, large numbers were observed facing into the current of the rivers connecting lac Victor to neighboring lakes, filtering out plankton (mostly Daphnia) being carried by the current. This type of behavior demonstrates the brook charr's ability to efficiently utilize readily available resources. Ouananiche parr are also partly planktivorous but to a lesser extent than coexisting brook charr.

The former ingest a larger volume of insect larvae. Forage fish, consisting of rainbow smelt (Osmerus mordax) and three spined sticklebacks (Gasterosteus aculeatus) constitute a large proportion of total ingested food volume by adult ouananiche. However, a wide range of food items have a relatively high percentage frequency-of-occurrence in their stomachs. Forage fish are evidently the major food item of the adult ouananiche while insects are an important secondary food resource. The adult lake dwelling brook charr are clearly generalists. As Behnke (1980) and Power (1980) have suggested, of all charrs, brook charr are probably the most generalized and adaptable. Coexistence with what appears to be a superior competitor in an unproductive lake, where food availability is unpredictable, has forced brook charr to maintain a wide niche to accommodate its resource demands. The apparent increase in the consumption of mayfly larvae in August by both adult ouananiche and brook charr, supports Keast's (1965) observations that the largest overlap in food consumption occurs during peak abundance of prey items. This again points to opportunistic behavior which these species have adopted to ensure continuing success.

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Table 1. Pooled Data for Vertical Distribution of Ouananiche and Brook Charr.

Depth	Ouananiche (N)	Brook Charr (N)
0- 3 m	76	149
5-10 m	16	30
HETEROGENEITY CHI-SQUARED TEST		
CRITICAL VALUE AT = 0.05		G = 1.197
HOMOGENEITY OF DIFFERENT SAMPLING DATES		G = 7.815
POOLED DATA		(0.75 < p < 0.90)
CRITICAL VALUE		G = 3.814
SPECIES INDEPENDENCE TO DEPTH		(0.95 < p < 0.975)

FIGURE CAPTIONS

- Figure 1. Study Site. Stations 1 to 3 indicated by arrows.
- Figure 2. Growth of ouananiche in lac Victor and Astray Lake. Fork length (cm) is related to age in years.
- Figure 3. Growth and brook charr in lac Victor and lac Chavary. Fork length (cm) is related to age in years.
- Figure 4. Condition factor and degree of infestation by Diphylobothrium sp. of ouananiche in lac Victor. Number of cysts on the stomachs of individuals were counted.
- Figure 5. Volume composition (percent) of different food items in fish stomachs from lac Victor. A. zooplankton (mostly Daphnia); B. Diptera larvae and adults; C. Hymenoptera adults; D. Megaloptera larvae; E. Ephemeroptera larvae and adults; F. Odonate larvae; G. Trichoptera larvae; H. Plecoptera larvae and adults; I. Lepidoptera adults; J. insect remains; K. sticklebacks; L. smelt; M. fish remains; N. Coleoptera adults; O. mammal remains.
- Figure 6. Frequency of occurrence of different food items in fish stomachs from lac Victor. Codes same as in Figure 5.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Figure 5

SEASONAL DYNAMICS OF SCHISTOCEPHALUS SOLIDUS IN THE
THREESPINE STICKLEBACK GASTEROSTEUS ACULEATUS OF MATAMEK LAKE.
PRELIMINARY RESULTS

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INTRODUCTION

One of the most striking characteristics of infections of Schistocephalus solidus in the threespine stickleback is the large size frequently attained by the plerocercoids. In multiple infections the total parasite biomass may approach that of the host. In the U.K., dead sticklebacks collected from the edges of a pond were found to have a higher parasite index for Schistocephalus, that is, a greater parasite biomass relative to host biomass, than live infected fish (Pennycuik 1971a). This suggests that a certain level of infection may cause host mortality. It is apparent that the abdominal distension of heavily infected fish severely impairs their swimming ability. In situations where sticklebacks are predated, selective predation of heavily infected fish is likely, the net effect on the parasite population depending on whether or not the predator is a suitable definitive host.

Thus, via parasite-induced host mortality and increased host susceptibility to predation, the parasites play a role in regulating both the host and parasite populations. There is also potential for the operation of regulatory mechanisms at the infrapopulation level. The so-called "crowding effect" has been reported for several parasite species when parasite intensity levels are high. As the parasite intensity increases the constraints operating on worm growth increase in severity, resulting in a smaller mean worm size.

METHODS

Samples of approximately 200 sticklebacks were collected twice monthly, using seine nets, at the North Camp of Matamek Lake, from June to September 1982. These samples, together with those collected similarly during the ice-free season in 1981, provide a data base of almost 3,000 fish. The fish, stored in 70% alcohol, were analysed for fish length, sex and dry weight and parasite number and dry weights.

At this point the data from samples collected between July and September 1982 is still being analysed, however, some of the findings from July 1981 to June 1982 are presented.

RESULTS AND DISCUSSION

From the frequency distribution of fish lengths for uninfected fish (Fig. 1) it can be seen that few sticklebacks, if any, complete a second year of life. This is in accordance with results from a study done by Coad (1972) who used otoliths to determine the age of threespine sticklebacks from the same location. Although the number of uninfected fish was small, we can follow the growth of the age classes through time. The co-existence of 0+ and 1+ age classes is best depicted by the two distinct cohorts shown in June 1982. Thus, the situation at Matamek Lake is different to that found in the U.K. where the hosts and parasites are reported to live for three years (Pennycuik 1971b). The mean parasite intensity, prevalence (percentage of infected fish) and the degree of dispersion of the parasites within the host population varies seasonally (see Fig. 2). The percentage of infected fish increases from approximately 76% in July 1981 to almost 100% in September. This suggests that parasite acquisition is occurring; however, the mean worm intensity remains fairly constant throughout the period. Thus, parasite acquisition must be balanced by the loss of parasites from the population. It is possible that selective predation by birds is high at this time as heavily infected fish are known to swim very close to the water surface during the warm months as the oxygen level is depleted (Lester 1972).

The degree of dispersion decreases in the fall and then drops dramatically over the winter. Also the prevalence drops from 100% in late August to approximately 6% after the winter. Both these phenomena constitute indirect evidence for parasite-induced host mortality, in the form of the death of more heavily infected hosts over the winter.

It is obvious that such heavy parasite burdens make great physiological demands on the host. The results shown in Fig. 3 illustrate that both fish weight and length decrease as the number of worms per fish increases. These data were taken from the September 1981 sample, which contained the highest number of fish. Although there were no uninfected fish in the September sample, an analysis of the July 1981 sample indicates that even the presence of a single parasite significantly reduces the mean weight and length of the host (Fig. 4).

With respect to the question as to whether any in situ constraints operate on worm growth, it can be seen in Fig. 5c that the mean worm weight decreases considerably with an increase in the number of worms per fish. Thus, we have evidence for the occurrence of density dependent growth. It is difficult to determine whether this results from some host response, that is immunity, or intraspecific competition between parasites for host limiting factors. The relationship between total worm biomass and worm intensity (Fig. 5a) illustrates that at first total worm biomass increases with increasing intensity of infection and then it levels off. To be sure that this relationship was not simply a reflection of variable fish size the relationship between parasite index and parasite intensity was determined (Fig. 5b). The same pattern emerges. Thus, it seems that

there is some limiting factor which becomes "fully operational" once parasite intensity has reached a certain level.

SUMMARY

Preliminary analysis of samples of the threespine stickleback infected with Schistocephalus solidus, taken from Matamek Lake between July 1981 and June 1982, has produced the following results:

1. Very few sticklebacks complete a second year of life, in contrast to the situation in the U.K.
2. Seasonal changes in parasite dispersion and prevalence provide indirect evidence for the occurrence of parasite-induced host mortality over the winter.
3. Infection by Schistocephalus impairs the growth of the host sticklebacks such that mean length and mean weight of infected fish are significantly lower than for uninfected fish.
4. Indirect evidence for the occurrence of density-dependent growth of the parasites is presented. A more detailed analysis in this direction may provide insight into the mechanics involved in the regulation of both host and parasite populations.

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I should like to thank all of those at Matamek Research Station whose cooperation vastly facilitated the setting up and carrying out of my field work. Special thanks are extended to Alan McNeill who collected the majority of the 1982 samples whilst working under a very tight schedule at the station.

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FIGURE CAPTIONS

Fig. 1. Frequency distributions of fish lengths for uninfected sticklebacks, July 1981 - June 1982.

Fig. 2. Frequency distributions of Schistocephalus solidus, July 1981 - June 1982.

n = number of fish examined.

x = mean number of parasites per fish.

Fig. 3. The relationships between parasite intensity and a) fish weight, b) fish length.

Fig. 4. The relationships between infection by Schistocephalus and the weight and length of the fish host.

Fig. 5. a) The relationship between total worm biomass and the number of worms per fish.

b) The relationship between parasite index and the number of worms per fish.

c) The relationship between mean worm weight (mg) and the number of worms per fish.

Fig 1

FREQUENCY DISTRIBUTIONS OF FISH LENGTHS
(uninfected fish)

Fig 2

Fig 5

RIVER ECOSYSTEM STUDIES

ENVIRONMENTAL MONITORING PROGRAM

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In 1982 data were routinely collected on stream water chemistry, precipitation, chemistry, discharge, and water temperatures. These are presented in the following tables and figures without comment. Methods of collection and analysis can be found in the annual reports for 1979 and 1980.

RAIN GAUGE: MATAMEK

RAIN GAUGE: MATAMEK

1982

1982

Table 1. Water Chemistry (mg. L⁻¹) Analyses for the Major Sampling Locations.

Date	NH ₄	NO ₃	NO ₂	Tot - N	PO ₄	Tot - P	Si
FIRST CHOICE CREEK							
12 May 82	.060	.095	.0010	.328	.156	.170	1.220
18 May 82	.066	.056	.0007	.207	.150	.161	1.051
25 May 82	.039	.134	.0007	.328	.113	.119	.528
1 Jun 82	.014	.097	.0010	.225	.041	.048	.437
8 Jun 82	.012	.082	.0004	.171	.031	.033	1.140
15 Jun 82	.020	.065	.0007	.132	.047	.052	.643
22 Jun 82	.028	.046	.0010	.229	.079	.090	.358
29 Jun 82	.024	.008	.0007	1.714	.073	.076	.750
6 Jul 82	.035	.030	.0009	.235	.129	.133	.502
20 Jul 82	.020	.011	.0009	.140	.071	.082	.350
3 Aug 82	.010	.018	.0016	.126	.007	.018	.083
17 Aug 82	.017	.011	<.0001	.258	.009	.013	.024
31 Aug 82	.005	.017	.0008	.150	.006	.008	1.426
7 Sep 82	.005	.011	.0008	.108	.004	.008	1.116
14 Sep 82	.008	.033	<.0001	.087	.004	.007	.498
20 Sep 82	.006	.006	.0002	.260	.003	.012	1.162
27 Sep 82	.004	.007	.0001	.040	.001	.008	.496
4 Oct 82	.004	.006	.0005	.130	.008	.042	.756
11 Oct 82	.001	.008	.0006	.052	.007	.011	.627
18 Oct 82	.014	.009	.0007	.860	.007	.016	.596
6 Nov 82	.002	.013	.0005	.161	.010	.026	.487
BEAVER CREEK RIFFLE							
18 May 82	.037	.012	.0008	.340	.095	.116	.042
25 May 82	.021	.008	.0007	.278	.063	.075	.106
1 Jun 82	.028	.013	<.0001	.415	.128	.134	.059
8 Jun 82	.019	.008	.0011	.303	.074	.084	.132
15 Jun 82	.044	.050	.0009	.351	.114	.140	.161
22 Jun 82	.022	.007	.0011	.315	.079	.092	.127
29 Jun 82	.027	.016	.0010	.334	.095	.112	.143
6 Jul 82	.077	.032	.0004	.822	.372	.416	.014
20 Jul 82	.124	.058	.0006	.702	.379	.401	.236
3 Aug 82	.035	.147	.0003	.648	.004	.012	.130
17 Aug 82	.022	.105	<.0001	.605	.008	.008	.017
31 Aug 82	.016	.073	.0024	.560	.002	.010	.089
7 Sep 82	.008	.102	.0011	.468	.002	.006	.044
14 Sep 82	.029	.237	.0009	.739	.008	.012	.126
20 Sep 82	.003	.009	.0005	.337	.002	.007	.113
27 Sep 82	.006	.021	.0005	.426	.002	.009	.230
4 Oct 82	.007	.014	.0003	.288	.0007	.010	.169
11 Oct 82	.003	.050	.0006	.230	.003	.011	.280
18 Oct 82	.003	.006	.0007	.297	.004	.011	.100
6 Nov 82	.005	.007	.0005	.411	.006	.016	.062

Table 1. (cont).

Date	NH ₄	NO ₃	NO ₂	Tot - N	PO ₄	Tot - P	Si
BEAVER CREEK DAM							
12 May 82	.076	.022	.0007	.505	.171	.191	.098
18 May 82	.065	.013	.0009	.374	.141	.171	.091
25 May 82	.030	.009	.0008	.293	.081	.095	.111
1 Jun 82	.015	.009	.0008	.346	.007	.077	.034
8 Jun 82	.018	.009	<.0001	.301	.085	.093	.098
15 Jun 82	.050	.027	.0007	.370	.168	.193	.275
22 Jun 82	.026	.008	.0008	.332	.096	.108	.107
29 Jun 82	.049	.088	.0004	.338	.137	.174	.017
6 Jul 82	.072	.067	.0003	.525	.282	.357	.784
20 Jul 82	.090	.044	.0013	.689	.335	.386	.355
3 Aug 82	.031	.133	.0010	.605	.002	.005	.305
17 Aug 82	.019	.112	.0006	.672	.004	.011	.155
31 Aug 82	.016	.027	.0002	.586	.001	.005	.132
7 Sep 82	.015	.045	.0010	.503	.002	.007	.055
14 Sep 82	.026	.170	.0012	.633	.005	.007	.011
20 Sep 82	.005	.011	.0012	.037	.002	.010	.055
27 Sep 82	.011	.002	.0010	.386	.002	.010	.258
4 Oct 82	.010	.013	.0001	.259	.0004	.008	.496
11 Oct 82	.004	.011	.0006	.304	.002	.008	.353
18 Oct 82	.003	.007	<.0001	.423	.005	.016	.031
MUSKRAT RIVER							
12 May 82	.081	.043	.0003	.505	.064	.076	.215
18 May 82	.058	.025	.0006	.290	.146	.161	.028
25 May 82	.013	.020	.0006	.279	.040	.048	.021
1 Jun 82	.035	.018	.0008	.414	.138	.162	.021
8 Jun 82	.016	.021	.0003	.244	.044	.054	.036
15 Jun 82	.073	.022	.0005	.345	.190	.214	.067
22 Jun 82	.041	.008	.0007	.284	.113	.128	.041
29 Jun 82	.017	.012	.0007	.267	.069	.079	.083
6 Jul 82	.034	.039	0	.311	.126	.165	.027
20 Jul 82	.093	.052	0	.519	.338	.406	.041
3 Aug 82	.018	.099	.0008	.514	.003	.006	.035
17 Aug 82	.007	.024	0	.319	.005	.005	.017
31 Aug 82	.007	.041	0	.403	.003	.004	.031
7 Sep 82	.005	.050	0	.347	.001	.004	.064
14 Sep 82	.007	.045	.0003	.362	.007	.008	.042
20 Sep 82	.002	.006	.0005	.279	.002	.007	.023
27 Sep 82	.008	.010	.0008	.410	.003	.012	.070
4 Oct 82	.003	.005	.0002	.174	.0004	.007	.039
11 Oct 82	.001	.006	.0003	.323	.002	.006	.080
18 Oct 82	.008	.020	.0004	.231	.001	.007	.015
5 Nov 82	.004	.024	<.0001	.486	.004	.027	.061
10 Dec 82	.022	.039	.0008	.273	.004	.010	.075

Table 1. (cont).

Date	NH ₄	NO ₃	NO ₂	Tot - N	PO ₄	Tot - P	Si
MATAMEK RIVER							
12 May 82	.035	.050	.0007	.352	.058	.067	.055
18 May 82	.059	.047	.0020	.370	.117	.132	.024
25 May 82	.032	.039	.0003	.259	.059	.069	.038
1 Jun 82	.029	.040	.0008	.267	.052	.061	.065
8 Jun 82	.039	.028	.0007	.275	.084	.098	.054
15 Jun 82	.023	.022	<.0001	.295	.096	.097	.019
22 Jun 82	.017	.026	.0007	.224	.047	.055	.059
29 Jun 82	.025	.026	.0006	.276	.063	.066	.012
6 Jul 82	.027	.017	.0007	.286	.101	.108	.033
20 Jul 82	.029	.012	.0008	.283	.099	.106	.033
3 Aug 82	.011	.027	.0003	.301	.002	.004	.023
17 Aug 82	.020	.039	.0012	.348	.002	.002	.008
31 Aug 82	.010	.027	0	.311	.001	.003	.027
7 Sep 82	.010	.020	.0001	.332	.002	.004	.033
14 Sep 82	.007	.034	0	.230	0	.004	.027
20 Sep 82	.002	.008	.0003	.232	.003	.007	.024
27 Sep 82	.003	.090	.0003	.179	.002	.004	.018
4 Oct 82	.002	.010	<.0001	.183	.003	.006	.019
11 Oct 82	.001	.012	.0003	.186	.003	.007	.011
5 Nov 82	.007	.028	<.0001	.357	.004	.016	.031
10 Dec 82	.011	.035	.0003	.199	.001	.004	.044
MOISIE RIVER							
12 May 82	.111	.059	.0007	.654	.274	.303	.082
18 May 82	.050	.051	.0010	.370	.127	.157	.222
25 May 82	.030	.051	.0019	.273	.079	.091	.199
1 Jun 82	.046	.040	.0012	.358	.144	.157	.110
8 Jun 82	.029	.032	.0006	.311	.098	.112	.104
15 Jun 82	.021	.056	.0010	.245	.051	.057	.340
22 Jun 82	.056	.033	.0017	.306	.125	.142	.209
29 Jun 82	.023	.051	.0006	.314	.066	.070	.235
6 Jul 82	.033	.034	.0006	.454	.113	.118	.271
20 Jul 82	.018	.032	.0007	.339	.092	.106	.369
3 Aug 82	.009	.027	.0005	.183	.003	.006	.815
17 Aug 82	.010	.047	.0020	.249	.007	.009	.414
31 Aug 82	.010	.089	.0004	.358	.001	.004	.386
7 Sep 82	.007	.018	.0002	.238	.001	.002	.121
14 Sep 82	.010	.014	.0003	.235	.001	.002	.160
20 Sep 82	.018	.039	.0003	.356	.001	.006	.216
27 Sep 82	.017	.038	.0008	.339	.001	.010	.437
1 Oct 82	.034	.041	.0005	.230	.001	.006	.358
4 Oct 82	.006	.041	.0004	.157	.0004	.005	.233
11 Oct 82	.009	.046	.0005	.181	.002	.004	.035
4 Nov 82	.003	.050	.0007	.230	.004	.014	.074

Table 1. (cont).

Date	NH ₄	NO ₃	NO ₂	Tot - N	PO ₄	Tot - P	Si
RAIN GAUGE							
1 Jun 82	.023	.022	.0012	.295	.126	.151	.003
3 Jun 82	.079	.178	.0006	.560	.109	.110	.004
17 Jun 82	.088	.069	.0007	.322	.089	.089	.056
19 Jun 82	-	.183	-	1.828	-	-	-
23 Jun 82	.052	.047	.0004	.200	.082	.088	.001
25 Jun 82	.056	.240	.0004	.475	.161	.170	.001
1 Jul 82	.040	.066	.0006	.227	.011	.117	.002
6 Jul 82	.187	-	-	.672	-	-	-
16 Jul 82	.251	.034	-	.973	.103	.132	.010
19 Jul 82	.295	.211	.004	.794	-	.114	.008
20 Jul 82	.449	.134	-	1.313	-	-	-
29 Jul 82	.118	.178	.0005	.532	.190	.250	.008
11 Aug 82	.125	.134	.0005	.343	.012	.016	.005
16 Aug 82	.009	.086	.0005	.197	.005	.004	.003
20 Aug 82	.153	.147	.0004	.559	.006	.011	.005
27 Aug 82	.225	.414	.0017	.882	.006	.011	.005
28 Aug 82	.225	.287	.0006	.615	.007	.007	.005
31 Aug 82	.081	.126	-	.453	.013	.019	.005

ALLOCHTHONOUS INPUTS TO THE MATAMEK RIVER WATERSHED, QUEBEC:
THE INFLUENCE OF STREAM SIZE

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ABSTRACT

The composition, seasonal pattern, and ash-free dry mass (AFDM) of particulate allochthonous input were studied on four streams of a pristine boreal watershed in eastern Quebec, Canada, from May 1980 to May 1982. Results were analyzed both for local descriptions of allochthonous input and for watershed trends in input characteristics. Annual litterfall per unit area of stream surface declined exponentially with increasing stream order ($r^2 = 0.98$), from 307-534 g AFDM $m^{-2} yr^{-1}$ in a first order stream to 15-17 g AFDM $m^{-2} yr^{-1}$ in a sixth order stream. Lateral input ranged from 25 to 70 g AFDM $m^{-1} yr^{-1}$ and showed no trend with stream order. Combined direct and lateral input per unit stream length increased logarithmically with increasing order ($r^2 = 0.87$), approaching an asymptotic value of 1000 g AFDM $m^{-1} yr^{-1}$. The proportional contribution of lateral input to total combined input was 41-54% in the first-order stream, but decreased with increasing stream order. When input-stream order relationships were extrapolated to the watershed scale it was estimated that streams in the 673 km^2 watershed received 729 mt/yr of particulate organic matter.

Direct litterfall to fifth and sixth order stream sites was measured near the shorelines and at several positions across the stream channel. Inputs showed high spatial variability, but 45-70% of the variation observed could be explained by an exponential decline in litterfall with increasing distance from shore. The parameters of the regression equations were site-specific.

The composition of litterfall at the study sites varied according to riparian vegetational structure. Although the forest in the watershed is dominated by conifers, deciduous leaves made up the largest fraction (46-60%) of terrestrial litterfall. Autumn leaf fall dominated the seasonal pattern of allochthonous input to the study sites; 44-80% of annual inputs for each year occurred between September 1 and November 1. Lateral input of material entrained by spring flooding was important at two sites.

Results of this and concurrent studies on these streams support some generalizations of the River Continuum Concept. When particulate allochthonous input is compared with periphyton and macrophyte production, 81-95% of the carbon supplied to the first and second order study sites is allochthonous, but 85-95% of the supply to the fifth and sixth order streams is autochthonous.

REFERENCE

- Conners, M. E. 1983. Allochthonous Inputs to the Matamek River Watershed, Québec: The Influence of Stream Size. M.S. Thesis. Massachusetts Institute of Technology, Cambridge, 73 p.

FIGURE LEGENDS

- Fig. 1 Location of study sites and trap placement. The Matamek Research Station is in southeastern Quebec, Canada, on the North Shore of the Gulf of St. Lawrence (50°10' N 65°00' W).
- Fig. 2 Sketch of lateral input samplers. Sides and retaining lip are of 5 mm mesh galvanized screening, endpieces are wood.
- Fig. 3 Allochthonous input to the litter traps at the terrestrial and small stream sites, $\text{g AFDM m}^{-2} \text{ d}^{-1}$. Each histogram cell represents one sampling interval: width indicates span of the interval, height indicates mean input from 10 replicate traps. Bars show standard errors of the mean.
- Fig. 4 Allochthonous input to the Muskrat and Matamek River array traps, $\text{g AFDM m}^{-2} \text{ d}^{-1}$. Each histogram cell represents one sampling interval: width indicates span of the interval, height indicates mean input from traps with the same number on 5 replicate transects (see Fig. 1, text). Bars show standard errors of the mean.
- Fig. 5 Allochthonous input to the lateral traps, $\text{g AFDM m}^{-1} \text{ d}^{-1}$. Each histogram cell represents one sampling interval: width indicates span of the interval, height indicates mean input from 6-10 replicate traps. Bars show standard errors of the mean.
- Fig. 6 Allochthonous input to the Muskrat River as a function of distance from shore. Annual litterfall to each array trap ($\text{g AFDM m}^{-2} \text{ yr}^{-1}$) is plotted against distance (m) from the trap to the nearest shore. The exponential regressions are drawn for each year:
- for 1980-81, $y = 190 e^{-0.459 \times} \quad r^2 = 0.71$
- for 1981-82, $y = 164 e^{-0.506 \times} \quad r^2 = 0.73$
- Fig. 7 Allochthonous input to the Matamek River as a function of distance from shore. Annual litterfall to each array trap ($\text{g AFDM m}^{-2} \text{ yr}^{-1}$) is plotted against distance (m) from the trap to the nearest shore. The exponential regressions are drawn for each year:
- for 1980-81, $y = 46.6 e^{-0.113 \times} \quad r^2 = 0.46$
- for 1981-82, $y = 43.4 e^{-0.089 \times} \quad r^2 = 0.65$

Fig. 8 Annual litter input (direct fall), g AFDM m⁻² yr⁻¹, vs. stream order for First Choice Creek, Beaver Creek (Closed Canopy site), the Muskrat River, and the Matamek River. The dashed lines indicate exponential regressions for data points from the individual years:

$$\text{for } 1980-81, \quad y = 1191 e^{-0.713 \times r^2} \quad r^2 = 0.99$$

$$\text{for } 1981-82, \quad y = 616 e^{-0.598 \times r^2} \quad r^2 = 0.99$$

The solid line indicates the regression using data from both years:

$$y = 856 e^{-0.598 \times r^2} \quad r^2 = 0.98$$

For each year, the annual litter input at the Beaver Creek Open Canopy site falls along the curve at approximately third order.

Fig. 2

ALLOCHTHONOUS INPUT - LITTER TRAPS

MAY 1980 TO MAY 1982

ALLOCHTHONOUS INPUT - ARRAY TRAPS

MAY 1980 TO NOVEMBER 1981

ALLOCHTHONOUS INPUT - LATERAL TRAPS

MAY 1980 TO MAY 1982

MUSKRAT RIVER

MATAMEK RIVER

Table 1. Physical and chemical characterization of the study sites (modified from Naiman 1982a, 1983).

Parameter	First Choice Creek	Beaver Creek	Muskrat River	Matamek River
Stream Order	1	2	5	6
Watershed Area (km ²)	0.25	1.83	207	673
Mean Width (m)	0.3	2.0	21.9	51.7
Mean Depth (m)	0.05	0.3	2.0	1.8
Mean Annual Discharge (m ³ /s)	0.013	0.033	8.4	13.7
Gradient (%; lower reaches)	1.5	1.0	0.14	1.33
Substrate	Detritus	Sediment/ cobble	Sediment/ cobble	Gravel/ cobble
Temperature Range (°C)	0.4–11.0	0.0–19.0	0.0–19.5	0.1–19.8
Annual Degree Days(°C/yr)	1702	2069	2157	2225
Nutrient Range (µg/L)				
NO ₃ -N	17–199	5–135	3–91	1–76
Total N	49–234	211–623	170–382	148–341
PO ₄ -P	2–8	1–7	1–5	1–17
Total P	7–29	6–26	6–22	5–16
Light Range (µEx10 ⁵ m ⁻² d ⁻¹)	7–24	20–56	77–330	47–339
Alkalinity Range (meq/L)	0.097–0.253	0.039–0.368	0.0–0.085	0.0–0.076
pH Range	6.2–7.2	6.0–7.0	4.9–6.1	4.8–6.0
Mean Dissolved Organic Carbon (mg C/L)	4.1	12.9	12.3	11.3
Forest Canopy Development	Closed	Mostly closed	Mostly open	Open
Benthic Organic Matter (g AFDM/m ²)	712	526	516	252

Table 2. Percent organic content of major litter fractions (ash-free dry mass/dry mass) as determined in July-September 1980. Values in parentheses were used for categories not measured directly.

Species	Type of Litter				
	leaves	wood	needles	bark	catkins
Alder	95.4	98.0	----	(95.0)	94.8
Birch	96.8	(95.4)	----	(95.0)	(94.8)
Aspen	95.2	96.4	----	(95.0)	(94.8)
Spruce	----	96.4	(91.9)	(95.0)	----
Fir	----	99.2	(91.9)	(95.0)	----
Miscellaneous	94.2	92.7	91.9	95.0	

Overall average (used for any other litter types)-----95.4

Table 3: Composition of allochthonous inputs on an annual basis. Inputs are divided into hardwood leaves, twigs and woody debris, conifer needles and cones, and hardwood seeds and catkins. The "other" category includes unidentified leaves, bark, and herbaceous litter.

Site	Study Year	Annual Input (g AFDM m ⁻² yr ⁻¹)	Percent of Annual Input				Percent of Leaf Input			
			Leaves	Wood	Needles	Catkins	Other	Birch	Alder	Aspen
<u>Terrestrial Sites</u>										
First Choice Creek	1980-81	327	58	15	26	2	1	85	4	11
	1981-82	229	51	13	23	6	7	75	3	22
Beaver Creek	1980-81	280	60	11	26	1	2	92	5	3
	1981-82	255	46	13	28	5	8	91	2	6
<u>Stream Sites</u>										
First Choice Creek Litter Traps	1980-81	534	46	33	18	2	1	79	2	17
	1981-82	307	52	19	13	5	11	71	1	29
Lateral Traps	1980-81	53	67	13	4	1	14	83	1	16
	1981-82	51	77	13	5	1	5	78	1	21
Beaver Creek Closed Canopy Litter Traps	1980-81	312	84	8	5	1	1	36	55	9
	1981-82	212	67	9	4	4	15	49	39	11
Lateral Traps	1980-81	53	56	30	1	1	10	68	22	8
	1981-82	55	83	8	2	1	5	72	16	11
Open Canopy Litter Traps	1980-81	120	79	9	5	1	6	47	47	3
	1981-82	103	73	5	2	3	16	42	52	5
Lateral Traps	1980-81	30	24	32	3	1	41	47	48	5
	1981-82	26	66	16	1	1	16	46	33	18

Table 3 continued.

Muskrat River

Litter Traps
Trap 1

1980-81	142	27	27	42	4	1	2	97	0
1981-82	139	27	27	24	1	22	7	91	2

Trap 2

1980-81	8	7	59	29	2	4	0	100	0
1981-82	8	0	71	21	4	3	--	--	--

Trap 3

1980-81	10	78	2	14	2	4	35	64	1
1981-82	3	9	24	33	12	22	0	46	54

Trap 4

1980-81	160	41	40	14	4	1	4	96	0
1981-82	106	56	14	19	1	11	3	52	1

Lateral Traps

1980-81	38	23	25	12	1	40	22	76	1
1981-82	25	43	23	6	1	26	7	85	5

Matamek River

Litter Traps
Trap 1

1980-81	49	58	5	34	2	1	29	28	1
1981-82	43	61	1	16	6	15	61	28	4

Trap 2

1980-81	4	22	11	16	1	50	38	37	25
1981-82	22	58	1	15	3	24	34	65	1

Trap 3

1980-81	2	89	0	4	0	7	9	91	0
1981-82	2	34	1	14	3	48	100	0	0

Trap 4

1980-81	2	5	1	43	45	6	21	78	0
1981-82	4	16	1	26	39	18	33	38	23

Trap 5

1980-81	99	37	15	40	6	1	29	66	1
1981-82	49	46	4	23	16	11	52	46	1

Lateral Traps

1980-81	70	27	36	5	0	32	53	45	1
1981-82	46	63	14	10	1	11	43	52	4

Table 4. Allochthonous inputs from 1 September to 1 November, expressed as the percentage of annual input for each year.

Site	Year	Percentage of the Annual Total 1 September - 1 November		
		Litter Traps	Lateral Traps	Total Income*
<u>Terrestrial Sites</u>				
First Choice Creek	1980	74.0		
	1981	67.2		
Beaver Creek	1980	64.3		
	1981	58.8		
<u>Stream Sites</u>				
First Choice Creek	1980	74.3	56.6	67.1
	1981	67.4	72.5	70.1
Beaver Creek Closed Canopy	1980	78.2	49.0	73.6
	1981	63.7	72.7	65.7
Open Canopy	1980	73.3	18.3	64.8
	1981	81.6	69.2	79.6
Muskrat River	1980	43.1	52.6	44.0
	1981	49.4	48.0	49.3
Matamek River	1980	69.4	7.1	57.9
	1981	55.0	63.0	55.9

*Calculated combined income per meter of stream length (see Table 5, text).

Table 5. Annual allochthonous inputs to the study sites. Standard errors of the estimates are in parentheses. The litter inputs for the Muskrat River and Matamek River are estimates from the regressions in Figures 6 and 7. See text for explanation of shore/stream ratios and total input calculations.

Site	Study Year	Litter Traps (g AFDM/m ²)	Lateral Traps (g AFDM/m)	Mean Width (m)	Shore Stream	Total Input (g AFDM/m)	Percent of Total as Lateral Input
<u>Terrestrial sites</u>							
First Chioce Creek	1980-81	327 (33)					
	1981-82	229 (19)					
Beaver Creek	1980-81	280 (15)					
	1981-82	255 (6)					
<u>Stream sites</u>							
First Choice Creek	1980-81	534 (83)	53 (10)	0.3	2.11	272	41.1
	1981-82	307 (31)	51 (4)			200	53.9
Beaver Creek Closed Canopy	1980-81	312 (19)	53 (16)	2.0	2.20	741	15.7
	1981-82	212 (26)	55 (10)			545	22.2
Open Canopy	1980-81	120 (17)	30 (16)	3.4	2.26	476	14.2
	1981-82	103 (36)	26 (6)			409	14.4
Muskrat River	1980-81	37	38 (12)	21.9	2.10	890	9.0
	1981-82	30	25 (6)			709	7.4
Matamek River	1980-81	15	70 (41)	51.7	2.32	938	17.3
	1981-82	17	46 (5)			986	10.8

Table 6. Particulate allochthonous loading to the Matamek River watershed. See text for calculation methods. Geomorphological data are from Naiman (1980, 1983).

Stream Order	Watershed Composition		Allochthonous Income	
	Total Length (km)	Percent of Total Length	Loading (10^3 kg AFDM)	Percent of Total Mass
1	726	50.5	165.2	22.7
2	322	22.4	179.8	24.7
3	176	12.2	159.3	21.9
4	92	6.4	98.4	13.5
5	95	6.6	100.7	13.8
6	26	1.8	25.4	3.5
Total	1437		728.6	

Table 7. Annual litterfall as reported in this study and in the literature.

Location	Stream Order	Litter Input (g m ⁻² yr ⁻¹)	Reference
New Hampshire	Terrestrial	570	Gosz et al. (1972)
Illinois		520-629	Bell et al. (1982)
Ontario		450-818	Merriam et al. (1982)
New Brunswick		152-197	MacLean and Wein (1978)
Quebec		229-327!	This Study
Denmark	1	655!	Iversen et al. (1982)
North Carolina		353	Webster (1977)
North Carolina		319	Webster (1977)
North Carolina		285	Webster (1977)
Quebec		307-534!	This Study
New Hampshire	2	578!	Fisher and Likens (1973)
Massachusetts		274*	McDowell and Fisher (1976)
Mississippi		400	de la Cruz and Post (1977)
North Carolina		273	Webster (1977)
Quebec		212-312!	This Study
Mississippi	3	386	Post and de la Cruz (1977)
North Carolina		572-638	Mulholland (1981)
Quebec		103-120!	This Study
Massachusetts	4	384	Fisher (1977)
Quebec	5	30-37!	This Study
Quebec	6	15-17!	This Study
Thames R, England		18-28	Matthews and Kowalczewski (1969)

!Input is in g AFDW, all others are in dry weight.

*Includes only autumnal input.

**From the Beaver Creek Open Canopy site, see discussion on litter input vs. stream order.

Table 8. Allochthonous input vs. autochthonous production. The average of annual particulate allochthonous inputs from the two years of this study is compared to estimates of primary production from Naiman (1982a). Original units are converted to grams carbon according to de la Cruz and Post (1977):

$$1 \text{ g O}_2 = 0.375 \text{ g C} \quad 1 \text{ g AFDW} = 0.45 \text{ g C.}$$

Stream	Carbon Supply $\text{g C m}^{-2} \text{ yr}^{-1}$			Percent of Total	
	Primary Production	Allochthonous Input*	Production + Input	Primary Production	Allochthonous Input
First Choice Creek	20.51	354.00	374.51	5.5	94.5
Beaver Creek	34.35	144.68	179.03	19.2	80.8
Muskrat River	96.49	16.43	112.92	85.4	14.6
Matamek River	168.09	8.37	176.46	95.3	4.7

*Does not include carbon supplied as DOM or POM in suspension

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

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Matamek Research Station

INTRODUCTION

Beaver (*Castor canadensis*) are again making impressive population gains in much of North America, and in some areas are as abundant as ever. From results of preliminary studies we feel that beaver act as a "keystone" species (sensu Paine 1966; Mann 1977) through their feeding and dam building activities to significantly influence the structure and dynamics of aquatic ecosystems. Some important effects are: (1) modification of channel geomorphology and hydrology by dam building, (2) retention of sediment and organic matter by dams high in the watershed, (3) creation and maintenance of wetlands, (4) modification of nutrient cycling and decomposition dynamics through wetting of soils, alteration of the hydrologic regime, and creation of extensive anaerobic zones in soils and sediments, (5) modification of the riparian zone, including the composition and form of plants, their quality (lignin, nitrogen, etc.), and the quantity of allochthonous inputs, (6) expansion of wetted areas and increased allochthonous inputs which influence the character of water and materials transported downstream, and (7) habitat modification which ultimately influence species such as migratory birds and large mammals. Surprisingly, few studies have seriously addressed the environmental effects of beaver on lotic ecosystems (see major reviews by Yeager and Hay 1955; Hodgdon and Larson 1980; Jenkins and Busher 1979).

The overall objective of this project is to evaluate the role of beaver as agents influencing the dynamics of aquatic ecosystems (Naiman et al. 1983 MS). The specific purpose of this paper is to present data on how beaver influence the pattern, diversity, and production of aquatic insects emerging from beaver ponds of various ages, and to compare these data to those from unmodified stream and river channels.

STUDY AREAS

The study sites are situated near Sept-Iles, Quebec, on the North Shore of the Gulf of St. Lawrence. 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 annual degree days ($^{\circ}\text{C}/\text{yr}$), and generally somewhat acidic brown waters (pH: 4.8-7.2). Five sites were used (Table 1): three small streams (Last Chance Creek, Cran Carré Creek, and Beaver Creek) and two rivers (Muskrat River and Matamek River). All watersheds are completely pristine boreal forest composed predominantly of black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). Various biological and physical aspects of these streams have been described by Naiman

(1982, 1983a, b, c), Melillo et al. (1983), Connors (1983), Naiman and Sedell (1981), and Power et al. (1973).

Last Chance Creek is a small second order stream draining 2.4 km² with 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 about 0.145 m³/s. All the secondary dams are in good repair and actively maintained.

Beaver Creek is a second order stream draining 1.8 km² that also has a large beaver pond in its headwaters. Over its 0.9 km length there are 12 abandoned or recolonized dams separated by riffles. Mean annual discharge is approximately 0.113 m³/s.

Cran Carré Creek is a third order stream draining 20.7 km². 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 estimated to be 0.944 m³/s.

The Muskrat River is a fifth order stream draining 207 km². In its lower reaches there are a few beaver dams that 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 m³/s.

The Matamek River is a sixth order stream draining 673 km². There are no dams in the lower reaches, although beaver are active (e.g., tree cutting, lodges) along the banks of slower flowing sections. The mean annual discharge is 13.7 m³/s.

METHODS AND MATERIALS

Insects were collected weekly at each site (Table 1) from May to mid-October in 1982 using emergence traps placed at the water surface in the center of the stream or pond. 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 m² (Mundie 1971). The traps were anchored to each shore with ropes. In all situations the traps were placed in the center of the stream or pond.

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 each genus in each collection was calculated by drying representative samples at 50°C for 24 h, weighing the specimen on a Cahn 25 automatic electrobalance, and then multiplying by the number of individuals in that collection. Annual emergence was then 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:

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

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

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

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

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

Analyses of variance (ANOVA) procedures were used to test for differences 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 collected from the 12 sites, with the Chironomidae being the best represented. The number of insects emerging annually ranged from 3296/m² in Last Chance Creek to 31,144/m² from the eroding beaver pond on Cran Carré Creek (Table 2). All sites 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 a significantly higher emergence.

In response to habitat there was no clear pattern for the annual biomass of emerging adults. In Last Chance Creek and Beaver Creek there was no significant difference in emerging biomass between beaver ponds and a riffle (Table 2). In Cran Carré Creek, where beaver ponds had annual emergences similar to those for 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 showed a significant difference from the other sites.

Beaver impoundments increase the percentage of the annual biomass composed of Chironomidae (Table 2). Beaver ponds in Last Chance Creek, Beaver Creek, and Cran Carré Creek had 19-74% ($x = 53\%$) of the total emergence as Chironomidae, whereas the percentage for riffles and eroding ponds only ranged from 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 comprised only 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 emergence over the season was similar between streams and for sites within the same stream (Fig. 1). Peak emergence was usually in July and August. Beaver Creek was the only exception. There, peak emergence from a beaver pond preceeded that from a riffle by about two months.

To better visualize community changes, insects were grouped into the four major orders (e.g., Diptera, Plecoptera, Trichoptera, and Ephemeroptera), and the percentage contribution to total numbers and biomass calculated (Fig. 2). In terms of numbers, Diptera comprised 60.2-94.2% ($x = 83.1\%$) of all emerging insects with 33 to 71 ($x = 48$) genera collected at a site. Nevertheless, in terms of biomass, diptera contributed only 12.1 to 87.3% ($x = 43.6\%$).

In Last Chance Creek the biomass composition was similar in both beaver ponds; in Beaver Creek Diptera dominated the pond while Trichoptera biomass was significantly larger in the riffle; and in Cran Carré Creek the two intact beaver ponds were quite different while the eroding pond and the riffle had a similar complement of emerging insect orders. In the Muskrat River there were more Ephemeroptera in the pool than in the riffle; other insect orders were roughly similar. In the Matamek River Plecoptera were dominant in the pool while Trichoptera were dominant in the riffle.

Diversity

Diversity was generally highest from June through August while equitability remained nearly constant from May to late-September (Fig. 3). There were no significant differences between sites in mean weekly generic diversity (H) or in equitability (E). Mean diversity ranged from 1.77 to 3.00 and mean equitability from 0.57 to 0.82, with no coherent patterns (Table 2). When diversity and equitability were calculated using genera collected for one site over the ice-free season the results were the same (Fig. 3). There were no significant differences between sites in the pattern observed from May to October.

DISCUSSION

The sites reported on here are similar to streams and beaver ponds described by Clifford (1978) and Hodkinson (1975) 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 similar to that reported here.

Although we could not consistently demonstrate an influence of beaver on the biomass of insect emergence, there are definite changes taking place in the stream community over both the short and long term. When beaver dam a stream water currents are slowed with substantial organic matter stored in ponds. As Hodkinson (1975), Cummins and Lauff (1969), and Reice (1980) have shown, substrate type has a strong influence on the nature of the benthic community and the particular species of which it is comprised. One consequence of shifting to a soft bottom substrate is an increase in Chironomidae as we have reported here.

Another consequence of beaver ponding streams less well appreciated is the reservoir effect (Baxter 1977, Duthie and Ostrofsky 1982). When impoundments are first created and flood adjacent terrestrial terrain, essential nutrients are leached, resulting in increased aquatic production for one or two years. Also, when impoundments are drained and refilled this trophic upsurge reappears as nutrients previously trapped in lake sediment are released. We believe this phenomenon to be responsible for the significantly higher production rates 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 the pond and allowing it 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 appears to enhance the productivity of the system (Duthie and Ostrofsky 1982).

Finally, beaver act to increase the total production in the system by increasing the aquatic surface area and the extent of the productive ecotone between the terrestrial and aquatic environments. When a new pond is formed the shoreline development (i.e., the ratio for 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). Ponds formed by beaver dams also differ from natural ponds in their longitudinal profiles. 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 latter phenomenon on benthic organisms is conjectural but it may be a strong influence in some situations. Where littoral zone processes are important, the total mass of aquatic insects emerging each year can be impressive.

The results of this study are complex at the level of examination attempted (i.e., generic) but are only one facet of a multidisciplinary project investigating how beaver influence the dynamics of stream ecosystems. Detailed analyses of the benthic invertebrate community in 1983 are expected to show strong shifts in community structures, even though areal productivity may not be strongly affected. Beaver appear to increase total aquatic production by providing a larger surface area and by creating long-term situations analogous to artificial fish ponds. We believe implications at the ecosystem level are clear.

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

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

Table 2. Emergence of major groups, generic diversity, and generic equitability.

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

FIGURE CAPTIONS

- Fig. 1. The annual emergence pattern and total biomass of aquatic insects emerging at the water surface for each site sampled in 1982.
- Fig. 2. The percentage composition (e.g., numbers and biomass) by insect order emerging at the water surface of each site in 1982.
- Fig. 3. The pattern of generic diversity and equitability of insects emerging at the water surface during the 1982 growing season.

1982

NUMBERS/m2

BIOMASS (mg DW/m2)

NUMBERS/m2

BIOMASS (mg DW/m2)

LAST CHANCE CREEK T-11

CRAN CARRE CREEK T-3

LAST CHANCE CREEK T-12

CRAN CARRE CREEK T-4

BEAVER CREEK T-5

MUSKRAT RIVER T-7

BEAVER CREEK T-6

MUSKRAT RIVER T-8

CRAN CARRE CREEK T-1

MATAMEK RIVER T-9

CRAN CARRE CREEK T-2

MATAMEK RIVER T-10

THE INFLUENCE OF BEAVER (*Castor canadensis*) ON
NITROGEN FIXATION IN BOREAL FOREST STREAMS

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ABSTRACT

Nitrogen fixation was measured in four boreal forest streams of eastern Quebec with varying amounts of beaver (*Castor canadensis*) activity. Acetylene-ethylene reduction analyses were used during the 1982 ice-free period (May-October) to estimate nitrogen fixation by micro-organisms colonizing wood and sediments associated with beaver dams. Mean seasonal fixation rates were low, ranging from zero to 2.3×10^{-3} $\mu\text{moles C}_2\text{H}_4 \cdot \text{cm}^{-2} \cdot \text{hr}^{-1}$ for wood, and from zero to 7.0×10^{-3} $\mu\text{moles C}_2\text{H}_4 \cdot \text{g AFDM}^{-1} \cdot \text{hr}^{-1}$ for sediment. Rates were also patchy; 77% of all wood and 63% of all sediment measurements showed no C_2H_2 reduction. Nonparametric analyses of variance Kruskal-Wallis tests showed no significant difference ($p > 0.1$) of C_2H_2 reduction rates between or within sites by organisms colonizing various wood species or sediment types (depths).

Nitrogen contributed by organisms colonizing wood in beaver influenced streams were small (e.g., $0.041 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at Beaver Creek) but slightly greater than those for streams without beaver (e.g., $0.003 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at First Choice Creek). Although weight specific nitrogen fixation rates do not change significantly as beaver transform riffles into ponds; nitrogen fixed by organisms colonizing sediment in pond areas are much larger (e.g., $20.4 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at the Beaver Creek lower dam area). The total nitrogen contributions are proportional to the larger quantities of sediment available for microbial colonization. We estimate that total nitrogen accumulations in sediments are enhanced 9 to 47 fold by beaver damming a section of stream.

INTRODUCTION

Beaver (*Castor canadensis*) significantly modify the structure and dynamics of streams through their wood cutting and dam building activities (Naiman et al. 1983 ms). An individual beaver annually cuts a metric ton of wood for growth and maintenance (Howard 1982), usually selecting species such as aspen, alder or birch which are high in nitrogen and low in lignin (Melillo et al. 1983). Alterations to the nutrient cycle may result as wood, and the sediment trapped behind dams, become available for colonization by microbes. In nutrient poor boreal forests, fixed atmospheric nitrogen may be a major proportion of available nitrogen, with streams manipulated by beaver appearing to present suitable conditions for nitrogen fixation to occur.

Recently, biologically fixed atmospheric nitrogen in terrestrial and aquatic northern ecosystems has been measured using the acetylene-ethylene reduction technique (MacGregor and Keeney 1973; Vanderhoel et al. 1974; Flett et al. 1980; Waughmann and Bellamy 1980). Several studies of stream systems have examined nitrogen fixation associated with terrestrial litter inputs (Buckley and Triska 1978; Ashton 1979; El Samra and Olah 1979; Dierberg and Brezonik 1981; Tam et al. 1981). Terrestrial litter physically acts as an available colonization substrate and biologically acts as a refractory nutrient-carbon source for nitrogen fixing organisms. Nitrogen fixation rates associated with beaver mediated litter inputs and accumulated sediments have not been investigated.

The objectives of this study were: first, to measure nitrogen fixation rates in boreal forest streams and, second, to determine whether the wood cutting and dam building activities of beaver establish a situation where substantial amounts of nitrogen are contributed to the ecosystem.

We thank B. Farr for supplying survey data of stream sites and for her assistance in the field, and E. M. Conners for allochthonous input data.

STUDY AREAS

The study sites are located ~25 km east of Sept-Îles, Quebec, on the North Shore of the Gulf of the St. Lawrence (Fig. 1). The streams are characterized by low concentrations of dissolved nitrogen (0.1 to 0.3 mg N/L, as nitrate) and phosphorus (~ 0.003 mg P/L, as orthophosphate), and concentrations of dissolved organic carbon ranging from 5-15 mg C L⁻¹ (Naiman 1982a, 1983a). All sites are typical of brown, low gradient, subarctic streams found on the Canadian Shield. Two of the four streams (Beaver Creek, Matamek River) are in the Matamek River watershed; First Choice Creek and Cran Carré Creek are adjacent to the watershed. Various characteristics of these streams have been previously described (Power et al. 1973; Naiman and Sedell 1981; Naiman 1982a, 1983a,b,c; Conners 1983).

First Choice Creek is a first order stream with no beaver activity. Most organic inputs (307-534 g DW · m⁻² · yr⁻¹ as leaves, needles, wood and herbaceous vegetation) originate from the closed canopy forest. The stream originates as a series of seeps, has an organic detrital substrate, and a mean annual discharge of 0.013 m³/s. The temperature ranges between 0.4 and 11.0°C, with about 1700 degree days per year (°C · yr⁻¹), and the pH ranges annually from 6.2-7.2.

Beaver Creek is a second order stream characterized by a series of 12 abandoned or recolonized beaver dams separated by long riffles over its 0.9 km length. Most wood (~70% of the ~42 kg/m²) in the stream was put there directly or indirectly by beaver. Sediment behind dams is flocculent detritus alternately layered with fine wood particles. Mean annual discharge is 0.033 m³/s; the temperature ranges from 0.1 to 19.0°C with about 2100°C · yr⁻¹, and the pH ranges from 6.0 to 7.0.

Cran Carré Creek is a third order stream. Thirteen dams, most of which are situated in open meadows, are separated by short, low-gradient riffles. Most wood in the stream was put there by beaver; loosely packed silt characterizes the ponds. Mean annual discharge is $0.95 \text{ m}^3/\text{s}$; the temperature ranges from 0.1 to 22.0°C , with about $1939^\circ\text{C} \cdot \text{yr}^{-1}$.

The Matamek River is a sixth order stream. There are no beaver dams although beaver cut wood along the banks of slower flowing sections. The mean annual discharge is $13.7 \text{ m}^3/\text{s}$. Wood cut by beaver makes up a minor proportion of the total wood mass. Sediments in slow flowing sections are firmly packed clay and silt. The temperature ranges from 0.1 to 19.8°C ; there are about $2300^\circ\text{C} \cdot \text{yr}^{-1}$, and the pH ranges from 4.9 to 6.1 .

METHODS AND MATERIALS

Five tree species (black spruce, Picea mariana; balsam fir, Abies balsamea; speckled alder, Alnus rugosa; trembling aspen, Populus tremuloides; and paper birch, Betula papyrifera) were debarked, cut into cross sections, attached to monofilament line, and anchored at five sites in June 1981. The sites were: First Choice Creek (FCC), Beaver Creek lower pond area (BC1), Beaver Creek riffle area (BCR), Cran Carré Creek lower pond area (CC1), and Matamek River (MTK). For wood species the percentage of nitrogen ranged from 0.04 to 0.32% and the lignin: nitrogen ratio ranged from 42 to 647 (Melillo et al. 1983).

Sediment samples were taken from each wood incubation site, from two additional pond sites on Cran Carré Creek (CC2, CC3) and a pond on Beaver Creek (BC2). All samples were collected biweekly during the 1982 ice-free (May–October) period. Similar samples taken during 1981 for technique and procedure development are not reported here.

Incubation: The acetylene–ethylene reduction technique was used for estimating nitrogen fixation potentials (reviewed by Hardy et al. 1973). Controls were run for inherent ethylene production from wood and sediment. Gas samples were stored for analysis in 3 ml disposable plastic syringes rather than fixing wood and sediment with trichloroacetic acid, which may cause ethylene adsorption from rubber stoppers.

Wood: Samples were placed in plastic bags with unaltered stream water and returned immediately to the laboratory. Three replicates per wood species per site were used. Wood pieces, taken from the outer perimeter of the disks, were measured for exposed surface area ($\sim 12 \text{ cm}^2$) and placed in 60 ml serum bottles with $5\% \text{ C}_2\text{H}_2$ and $\sim 5 \text{ ml}$ filtered ($0.2 \mu\text{m}$) water from the sample site. Initial 2.5 ml gas samples were then collected in disposable plastic syringes for later analysis. Samples were incubated for a precise time period (either 2 , 5 , or 7 hr depending upon expected activity) before final 2.5 ml gas samples were extracted for C_2H_4 concentrations. About 700 samples were examined during 1982.

Sediment: Cores were taken behind beaver dams and in riffle areas with 6.5 cm diameter plexiglass tubes. Redox potential and the pH of surface and 10 cm depth sediment were measured in the laboratory using a Coleman model 80 Metrion pH meter. Four replicate samples each of aerobic and anaerobic sediments (occupying ~10% of the reaction volume) were incubated in 120 ml syrum bottles with ~5 ml filtered (.02 μ m) stream water. Water used for incubation of anaerobic sediments was bubbled with argon for 5 min to remove oxygen both before and after adding sediment samples, and prior to C_2H_2 injection. Following final gas collection sediment samples were dried at 50°C, weighed for dry mass (DM), and weighed again after 12 hrs at 500°C to calculate ash-free-dry-mass (AFDM). About 460 samples were examined during 1982.

Gas Analysis: Ethylene concentrations were measured within 48 hrs on a Carle AGC211 Flame Ionization Detector Gas Chromatograph using a propopak Q column at 75°C. Pre and post-incubation ethylene concentrations ($[C_2H_4]$), reported on a Hewlett Packard 3390A integrator, were corrected for $[C_2H_4]$ absorption by plastic syringes over time using the following equation:

$$\frac{X_o}{X_f} \times F - \frac{X_i}{X_i} \times I = \text{ETHYLENE PRODUCTION}$$

where:

X_o = mean $[C_2H_4]$ of 3 replicates of 5% C_2H_2 samples at $t = 0$ in syringe,

X_f = mean $[C_2H_4]$ of 3 replicates of 5% C_2H_2 at $t = \text{No. hours final}$

samples remained in syringe prior to analysis,

X_i = mean $[C_2H_4]$ of 3 replicates of 5% C_2H_2 at $t = \text{No. hours initial}$ samples

remained in syringe prior to analysis,

F = final (post-incubation), post-syringe storage $[C_2H_4]$ for each sample, and

I = initial (pre-incubation), post-syringe storage $[C_2H_4]$ for each sample

Ethylene production was calculated per g AFDM and g DM of sediment, or surface area (cm^2) of wood per hour. There was no relationship between sediment sample size and the specific rate of ethylene production on an AFDM ($r^2 = 0.01$) or a DM ($r^2 = 0.01$) basis, or for wood surface area and ethylene production. Mean acetylene reduction rates were used for interpretation since parametric Student-Newman-Kuels analysis of variance tests were not valid (based on Bartlett's test of homogeneity of

variances) for raw or log transformed data (Sokal and Rohlf 1969). Nonparametric Kruskal-Wallis analysis of variance tests showed no significant differences ($p > 0.01$) between sites, between wood species, or between sediments (Sokal and Rohlf 1969). Nitrogen fixation potentials were estimated from C_2H_2 reduction rates using the accepted 1/3 conversion factor (Bergensen 1970, 1980), although the universality of the factor for specific microbes can be disputed (Hardy et al. 1972; Graham et al. 1980).

The total nitrogen contribution by sediment organisms was estimated by using mean seasonal reduction rates, an equation estimating average stream width as a function of stream order (Naiman 1983a), and data on sediment volume at each sample site (Naiman 1982b). Sediment volumes behind dam areas were calculated using survey techniques and trigonometric interpolations of valley contours to estimate the extent of sediment accumulations. Sediment mass was calculated assuming $1 \text{ cm}^3 = 1 \text{ g dry weight}$, and that sediment from typical riffle areas extended to only 15 cm.

Estimates were also made for the total nitrogen contributed by organisms associated with wood species by interfacing mean seasonal rates with data on the surface area of wood in each stream (Naiman 1982b). The volume of small wood (1 cm - 10 cm diameter) was estimated by measuring the dimensions of all wood in 1 m transects every 10 m of stream length. Wood greater than 10 cm diameter was measured for either the entire stream or 500 m. The wood was identified to species and categorized by the method of input to the stream (e.g., erosion, wind, directly by beaver, indirectly by beaver). Wood volume was calculated from diameter and length measurements treating each piece of wood as a cylinder; whole tree volumes were estimated using the diameter at breast height (DBH) method. Wood buried in sediments or as a structural part of dams was not included.

RESULTS

Nitrogen fixation studies in field situations have historically yielded patchy data, which were incompatible with standard methods of statistical analysis. In studies similar to ours investigators discarded zero values or reported only maximum values to overcome statistical problems; few included long term repetitive sampling schedules. We feel these shortcomings bias readers into believing that highest rates are the norm. We believe it is essential to report observed, though statistically insignificant trends, if insights into the stream ecosystems are to be achieved.

Wood - Acetylene reduction rates were consistently low and patchy with 77% of all wood incubations showing no activity. Paper birch at BCR (Fig. 2) exemplifies the patchiness and the distributional range of reduction rates observed at all sites (e.g., 15 zero values for 22 incubations; max value = $2.3 \times 10^{-2} \mu\text{moles } C_2H_4 \cdot \text{cm}^{-2} \cdot \text{hr}^{-1}$). Patchiness accounts for there being no homogeneity of variances and no significant difference between reduction rates for wood species and sample sites (chi square < 9.5 , $P > 0.1$).

Mean seasonal rates for wood species ranged from 4.7×10^{-3} $\mu\text{moles C}_2\text{H}_4 \cdot \text{cm}^{-2} \cdot \text{hr}^{-1}$ for black spruce to 4.9×10^{-2} $\mu\text{moles C}_2\text{H}_4 \cdot \text{cm}^{-2} \cdot \text{hr}^{-1}$ for paper birch (Table 1). Hard woods (birch, aspen, alder), with low lignin:nitrogen ratios, showed higher mean seasonal activity than soft woods (spruce, balsam; Table 1). Mean seasonal rates for each wood species increase downstream in beaver manipulated watersheds; every species at BCR (e.g., 2.42×10^{-2} $\mu\text{moles C}_2\text{H}_4 \cdot \text{cm}^{-2} \cdot \text{hr}^{-1}$ for aspen) showed higher rates than the same species in an upstream pond area, BCl (e.g., 2.3×10^{-3} $\mu\text{moles C}_2\text{H}_4 \cdot \text{cm}^{-2} \cdot \text{hr}^{-1}$ for aspen) (Table 1).

Sediment - Acetylene reduction rates were low and patchy; 63% of the sediment samples showed no nitrogen fixation. Mean seasonal rates ranged from 0.2×10^{-3} to 1.5×10^{-3} $\mu\text{moles C}_2\text{H}_4 \cdot \text{g AFDM}^{-1} \cdot \text{hr}^{-1}$ for anaerobic sediments and from 0.6×10^{-3} to 7.0×10^{-3} $\mu\text{moles C}_2\text{H}_4 \cdot \text{g AFDM}^{-1} \cdot \text{hr}^{-1}$ for aerobic sediments (Table 2). Mean seasonal rates for aerobic and anaerobic sediments at each site, like wood species, followed a trend for rates to increase proceeding downstream in beaver manipulated watersheds (Table 2). Three dams in Cran Carré Creek [CC3 (upstream) $\rightarrow$ CC2 $\rightarrow$ CC1(downstream)] showed aerobic nitrogen fixation rates consecutively increasing from $1.0 \times 10^{-3} \rightarrow 3.3 \times 10^{-3} \rightarrow 5.0 \times 10^{-3}$ $\mu\text{moles C}_2\text{H}_4 \cdot \text{g AFDM}^{-1} \cdot \text{hr}^{-1}$, and anaerobic sediments increasing from $0.8 \times 10^{-3} \rightarrow 1.1 \times 10^{-3} \rightarrow 2.8 \times 10^{-3}$ $\mu\text{moles C}_2\text{H}_4 \cdot \text{g AFDM}^{-1} \cdot \text{hr}^{-1}$. In Beaver Creek, proceeding from BC2 (upstream) $\rightarrow$ BCl $\rightarrow$ BCR (downstream), rates for aerobic sediments increase from $0.6 \times 10^{-3} \rightarrow 5.3 \times 10^{-3} \rightarrow 7.0 \times 10^{-3}$ $\mu\text{moles C}_2\text{H}_4 \cdot \text{g AFDM}^{-1} \cdot \text{hr}^{-1}$, while anaerobic sediment nitrogen fixation rates increase from $0.5 \times 10^{-3} \rightarrow 2.8 \times 10^{-3} \rightarrow 5.2 \times 10^{-3}$ $\mu\text{moles C}_2\text{H}_4 \cdot \text{g AFDM}^{-1} \cdot \text{hr}^{-1}$.

There is a statistically insignificant difference in average nitrogen fixation rates between aerobic and anaerobic sediments of watersheds with and without beaver. At First Choice Creek, with no beaver activity, anaerobic sediments show a higher mean seasonal rate (5.5×10^{-3} $\mu\text{moles C}_2\text{H}_4 \cdot \text{g AFDM}^{-1} \cdot \text{hr}^{-1}$) than aerobic sediments (2.4×10^{-3} $\mu\text{moles C}_2\text{H}_4 \cdot \text{g AFDM}^{-1} \cdot \text{hr}^{-1}$, Table 2). In contrast, sites at Beaver Creek and Cran Carré Creek, where beaver are present, show higher reduction rates for aerobic sediments than anaerobic sediments (Table 2).

DISCUSSION

Beaver physically influence the structure and dynamics of stream ecosystems by creating new habitats which, as a function of area or volume, establish the magnitude of ecosystem-level processes. Absolute increases in nitrogen are related to the creation of new colonization substrates, moreso than to an increase in nitrogen fixation rates.

Estimates of annual nitrogen contributions per unit area by organisms colonizing wood in Beaver Creek and First Choice Creek were calculated

from mean acetylene reduction rates (Table 1) and the surface area of wood in these streams (Table 3). Nitrogen fixation associated with wood in Beaver Creek riffle, although supplying only $20.0 \times 10^{-2} \text{ g N m}^{-2} \text{ yr}^{-1}$, contributes more than fixation associated with wood in First Choice Creek ($8.1 \times 10^{-2} \text{ g N m}^{-2} \text{ yr}^{-1}$) (Table 3). These estimates are considerably lower than reports of $70.0 \times 10^{-2} \text{ g N m}^{-2} \text{ yr}^{-1}$ in a wood choked Oregon stream (Buckley and Triska 1978).

Annual nitrogen contributions by sediment organisms behind dams, calculated from mean seasonal reduction rates (Table 2) and survey data of sediment volumes (Table 5) are larger on an areal basis than for wood (0.75 g N/m^2 for wood, 20.4 g N/m^2 for sediment at BC1). Furthermore, the volume of wetted sediment in a ponded reach of stream is vastly increased by beaver activity. The resultant nitrogen contribution by sediment organisms is potentially several orders of magnitude greater than that for wood. For instance, nitrogen contributed to the ecosystem from 3 of 13 ponded areas on Cran Carré Creek is $209.5 \text{ kg N yr}^{-1}$, assuming mean fixation rates occur in all accumulated sediments. Nitrogen contributions from sediment organisms behind two dams on Beaver Creek ($23.1 \text{ kg N yr}^{-1}$) are less than those for Cran Carré, but still significantly greater than N inputs from the entire mass of wood in the stream system (Table 4). Nitrogen contributed to the system from ponded areas ($204 \text{ g N hectare}^{-1} \text{ yr}^{-1}$ based on BC1) is substantial compared to a study of alder stands in northeastern Connecticut (Voight and Stevcek 1969).

Applying an equation relating stream order with average stream width ($\log_{10} \text{ width} = 2.98 \log_{10} \text{ order} - 0.57$; Naiman 1983), estimates were made of the nitrogen contribution at each ponded area should that area be a typical riffle (i.e., with sediment volume equal to average stream width $\times$ 15 cm sediment percolation depth $\times$ stream length within the corresponding ponded area). Total nitrogen contributions were enhanced 9 (at BC1) to 47 (at CC2) fold due to beaver damming stream reaches that would normally be riffles (Table 4). The calculated increase is proportional to the volume of sediment trapped by beaver dams.

Comparisons of potential nitrogen inputs from several sources (e.g., allochthonous organic matter which supply a nutrient source to the ecosystem equal to the nutrient content of the litter; large wood inputs which sporadically enter the ecosystem either through beaver activity or storms; nitrogen in direct precipitation, and nitrogen accumulating from microbial fixation) indicate that the potential nitrogen input from litter is orders of magnitude greater than microbial nitrogen fixation. Groundwater nitrogen input is now being investigated.

It is important to note, however, that nitrogen from decomposing litter inputs, is not in a readily available form; rather it is slowly released as decomposition proceeds. Nitrogen fixation, although at low levels, may be more accessible to higher trophic levels because it is in a form available for immediate uptake. Conversely, nitrogen fixing organisms, by using allochthonous inputs as carbon sources, may enhance the litter decomposition rate and thus its availability to the stream community.

It appears that nitrogen fixation may be enhanced downstream of beaver influenced areas. In fact, both the nitrogen fixation and wood decomposition studies in the Matamek River watershed show increasing rates proceeding downstream within a beaver manipulated watershed (this study and Melillo et al. unpublished data). A lack of sufficient nitrogen, or an abundance of available phosphorus with ample carbon, could explain this trend.

Beaver ponds may act as sources or sinks of essential nutrients (P and N) and carbon, the relative levels of which influence nitrogen fixation rates and decomposition dynamics. Beaver utilize wood which decomposes rapidly (Jenkins 1975; Melillo et al. 1983) and thus continuously supplies downstream waters with carbon (Naiman 1983c). In addition, phosphorus may be a contributing factor to enhancement of downstream fixation and decomposition rates with continuous leaching of phosphorus as beaver ponds dry and flood over many years (Baxter 1977).

From our studies it is clear beaver not only influence the structure of stream ecosystems but also have a pronounced influence upon the magnitude of stream processes. Primarily from the massive volume of sediment trapped behind dams, the amount of nitrogen accrued annually to small watersheds is increased by over an order of magnitude. The implications for aquatic productivity and ultimate terrestrial succession are clear. The activities of beaver result in increased absolute productivity in headwater streams, providing a source of essential nutrients to downstream communities as ponds and meadows erode during their normal ontogeny. Without beaver, the absolute productivity and diversity of aquatic systems would be vastly decreased.

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Table 1: Mean seasonal C_2H_2 C_2H_4 reduction rates of organisms colonizing wood species in 1982 (10^{-4} umoles C_2H_4 cm^{-2} hr^{-1}); SEM = standard error; n = sample size; 0 = Percent of total incubations showing no C_2H_2 reduction.

Site	Black Spruce			Balsam Fir			Specked Alder			Trembling Aspen			Paper Birch			Mean Rates	
	(n)	x	SEM	(n)	x	SEM	(n)	x	SEM	(n)	x	SEM	(n)	x	SEM	All Species	(n) x SEM
First Choice Creek	24	.70	.21	63	24	.40	.19	83	24	7.77	3.67	63	27	.49	.19	81	123 1.93 .20
Beaver Creek, Lower Dam	25	.28	.08	76	25	.31	.12	68	28	.23	.06	79	26	.16	.04	69	127 .24 .01
Beaver Creek, Riffle Area	27	.68	.23	78	26	1.14	.56	81	27	1.16	.29	56	26	23.07	11.78	73	130 5.69 .85
Cran Carré Creek, Lower Dam	23	.41	.11	70	23	.27	.13	61	23	.31	.15	78	23	.45	.15	65	115 .45 .02
Matamek River	26	.28	.08	77	26	.74	.35	85	26	.23	.90	77	26	.09	.03	85	126 .41 .03
Average	125	.47	.01		124	.57	.03		128	1.94	.29	0	116	.89	.08	0	621 1.75 ± .09

Table 2: Mean-Seasonal $C_2H_2 \rightarrow C_2H_4$ Reduction Rates for Sediment Organisms in 1982 (10^{-3} μ moles C_2H_4 g AFDM $^{-1}$ hr $^{-1}$); SEM = standard error; n = sample size; 0 = Percent of total incubations showing no C_2H_2 reduction.

Site	Aerobic Sediment				Anaerobic Sediment				Mean Rate; All Sediment Types		
	n	x	SEM	0	n	x	SEM	0	n	x	SEM
First Choice Creek	30	2.4	0.8	77	30	5.5	1.5	70	60	4.0	0.3
Beaver Creek, Upper Dam	28	0.6	0.1	61	28	0.5	1.4	57	56	0.6	0.1
Beaver Creek, Lower Dam	30	5.3	1.9	60	30	2.8	1.1	53	60	4.1	0.2
Beaver Creek, Riffle Area	29	7.0	1.8	59	29	5.2	1.0	55	58	5.1	0.2
Cran Carre Creek, Upper Dam	23	1.0	0.3	74	30	0.8	0.2	63	53	1.0	0.0
Cran Carre Creek, Middle Dam	29	3.3	0.7	59	20	1.1	0.5	90	49	2.2	0.2
Cran Carre Creek, Lower Dam	31	5.0	1.0	61	30	2.8	0.6	77	61	3.9	0.2
Matamek River	25	2.3	0.6	64	26	2.8	0.4	38	51	2.6	0.1
Mean Rate, All Sites	235	3.4	0.1		223	2.7	0.1		458	3.0	1.8

Table 3: Estimated nitrogen contributions by organisms colonizing wood in streams with and without beaver.

Species	First Choice Creek (No Beaver)				Beaver Creek (Beaver)			
	Rate	N input	Rate	N input	Rate	N input	Rate	N input
	(10^{-4} Mol C H ₂ O ₂ hr ⁻¹)	(10^{-2} g N m ⁻² yr ⁻¹)	(10^{-4} Mol C H ₂ O ₂ hr ⁻¹)	(10^{-2} g N m ⁻² yr ⁻¹)	(10^{-4} Mol C H ₂ O ₂ hr ⁻¹)	(10^{-2} g N m ⁻² yr ⁻¹)	(10^{-4} Mol C H ₂ O ₂ hr ⁻¹)	(10^{-2} g N m ⁻² yr ⁻¹)
Wood	2. -2	-2. -1	2. -2	-2. -1	2. -2	-2. -1	2. -2	-2. -1
(cm m)	(cm m)	(cm m)	(cm m)	(cm m)	(cm m)	(cm m)	(cm m)	(cm m)
Species	(cm m)	(cm m)	(cm m)	(cm m)	(cm m)	(cm m)	(cm m)	(cm m)
Alder	1105	7.70	6.96	0.79	1154	0.79	0.23	0.22
Balsam	1453	0.19	0.23	0.12	324	0.12	0.31	0.08
Spruce	396	0.70	0.23	0	256	0	0.28	0.06
Aspen	138	0.30	0.03	0.96	732	0.96	0.23	0.14
Birch	1636	0.49	0.66	18.84	1879	18.84	0.16	.25
Total		8.11		20.71		20.71		0.75

Figure 1. Study sites on the north shore of the Gulf of the St. Lawrence River
~ 25 km east of Sept-Îles.

Figure 2. C_2H_2 reduction of paper birch at Beaver Creek riffle area showing
typical patchiness of fixation rates during the course of the 1982
season.

WOOD DECOMPOSITION STUDIES

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Ecosystems Center, Marine Biological Laboratory
and The Woods Hole Oceanographic Institution

C_2H_2 REDUCTION PAPER BIRCH @
BEAVER CREEK RIFFLE

Questions

Conclusions

WOOD DECOMPOSITION STUDIES

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Questions

During 1982, our work on wood decomposition focused on three questions:

- (1) How does wood decay in forest ecosystems compare with wood decay in adjacent stream ecosystems?
- (2) How does the addition of inorganic P influence wood decay rate and magnitude of N and P immobilization in decaying wood?
- (3) What is (are) the mechanism(s) responsible for N and P immobilization in decaying wood?

Conclusions

Q1: In a field experiment using a litter bag technique we compared decay rates of five woody materials (wood chips of speckled alder, paper birch, trembling aspen, black spruce and balsam fir) in a black spruce forest with decay rates of the same five materials in four stream sites (first, second, sixth and ninth order streams - see Melillo et al. 1983). Several general trends were apparent. First, for a single wood litter type, decay rate was highest in the first order stream, intermediate in the second and sixth order streams, and lowest in the ninth order stream and the terrestrial site. Aspen wood clearly exhibits this pattern (Fig. 1).

Second, at each of the five sites, there was a good relationship between decay rates of the five wood materials and some chemical parameter of the wood. Decay rates of wood in the terrestrial site were directly related to their initial nitrogen concentrations (Fig. 2a). Decay rates of woody materials in the first order stream were inversely related to their initial lignin to nitrogen ratios (Fig. 2b). Decay rates of woody materials in the larger streams were inversely related to their initial lignin concentrations (Fig. 2c).

Q2: In a recent publication (Melillo et al. 1983) we speculated that woody materials decayed faster in the first order stream than in other streams because inorganic P concentration in the water column in the first order stream was highest. To test this hypothesis we conducted a laboratory microcosm experiment in which we decomposed alder and spruce wood chips under two P regimes: "low P" where P concentration in the water was

0.003 ppm $\text{PO}_4\text{-P}$ (comparable to P level in the Matamek River water); and "high P" where P concentration in the water was 0.150 ppm $\text{PO}_4\text{-P}$ (comparable to 50 x P level in the Matamek River water). All other nutrients (e.g., N, Ca, trace elements) were delivered at high rates so as to make them non-limiting.

The design of the laboratory microcosms (chambers) appears in Fig. 3. The chambers are glass filter tubes with a narrow stem drawn at the bottom. Coarsely chopped litter is retained within the chamber by a square of fiberglass screening supporting a thin layer of glass wool. Water containing a specific nutrient mix is delivered to the top of the chamber, drains through the litter and down the stem, where it bifurcates either to the recirculating or to the outflow limb. The height of the outflow limb determines the water level in the chamber, which for our purposes is set at the glass wool, so that the litter is moist but not waterlogged. The recirculating limb operates as an airlift, such that the pressure head in the stem pushes water past a "Y"-shaped junction, where an air-stream bubbles it up and over into the top of the chamber again. The inflow and outflow rates are slow and equal each other (~17 ml/hr), resulting in a steady-state with respect to water level. Water flows in from above the chambers by means of a Marriot bottle and a siphon that achieves constant flow independent of water level.

For both alder and spruce, decay rates (calculated after 56 d of incubation) were higher in the "high-P" treatment (Table 1). These results are consistent with the findings of other studies (laboratory and field) designed to evaluate the relationship between P concentration in the water column and decay rate of plant litter (e.g., Howarth and Fisher 1976; Elwood et al. 1981).

Preliminary analysis of the data indicate that the P concentration in the irrigation water influenced N and P immobilization potentials in both materials (Table 1). The higher P concentration in the water resulted in higher N and P immobilization potentials for both materials. The level of P in the water had a more dramatic influence on P immobilization than on N immobilization for both materials.

Q3: The mechanism(s) responsible for N and P immobilization in decaying litter is (are) not known. While some reports suggest that much of the absolute N accumulation during decay can be attributed to increases in fungal biomass (Newell and Hicks 1983), most evidence suggests that the nitrogen accumulated in decaying litter is not directly associated with microbe mass (Rice 1982). We made direct counts of fungi on alder wood undergoing decay in a laboratory microcosm system to evaluate the fraction of the accumulated N associated with fungal biomass.

Depending on the assumptions we used in interpreting the direct fungal counts and converting them to N mass in fungae, we calculate that only between 13% and 23% of the absolute accumulation of N can be accounted for in fungal biomass. We are currently persuing the hypothesis that most of

the N (and P) accumulation is associated with the condensation of reactive compounds produced when microbial enzymes depolymerize the initial detritus substrate.

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Table 1. Decay rates and maximum N and P immobilization potentials of alder and spruce wood chips decomposing under 2 levels of P.

Woody Material	P Concentration in the water column	K	Maximum N immobilization (mg/g initial material)	Maximum P immobilization (mg/g initial material)
Alder (1x)	0.003	0.91	8.0	.23
Alder (50x)	0.150	3.25	8.5	.83
Spruce (1x)	0.003	0.58	4.8	.19
Spruce (50x)	0.150	0.87	5.9	.83

FIGURE CAPTIONS

Figure 1. Decay rates (k) for aspen wood chips decomposing at 5 sites in the Matamek area.

Figure 2. The decay constant k expressed as a function of the initial N concentration of all litter types in the terrestrial site (2a); initial lignin:N concentration of all litter types in the first order stream (2b); and as a function of the initial lignin concentration of all litter types in the larger streams (2c).

Figure 3. Design of laboratory microcosms.

pH CHANGES IN THE MATAMEK WATERSHED AS SHOWN BY
SEDIMENTARY DIATOM ANALYSES

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INTRODUCTION

The acidification of lakes through acid precipitation has become a major environmental concern in the last 10 years. Lakes located on the Canadian Shield are particularly susceptible because granite has a very poor buffering capacity.

The most visible effects of acid precipitation are noted on the fish populations. According to Webb (1980), reproduction is reduced and juvenile mortality is increased. In general, a pH below 5.5 is felt to reduce fish populations.

Diatoms have been utilized by paleolimnologists to determine the pH history of a lake. Their siliceous frustules accumulate in lake sediments and provide information on past environmental conditions.

The purpose of this report is to describe the utilization of sedimentary diatom analysis in determining whether or not acidification is occurring in the Matamek watershed. It, like most of the province of Quebec, is in a region which has been identified as highly sensitive to acidification (LRTAP 1979).

The Matamek Research Station has been active in fisheries research, particularly with respect to salmonids, a group very sensitive to acidification. As well, information on the pH histories of Canadian Shield Lakes is greatly lacking. It is difficult to illustrate the effect of acid precipitation and the threat that it poses to much of Eastern Canada without such data.

MATERIALS AND METHODS

Lake C22, a lake in the Matamek watershed, was sampled off the pontoons of a Beaver aircraft using a gravity corer on June 11, 1982. Two cores were taken at the centre of the lake, which according to the bathymetric map, is an undisturbed sediment basin. The cores were taken at a water depth of 21 metres. The chosen cores had an undisturbed sediment-water interface and were capped for transportation back to the lab. Before extruding, the total length of the core was measured, the physical characteristics of the core were described, and the surface water was carefully pipetted off and saved for analysis. Each core was extruded using a piston-like device which allowed sectioning of the core, from the top downwards, using thin metal sheeting. Sections were taken every 2 mm for the first 60 mm, every 5 mm for the next 100 mm and every 10 mm for the

remainder of the core. Sections were stored in labelled, wide-mouthed plastic containers with screw-on lids which had been pre-weighed on a Sartorius 3704 balance of the Matamek Station. After transportation to the University of Waterloo, the sample containers were weighed on a Mettler balance to enable calculation of wet weights. The sample containers were then frozen and freeze-dried for 24 to 48 hours, after which they were reweighed for dry weight determination. One core was retained at the University of Waterloo for diatom enumeration. The second core was sent to Dr. Marcel Ouellet at the Université du Québec for Cesium-137 dating and metal analysis.

To prepare a diatom slide for enumeration, 0.05 g of the freeze-dried sample was placed in a glass beaker to which 20 ml of a 1:1 solution of H_2SO_4 and HNO_3 was added. The solution was heated on a hot plate in a fumehood for approximately half an hour, until the solution cleared and a white, powdery precipitate was visible. After the solution cooled, the frustules were centrifuged and washed with distilled water. The frustules were washed and centrifuged three times. The solution was then made up to 200 ml using deionized water. A magnetic stirrer was used to agitate the solution and 10 ml were removed and settled in a Battarbee chamber to prepare four cover-slips. When dry, the cover-slips were mounted using Clearax mounting medium.

Four to five hundred diatoms were counted for each core section examined. Identifications were made with reference to the works of Patrick (1966, 1975), Germain (1981), Foged (1977, 1979), and Cleve-Euler (1968). Photographs were taken of many of the species observed.

RESULTS AND DISCUSSION

The core used in this study was 250 mm in length and was composed of soft-brown to olive-grey flocculant sediment. The sediment-water interface was slightly sloped at the time of coring and was in this position at the time of extruding. The core had not been disturbed by transportation.

Two distinct bands were visible through the clear plexiglass coring cylinder when the core was taken and both were still visible at the time of extruding. Both were grey to light brown in colour and were found at 124-145 mm and 180-190 mm respectively, measured from the sediment-water interface. Several other bands became visible as sectioning was carried out. A very distinct band, similar in appearance to creamy grey putty, was found at 111-115 mm. These bands have not yet been examined. It has been suggested that their presence is due to sediments washed into the lake during heavy spring flooding (M. Ouellet, personal communication). Diatom analysis may elucidate this by use of indicator species. The moisture content of the sections varied from 81.4% to 95.1%. A distinct grey band at 111-115 mm had a moisture loss of 54.3% suggesting a clay composition. Clay is composed of very fine particles, which can pack very tightly together, resulting in less trapped moisture.

A Cesium-137 profile was prepared by plotting Cesium-137 values against the midpoint of the core section analyzed (see Table 1). The Cesium-137 dating method is based on the knowledge that Cesium-137 was not widespread in the environment until 1954, when nuclear testing began. Thus, the first peak in a Cesium-137 profile is considered to be 1954. In many European lakes, the maximum peak represents 1963, but this is not consistent in North American lakes (Nancy MacNeill, personal communication). Assuming that the first value represents 1954, the sedimentation rate can be determined. The depth of the core at this point divided by the years since 1954 yields the sedimentation rate. Using our data, the sedimentation rate of Lake C22 is approximately 3.75 mm/yr.

Chemical analysis for trace metals (Cu, Zn, Pb, As, Co and Cd) is presently being carried out by Dr. Marcel Ouellet. Results are not yet available.

Diatoms have varying pH preferences. Hustedt (1937 - 1939) divided the diatoms into five categories based on their preferences:

- alkalibiontic: occurring at pH values above 7
- alkaliphilous: occurring at pH values above 7 and with widest distribution at pH above 7
- indifferent: occurrence around pH 7
- acidiphilous: occurring at about pH 7 and with widest distribution at pH values below 7
- acidibiontic: occurring pH values below 7; optimum distribution at pH 5.5 or less

Nygaard (1956) developed several indices which quantified Hustedt's groups:

$$\text{Index } \alpha = \frac{\text{acid units}}{\text{alkaline units}}$$

$$\text{Index } \omega = \frac{\text{acid units}}{\text{number of acid taxa}}$$

$$\text{Index } \epsilon = \frac{\text{alkaline units}}{\text{number of alkaline taxa}}$$

The acid units are calculated by adding the relative frequency of the acidibiontic species multiplied by five to the relative frequency of the acidiphilous taxa. The alkaline units are calculated in the same manner. The relative frequencies of the acidibiontic and alkalibiontic species are multiplied by five to emphasize that they are extreme groups (Nygaard 1956).

Merilainen (1967) calculated Nygaard's α , ω and ϵ indices for 14 Finnish lakes and ponds. These were plotted against the pH scale. The resulting curves revealed that it was possible to make accurate estimates of the pH of natural waters from their diatom floras.

Paleolimnologists have since utilized this knowledge by plotting the α -indices for surficial sediments against lake pH. The regression of lake pH vs log (α index) can be determined from this graph. The equation for this regression can then be used in determining the pH history of a sediment core because the α -index can easily be determined for any section of the sediment core based on its diatom assemblages.

Del Prete and Schofield (1981) used data from Scandinavian studies by Nygaard and Merilainen as well as 7 Adirondack lakes to determine the equation for the regression of lake pH vs log (α -index) shown below:

$$\text{pH} = 6.63 - 0.81 (\log_{10}\alpha)$$

At present an equation has not been developed for lakes in the Canadian Shield.

About 120 diatom taxa were identified in the sediments. As expected, alkalibiontic species were not present. The pH of the surface water was 5.75. Actinella punctata, Eunotia bidentula, E. exigua, E. fallax, E. flexuosa, E. meisteri, E. praerupta, Navicula cocconeiformis, Semiorbis hemiyclus, Surirella delicatissima and Tabellaria flocculosa were the acidobiontic species noted.

The α -indices and pH values are given in Table 2. The results indicate that the pH values for the surface sediments are in excellent agreement with the actual lake pH of 5.75.

A slide was also examined at 131-141 mm. The calculated pH was 5.75, which could be taken as an indication that no acidification has occurred in the system. However, this was the first slide enumerated and errors could exist in the counts or it may or may not be a random event. More slides of the core will be examined to verify this finding.

According to the Cesium-137 data recently received and presented in this report, the actual rate of sedimentation is 3.75 mm/yr. This means that the slides examined for the surface sediments represent a time period of only two years. Therefore it is not possible to make a statement regarding acidification in the watershed until deeper regions of the core are examined.

The high sedimentation rate also indicates that deeper cores should be obtained if a long-term history of Lake C22 is required. Based on the sedimentation rate of 3.75 mm/yr, the present core represents a time span of 66 years. In the future, larger diameter cores should be taken for Cesium-137 dating purposes so that it is not necessary to group sections

of the core together to obtain enough sediment for Cesium-137 analysis. With larger diameter cores more Cesium-137 values could be obtained and a more accurate dating and sedimentation rate could be determined. Core sections enumerated for diatoms could be adjusted accordingly.

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Table 1. Cesium-137 dating results from a sediment core taken from Lake C22. Depths are measured from the sediment-water interface.

CORE DEPTH (mm)	pCi/g
0- 34	5.919
34- 60	8.580
60- 90	1.466
90-120	1.314
120-140	0.257
140-160	-----
160-190	-----
190-210	-----
210-230	-----
230-250	-----
250-270	-----
270-290	-----
290-310	-----
310-330	-----
330-350	-----

Table 2. Nygaard's α -index and the calculated pH of the surface sediments of Lake C22 based on Del Prete et al. (1981). The actual lake pH was 5.75.

CORE SECTION (mm)	NYGAARD'S α -INDEX	CALCULATED pH
0- 2	14.105	5.70
2- 4	37.714	5.38
4- 6	15.040	5.68
131-141	12.200	5.75

GEOGRAPHIC VARIATION IN THE LIFE HISTORY CHARACTERISTICS
OF AQUATIC INSECTS IN EASTERN NORTH AMERICA

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This report briefly summarizes two years of research on life history characteristics of selected aquatic insect species in streams and rivers near the Matamek Research Station. These studies were part of a much larger project concerning the effects of natural temperature gradients on the geographic distribution, life history characteristics, and population dynamics of aquatic insects in eastern North America. Our central hypothesis for the overall project was that the stability of a given population (i.e., the ability to recover from serious reduction in population size by perturbations or natural fluctuations of the environment) within the geographic range of a species reflects mainly a dynamic equilibrium between temperature and individual growth, metabolism, reproductive potential, and generation time (Vannote and Sweeney 1980). In this context, a thermal regime is viewed as optimum for a species when individual body weight and fecundity is maximized. Geographic dispersal to the North or South of a location with an optimum thermal regime would be associated with temperature induced changes in the rate and efficiency of energy use, developmental processes, and generation time. The net result of these changes would be altered life history patterns and reduced reproductive effort.

The overall project involved studies on a large number of aquatic species in an array of rivers distributed along the Atlantic drainage from northern Florida to the Province of Quebec. As part of this project, we selected nine sites near the Matamek Research Station and initiated field studies in June 1981. A total of 27 species of aquatic insects, largely belonging to the orders Ephemeroptera, Plecoptera, and Trichoptera, were studied intensively from June through August 1981 and May through September 1982 (Table 1). Although many more species occur and were collected at these sites, we only performed detailed studies on those species that were previously studied at more southern latitudes (Florida to Vermont).

Study parameters for each species included: (1) the rate and magnitude of larval growth; (2) timing of adult emergence; and (3) the size and fecundity of adults or mature larvae. In addition, the larvae of many species were reared to the adult stage at the Matamek Research Station. These reared adult specimens were used for taxonomic verification and detailed population genetic studies (i.e., gel electrophoresis studies of 18-22 loci for at least 30 adult specimens per species).

Results of field studies indicate that most species emerge significantly later (i.e., 4-8 weeks) in the spring and summer at the nine study sites relative to rivers at more southern latitudes. The delayed emergence is probably due to cool seasonal temperatures that occur in rivers

near the Matamek Station (e.g., see Fig. 1 for a partial temperature record at four study sites).

There was also evidence that the duration of the life cycle for two species (viz. Eurylophella verisimilis and Eurylophella funeralis) increased from one year at lower latitudes to at least two years in rivers near the Matamek Station. In addition, adult size and fecundity of many species appeared to be consistently lower at the nine sites relative to populations at lower latitudes.

Electrophoretic analysis of proteins has been completed on two populations occurring in study sites near the Matamek Research Station. One population, Eurylophella funeralis, appears to be genetically similar (but not identical) to most other populations of the same taxa distributed at lower latitudes (viz. from South Carolina to Vermont). The life history characteristics of these populations, however, vary significantly, especially in rivers near the Matamek Station. This variation may largely reflect an ecophenotypic response to environmental gradients but more data are clearly needed.

We also completed electrophoretic studies on a population in the genus Siphloplecton from the Matamek River. These results indicate that this population is genetically very different from populations at southern latitudes (i.e., populations identified as Siphloplecton basale). We are presently evaluating whether individuals of Siphloplecton in rivers near the Matamek Research Station should be assigned to a new species. Additional electrophoretic studies on several other populations from the Matamek Research area are presently underway.

Table 1. A list of insect species and river sites where they were studied in 1981 and 1982.

	Study Sites*								
	CHO1	TRA2	BEA2	PIG6	TRU4	CRA3	LOU6	MAT7	MUS4
Ephemeroptera									
Ameletus subnotatus				X			X		
Arthroplea bipunctata								X	
Baetis sp.						X			
Baetisca laurentina								X	
Cinygmula sp.				X					
Dannella simplex				X					
Drumella cornutella				X			X		
Epeorus fragilis				X			X		
Epeorus pleuralis				X		X	X		
Epeorus vitreus				X					
Ephemerella aurivillii		X		X	X				
Eurylophella funeralis		X	X			X			
Eurylophella verisimilis				X		X	X	X	
Heptagenia pulla			X	X		X	X		
Leptophlebia sp.		X							
Leptophlebia cupida		X		X		X		X	
Litobrantha recurvata				X					
Paraleptophlebia debilis		X	X	X		X	X	X	X
Siphonurus sp.				X				X	
Siphonurus barbaroides				X					
Siphloplecton sp.				X		X	X	X	X
Stenonema modestum				X		X			X
Stenonema vicarium				X					
Trichoptera									
Neophylax sp.	X	X	X	X					
Pycnopsyche gentilis		X	X						
Plecoptera									
Nemoura sp.							X		
Taeniopteryx sp.							X		

*CHO1 = First Choice Creek, TRA2 = Trapper Cabin Creek, BEA2 = Beaver Creek, PIG6 = Pigou River, TRU4 = Riviere la Truite, CRA3 = Cran Carre River, LOU6 = Loup Marin River, MAT7 = Matamek River, MUS4 = Muskrat River.

Fig. 1 - Partial temperature record at four study sites near the Matamek Research Station. Daily maximum and minimum temperatures are depicted by the upper and lower solid lines in each plot; data are mean daily temperatures.

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