Aquatic Insect Histories and Atlantic Salmon Fry Diets in the St. Croix River, New Brunswick, Canada.

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AQUATIC INSECT HISTORIES AND ATLANTIC SALMON FRY DIETS IN THE ST. CROIX RIVER, NEW BRUNSWICK, CANADA

by

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ABSTRACT

Peterson, R. H., and D. J. Martin-Robichaud. 1986. Aquatic insect histories and Atlantic salmon fry diets in the St. Croix River, New Brunswick, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 1485: iii + 27 p.

Benthic invertebrate communities in riffle areas near the outfall of Spednic Lake on the St. Croix River, N.B. (latitude 45°11'; longitude 67°17') were found to differ from those in similar habitat farther downstream. Downstream sites were also characterized by less suspended chlorophyll a. Life history data on nine Trichopteran taxa and 15 Ephemeropteran taxa are presented.

In general, mayflies were more important food items for salmon fry than were caddisflies. Baetis spp. were the most important food item. Leucrocuta sp. and Paraleptophlebia sp. nymphs were most important at earliest feeding in June. Rhithrogena sp. was most important in October.

Relative "preferences" for various taxa depended on the estimate of relative availabilities used (drift vs benthos). Some taxa (e.g. Baetis, Chironomidae) were apparently foraged from the drift, whereas others (e.g. Leucrocuta, Rhithrogena) were probably foraged from the benthos. Ivlev's selectivity index was modified to analyze these tendencies and appears to be a useful method to assess foraging strategies for various taxa.

RÉSUMÉ

Peterson, R. H., and D. J. Martin-Robichaud. 1986. Aquatic insect histories and Atlantic salmon fry diets in the St. Croix River, New Brunswick, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 1485: iii + 27 p.

Les communautés d'invertébrés benthiques des hauts-fonds qui se trouvent près de l'endroit où le lac Spednic se déverse dans la rivière Ste-Croix (N.-B.) (Latitude 45°11'; longitude 67°17') diffèrent d'autres communautés occupant un habitat similaire plus en aval de la rivière. De plus, les emplacements en aval de la rivière contiennent moins de chlorophylle a en suspension. Le rapport présente des données relatives au cycle évolutif de neuf taxons de l'ordre des Trichoptères et de quinze taxons de l'ordre des Ephéméroptères.

Règle générale, les éphéméridés représentaient, par rapport aux phryganes, une part plus importante du régime alimentaire des alevins de saumon. L'espèce Baetis spp. était cependant le principal aliment des alevins de saumon. En juin, les nymphes de Leucrocuta sp. et Paraleptophlebia sp. étaient les princiaux constituants de l'alimentation des alevins de saumon tandis qu'en octobre les nymphes de Rhithrogena sp. avaient préséance.

Les préférences relatives pour divers taxons étaient déterminées par l'évaluation de la disponibilité de ces derniers (dérive versus benthos). Certains taxons (par ex. Baetis, Chironomidae) semblaient avoir été recueillis à partir de la dérive tandis que d'autres (dont Leucrocuta, Rhithrogena) avaient sans doute été puisés du benthos. L'indice de sélectivité d'Ivlev a été modifié pour analyser ces tendances et il semble utile pour l'évaluation des stratégies de l'approvisionnement en nourriture liées à divers taxons.

INTRODUCTION

Juvenile salmonid diet has been the subject of several studies, most suggesting that stomach contents qualitatively resemble stream invertebrate drift more closely than benthic standing crop. Elliott (1969, 1970, 1973) emphasized the importance of stream drift to the feeding of juvenile Salmo trutta and S. gairdneri, particularly the 0+ age group. McCormack (1962) emphasized the importance of Baetis nymphs in the diet of juvenile S. trutta. McNicol et al. (1985) reported that brook trout fry (Salvelinus fontinalis) fed more on subsurface drift than from either substrate or surface drift. Lillehammer (1973) studied the food habits of 0-age Atlantic salmon in streams below the outfall of lakes where zooplankton dominated the drift. These organisms were most abundant in salmon stomachs, with Chironomidae larvae ranking next in importance.

Others have reported conflicting results. Neveu (1981) found that, although feeding of juvenile S. trutta occurred primarily at dawn and dusk, there was no correlation between stomach and drift compositions. Williams (1981) concluded that salmon fry feed more from the substrate than do brook trout fry, with Plecoptera, Chironomidae pupae and larval Dytiscidae being important components of the diet.

In view of the conflicting observations reviewed in the above paragraphs, the relationship of juvenile salmon diet to specific life-history patterns of salmon prey is still not well understood. In a given river, are there certain "key" species which vary in importance, depending upon life-history strategies?

Several methods to determine the relative importance of available food items in diets have been elaborated. Ivlev (1961) developed an index of selective feeding (electivity index) based upon the relative percentages of numbers of a given organism in stomachs and in the total fauna. One of the most difficult aspects of studying natural diets of organisms lies in determining what component of the fauna is available to the predator. Thus, an electivity index may indicate either relative "preference" or relative availability. Johnson (1980) has discussed this aspect of feeding ecology, and has developed a parametric ranking method to assess relative "preferences" for various food organisms.

Sweeney and Vannote (1981) have shown how interspecific physiological differences among ephemerellid mayflies may result in asynchronous life cycles of several species occupying the same habitat. Coleman and Hynes (1970), Kovalak (1978), MacKay (1969), Krueger and Cook (1984) and others have established life histories for some species with Krueger and Cook (1984) emphasizing relationships among stage of development, incidence in stream drift and benthic densities.

In this paper we present life-history data on mayflies and caddisflies, and describe the occurrence of these taxa in stomachs of salmon fry in relation to these life histories. We also report the relative abundances of these taxa in benthic and drift samples, and summarize salmon fry diets in relation to various temporal and spatial components of benthic and drift fauna. Finally, we present data on food particle sizes of salmon fry, and relate this to particle size preferences determined in laboratory studies (e.g. Wankowski and Thorpe 1979).

STUDY SITE DESCRIPTION

The main stem of the St. Croix River forms the Maine-New Brunswick border from Vanceboro, Maine (45°34'N; 67°25'E) to St. Stephen, N.B. (45°11'N; 67°17'E). It has an annual mean discharge rate of 20 m³/s at the Spednic Lake dam with a width of ca. 70 m. The first 15-20 km below the dam include extensive dead-water areas interrupted by shorter stretches of turbulent "rips" (Fig. 1). From Hall's Rips to Meetinghouse Rips, the river consists of nearly continuous riffles and rapids with the stream gradient gradually decreasing downstream. Gravel Island, selected as the study site, is located in this latter segment of the river. Physical-chemical parameters of water quality are given in Table 1 (from Edmunds et al. 1968). Dissolved total phosphorus and NO_3-NO_2 levels were usually below detection limits. Mid-day water temperatures in the St. Croix River were typically 5-7°C in early May, rising to summer maxima of 20-26°C. Temperatures declined after early August, reaching 5°C by early November.

METHODS

Temperatures were recorded with a mercury thermometer to ±0.1°C whenever sampling was performed. Some water temperatures as well as various water chemistry parameters were available from the NAQUADAT data base maintained by Inland Waters Directorate, Canada Department of Environment, which operates a gauging station at the Spednic Lake dam.

Chlorophyll a was determined by standard fluorometric methods (Yentsch and Menzel 1963) on 1-L samples filtered through 50-µm mesh in the field. Since phaeopigment values were usually negative, no correction was made.

Invertebrate drift was sampled biweekly for 24 h continuously. The drift sampler consisted of a galvanized metal funnel, the narrow opening (3 x 20 cm) facing upstream, with a 1-m long nylon mesh bag (pores 475 µm on a side) attached to the downstream end (10 x 20 cm). A 250-mL plastic beaker was clamped to the downstream end of the bag. The side of the beaker contained a 2.5-cm diameter hole covered with nylon mesh (475-µm pore size). The upstream end of the sampler was threaded onto an iron rod driven into the stream bottom. The rods were in the same location throughout the period of drift sampling. When water levels were high, two samplers were stacked so that the top one was partially emergent and sampled surface drift. Samplers were emptied at 1000 h and 1800 h. The overnight sampling period thus included dawn and dusk. The contents of the samplers were removed by washing them into the beaker, which was then unclamped, and the contents preserved in 95% ethanol. Invertebrates were sorted from the samples manually under low-power magnification of a stereoscopic microscope. Sampling was discontinued Oct. 5 due to problems associated with drift of newly fallen leaves.

Water current velocities in the openings of the drift samplers were measured at the beginning and end of each sampling period, halfway up the drift sampler or at mid-depth, whichever was less. Mean velocities were used in calculating volumes filtered by the drift samplers.

The benthos was sampled with a standard Surber-type bottom sampler which sampled 0.09 m^2 of bottom. All large stones within the sampling area were scrubbed in the sampler bag, then the substrate within the sampling area was stirred vigorously at a depth of about 10 cm with a claw-type garden cultivator for 1 min. Samples were transferred to jars of 80% ethanol and sorted manually, with specimens stored in 70% ethanol. A grid of 20 ft x 10 ft (6 m x 3 m) was marked off in a subjectively selected riffle area by driving metal stakes at each corner. Each sampling area was subdivided into 200, 0.09-m^2 sampling locations by stretching ropes graduated in 0.3-m divisions between the stakes, and connecting appropriate graduations on the ropes with graduated PVC tubing. Squares within each grid were numbered from 001 to 200 and sampling locations selected with the use of a table of random numbers. Ten random benthic samples were taken within the grid every 2 wk from May to October. The particle size distribution of the substrate from which benthos was sampled has been described previously (Peterson 1978). The surficial 10 cm typically had 60-80% by weight in the 22-256 mm particle size range, 10-20% of 20-22 mm particle size and 1-10% sand (0.06-2.0 mm).

Streamside vegetation was swept with a butterfly net to collect adults, which were preserved in 70% ethanol.

Atlantic salmon eggs and alevins (30,000) of Waweig River stock were reared at the St. Andrews Biological Station until "swim-up." They were then transported to the St. Croix River in mid-May 1979 and planted in suitable habitat, both upstream and downstream of the drift and benthic sampling locations. In the fall of 1980, 400 adult Atlantic salmon of Saint John River origin were stocked at several St. Croix sites, including Gravel Island, by the Canada Department of Fisheries and Oceans, Freshwater and Anadromous Division. The progeny of these adults were also sampled monthly at Gravel Island.

Fry were sampled monthly by electrofishing, and preserved in 80% ethanol. Stomachs were removed and dissected within 48 h of capture, prey items were identified and counted and head capsule widths of prey items measured.

STATISTICAL METHODS

Distribution of numbers of various taxa in the benthic samples were highly skewed, and were not normalized with routine transformations (square root, natural logarithm), nor did they approximate a Poisson distribution significantly. Therefore, a non-parametric Wilcoxon two-sample test (Sokal and Rohlf 1981) was used to test the significant differences in numbers of a given taxon between study sites for a common sampling date.

Polar ordination (Poole 1974) was utilized to categorize mayfly and caddisfly communities at nine sampling sites in a preliminary survey of the river.

The drift samples were divided into "day" and "night" drift - the latter including the dawn and dusk periods. These were further subdivided into "surface" and "subsurface" drift. The tendencies of various drift components to occur in these drift subdivisions were tested by a X^2 analysis. Comparisons of "availability" of various organisms in the various drift components and in the benthic fauna were made with usage by salmon fry (0+), using the methods developed by Johnson (1980). In addition, the degree to which availability in the drift determines usage by salmon fry was assessed by an extension of the Ivlev formula.

Due to manpower constraints, different phases of the investigation were performed in different years (Table 2). We have therefore assumed that there is sufficient synchrony in caddisfly and mayfly life histories from year to year to permit temporal comparisons among drift, benthic and diet data. The assumption seems warranted, based on the apparent agreement of drift and benthic temporal patterns for the various taxa.

RESULTS AND DISCUSSION

STUDY SITE SELECTION

The investigation consisted of two phases, a preliminary survey and a more intensive subsequent study of two selected sites. The preliminary survey consisted of six benthic samples in late August of 1976 and 1977 at each of nine sites (Fig. 1, Table 2), ranging from 0.5-37.5 km downstream of Spednic Lake, plus an analysis of the chlorophyll a content of the water at the various sites at the time of sampling.

Polar ordination of both the Ephemeropteran and Trichopteran generic composition at the various study sites indicated a dominant axis associated with upstream-downstream differences in community composition (Fig. 2, 3). The Vanceboro site was well separated from more downstream sites for both orders.

Based upon the above surveys, two sites were selected for more intensive study and planting of salmon fry: Vanceboro, representing the near-lake benthic community, and Gravel Island, representative of the downstream community.

COMPARISONS OF THE TWO SITES

The chlorophyll a content of river water at Gravel Island was consistently about 5 µg/L less than that at Vanceboro (Fig. 4) ($Cha_{V.} = 4.86 + 1.004\ Cha_{G.I.}$, r = 0.90, n = 13). Concentrations were highest from April to early July with peaks in late April and early July. From late July to October, they were fairly constant at 10 and 5 $\mu g L^{-1}$ for Vanceboro and Gravel Island, respectively.

TRICHOPTERAN LIFE HISTORIES

Forty-one taxa of Trichoptera were identified from the benthic sampling (Table 3), of which 24 were identified to the species level. Only nine taxa, however, were sufficiently numerous to yield sufficient data to elucidate life histories and permit an assessment of importance in salmon diet.

Hydropsyche was an abundant Trichopteran genus at both study sites, significantly more so at Vanceboro where the number sampled in benthic samplers was usually more than double that at Gravel Island at corresponding times (Fig. 5A, B). The genus was probably represented by a complex of at least four species as identified from adults swept from streamside vegetation. Fewer species might be represented at Gravel Island as only H. morosa was identified. Since the species were not separated as larvae, the genus was treated as a single entity. MacKay (1984) found H. morosa to be bivoltine in southern Ontario with trivoltinism occurring in H. bronta. The species sampled from the St. Croix were probably multivoltine as well, judging from the wide ranges of larval sizes present throughout most of the sampling period. Early instars were most abundant in benthic samples from late June to late August at Vanceboro, while they continued to be present at Gravel Island until early October. The partly grown larvae overwintered. The numbers collected in benthic samples at Gravel Island are maximal in mid-August, and numbers collected in drift samplers showed a trend approximating that of benthic collections. At Vanceboro, a peak in numbers sampled from the benthos coincided with the recruitment of early instars into the population, and an abundant drift of these early instars occurred at this time as well.

Cheumatopsyche campyla was identified from adults collected at Vanceboro and Gravel Island. Many larvae at Gravel Island lacked a fronto-clypeal notch, which was present in those collected at Vanceboro. Therefore, there probably was an additional, unidentified species at Gravel Island. The life histories were similar at the two study sites, with adults in flight from mid-June to early August (Fig. 5C, D). Early instars are recruited from late June to October, peaking in July and August, and the genus overwintered as partly grown larvae. A drift of early instar larvae occurred at Vanceboro in early July, probably correlated with peak recruitment, but was not observed at Gravel Island. The only Cheumatopsyche taken in drift at the latter study site were mature larvae in early June.

Macronema zebratum is a large Hydropsychid, probably having a semivoltine life history. Thus, there was a wide range of larval instars present at most times (Fig. 6A). Adults were in flight in late June-early July and early instars were recruited in late July-early August. M. zebratum larvae were usually not collected in drift samplers, the only drift being associated with very high water in late May. The genus was much less abundant at Gravel Island.

Two species of Chimarra, C. socia and C. obscura, were identified at Gravel Island. The life histories of the two species appeared very similar, and no clarification was obtained by analyzing them separately; therefore, head capsule data for the two species were combined (Fig. 6B). Numbers collected from the benthos were minimal in late May to early July, consisting mostly of late instar larvae. Adults were captured from June to September, and recruitment of early instars occurred from July to October. Probably at least two generations occurred per year. Chimarra larvae were not frequent in the drift.

Brachycentrus appalachia was clearly univoltine (Fig. 6C) with earliest instars appearing in June. The species overwinters as mature larvae or pupae, and adult emergence occurred prior to start of sampling. B. appalachia was collected in drift only in July and was not collected at Vanceboro.

Lepidostoma larvae were not identifiable to species; however, the genus seemed to be represented by single, but different, species at each study site. Life histories were similar at each study site with larvae overwintering and maturing the next July (Fig. 7A, B). Early instars appeared in early August. Lepidostoma larvae were not collected frequently in the drift; samples were mainly associated with either eclosion or high water.

Agarodes sp. had a very short larval phase at Gravel Island with early instars first appearing in late July (Fig. 7C). The overwintering phase may have been mature larve or pupae, or emergence may have occurred in late fall with the egg overwintering. At any rate, there must have been a long egg diapause from May until July.

Oecetis avara larvae were collected in numbers only from late June to early August (Fig. 7D) with emergence presumably occurring in August. Occasional early larvae were collected in August-October, indicating a partial hatch of early larvae throughout this period.

Three species of Ceraclea were identified, with C. arielles and C. annulicornis collected only from Vanceboro and C. submacula present at both sites. The life histories of the first two species were similar (Fig. 7E), with May sampling yielding late instar larvae which probably emerge in June, at which time few were collected from the benthos. Hatching occurred somewhat later in C. arielles than in C. annulicornis. These early instars contributed to the peak numbers collected from the benthos in early August. The third species, C. submacula, occurred in low numbers at both sampling sites. The life history is less clearcut due to smaller numbers sampled and possibly more complex life cycle. Early instars appeared in July, contributing to the drift illustrated in Fig. 7E. Overwintering probably occurred as partly grown larvae, and late instar larvae were collected in small numbers from late June to mid-August.

Stream insect life histories may be classified into "fast" and "slow" univoltine (Krueger and Cook 1984; Hynes 1961), multivoltine or semivoltine. Examples of fast univoltine cycles for Trichoptera presented in this paper were Agarodes sp. at Gravel Island and Oecetis avara at Vanceboro.

Brachycentrus appalachia exhibited a typical slow univoltine life cycle, very similar to that described for B. occidentalis by Krueger and Cook (1984). These authors classified Lepidostoma byanti as having a "fast" univoltine life cycle with most growth occurring after leaf-fall. The Lepidostoma species at Gravel Island and Vanceboro apparently required a longer period of time with considerable growth occurring in May and June of the year following hatching. Chimarra spp., Hydropsyche and Cheumatopsyche were multivoltine, with recruitment of early instars occurring from June or July until September. Macronema zebratum was a semivoltine caddisfly, with many instars present at one time.

Caddisflies, in general, are not prominent in stream drift. Elliott (1969) found that, although caddisflies were the dominant order in the benthos, they contributed to only 3% of the drift. In our study, most caddisfly species did not drift significantly. Hydropsyche contributed most to stream drift, particularly at Vanceboro where drift densities exceeded 50/100 m^3 during peak recruitment. Macronema and Lepidostoma did not drift significantly. Cheumatopsyche drifted in numbers at Vanceboro, but not at Gravel Island, perhaps due to greater benthic densities of this genus at Vanceboro. In general, Trichoptera drift occurred in one of two situations: drift associated with recruitment of early instars (e.g. Hydropsyche, Cheumatopsyche at Vanceboro, Chimarra and Brachycentrus at Gravel Island), or with high water levels and/or with pupation (e.g. Lepidostoma and Macronema at Vanceboro). Krueger and Cook (1984) noted similar drift tendencies for Lepidostoma.

EPHEMEROPTERA LIFE HISTORIES

At both Gravel Island and Vanceboro, the most abundant Ephemerellid species were of the genus Drunella (D. tuberculata at Vanceboro, D. lata at Gravel Island) and Ephemerella rotunda/invaria (Fig. 8A). E. rotunda/invaria nymphs hatched in mid-July at Vanceboro and late July-early August at Gravel Island. They overwintered as immature nymphs and matured in late May-early June. Both Drunella species probably overwintered in the egg stage, as the most immature nymphs were collected in May. D. tuberculata nymphs at Vanceboro matured in late July, while D. lata nymphs at Gravel Island did not mature until late August. Three other Ephemerellid species were sampled at Vanceboro. Serratella serratoides had a life history similar to that of D. tuberculata, but matured about a month later. Attenella attenuata and S. deficiens both appeared as immature nymphs in late summer (early August in the case of A. attenuata; early September for S. deficiens). They overwintered as partly grown nymphs and matured somewhat later than E. rotunda/invaria - late June for A. attenuata and late July for S. deficiens.

The temporal pattern of numbers of Ephemerellid nymphs collected in benthic and drift sampling reflected the life-history pattern (Fig. 8B). Maturing E. rotunda/invaria nymphs were abundant in both the benthic and drift samples in mid- to late May. Much of the early E. rotunda/invaria drift at Gravel Island was probably missed as the site was not accessible for earlier sampling. Numbers of nymphs in both drift and benthic samples declined in late June, then peaked again in mid- to late July. This peak was associated with D. lata at Gravel Island and primarily D. tuberculata plus A. attenuata and S. serratoides at Vanceboro. For Ephemerellid nymphs, as well as for the other taxa discussed, the maximal number obtained in benthic samples may not have reflected true benthic densities. Suter and Bishop (1980) have demonstrated that Surber samplers with 100-µm mesh is more efficient at collecting earliest instars than are samplers with the 400-µm mesh size used here. Numbers of D. tuberculata (and other taxa) were greatest for the earliest instars. The peak in sampling may reflect increased sampling efficiency for larger nymphs, then a decline reflecting reduced numbers due to mortality. It may also reflect hatching asynchrony. After an August minimum in numbers of Ephemerellid nymphs, the numbers collected increased through September and early October, due primarily to the hatching of a new cohort of immature E. rotunda/invaria nymphs.

The life cycles of various Ephemerella mayflies in the St. Croix appear to be temporally segregated in the manner described by Sweeney and Vannote (1981) for this genus in White Clay Creek, Pennsylvania. The E. deficiens life history was similar to that described by those authors for the species, except that it apparently matured about a month later, most growth occurring in early June rather than in May. This discrepancy may be due to latitudinal differences in the two studies. The E. invaria representative in the St. Croix hatched at about the time of E. subvaria in White Clay Creek, but emerged in late May-June rather than April.[1] The Drunella species have fast univoltine cycles, hatching in May or June and emerging in late August. Thus, most of this growth occurred when E. invaria was either in egg diapause or in very early instars. S. serratoides also has a fast univoltine life cycle which was delayed by about a month relative to that of D. tuberculata.

Paraleptophlebia sp. which overwintered as partly grown nymphs (Fig. 8C) probably matured in the spring, before benthic sampling was begun. There was apparently continuous egg production and recruitment of nymphs through May and June. Egg diapause probably occurred from mid-July to early August. The overwintering cohort hatched from early August to mid-September. Drift densities of Paraleptophlebia were high in early June. The reasons for this may be twofold. There were large numbers of nymphs maturing then, and stream discharge was relatively great. The pattern generated from numbers obtained in the benthic samples (Fig. 8C) was typical of that for taxa which have more than one generation per season, with two periods of relatively high abundance. Again, real peaks of benthic densities may have been slightly earlier than those estimated from benthic sampling, due to inefficiency in sampling the earliest instars.

Baetis nymphs were not further identified, and probably represent a complex of several species or genera. Benthic and drift densities increased through the summer, peaking in mid-August and mid-September, respectively (Fig. 9A, B). Drift densities were fivefold greater at Gravel Island than at Vanceboro although maximal numbers taken in benthic samples at Vanceboro were usually about double those at Gravel Island. This apparent anomaly may reflect differences in suitability of sampling sites, but more probably was due to the extensive riffle habitats upstream of the drift samplers at Gravel Island. Such habitat was absent 10 m upstream of the Vanceboro samplers. Baetis probably overwintered primarily in the egg stage as both benthic standing crop and drift fell to low levels by early October. Recruitment of early instars occurred primarily in July and August with benthic density peaking in late August. Baetis spp. were characterized as having a fast 1-yr cycle in Lapland streams (Ulfstrand 1968). The St. Croix Baetis populations were either multivoltine or composed of several species each with fast 1-yr cycles.

[1] E. subvaria may have been confused with early instars of E. invaria/rotunda. In more recent sampling, E. subvaria has been found to hatch earlier than E. invaria/rotunda. E. subvaria may not have been identified in this study because sampling was discontinued in October.

The data obtained for Isonychia sp. indicate different life histories at the two study sites (Fig. 9C, D), although the genus was not particularly abundant at either site. Possibly, different species existed at each site. At Gravel Island, the life history was apparently bivoltine with a fairly strong summer cohort hatching in July and maturing in late September, and a weaker overwintering cohort. At Vanceboro, a few specimens were sampled in May, then none until August when a fairly strong cohort appeared. None was taken in the drift at any time. It is possible the species overwintered as mature nymphs and emerged prior to initiation of sampling in early spring.

Tricorythodes atratus was sampled only infrequently at Gravel Island, but early instars became very abundant in the benthic samples at Vanceboro in mid-July (Fig. 9C, lower panel). Numbers sampled then declined quickly as the nymphs matured. The entire life cycle appeared complete by mid-September. Drift sampling yielded an entirely different picture. Tricorythodes nymphs were continually found in the drift throughout the summer with an early abundance, which may have peaked prior to the start of sampling, and a second peak coinciding with the peak of numbers sampled in the benthos. A reasonable explanation is that much of the drift was derived from the lake, and the sampling site was colonized by adults from the lake, resulting in a mid- to late summer population peak in the riffle. This contributed to the drift in mid-July.

Stenonema life histories were similar at Gravel Island (mainly S. vicarium) and Vanceboro (mainly S. mediopunctatum) (Fig. 10A, B). There was considerable scatter in head capsule width, probably due to lack of synchrony within a generation. The new cohort hatched in early July, and increasing numbers were sampled in benthic samples from then until sampling was terminated in October. The high drift density from April to early June may have been due to high stream discharge. Drift densities were higher in late summer, as were benthic densities.

Epeorus vitrea was an important benthic species only at Gravel Island. The life history (Fig. 10C) was similar to that described for Stenonema. It appeared to be univoltine with considerable asynchrony within a generation. Synchrony was greatest in the early instars, imposed by mid-summer egg diapause. Benthic densities were low in May to early July, consisting of mid- to late instars. Nymphs were essentially absent from the benthic fauna in late July, and numbers increased from early August to October with the appearance of the new cohort. Drift densities of late instars were high in early June, decreasing to zero in late July. Drift in the early instars began in early August, peaked in late August, then declined to near zero again in late September.

Rhithrogena sp. appeared to be bivoltine (Fig. 10D) with one generation hatching in late summer and overwintering as immature nymphs, and a summer generation hatching near late May and maturing in late July-early August. The presence of two species is another possible explanation. Benthic densities of Rhithrogena were lowest in August when there was a gap between the generations. Drift densities were notable only in late May to mid-June, declining to near zero by mid-July. As with Epeorus, synchrony of development seemed to be imposed by an egg diapause period in August.

A wide range of Leucrocuta instars was present during most of the summer (Fig. 11A). It is possible that at least a partial summer generation may have occurred, or more than one species. The overwintering stage was the partly grown nymph. As with E. vitreus and Rhithrogena sp., Leucrocuta was found only infrequently at the Vanceboro site.

SALMON DIET

Trichoptera occurred less frequently in the stomachs of salmon fry than did Ephemeroptera. Hydropsyche, the caddisfly most important in the diet (Fig. 5B), was ingested in greatest numbers in July when early instars were most numerous and Hydropsyche drift was relatively great. Brachycentrus was a minor component of the diet (Fig. 6C) in early July when benthic densities of early instars were near maximal. Lepidostoma was of minor importance in early October (Fig. 7B), again coinciding with maximal benthic densities of early instars, and Chimarra was an occasional dietary item (Fig. 6B).

Paraleptophlebia was an important food item in early summer when drift densities were still high (Fig. 8C, 11B) relative to the drift of other invertebrates. Approximately 20% of the items ingested in late June were Paraleptophlebia nymphs. Leucrocuta was also an important early summer food item for salmon fry (Fig. 11B). The proportion of Leucrocuta in the diet appears related to drift density rather than number collected in benthic samples. Baetis was the major component of salmon fry diet from mid-July to October (Fig. 9B, 11B) amounting to more than 50% of the ingested items in August and early September. Forty-three of the 46 items in the stomach of the single fry collected at Vanceboro in August were Baetis nymphs. Epeorus vitrea was an important dietary item in June, when later instars comprised nearly 10% of ingested items, and in late August, corresponding to the peak of the early instar drift, when nearly 25% of ingested items were E. vitrea (Fig. 10C, 11B). Stenonema was a dietary component only in late summer and fall when benthic densities were high, but it was never a major component (Fig. 10B, 11B). Rhithrogena sp. was a dietary component both in June-July, and particularly in October (Fig. 10D, 11B). The relatively high proportion of Rhithrogena in the diet in October is noteworthy, considering that the drift densities were low at this time.

While Ephemerellidae nymphs were never a major component of the diet of Atlantic salmon fry, they were eaten most in late July when D. lata nymphs were consumed (Fig. 8B). Proportions were also relatively high in the latter part of June (also D. lata) and in October when the early instars of E. rotunda/invaria were consumed. Only six salmon fry were recovered at Vanceboro; one collected in mid-August contained no Ephemerellidae. Of four collected on June 10, two contained one E. tuberculata each; and for the single fry recovered on Oct. 5, seven of 14 items in the stomach were immature E. rotunda/invaria.

Salmon fry in streams are not presented with a graded series of food particle sizes matched to fry size as growth proceeds. Large nymphs of Paraleptophlebia, Leucrocuta and Epeorus were predominant components of the drift at time of first feeding (early to mid-June), and these organisms predominated in stomachs of fry sampled in June, both numerically and gravimetrically (Fig. 12, Table

5). Mean head capsule widths for the remaining months were 0.6-0.77 mm, largely reflecting the head capsule widths of Baetis nymphs, the dominant food item for July-October. The mean head capsule width increased again in October due to increased consumption of the Heptagenia, Rhithrogena and Stenonema. Ranges of food particle lengths were similar for all organisms ingested (Fig. 13) with >90% of all ingested items being 2-5 mm in length (excluding caudal filaments). McCormack (1962) commented on the relatively large size (up to 7.5 mm) of food organisms of newly feeding S. trutta. The gape of newly feeding salmon fry is about 3.0 mm (Allen 1940), about 50% greater than the largest head capsule widths ingested.

Though the size of food particles does not increase through the summer, the number of items found in salmon stomachs increased dramatically (Fig. 14) from about three items/stomach in June to 50 in late September. This rise was paralleled by the rise in drift densities of "consumable" items (items found in fry stomachs throughout the summer). Although we have not shown it with the lines indicating trends in Fig. 14, both drift rates and feeding rates declined in October. Fry growth, as indicated by length in Fig. 14, was rapid for June and mid-July with fork length increasing from 35-50 mm. Little increase in length occurred from mid-July to mid-August, implying that food consumed was entirely utilized for maintenance and locomotion. The mid-July to mid-August period had seasonally maximal mid-day temperatures (ca. 25°C), so that temperatures may have been supra-optimal for fry growth. From late August to late September, growth was again rapid with mean length increasing from 55-70 mm, corresponding to high feeding rates.

Analysis of temporal and spatial drift density patterns (Table 5) demonstrated the tendency of most organisms to drift between dawn and dusk. The only exception was the tendency of Trichoptera adults at Gravel Island to drift during the day. Most organisms also drifted in significantly greater densities in the "subsurface" (i.e. bottom 20 cm) water column, exceptions being Ephemeroptera imagos, and Trichoptera adults. Terrestrial insects (not shown in Table 2, 3, 4) also drift primarily on the surface. Caddisfly and mayfly adults, and terrestrial insects were never found in fry stomachs, a possible conclusion being that the fry did not feed on surface drift. It is also possible that our drift sampling missed some emergence periods of importance in this regard.

Baetis spp. were overwhelmingly the single most important food item consumed by salmon fry from July through October. About 50% of the items ingested were of this taxon. McCormack (1962) made similar observations on the importance of Baetis as food for S. trutta.

Baetis was not the most important food item in June when fry began feeding. Paraleptophlebia and Leucrocuta combined to form nearly 50% of the food items ingested in June. E. vitrea was also an important food item at this time. All three of these taxa were present as mature nymphs during this period, so they represented relatively large food items as well.

Rhithrogena sp. approached the importance of Baetis in the diet in October, and S. vicarium was also of greatest importance in the diet at this time. The utilization of these two species occurred when standing crop densities of early instars were maximal, but incidence in drift very low (<1/100 m^3). Either the salmon fry were foraging them from the substrate, or they were migrating on the substrate surface and were not being collected in the drift samplers.

The temporal sequence in which various Ephemeroptera taxa appeared as important salmon fry food items is summarized in Fig. 11. A varied Ephemeropteran fauna provided a continuing food source throughout the growing season.

Salmon fry diets usually correlate more closely with drift composition than with the benthos (Elliott 1970, 1973; Lillehammer 1973), although Williams (1981) reported otherwise. In our study, Hydropsyche, the most abundant caddisfly in the drift, was also the most frequently encountered in salmon stomachs. Hydropsyche was most important in the diet in late July and early August when early instars were recruited into the population, and when drift densities were high, although the peak of utilization does not coincide with the observed peak in benthic density. This may reflect inadequacies of the Surber samplers in retaining the smallest instars. Lepidostoma was a component of the diet only in October when benthic densities were high. Since they were not taken in drift samplers at this time, they may have been foraged from the bottom. B. appalachia was a minor component of the diet in early July, coinciding with peak drift and benthic density.

Caution is suggested when drawing inferences from stomach analyses as to quantities of food ingested since feeding frequencies and digestion rates are unknown. Neveu (1981) found S. trutta to feed mainly twice per day, at dusk and dawn, with the former most important. Elliott (1972) showed that gastric evacuation of several aquatic invertebrates by juvenile brown trout was 50% complete in 2-3 h at 15°C, and 75% complete in 7-10 h. Our fry were sampled at 1000-1200 h (ca. 5-7 h after daybreak), so that it is probable that the stomachs contained nothing from the previous dusk feeding and perhaps less than 50% of the dawn feeding, plus whatever had been ingested more recently. The daily total of ingested organisms, particularly for July-September, is probably more than twice the number counted in the stomachs.

The relation of incidence of various taxa in fry diets to incidence in drift suggests that the fry were depending upon the drift for prey, agreeing with previously reported findings (Elliott 1970, 1973; Lillehammer 1973). Johnson (1980) developed a parametric method for testing relative usages of various taxa in relation to availability estimates, based upon differences in rank between usage and availability. This test does not provide absolute values for "preference" or "avoidance," but only relative assessment. We used this method to compare relative "preferences" for various food organisms with "availability" in both drift and benthos (Table 7). Taxa such as Heptagenia and Epeorus usually rank high on the basis of either availability estimate, while Chironomid larvae and Paraleptophlebia usually ranked low. Baetis ranked high on the basis of benthic availability, but not in relation to drift, suggesting (by reverse logic) that fry are preying on it primarily from the drift. Rhithrogena, on the other hand, ranked low on the basis of benthic availability, but high in relation to drift, indicating they may be foraged primarily from the benthos. In an attempt to determine more accurately to what extent the drift is the source of prey items, we utilized an extension of the "selectivity index" devised by Ivlev (1961). The selectivity index is the term used to describe r_i-p_i/r_i+p_i where r_i is the proportion of the ith item in the diet, and p_i is the proportion of that item in the fauna. In our study, we had two estimates of the fauna from which proportions can be drawn, the drift and benthic data. We have utilized the proportions of various important food taxa in diet, drift and benthos in an Ivlev paradigm as follows:

if r_i = proportion of the ith taxon in the diet
p_i = " " " " " " " drift
q_i = " " " " " " " benthos,

then the selectivity index of diet vs drift $= \dfrac{r_i-p_i}{r_i+q_i}$

and " " " " " " benthos $= \dfrac{r_i-q_i}{r_i+q_i}$

We can also calculate an index of "propensity to drift" relative to proportion of the benthos p_i-q_i/p_i+q_i. Now if we let r_i-q_i/r_i+q_i = p_i-q_i/p_i+q_i, then $r_i = p_i$, so that the locus of points where ratios of r_i-q_i/r_i+q_i : $p_i-q_i/p_i+q_i = 1$ is the line of equivalence between proportion in stomachs and proportion in drift. Thus in Fig. 15 where r_i-q_i/r_i+q_i is plotted vs p_i-q_i/p_i+q_i, the diagonal indicates the locus of points where $r_i-p_i/r_i+p_i = 1.0$. Dietary items obtained primarily from the drift, with no selectivity, will fall along this line. Baetis nymphs, Hydroptilid larvae, Ephemerella nymphs, Hydropsyche larvae, Paraleptophlebia nymphs, Chironomid larvae and Chimarra larvae all follow this line closely, indicating that fry may be obtaining these items almost solely from the drift. The relative tendencies of these taxa to drift are indicated by their positions along this line. Baetis drifts in high proportions relative to proportions in the benthos. Chimarra, at the other extreme, occupies a very small proportion of the drift relative to its proportion in the benthos. The proportion of the diet composed of Lepidostoma, on the other hand, is identical to its proportion in the benthic standing crop, somewhat higher than its proportion in the drift. Either it is being taken from the substrate or the fry are exercising some selectivity in taking it from the drift. The Heptageneid nymphs all lie well above the "drift" line and, in fact, were eaten in greater proportion than would be predicted from either benthic or drift frequencies. There are at least two possible explanations. Either the fry are selecting these organisms from the drift, benthos or both, or our two methods of sampling prey items (drift and substrate sampling) have underrepresented the faunal proportions available to fry. Most fry, particularly in early summer, were sampled within 1-2 m of the shoreline whereas our substrate sampling grid and drift sampler were somewhat farther out in the stream. These nymphs may have been present in higher proportions in near-shore habitat. Conversely, Plecoptera and Anisoptera nymphs were found in lower proportions in the diet than in either the drift or benthic samples, indicating that fry were possibly avoiding these organisms or vice versa.

The unsuccessful stocking of salmon fry at the Vanceboro site was probably a result of the extremely high discharge rates occurring soon after fry release (c.f. Fig. 16). It is likely that fry were flushed downstream in these pulses. These pulses would be damped at the Gravel Island site due to storage capacity in the deadwater areas downstream of the dam. This damping was apparently sufficient to allow fry stocked at Gravel Island to retain position.

The results reported here emphasize the importance of a varied benthic community for Atlantic salmon fry foraging, and support the findings of others that the Baetine mayfly production is of particular importance.

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Table 1. Physico-chemical characteristics of St. Croix River water. Chemical concentrations are given as μM. DOC is in mg/L (from Edmunds et al. 1968).

	Parameter										
	DO	HCO_3^-	Ca^{2+}	Na^+	Cl^-	SO_4^{2-}	Mg^{2+}	pH	Specific conductance	Color	DOC
Mean value	95%	100	75	60	50	40	20	6.7	32		
(Range)	(65-100)							(6.5-6.9)	(27-38)	(5.0-30)	1.5-9.0

Table 2. Sampling schedule for various components of the St. Croix study.

	1976	1977	1978	1979	1981	1982
	4 5 6 7 8 9 10	4 5 6 7 8 9 10	4 5 6 7 8 9 10	4 5 6 7 8 9 10	4 5 6 7 8 9 10	4 5 6 7 8 9 10
Vanceboro	• +	• +		× • • • • • • ✲ ✲ ✲ ✲ ✲ ✲		× × + + + + + + +
Mile Rips	• +	• +				
Hall's Rips	• +	• +				
Duck Pt.	• +	• +				
Scott Bk.	• +	• +				
Albie's Rips	• +	• +				
Gravel Is.	• +	• +		× × × × × × • • • • • • ✲ ✲ ✲ ✲ ✲ ✲	× × × × ×	+ + + + + +
Meetinghouse Rips	• +	• +				
Canoose Rips	• +	• +				

\+ -Benthic Sampling
✲ -Drift Sampling
× -Fry Sampling
• -Chlorophyll Sampling

Table 3. Checklist of Trichoptera with relative abundances at Gravel Island and Vanceboro study sites (0 - not collected; 1 - occasional; 2 - common; 3 - abundant)

Family	Species	Vanceboro	Gravel Is.
Philopotamidae	*Wormaldia* sp.	0	1
	Chimarra socia	1	3
	Chimarra obscura	1	2
Pyschomyiidae	*Lype diversa*	1	0
Polycentropodidae	*Neureclipsis bimaculata*	2	1
	Polycentropus sp.	0	1
Hydropsychidae	*Cheumatopsyche campyla*	2	3
	Hydropsyche morosa		
	Hydropsyche walkeri	3	3
	Hydropsyche scalaris		
	Hydropsyche recurvata		
	Macronema zebratum	3	1
Rhyacophilidae	*Rhyacophila fuscula*	2	1
	Rhyacophila manistee	1	0
	Rhycophila sp. (*melita* group)	1	0
Glossosomatidae	*Glossosoma* (*lividum*?)	0	2
	Agapetus sp.	0	2
	Culoptila sp.	0	3
	Protoptila sp.	0	1
Hydroptilidae	*Hydroptila amoena*	1	1
	Ithytrichia sp.	0	1
	Mayatrichia ayama	0	1
	Neotrichia sp.	1	1
	Ochrotrichia sp.	1	0
	Oxyethira sp.	1	0
Brachycentridae	*Brachycentrus appalachia*	0	3
	Micrasema sp.	1	1
Limnephilidae	*Pycnopsyche* sp.	1	0
	Nemotaulius hostilis	1	0
	Apatania sp.	1	1
Lepidostomatidae	*Lepidostoma* spp.	3	3
Sericostomatidae	*Agarodes* sp.	0	2
Odontoceridae	*Psilotreta* sp.	0	2
Helicopsychidae	*Helicopsyche borealis*	1	1
Leptoceridae	*Ceraclea submacula*	2	2
	Ceraclea arielles	3	0
	Ceraclea annulicornis	3	0
	Mystacides alafimbrata	1	1
	Nectopsyche sp.	1	0
	Oecetis avara	2	1
	Setodes oligia	1	1

Table 4. Checklist of Ephemeroptera with relative abundances at Gravel Island and Vanceboro study sites on the St. Croix River (0 - not collected; 1- occasional; 2 - common; 3 - abundant)

Family	Species	Vanceboro	Gravel Island
Leptophlebiidae	Paraleptophlebia (mollis?)	1	3
Siphlonuridae	Isonychia sp.	1	2
Tricorythidae	Tricorythodes atratus	3	1
Ephemerellidae	Ephemerella rotunda (invaria?)	3	2
	Ephemerella needhami	1	0
	Drunella tuberculata	3	1
	Drunella lata	0	3
	Drunella walkeri	0	1
	Attenella attenuata	2	0
	Serratella serratoides	2	1
	Serratella deficiens	2	1
	Serratella serrata (?)	0	2
Heptageniidae	Stenonema mediopunctatum	3	0
	Stenonema vicarium	0	2
	Stenonema modestum (?)	2	1
	Epeorus vitrea	1	3
	Leucrocuta sp.	1	2
	Rhithrogena sp.	0	3
Baetidae	Baetis spp.	3	3

Table 5. Dry weights (mg/stomach) of various items in salmon stomachs. (Leuc. = Leucrocuta, Sten. = Stenonema, Ep. = Epeorus, Chir. = Chironomids, Rhith. = Rhithrogena.)

Time	Para.	D. lata	Leuc. Sten. Ep.	Chir.	Baetis	Rhith.	Ep.	Ephemerella invaria	Stenonema	Hydropsyche	Simuliidae	Totals
June	0.40	0.16	1.91	0.032	0.05	-	-	-	-	-	-	2.55
July	0.17	-	0.38	0.083	0.34	0.10	-	-	-	0.48	-	1.25
Aug	-	-	0.53	0.101	0.54	-	0.51	-	-	0.09	-	1.77
Sept	-	-	0.03	0.023	1.10	-	0.10	-	-	0.48	0.21	1.94
Oct	-	-	-	0.014	0.85	0.68	-	0.43	0.35	-	-	2.32

Table 6. Chi-square (X^2) values and probabilities (d.f.=1) for drift patterns of various taxa. "Preferred" indicates significantly greater drift than would be expected on the basis of volume filtered.

Taxon	Day (D) vs Night (N)			Surface (T) vs Subsurface (B)		
	X^2	p	"Preferred"	X^2	p	"Preferred"
Vanceboro						
Stenonema spp.	0.004	>0.995	-	2.36	<0.25	B
Baetis spp.	40.41	<0.005	N	0.37	0.5	-
Ephemerella spp.	38.2	<0.005	N	4.60	<0.05	B
Tricorythodes atratus	97.3	<0.005	N	573	<0.005	B
Eph. Imagos	356	<0.005	N	177	<0.005	T
Cheumatopsyche campyla	22.1	<0.005	N	27.2	<0.005	B
Hydropsyche spp.	0.01	<0.995	-	56.4	<0.005	B
Trichoptera adults	54.1	<0.005	D	39.6	<0.005	T
Gravel Island						
Stenonema spp.	36.6	<0.005	N	1.60	0.1	B
Leucrocuta sp.	69.1	<0.005	N	9.87	<0.005	B
Epeorus vitrea	67.0	<0.005	N	4.70	<0.1	B
Ephemerella spp.	31.9	<0.005	N	2.37	<0.1	B
Paraleptephlebia	231	<0.001	N	2.74	<0.1	B
Eph. Imagos	55.1	<0.001	N	139	<0.001	T
Micrasema sp.	4.67	<0.05	N	0.71	0.05	
Hydropsyche spp.	0.13	>0.9	-	5.46	<0.025	B
Trichoptera adults	61.9	<0.005	N	293	<0.001	T

Table 7. Relative "preference" of salmon fry for various prey taxa, when tested against relative "availabilities" in benthos and drift. Taxa enclosed within a common bracket do not differ significantly (F test; p 0.05) in "preference" rank

June		July		August		September		October
Benthos	Drift	Benthos	Drift	Benthos	Drift	Benthos	Drift	Benthos
Heptagenia	Rhithrogena	Baetis	Hydropsyche	Epeorus	Heptagenia	Simuliidae	Epeorus	Baetis
Epeorus	Heptagenia	Hydroptilidae	Rhithrogena	Baetis	Plecoptera	Baetis	Plecoptera	Stenonema
Baetis	Epeorus	Heptagenia	Paraleptophleb.	Stenonema	Epeorus	Hydroptilidae	Hydropsyche	Ephemerella
Ephemerella	Ephemerella	Glossosoma	Baetis	Heptagenia	Stenonema	Ephemerella	Baetis	Lepidostoma
Paraleptophleb.	Baetis	Ephemerella	Hydroptilidae	Ephemerella	Baetis	Epeorus	Chironom.larv.	Epeorus
Rhithrogena	Chironom.larv.	Rhithrogena	Heptagenia	Plecoptera	Chironom.larv.	Heptagenia	Stenonema	Hydropsyche
Chironom.larv.	Paraleptophleb.	Hydropsyche	Chironom.larv.	Chironom.larv.	Hydropsyche	Chironom.larv	Ephemerella	Plecoptera
		Chironom.larv.	Ephemerella	Hydropsyche		Stenonema		Rhithrogena
		Paraleptophleb.				Plecoptera		Paraleptophleb.
						Hydropsyche		Chironom.larv.

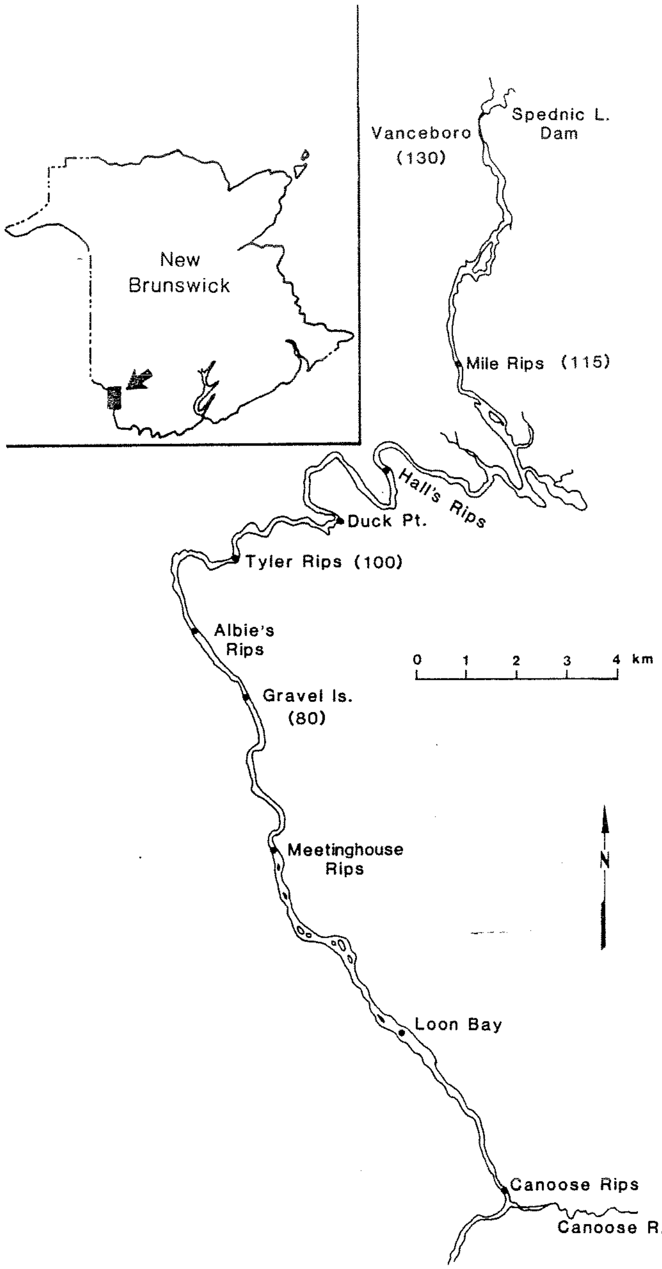

Fig. 1. Study segment of the St. Croix River, indicating sampling sites and elevations (m).

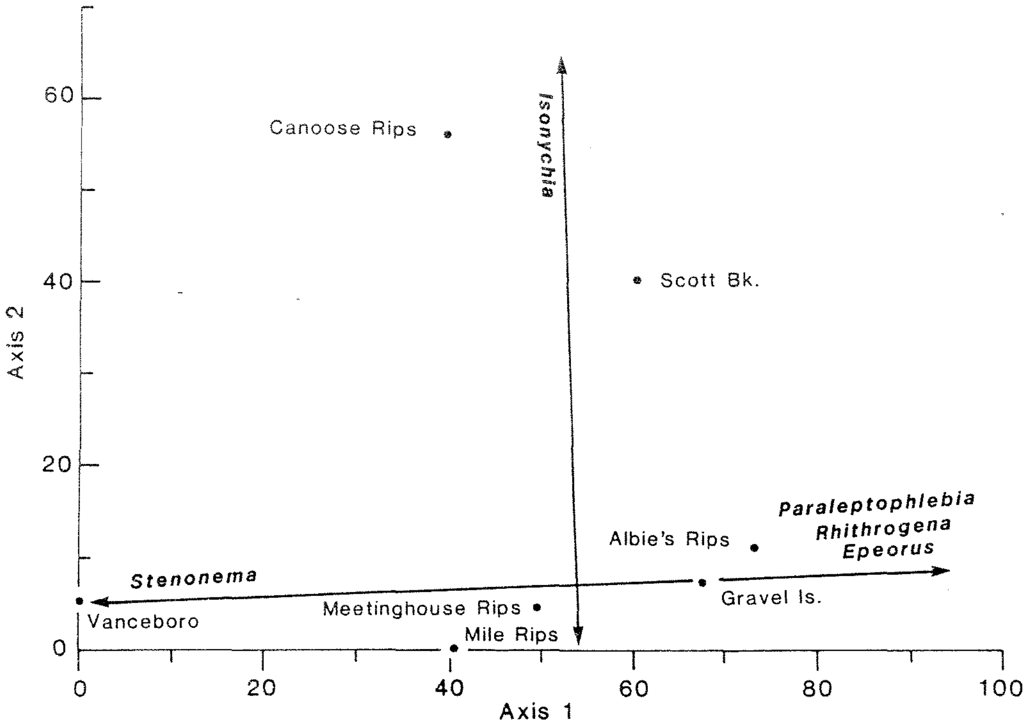

Fig. 2. Ordination analysis of nine sampling sites on the St. Croix River with respect to mayfly genera. Axes 1 and 2 are arbitrarily selected to maximize differences. Ecological significance of indicated vectors is discussed in the text. Genera indicated on vectors are considered as important in determining indicated trends.

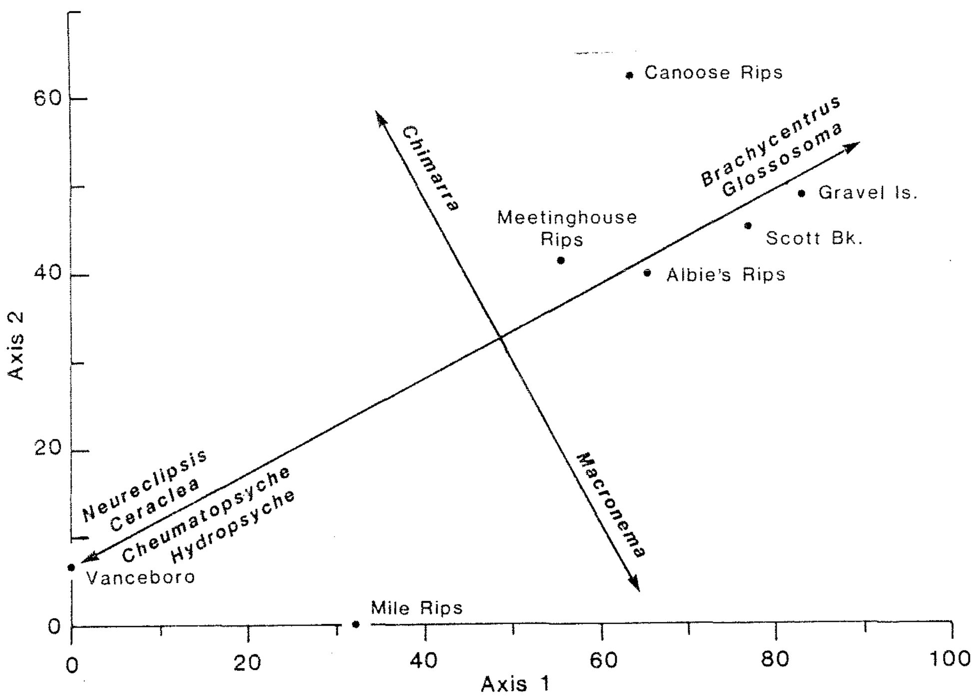

Fig. 3. Ordination analysis of nine sampling sites on the St. Croix River with respect to caddisfly genera. Genera indicated on vectors are considered as important in determining indicated trends.

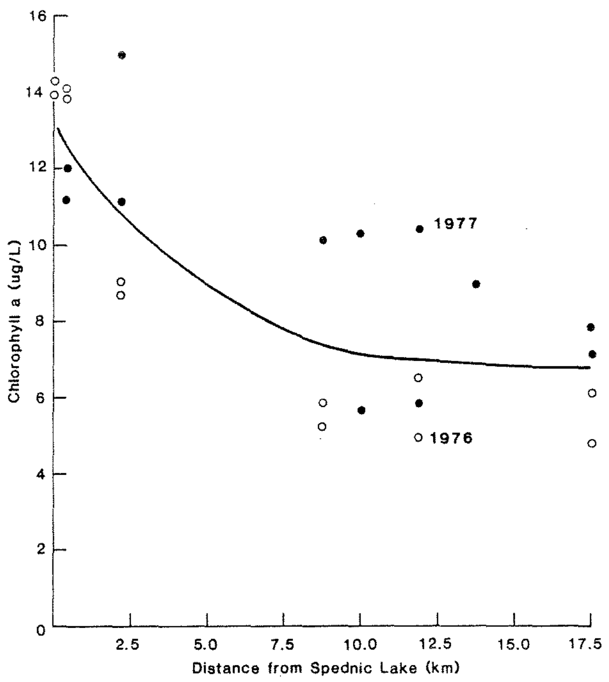

Fig. 4. Spatial trends of chlorophyll a concentrations in the St. Croix River water with increasing distance downstream of Spednic Lake.

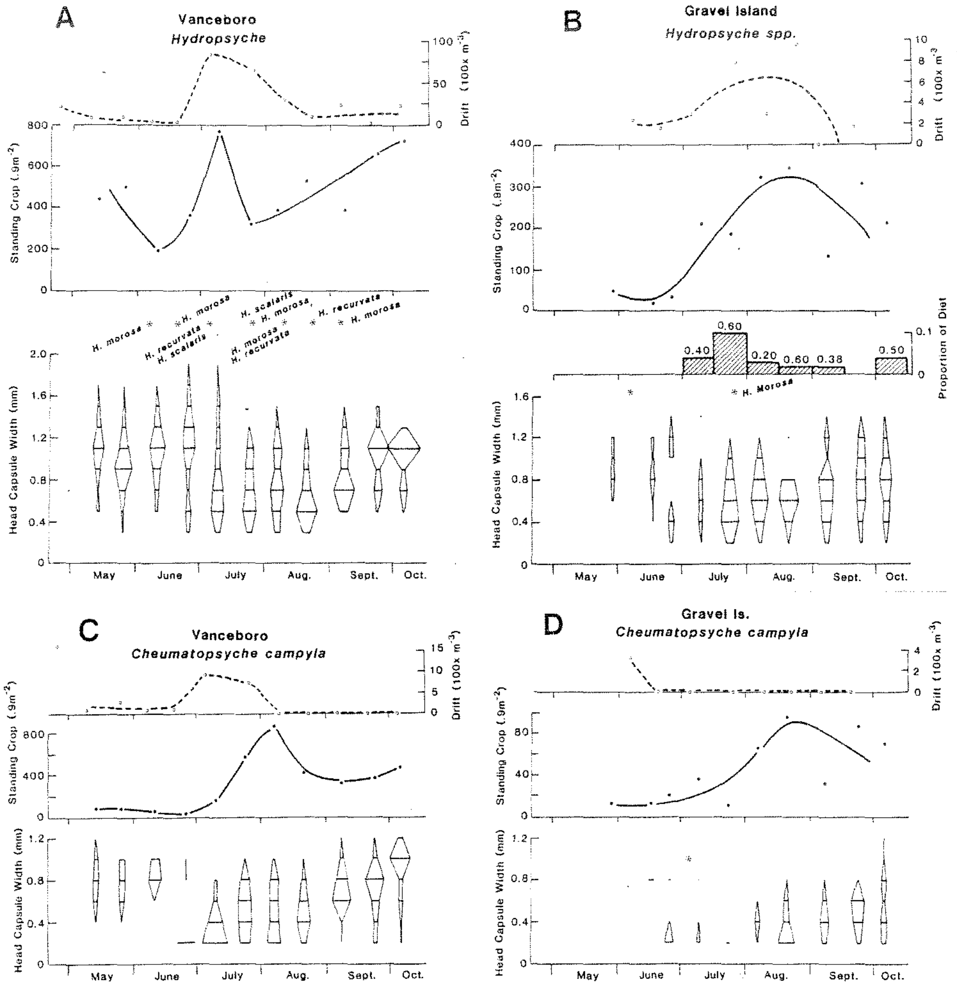

Fig. 5. Seasonal fluctuations in drift and benthic densities and head capsule measurements for the indicated larvae at the two study sites. Asterisks indicate times when adults of the indicated species were collected. Width of bars on head capsule measurements is proportional to numbers of capsules measured. Calibrations bar is shown at upper right of lower panel.

Decimal fractions above hatched bars indicate proportion of stomachs analyzed containing a given taxon.

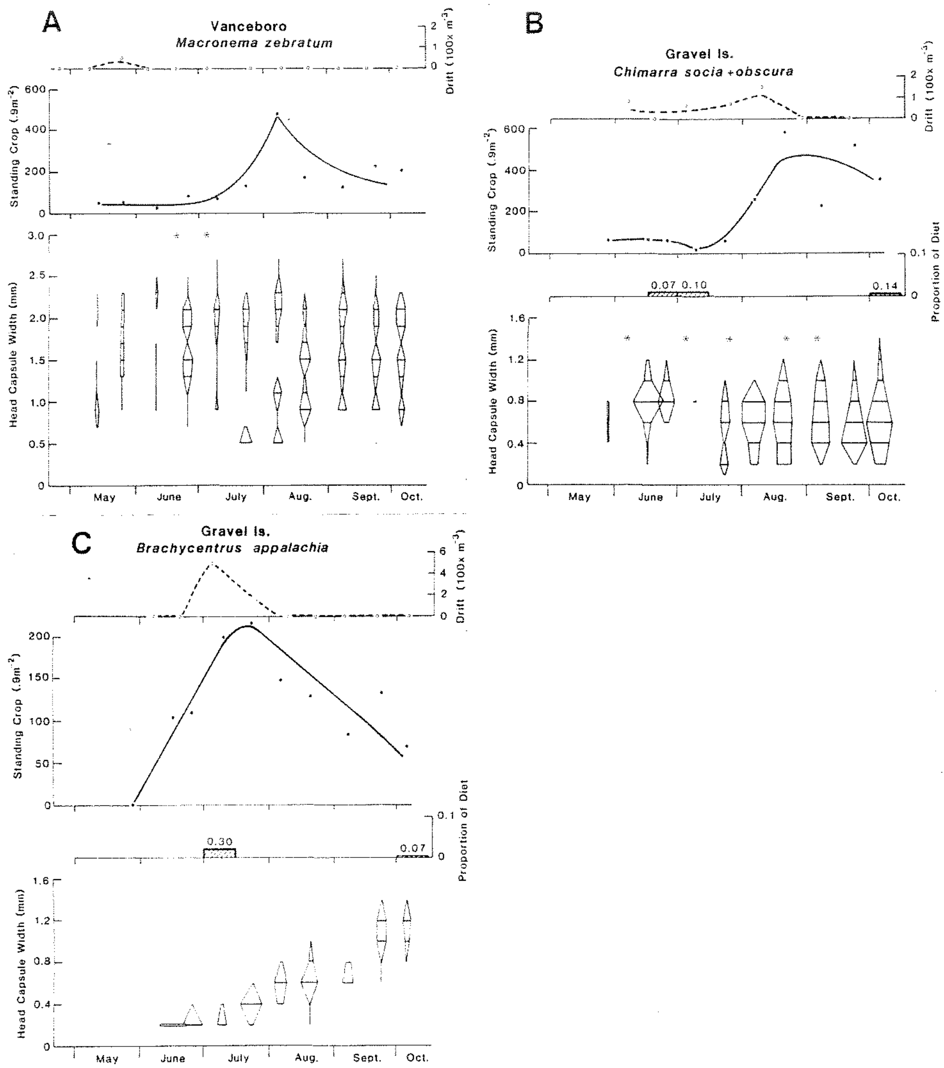

Fig. 6. Seasonal fluctuations in drift and benthic densities, and head capsule measurements for the indicated larvae at the two studies sites. Asterisks indicate times when adults of the indicated species were collected.

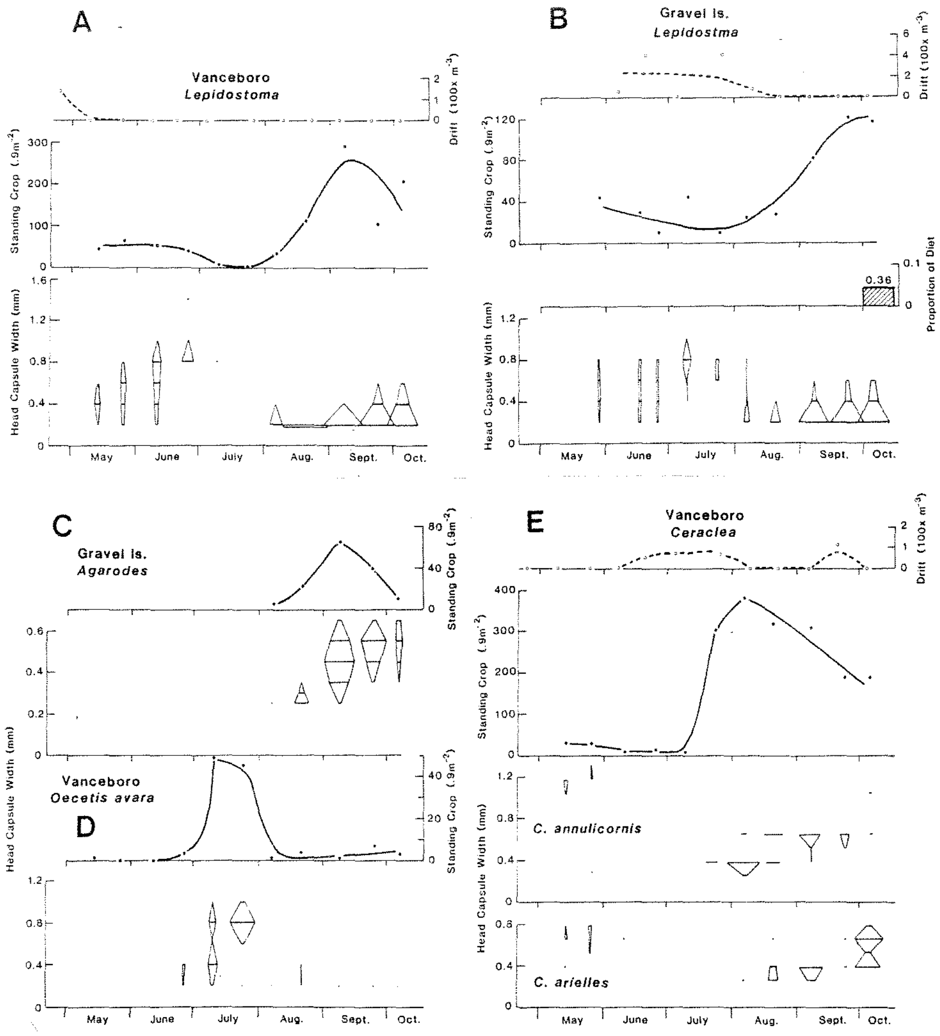

Fig. 7. Seasonal fluctuations in drift and benthic densities, and head capsule measurements for the indicated larvae at the two study sites.

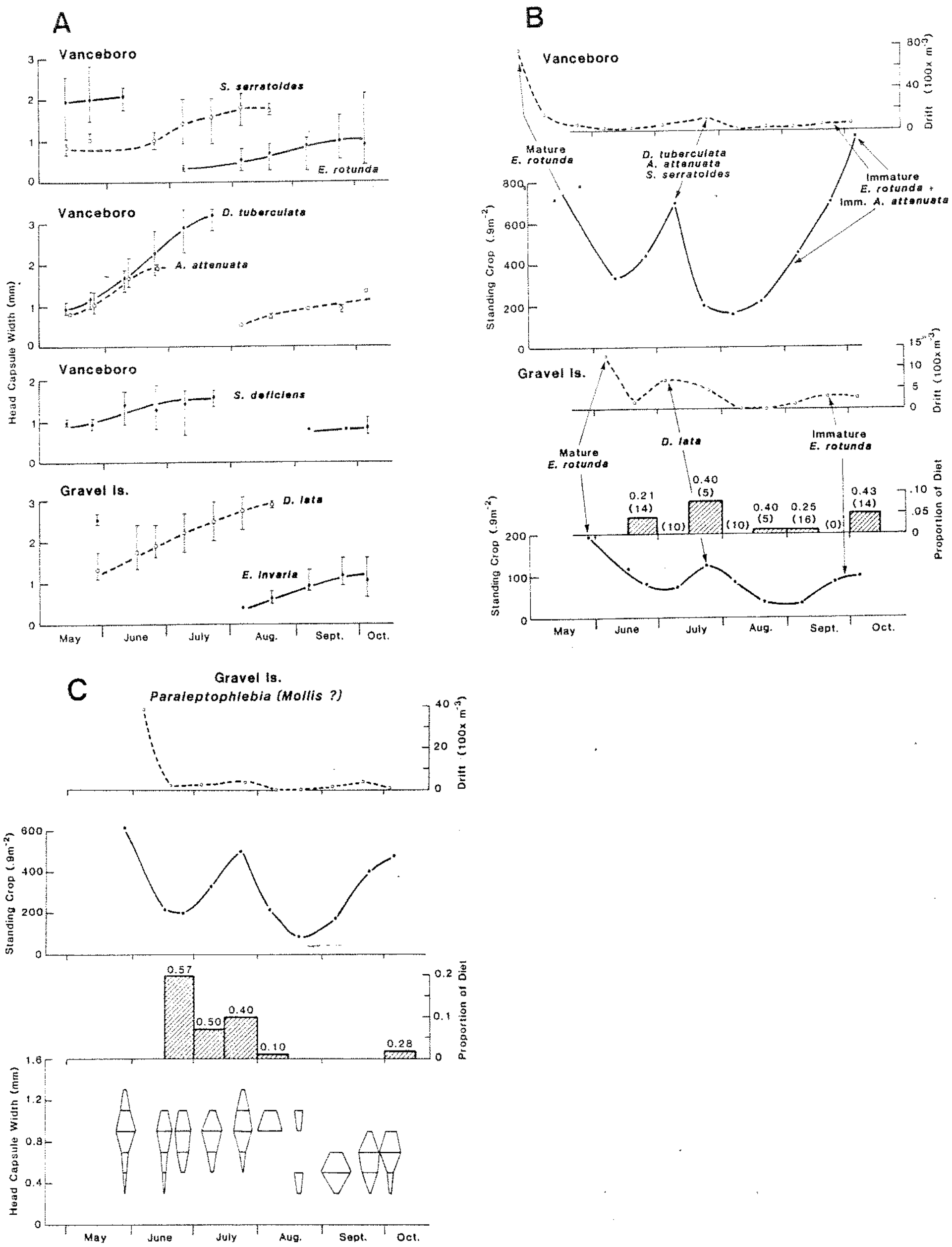

Fig. 8. Seasonal ranges of head capsule widths for the indicated mayfly nymphs sampled at the indicated study sites. Seasonal drift and benthic densities and proportions of salmon diet for the indicated Ephemerellidae mayfly nymphs and for Paraleptophlebia at the indicated study sites. For the Ephemerellidae, stomachs dissected are indicated in parentheses above each hatched bar. For Paraleptophlebia, lower panel gives numbers of measured head capsule widths for nymphs collected seasonally. Maximum bar width for head capsules equals 40 measurements.

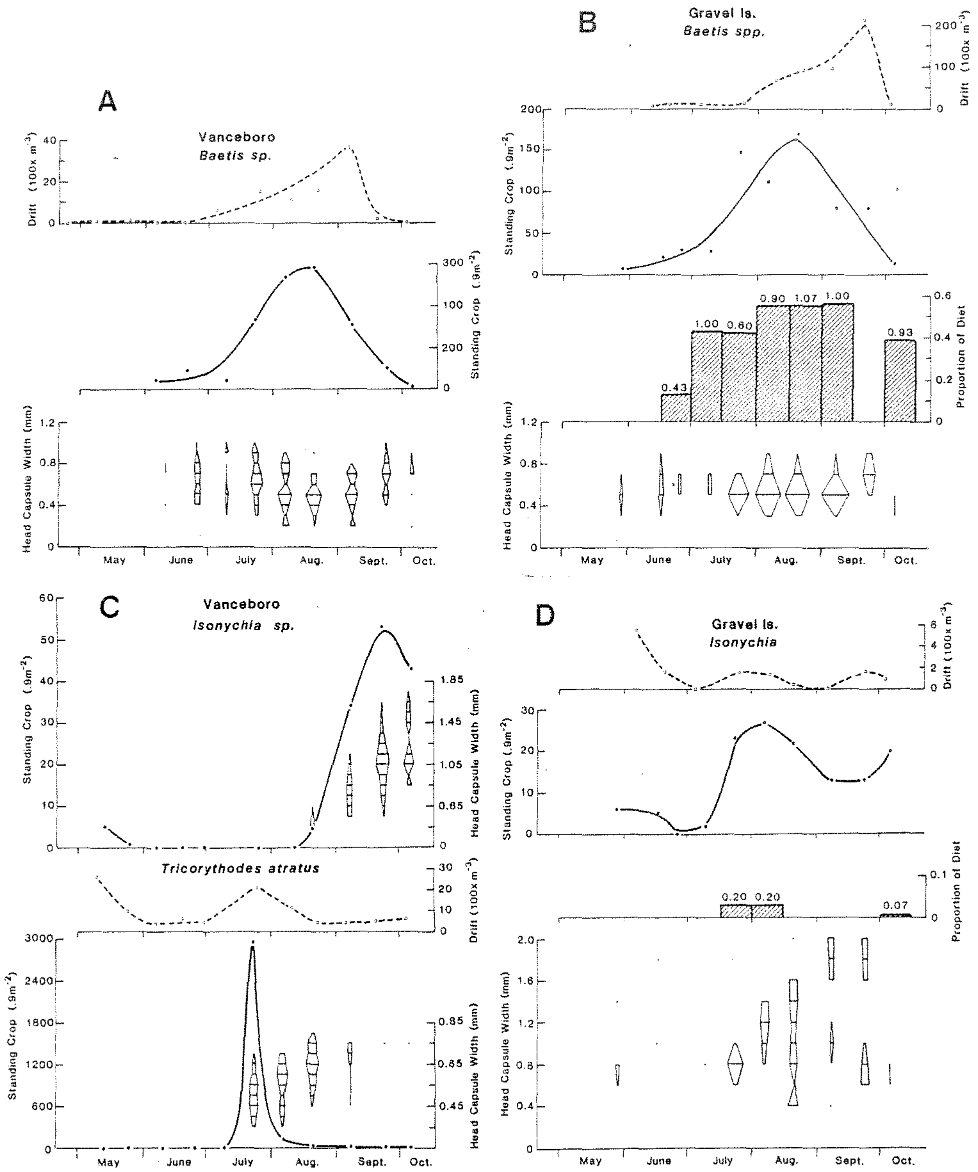

Fig. 9. Seasonal fluctuations in drift and benthic densities, and head capsule measurements for the indicated nymphs at the indicated study sites.

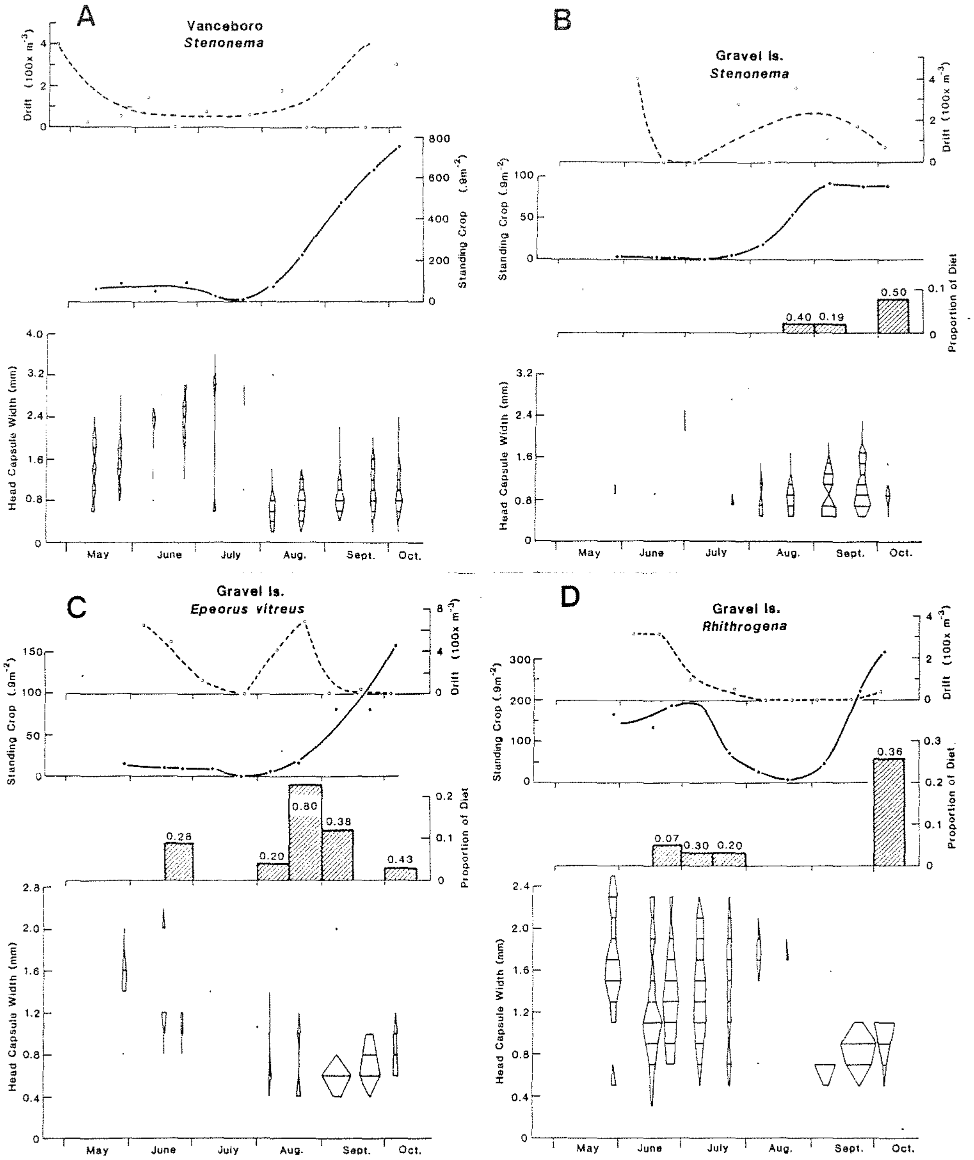

Fig. 10. Seasonal fluctuations in drift and benthic densities, and head capsule measurements for the indicated nymphs at the indicated study sites.

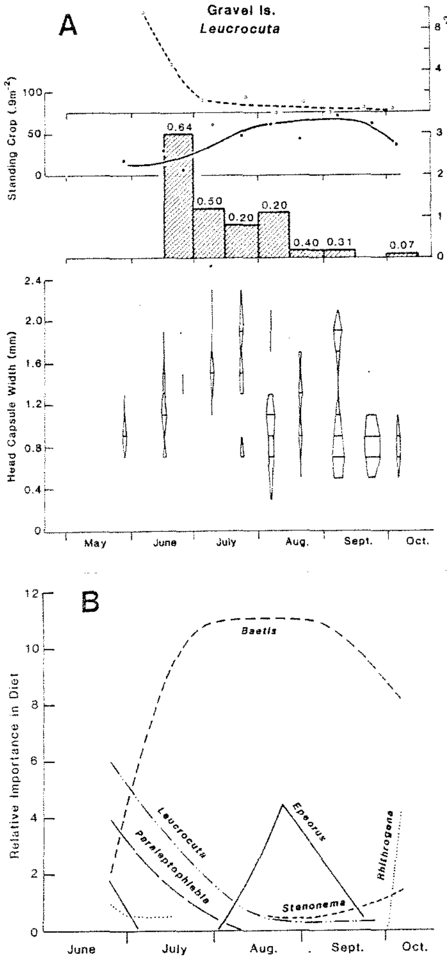

Fig. 11. Temporal variation in relative importance of various mayfly genera in salmon fry diets. Ordinate scale is arbitrary.

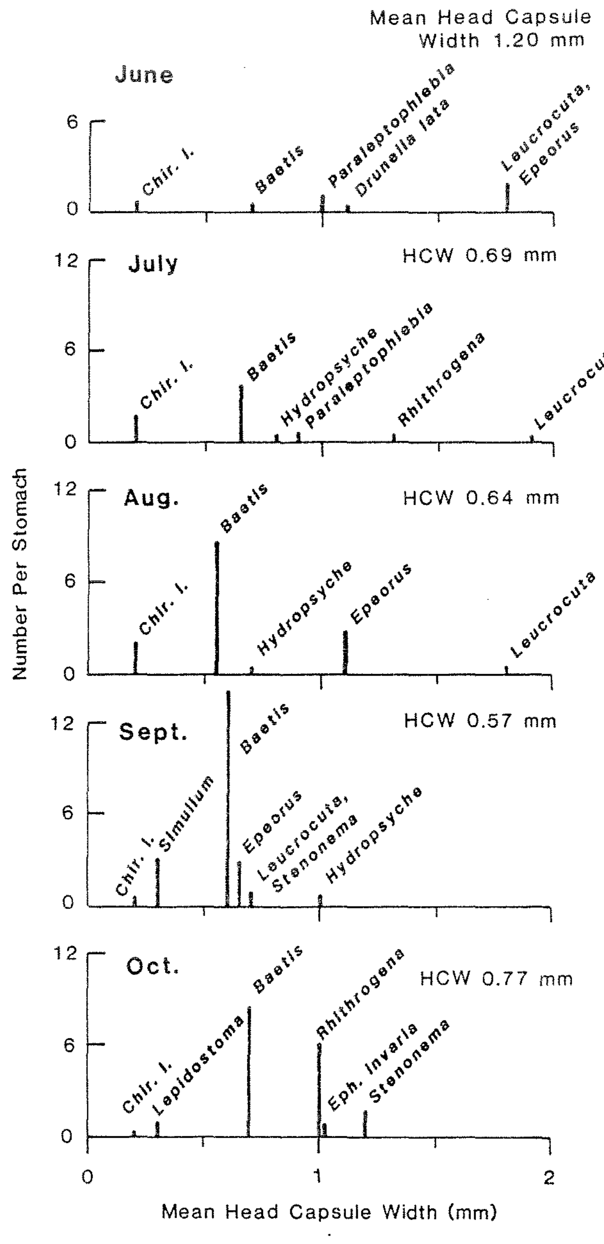

Fig. 12. The contribution of various taxa to Atlantic salmon fry diet for June-October. Taxa are arranged according to mean head capsule width. Mean head capsule widths for all taxa ingested are given at upper right for each month.

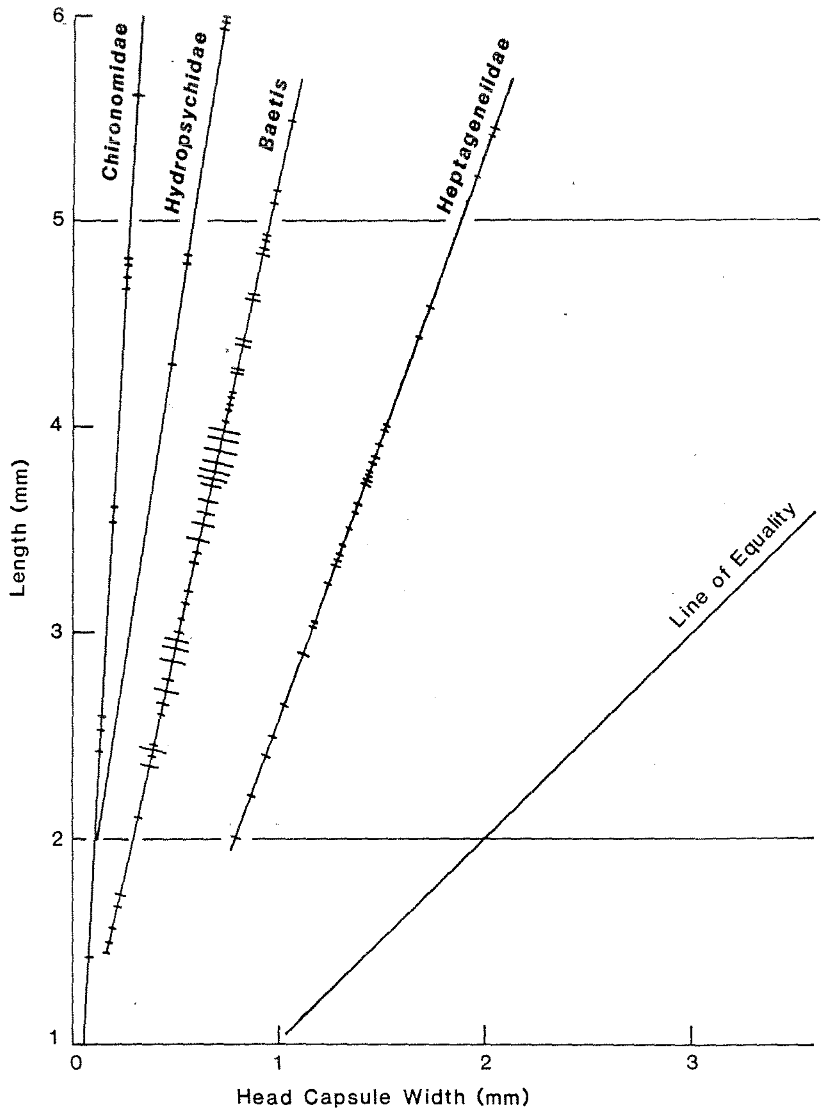

Fig. 13. Dimensions of organisms ingested by Atlantic salmon fry in the St. Croix River. The lines were fitted by eye from scatter diagrams generated from organisms collected in benthos samples. The slopes indicate length-head capsule width ratios. The crossbars indicate measurements from food items with the width of the crossbar proportional to the number of organisms measured. Maximum crossbar width is equivalent to five organisms.

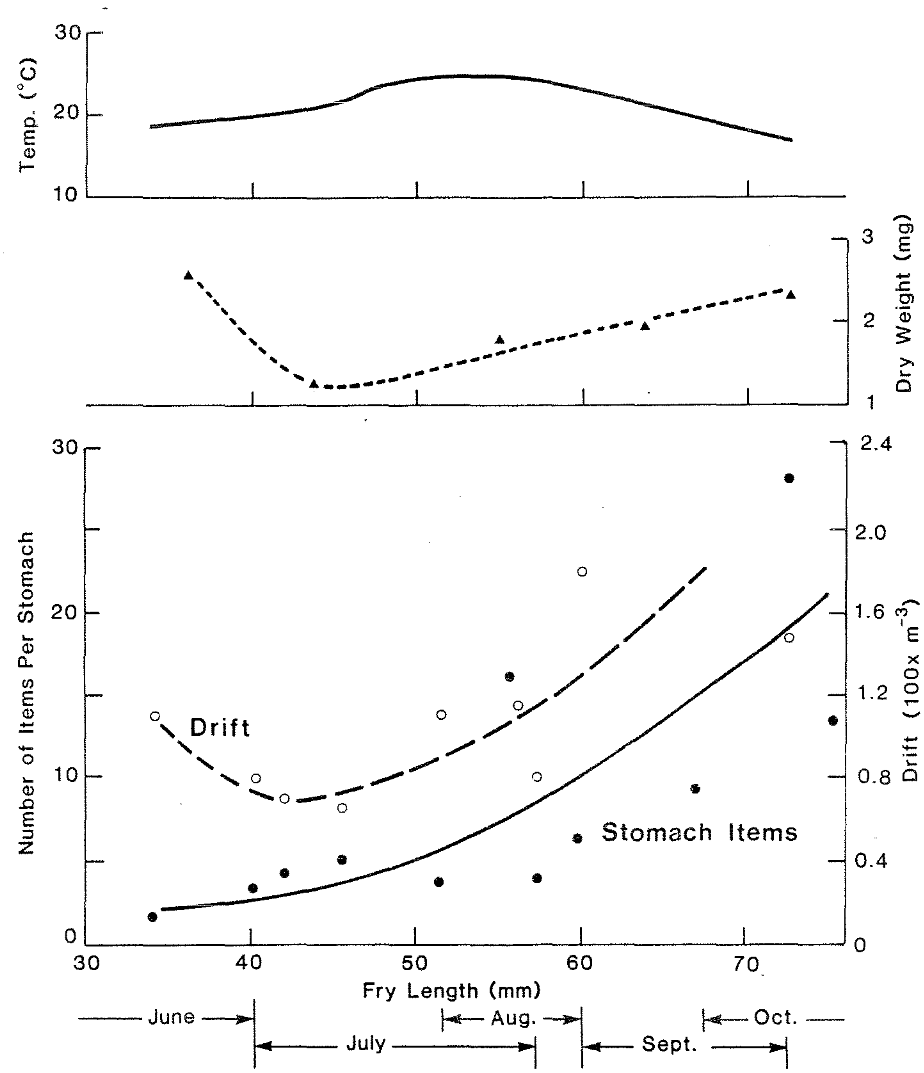

Fig. 14. Routine daytime St. Croix River temperatures (upper panel) and dry weights of salmon fry stomach contents (middle panel) are shown. Drift densities of consumable items (lower panel, open circles) and number of items per stomach (closed circles) are plotted versus fry fork-length. The range of fry lengths for each month of sampling is also indicated on the abscissa.

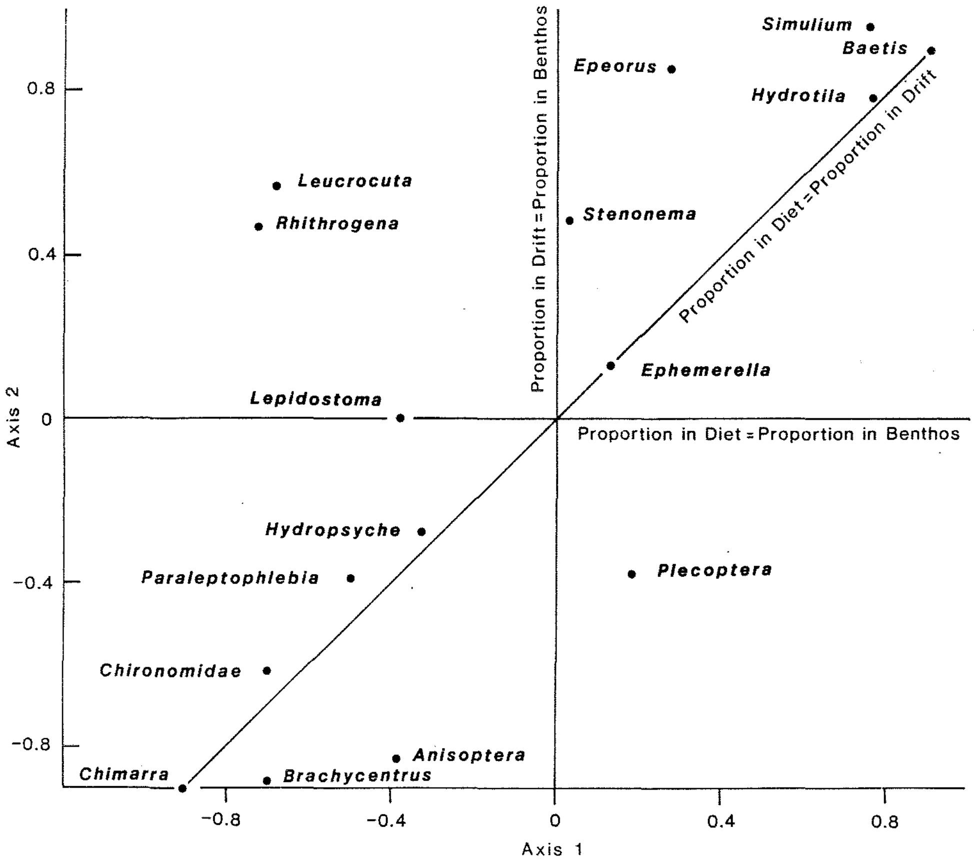

Fig. 15. Various organisms ingested by Atlantic salmon fry in the St. Croix River are arrayed on a "selectivity index" grid. Axis 2 represents drift densities relative to benthic densities. Axis 1 indicates selectivity indices relative to benthic densities. The diagonal is the locus of points equating selectivity index to drift density.

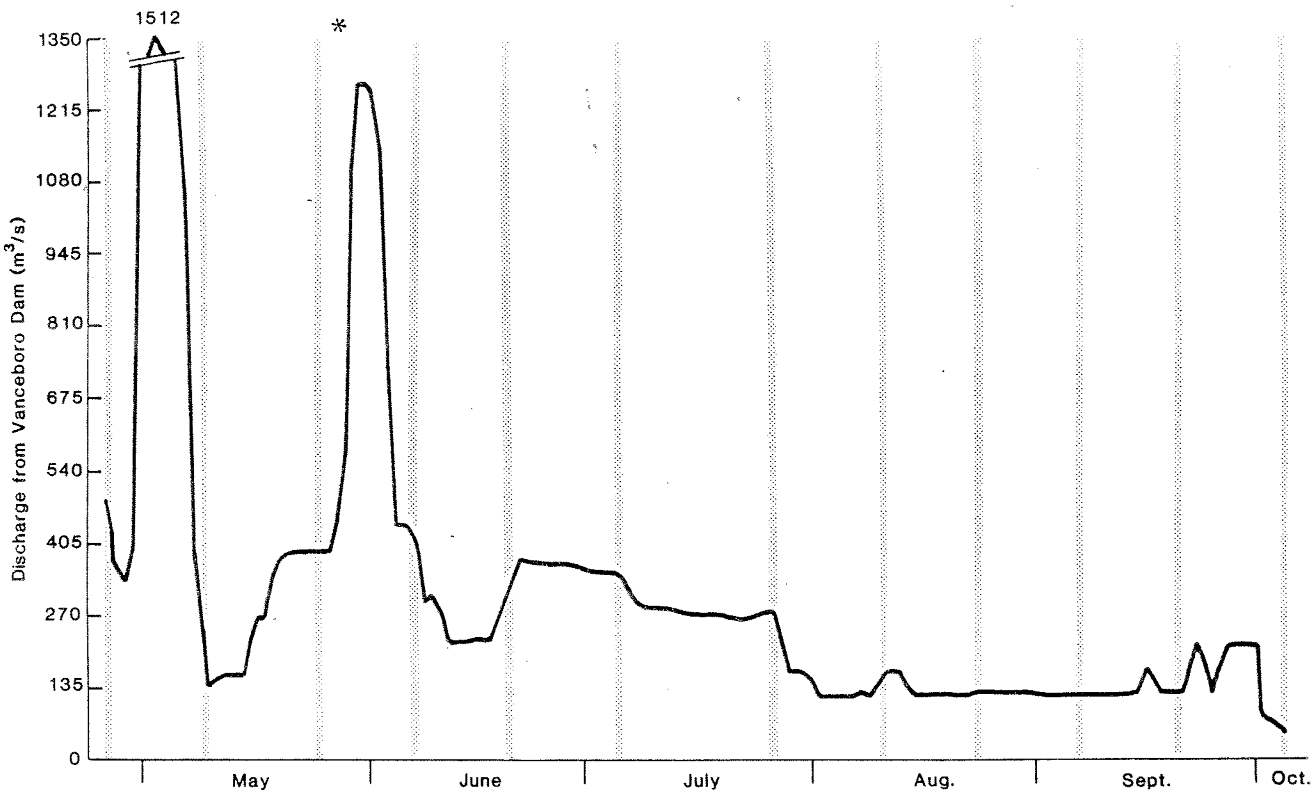

Fig. 16. Stream discharge at Vanceboro for April-October 1979 is indicated by the solid line. Stippled bars indicate periods of drift sampling. Asterisk indicates time of salmon fry releases.