THE ECOLOGY OF NET-SPINNING CADDISFLIES IN A NEWFOUNDLAND LAKE OUTLET

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The Ecology of Net-spinning Caddisflies
in a Newfoundland Lake Outlet

by

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ABSTRACT

The community of dominant species of net-spinning caddisflies found in the Axes Pond outlet -- an oligotrophic lake-stream system near Torbay, Newfoundland was investigated. The dominant species in the system included: Cheumatopsyche pettiti, Hydropsyche betteni, Hydropsyche slossonae, Hydropsyche sparna, Neureclipsis crepuscularis and Chimarra aterrima. Zonation existed in the abundance and distribution of these species along the stream within short distances from the lake outlet. H. betteni, C. pettiti and N. crepuscularis were predominant at the immediate lake outlet, while 60 meters downstream H. slossonae and H. sparna were predominant with large numbers of C. pettiti and N. crepuscularis present. Downstream from this point, C. aterrima was predominant. Biomass of net-spinning caddisfly larvae varied throughout the year and between stations. Highest values were generally reached at the immediate outlet during late spring or late fall and winter. Lowest values were observed at the sampling station furthest from the outlet during mid summer.

It is strongly suspected that density dependent drift resulted in a developmental gradient within the densest populations at the outlet. For any one generation, the modal instar number for a species population decreased with distance below the outlet.

Life-history patterns of the net-spinning caddisflies studied at Axes Pond were not necessarily comparable with those described for the same species on the mainland. Larvae of most species of hydropsychids studied at Axes Pond were larger at a given larval instar and overwintered in earlier larval instars than the same species studied on the mainland. With the exception of H. slossonae, which had a univoltine life cycle, all species studied had univoltine and/or semivoltine life cycles. This is the first report of a semivoltine life history in net-spinning caddisflies.

Large particles of lake-derived seston disappeared from the stream faster than smaller particles. This reduction in mean food particle size over distance downstream from the outlet corresponded with the feeding habits and zonation of the net-spinning caddisflies. In addition to differences in feeding habits it is postulated that these species may be able to exist together as a result of several other factors including temporal variation in life history and differences in habitat preference. These factors permit the existence of a complex guild of net-spinning caddisflies at a lake outlet.

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INTRODUCTION

Benthos production has not been measured in Newfoundland streams. Newfoundland streams are oligotrophic and, consequently, standing crop biomass would be expected to be low, with one notable exception -- lake outlets. From preliminary investigations and the work of others, it is known that the distribution of organisms along a stream system is not uniform and that enhanced productivity is found in stream outflows of lakes (eg. Oswood 1979). High outflow productivity is largely contributed by high densities of filter feeding insects such as net-spinning caddisflies and blackflies.

Lake outlets are unique in that biological and physical characteristics of lotic and lentic habitats merge. Variation in both the lake and stream characteristics produce a variety of lake outlet situations. Eutrophic lakes provide different inputs to the outlet stream than do oligotrophic lakes. Likewise, a shallow, fast flowing stream with rocky substrates may influence lake water in a far different way than a deep, slow moving stream with a sandy substrate. Moreover, within a given lake outlet system, seasonal and diurnal variation of biotic and abiotic components of both the lake and the stream add a dynamic dimension not normally seen in either habitat alone.

Stream temperatures at the outlet tend to reflect water temperature in the surface water of the lake. In temperate climates, outlet stream temperatures are generally warm in the summer, especially after lake stratification, and cold in winter although perhaps not as cold as areas further downstream as evidenced by the ice free character of the outlet. In fact, the lake acts as a buffer to rapid changes in temperature producing slower warming in spring and slower cooling in fall (Ulfstrand 1968). It should be noted that this effect is observed primarily at the outlet and its immediate area. As water travels downstream, even a short distance, the water temperature begins to reflect the air temperature, particularly in shallow turbulent streams.

The most important influence of lakes on streams is the movement of organic material produced in the lake into the stream. Chandler (1937), Cushing (1963), Maciolek and Tunzi (1968), Ulfstrand (1968), Ward (1975) and Carlsson et al. (1977) among others, have shown that lakes supply large amounts of organic materials to downstream areas. Again, there are large temporal variations in densities of phyto- and zooplankters of lakes producing corresponding pulses in the lake effluent. Furthermore, many plankters, particularly zooplankters, undergo circadian changes in behaviour and location, particularly in depth. This imposes diurnal changes in organic inputs to the stream, superimposed on the seasonal changes. A lake may further change the character of organic matter in the lake effluent by acting as a settling basin for incoming detritus (Maciolek 1966). Thus water at the outlet is enriched in cellular material (plankters) and diminished in detritus.

Interest in detrital processes in aquatic systems has steadily increased during the last decade. Both the trophic importance of detritus and the role of detritus as an organizing factor in aquatic systems have been emphasized. "It is becoming apparent ... that the trophic dynamic structure of aquatic systems depends operationally on a dynamic detrital structure. Common to both lake and stream system is the total dominance of detrital metabolism which gives the system a metabolic stability" (Wetzel 1975). Most running water systems are based largely ~~on~~ allochthonous energy resources which enter the food chain as detritus (Fisher and Likens 1972, Hynes 1963, Boling et al. 1975, Hynes 1970, Cummins 1974, Vannote et al. 1980, Wetzel 1975). However, most work on detrital processing in lotic systems has been focused on large particulate detritus especially leaf material. Much less is known about the dynamics of suspended particulate matter (seston). "A large part of consumer production in mountain streams is based on the occurrence of organic particles carried in suspension. This is especially manifest in the relative abundance of primary consumers, such as simuliid larvae, that are uniquely adapted for feeding upon transient seston particles. Seston contributes secondarily to stream trophic ecology when it settles or adheres to the substrate and is utilized there by grazing fauna. Despite its trophic importance, suspended organic matter in rhithron type streams is poorly known" (Maciolek 1966). The components of seston include not only detritus (including dead organisms and colloidal material) but also phyto- and zooplankton.

In many ways lake outlets are ideal locations for the study of suspended organic material. The lake provides a point source of seston (particularly the plankton component). Changes in seston concentration and composition downstream from the outlet may then be examined. Reif (1939) collected phyto- and zooplankton in small lake outlet streams. He noted a general decrease in concentration downstream and a change in composition. This was also observed by several other authors (Chandler 1937, Ulfstrand 1968, Gibson and Galbraith 1975). Reif noted in particular that colonial algae and robust diatoms traveled further downstream than zooplankton. Similar results were observed by Maciolek (1966) and Egglishaw and Shackley (1971). Cushing (1963) compared plankton above and below a series of lakes on the Montreal River, Saskatchewan. Both phyto- and zooplankton were more numerous below the lakes than above. Particulate amorphous organic matter was, however, less abundant below the lakes than above.

Maciolek and Tunzi (1968) studied longitudinal patterns of seston concentration and composition below a lake outlet. They concluded that changes in seston composition and concentration were the result of a dynamic balance between supply and removal. The most important component of supply was the effluent limnoplankton, followed in importance by terrestrial vegetation and in turn by aufwuchs. Seston losses were primarily due to the large numbers of filter-feeding invertebrates (almost entirely larvae of Simuliidae). Sedimentation and physical breakdown of seston were of much lesser importance. This relationship between outlet production and the nature and quantity of seston originating from the lake has been observed by several other workers (Carlsson et al. 1977, Wotton 1978, Oswood 1979). Muller (1955) made a similar association. He stated, "Investigations of the nutrition of these larvae (Hydropsyche, Neureclipsis, Plectrocnemia, Simulium, Orthocladiinae) showed that they are almost exclusively restricted to feeding on the phyto- and zooplankton, which are drifting out of the lake into the river. On this account, the amount of the larvae always depends on the production of the plankton in the lake lying above the rapids." While this is basically true, it is not clear if specific portions of lake-derived seston are more important than other portions in producing the "lake outlet effect". It is furthermore not clear whether lake outlets create secondary effects (eg. changes in flora) which are in part responsible for densities of filter-feeders.

Hynes (1970:259) summarized the results of most previous investigations as follows: "We can conclude, therefore, that although a lake or pond on the course of a river or stream produces a great increase of passively feeding organisms and to some extent of others as well, possibly indirectly, the effect is manifest over only a fairly short distance. This is doubtless because ... the still-water plankton is rapidly eliminated, and presumably much of this elimination is caused by the benthic fauna itself." Hynes (1970) noted three major features of the fauna (particularly insects): 1) an increase, often dramatic, in the density of filter-feeding organisms, 2) general increases in the production of biomass, and 3) rapid changes in the fauna as one progresses downstream. Particularly prevalent at lake outlets are large numbers of filter-feeding Trichoptera (particularly Hydropsychidae) and/or Diptera (Simuliidae). In fact, some species of Simuliidae appear to be confined to lake outlets (Colbo 1979, Larson and Colbo 1983, Hynes 1970, Ulfstrand 1968).

In both composition and density, the fauna of lake outlets is unique. The enhanced benthic fauna production at lake outflows has been studied by several limnologists (eg. Armitage 1976, Illies 1956, Muller 1955, Oswood 1976, 1979, Sheldon and Oswood 1977) but only a few studies dealt with boreal systems (eg. Gibson and Galbraith 1975, Ulfstrand 1968, and Wotton 1978). In addition, the studies vary widely in terms of distance between sampling stations and the outlet. The lake outlet community is often dominated by filter-feeders. The net-spinning caddisflies (Hydropsychidae, Polycentropodidae, Philopotamidae) and/or blackfly larvae (Diptera: Simuliidae) may reach astounding numbers. Muller (1956, cited by Hynes 1970) found <u>Hydropsyche</u> larvae in densities of over 50 million per hectare. Cushing (1963) found 3,340 campodeiform Trichoptera per square foot below a series of lakes on the Montreal River, Saskatchewan. In contrast, Ulfstrand (1968) in a comparison of Lapland rivers, found no evidence of increased dominance of Hydropsychidae. He did, however, find a remarkable production of blackfly larvae (3 grams per square meter per day). He estimated annual blackfly production at a lake outlet at 100 kg. over an area of approximately 100 square meters.

Given the extremely high densities of filter-feeders, Oswood (1976) suggested that competition might give rise to two observable phenomena. The first was development of behavioural, physiological, and/or morphological adaptations to lake outlet conditions such that some species were particularly dependent on lake outlet conditions. The second, and more important, was ecological divergence of the competing species.

As Muller (1956) and Hynes (1970) pointed out, high densities of passive feeders do not usually persist far below the lake outlet. Illies (1956) demonstrated a reduction in passive feeders (3197.0 mg/1000 square centimeters to 767.5 mg/ 1000 square centimeters) within 200 meters. He, furthermore, showed a sequential replacement of filter-feeders from Polycentropus at the outlet to Neureclipsis, Hydropsyche, and Simulium.

Newfoundland stream systems have been commonly found with high densities of Hydropsychidae at lake outlets (Larson and Colbo 1983). Hydropsychid larvae are an important member not only of lake outlet faunas but of running water in general. The caddisflies compose 8 to 13 percent of all river fauna and the Hydropsychidae constitute approximately 80 percent (by number) of all stream Trichoptera larvae (Roback 1962, cited by Gordon and Wallace 1975). The study of a lake outlet seemed ideal for the investigation not only of the biology of the Hydropsychidae and other net-spinning caddisflies as components of the lake outlet fauna as it pertains to an oligotrophic lake but also their comparative ecology as important members of the stream fauna.

The comparative approach to the ecology of related stream insects seems to be a particularly fruitful one. As pointed out by Grant and Mackay (1969), related species should inherit similar adaptive systems. When sympatric, such species must compete for commonly required resources. There are three principal niche components available for diversification: time, food and space (Pianka 1975). Competing organisms may decrease competition by diverging along any or all of these axes. The relative importance of time, food, or space in allowing coexistence is dependent, of course, on the organisms involved and the ecological situation. Grant and Mackay (1969) studied pairs of related stream insects in several orders and found time (life history) differences to be more important than habitat differences. Hynes (1970) mentioned several examples of habitat segregation in similar species. Mackay and Kalff (1973) studied two species of Pycnopsyche (Trichoptera: Limnephilidae) and found differences in the allochthonous organic materials (leaves and detritus) utilized as habitat. Williams and Hynes (1973), in a comparison of microdistribution, feeding and life history patterns, found no differences in two species of Hydropsychidae but found interfamilial differences in microhabitat and food (especially on a seasonal basis) between the two hydropsychid species and Chimarra (Trichoptera: Philopotamidae). Wallace (1975a,b) has investigated the ecology of Hydropsychidae in a comparative systematic manner. Comparison of three species of Hydropsychidae (in three genera) showed differences in construction of the feeding nets and retreats, spatial distribution within and on the substrate, and size and type of food particles ingested.

Hydropsychid life history patterns as described by Edington (1965), Ross (1944), Sprules (1947) and Williams and Hynes (1973) have several points in common. The hydropsychids have a univoltine life cycle. Adults emerge in spring to early fall. The eggs hatch over a considerable length of time, leading to prolonged recruitment of early instars. However, Sprules (1947) and Mackay (1979) have found evidence from emergence data that some Canadian Hydropsychidae produce two generations per year. Multivoltine life history patterns appear to be very rare in the Trichoptera as a whole. As Grant and Mackay (1969) point out, since feeding structures and habits change with age, life history separation may be particularly effective in partitioning of food by size and type between species.

Food habits of the Hydropsychidae and many of the other net-spinning caddisflies have been investigated by many workers (Percival and Whitehead 1929, Cummins et al. 1966, Coffman et al. 1971, Wallace 1975a,b). An excellent paper by Fuller (1980) describes the feeding ecology of many hydropsychid caddisfly larvae, some of which occur at Axes Brook.

Microhabitat (ie, substrate preference, velocity requirements etc.) of the Hydropsychidae has been investigated in a variety of ways. Some papers were largely observational (Percival and Whitehead 1929, Scott 1958, Sprules 1947). In general, these authors have shown that the hydropsychids prefer shallow, fast water flowing over relatively large substrate particles. An experimental approach was taken by Edington (1965, 1968) and Philipsen (1954, 1969). Their studies showed that velocity strongly influences distribution of Hydropsychidae. Net-spinning behaviour is positively correlated with velocity. Hydropsychidae nets appear to function in relatively rapid (15-100+ cm/sec) water velocities (Edington 1968). Experimental blockage of stream flow with baffles results in dispersal of hydropsychid larvae from the area of lowered flow (Edington 1965, 1968). Hydropsychidae, furthermore, appear to require relatively high oxygen concentration in still water but are similar to other Trichoptera if the water is flowing (Philipson 1954).

At this point, it should be reemphasized that lake outlets are much more complex than a guild of filter-feeders straining lake organisms. The lake is a perturbation of the stream ecosystem. The manner in which variables return to steady state values can tell us much about the "normal" dynamics of streams. By examination of concurrent changes in important variables as water proceeds from the outlet downstream, one can frame hypotheses about the functional relationships between such variables. The existence and nature of these relationships constitute a portion of the knowledge necessary to make functional such general models of the stream ecosystem as those of Boling <u>et al.</u> (1975) and Hynes (1970) and the river continuum concept (Vannote <u>et al.</u> 1980). Furthermore, the changing physical and biological conditions downstream from the lake outlet form a succession of environments. Observance of species replacement may lead to indirect information about differing functional niches and the changing competitive patterns.

Should these observations be associated with more direct measurements of niche make-up for each species, including resource and habitat partitioning, some theoretical basis of community structure may be obtained.

Preliminary surveys of Axes Pond outlet indicated a species complex of net-spinning caddisfly larvae with very high densities at the lake outlet and rapidly declining densities downstream. These larvae, furthermore, appeared to have species specific patterns of longitudinal distribution below the lake outlet, particularly among members of the Hydropsychidae. With this in mind, the overall objectives of this study were to examine: the life history of the dominant net-spinning caddisflies in a Newfoundland lake outflow; aspects of their ecology which relate directly to the existence of a lake outlet in the immediate area; and the effects of a trophic gradient of lake seston, as it is progressively reduced by filter feeders, on the standing crop and structure of stream benthos communities.

MATERIALS AND METHODS

Benthic insect samples were taken from January to December, 1983, with either a 0.1 square meter Hess-type sampler (March-August) or a standard Surber sampler (0.093 square meters).

The Hess-type sampler (Figure 1) was constructed out of 3.17 mm steel plate. Four large holes were cut in the upstream face of the cylinder and covered with 1 mm. copper mesh. The downstream face had one large hole (24x24 cm) which led into the capture net. The capture net consisted of a cone shaped section of fine mesh nylon netting (80 mesh/cm) which lead from the sampler to the end of a 10 cm piece of metal piping, 13.5 cm in diameter, to which it was fastened with a ring-clamp. To the other end of this piping was attached a 50 cm long 'bag' of coarser nylon netting (45 mesh/cm). This 'bag' was designed to be detachable, being held in place by a series of metal hooks. The main disadvantage of this sampler was its weight but this was an asset when sampling during spring floods.

FIGURE 1. Photograph showing details of the Hess-type benthic sampler. (Taken at Station 'C')

The Surber sampler (1mm mesh) was used during the winter months because of its portability and the assumption that, during these months, a large proportion of the larvae would be in their later instars (IV and V) (Mackay 1979) and thus easily retained in a Surber sampler. This assumption proved to be invalid in several cases.

Preliminary surveys indicated that changes in faunal density and diversity occurred very rapidly near the outlet. Therefore, sample stations were closer together near the outlet than downstream. Sampling stations 'A'-'D' were established at four sites which appeared similar physically but which differed in location relative to the lake outlet. Distances between stations were measured directly during a topographic survey of the stream (Figure 2). Sites were selected which contained similar habitats (ie fairly fast flowing water (>=20 cm/sec), rocky substrate and similar mean depth) (Table 1). Mean stream width and its components, riffle width and pool width, were determined from 5 transects at each station. Mean substrate composition was determined by measuring the length of each transect over which substrates were present. Subtrates ranged in size from boulder (>30cm) to fine organic debris and silt. Bank vegetation was quantified using a simple index. The index total for each station was 2 units (1 unit for each bank). Percent composition of the various types of vegetation was estimated for each bank and summed to give a final index value for each vegetation type at each station.

FIGURE 2. Vertical profile of Axes Brook showing Stations 'A' - 'D'.

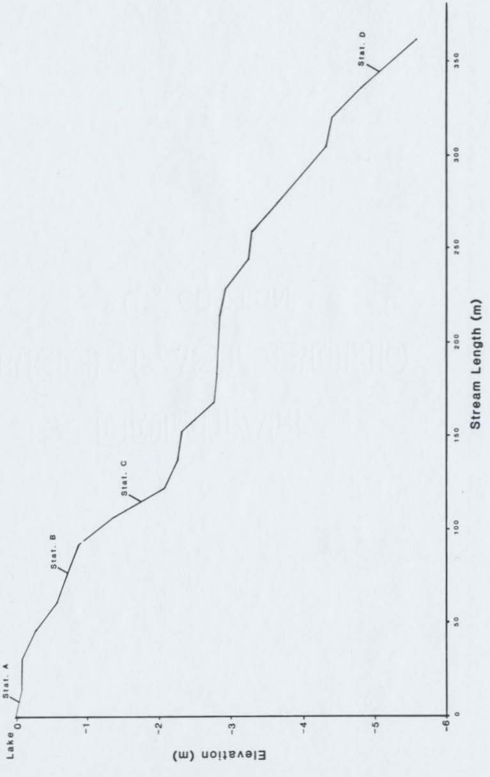

Lake
Stat. A
Stat. B
Stat. C
Stat. D
Elevation (m)
0
-1
-2
-3
-4
-5
-6
Stream Length (m)
0
50
100
150
200
250
300
350

TABLE 1. Physical attributes of Axes Brook sampling stations 'A' - 'D'. (Note: Standard deviations for Depth and Velocity are given in parentheses).

Parameter	A	%	B	%	C	%	D	%
Total Width (m)	4.66	-	4.48	-	3.93	-	3.54	-
Riffle Width (m)	3.75	80.5	3.54	79.0	3.60	91.6	3.35	94.6
Pool Width (m)	0.91	19.5	0.94	21.0	0.34	8.7	0.18	5.1
Substrate (m)								
(a) Boulder(>30cm)	0.37	7.9	0.82	18.3	0.52	13.2	0.79	22.3
(b) Rubble(30-3.75cm)	3.20	68.7	3.02	67.4	3.26	83.0	2.29	64.7
(c) Gravel(<3.75cm)	0.82	17.6	0.24	5.4	0.09	2.3	0.27	64.7
(d) Sand and Silt	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(e) Organic	0.09	1.9	0.40	8.9	0.03	0.8	0.12	3.4
Bank Vegetation								
(a) Forest	0.4		1.4		2.0		0.4	
(b) Brush	1.6		0.6		0.0		0.8	
(c) Open	0.0		0.0		0.0		0.8	
Channel Depth (cm)	20.2 (4.00)		19.7 (5.39)		19.8 (5.91)		18.9 (5.40)	
Velocity (cm/sec)	20.0 (11.8)		22.0 (23.5)		26.0 (12.7)		32.0 (15.4)	
Gradient (m/15.25m)	0.1		0.16		0.69		0.45	
Chemistry (means values for 1982)								
(a) pH	5.95							
(b) conductivity (umho)	42							

Mean channel depth and current velocity were calculated from 15 sets of measurements made at each station (3 measurements each per transect).

Selection of sample sites from within stations in running water studies presents several difficulties. Random sampling is too inefficient (Cummins 1975, Elliott 1971). Instead, some form of stratified random sampling is usually recommended. This is the method I used in as much as locations were randomly selected within the sampling station from areas which had a current of at least 20 cm/sec on the given sampling day. Between March and August, three samples were taken from each station with the Hess-type sampler. At other times of the year only a single sample was taken from each station with the Surber sampler. Sampling of the same location within a sample site was avoided for at least 2 months so as to avoid areas of recently disturbed substrate.

The benthic insect samples were preserved in Kahle's fluid (Wiggins 1977) until sorted. Sorting was performed in a white enamel pan without the aid of magnifying lenses. The insects thus collected were stored in 70% ethanol for further species and instar identifications. Trichopteran larvae and associated pupae and adults were sorted to genus according to Wiggins (1977). Specimens were identified to species using the literature when adequate taxonomic keys were available. Also, identifications were made and checked through association of larvae with pharate male pupae (metamorphotype method of identification, Milne 1938).

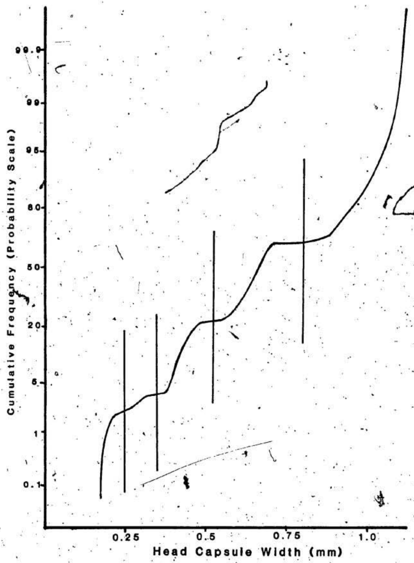
Interocular head capsule widths were measured to the nearest 0.05 mm using an ocular micrometer. Instars were readily determined by using head capsule width - frequency distributions plotted on probability graph paper (Mackay 1978) (Figure 3). Non-caddisfly insects were stored for future considerations, but were not dealt with in this study.

Adults were sampled with aerial nets and emergence traps from June - August.

Six species of net-spinning Trichoptera were examined in some detail: Cheumatopsyche pettiti (Banks), Hydropsyche betteni Ross, Hydropsyche slossonae Banks, Hydropsyche sparna Ross, Neureclipsis crepuscularis (Walker), and Chimarra aterrima Hagen. Biomass for each species was calculated based on mean wet weights of instars III-V obtained from a Cahn milligram balance (Appendix 1). Smaller instars, it was assumed, contributed little to the biomass of each species. Weighed larvae were freshly killed in Kahle's fluid and two hours later patted dry and weighed to the nearest hundredth of a milligram.

Gut contents of fifth instar larvae were examined for 4 specimens of each species. Data thus obtained was strictly qualitative and meant to be used for comparison with mainland data (Fuller 1980), comparison of diet between species and to determine the presence or absence of lake derived plankton.

FIGURE 3. Instar determination using a plot of head capsule width cumulative frequencies. Vertical lines delimit the range within each instar while the ascending portion of the graph illustrates the most abundant head capsule widths per instar. (Figure depicts the data for <u>Cheumatopsyche pettiti</u>)


99.9
99
95
80
50
20
5
1
0.1
Cumulative Frequency (Probability Scale)
0.25
0.5
0.75
1.0
Head Capsule Width (mm)

Zooplankton samples were collected by submerging a plankton tow net for 1 minute. Each sample was associated with a measurement of average depth and current velocity (Appendix 2). Velocity was determined using a float over a measured distance. Velocities thus obtained were related to a standardized propellered flow meter for actual mid water velocities. The volume filtered was determined using the current velocity and cross-sectional area of the plankton net opening. Samples thus collected were preserved in 70% ethanol. Phytoplankton samples were collected in Lugol's iodine solution. One liter of water was filtered at the site on glass fibre filter paper and stored in the dark until returning to the lab. At the lab, these filtered samples (seston) were frozen at -20° C (an elapsed time between filtering and freezing of approximately 2 hours).

Zooplankton samples were subsampled (10% of each sample) and individual plankters were counted and body length measured using the Zeiss MOP-3 digitizer. Each phytoplankton sample was placed in a 5 ml settling tower for 48 hours, after which time the excess fluid was removed and the settled material allowed to dry on a glass slide at 30° C. This slide was later examined on an inverted microscope and quantified. Frozen seston samples were dryed at 60° C for at least 4 days, weighed on a Cahn microgram balance and then ashed at 430° C in a muffle furnace for 6.5 hours and weighed again as before. The difference in weight was then recorded as the ash-free dry weight of the seston.

RESULTS

The Study Area

The study area is located in the Piccos Brook drainage area of the northeast Avalon Peninsula, Newfoundland. Piccos Brook originates in Piccos Pond at an elevation of 229 meters (750 feet) and flows into Tor Bay.

The lake outlet system studied was that of a presently unnamed stream which drains out of Axes Pond. The outlet itself is easily defined by an acute narrowing of the pond and a readily observable increase in water flow rate. This tributary of Piccos Brook (henceforth called Axes Brook) and Axes Pond lie on deposits of Hadrynian slate, siltstone, greywacke, conglomerate and various minor volcanic rocks. Some of the water entering Axes Pond, however, may pass through areas of acidic volcanic rock (Murray and Harmon 1969). Axes Pond, as are many ponds in the area, is oligotrophic. This is due in part to the regional geology already mentioned, low conductivity (42 umho) and a mildly acidic pH (5.95) due primarily to bog run-off.

Axes Brook is a rhithron-type stream, approximately 1.125 km in length, which drains Axes Pond at its eastern end. Direct discharge measurements were not obtained but measurements from a nearby monitered stream (Northwest Brook) (Figure 4) indicate a peak flow during the spring followed by a short period of very low discharge during July and August. It does not freeze during winter but does have intermittent ice cover. Surrounding vegetation consisted largely of Black spruce (<u>Picea mariana</u>), Balsam fir (<u>Abies balsamae</u>) and Ericaceous shrubs.

Air temperatures were cool (Figure 5), seldom reaching temperatures in excess of 20^{0} C. Mean temperatures in excess of 10^{0} C were observed over a short period during the summer (June-September). Water temperatures were not taken due to their variable nature but streams in the area of Axes Pond which have had continuous temperature monitering seldom exceed 20^{0} C and show a slight lag behind major air temperature shifts (Larson and Colbo 1983, Figure 6).

The outlet itself comprised station 'A'. It was fairly uniform in depth and remained submerged at all times during the year. The right bank was open, the vegetation consisting mainly of typical wet land vegetation (Erecaceous shrubs, sedges etc). The left bank was more shaded, having a few stunted black spruce and larger shrubs. Station 'B' was located a short distance downstream at the first major bend in the stream (60 meters below the outlet). Its depth profile was skewed such that the deepest channel of water

FIGURE 4. Mean monthly discharge for Northwest Brook, Newfoundland. (1982 and 1983)

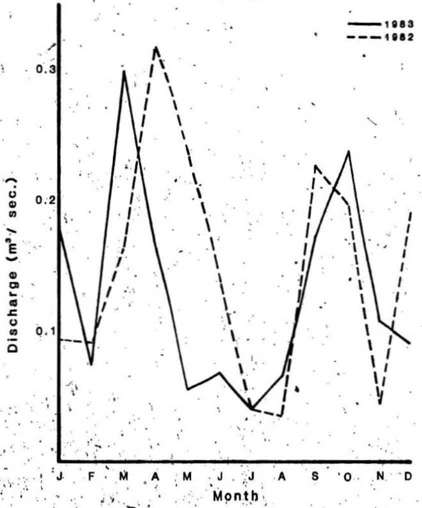
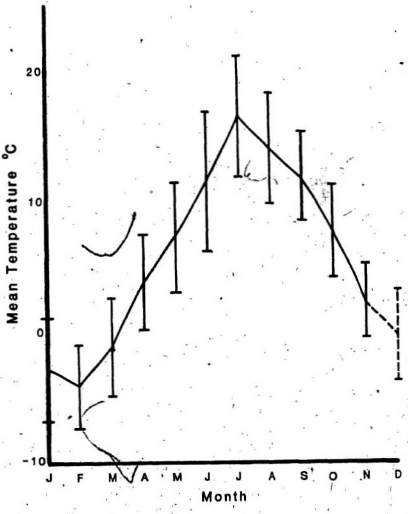

1983
1982
Discharge (m³/ sec.)
0.3
0.2
0.1
J
F
M
A
M
J
J
A
S
O
N
D
Month

FIGURE 5. Mean monthly air temperatures for Torbay, Newfoundland. (1983) (Vertical bars denote temperature range) (Note: December value based on one half month's data)


Mean Temperature °C
20
10
0
-10
J
F
M
A
M
J
J
A
S
O
N
D
Month

was observed near the right bank. During the summer the stream bed nearest the left bank was often dry. The right bank was densely forested, with some low lying evergreen branches shading large portions of the stream. The left bank was largely open, the vegetation consisting mainly of larger shrubs and sedges. Station 'C' was a little further downstream, just beyond the second major bend in the stream (90 meters below the outlet), The stream depth was fairly uniform with a slightly raised central ridge and remained submerged at all times during the year. Both banks were heavily forested with black spruce and balsam fir, only allowing direct sunlight during a few hours at mid day. Station 'D' was several hundred meters further downstream, just upstream from a culvert (325 meters below the outlet). It was fairly uniform in depth and remained submerged at all time during the year. Both banks were open, the vegetation consisting of larger shrubs or sparse grasses and herbs. The right bank had been disturbed by the construction of a farmer's dirt road, however, very little of the road construction materials were seen in the stream station itself.

Benthic Sampling

As two benthos sampling devices (Surber sampler (Jan.-Feb. and Sept.-Dec.) and Hess-type sampler (Mar-Aug)) were employed in this study it was necessary to compare them statistically to see if the sampling error was similar for each. Using a Kruskal-Wallis test (Gibbons 1976) (Appendix

3), the population data for Cheumatopsyche pettiti was examined and it became apparent that the Surber sampler under-sampled larvae of instar III and smaller. Since the Surber sampler was used largely in the winter months, this was not considered a great hindrance to the study as most species exist predominately in the fourth and fifth instars at this time. Nevertheless, the population composition was significantly different ($P<.05$) between February (Surber) and March (Hess-type). Comparison of January and February with September-December (Surber) proved to be insignificant. In addition, March and April were not significantly different in composition. It was therefore thought that both February and March represent winter populations--any differences observed being due to the change in sampler. Each of the late spring and summer months (May-August (Hess-type)) had significantly different ($P<.05$) population compositions from any other adjacent month.

Life History Patterns

As the area studied occupied such a short distance and the sample sites were so similar, it is perhaps not surprising that many of the Trichoptera collected were found at all stations. Given in Table 2 is the number of larvae of each species of Trichoptera collected over a 12 month period at each station. Non-caddisfly material will be analyzed and incorporated into future work so that a more complete picture of overall community structure may be obtained.

TABLE 2. Species list and the total number of Trichoptera larvae collected at each Axes Brook sample station (A' - D') over 12 months.

SPECIES	Stations A	B	C	D
HYDROSYCHIDAE				
Cheumatopsyche pettiti (Banks)	7308	2643	859	11
Hydropsyche betteni Ross	1514	144	12	4
H. slossonae Banks	46	853	660	113
H. sparna Ross	129	810	492	103
HYDROPTILIDAE				
Hydroptila metoeca B. & M.	16	60	65	54
Oxyethira obtatus Denning)	14	39	9	21
LEPIDOSTOMATIDAE				
Lepidostoma spp.	13	66	49	22
LEPTOCERIDAE				
Ceraclea *(diluta (Hagen))	13	9	10	1
Mystacides sepulchralis (Walker)	6	15	7	0
Oecetis *(persimilis (Banks))	584	636	742	37
Trianodes injusta (Hagen)	0	2	0	0
LIMNEPHILIDAE				
Limnephilus spp.	3	2	0	0
ODONTOCERIDAE				
Psilotreta frontalis Banks	0	2	11	1
PHILOPOTAMIDAE				
Chimarra aterrima Hagen	162	1865	2413	276
Dolophilodes distinctus (Walker)	1	5	1	21
POLYCENTROPODIDAE				
Neureclipsis crepuscularis (Walker)	3401	1911	1154	16

(contd.)

SPECIES	Station A	B	C	D
POLYCENTROPODIDAE				
Nyctiophylax affinis (Banks)	4	2	1	0
Polycentropus *(cinereus Hagen)	132	43	23	5
RHYACOPHILIDAE				
Rhyacophila fuscula (Walker)	57	73	59	44
TOTAL	13403	9180	6567	729

*Adults captured in emergence nets; no direct larval association

Overall caddisfly larval numbers found at each station decrease rapidly as one progresses from station 'A' to station 'D' (Table 2). This trend was observed throughout most of the year and is statistically significant for net-spinning caddisflies (ANOVA $P<0.05$; Table 3). Similarly, biomass of net-spinning caddisflies tended to be higher at the upper stations (station 'A') and decreased rapidly downstream (Figure 6) although a shift in peak biomass to station 'B' took place during the summer. Winter samples appear highly variable due to a lack of replicate samples. However, the overall biomass is much higher than that observed during the summer.

a) Cheumatopsyche pettiti

Cheumatopsyche pettiti, the smallest of the hydropsychids found in Axes Brook, was also the most numerous. C. pettiti was found in very large numbers at station 'A' and numbers declined very rapidly as sampling progressed further downstream (Figure 7; Table 4). Its life history was typical of many of the small net-spinning caddisflies encountered in this study (Figure 8).

Cheumatopsyche pettiti exhibited a largely univoltine life cycle consisting of 5 instars with a mean proportional increase in head capsule width between successive instars of 1.48 ± .07 S.D. per instar (See Table 5 for head capsule measurements and partial comparison with mainland representatives). Mean head capsule width of instars III-V

TABLE 3. Analysis of variance for the total number of net-spinning caddisfly larvae collected, per sample, from each of the sampling stations on Axes Brook.

SOURCE	DF	SS	MS.	F
STATIONS	3	2883730	961243	9.07
ERROR	91	9649362	106037	
TOTAL	94	12533092		

LEVEL	N	MEAN	STDEV.
STAT. A	25	502.40	317.85
STAT. B	24	342.75	364.75
STAT. C	23	243.04	433.78
STAT. D	23	22.74	33.82

```
INDIVIDUAL 95 PCT CI'S FOR MEAN BASED ON
POOLED STDEV
-----+---------+---------+---------+-
                          (----*----)
                   (-----*-----)
               (----*-----)
(------*-----)
-----+---------+---------+---------+-
     0        240       480       720
```

POOLED STDEV = 3E + 02

FIGURE 6. Net-spinning caddisfly larvae (instars III-V) wet weight biomass estimates per 0.1 square meters for 1983 at Axes Brook, stations 'A' - 'D'. Figure includes both total biomass and individual species contributions. (Note: Only stations 'A' and 'B' were sampled in January)

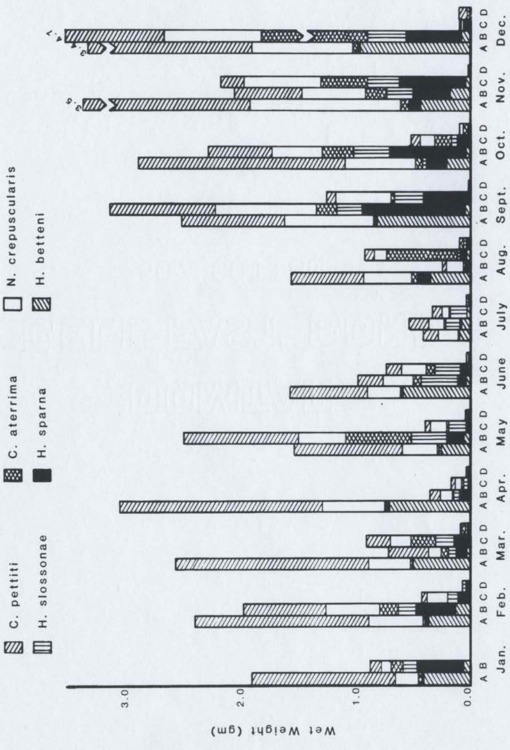

C. pettiti
C. aterrima
N. crepuscularis
H. slossonae
H. sparna
H. betteni
Wet Weight (gm)
0.0
1.0
2.0
3.0
A B
Jan.
A B C D
Feb.
A B C D
Mar.
A B C D
Apr.
A B C D
May
A B C D
June
A B C D
July
A B C D
Aug.
A B C D
Sept.
A B C D
Oct.
A B C D
Nov.
A B C D
Dec.
3.5

FIGURE 7. Abundance profile for Cheumatopsyche pettiti at Axes Brook, stations 'A' - 'D', during 1983. (Note: Only stations 'A' and 'B' were sampled in January).

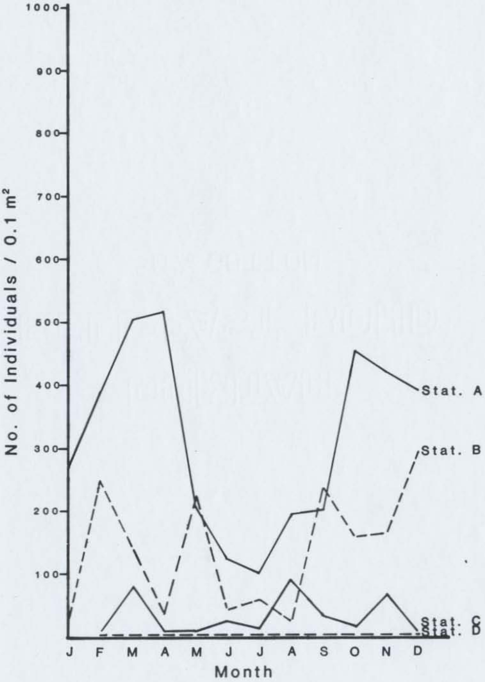

No. of Individuals / 0.1 m²
1000
900
800
700
600
500
400
300
200
100
Stat. A
Stat. B
Stat. C
Stat. D
J F M A M J J A S O N D
Month

TABLE 4. Mean sample size per sampling date and station at Axes Brook for 6 species of net-spinning caddisfly larvae. Standard deviation is given in parentheses where replicate samples were taken.

MONTH	STAT.	Cheumatopsyche pettiti	Neureclipsis crepuscularis	Chimarra aterrima
JAN	A	250	34	11
	B	26	18	50
FEB	A	361.0 (131.5)	98.0 (28.3)	6.5 (2.1)
	B	290	128	83
	C	10	50	4
	D	0	0	0
MAR	A	505.7 (294.5)	139.3 (43.1)	2.7 (3.8)
	B	143.7 (89.4)	86.0 (47.1)	45.3 (44.0)
	C	80.7 (97.4)	72.7 (24.1)	137.3 (218.8)
	D	0.3 (0.6)	0.3 (0.6)	20.0 (19.7)
APR	A	518.3 (346.0)	164.7 (72.8)	4.7 (4.2)
	B	36.7 (35.8)	39.3 (36.6)	15.0 (14.1)
	C	12.0 (9.0)	23.7 (14.0)	10.7 (10.6)
	D	0	0	7.3 (10.1)
MAY	A	207.3 (81.6)	88.0 (43.6)	2.7 (2.1)
	B	220.7 (218.6)	111.7 (86.2)	142.0 (152.2)
	C	11.3 (12.7)	34.3 (40.4)	3.7 (2.9)
	D	1.3 (1.5)	1.3 (0.6)	3.3 (1.5)
JUN	A	126.3 (156.5)	33.3 (29.5)	0.7 (0.6)
	B	43.7 (60.7)	33.3 (16.0)	15.0 (26.0)
	C	27.0 (14.1)	28.3 (2.3)	14.0 (18.2)
	D	0.3 (0.6)	0.3 (0.6)	0.3 (0.6)
JUL	A	104.3 (88.1)	138.3 (140.4)	0.7 (1.2)
	B	60.3 (61.1)	38.7 (27.5)	13.0 (19.1)
	C	12.3 (10.7)	11.0 (5.2)	3.0 (3.5)
	D	0	0.3 (0.6)	1.7 (2.9)
AUG	A	196.0 (138.0)	215.0 (113.3)	19.3 (22.7)
	B	25.0 (20.2)	50.3 (34.5)	14.3 (20.6)
	C	94.0 (80.2)	108.3 (90.0)	559.3 (760.0)
	D	0	1.0 (1.0)	41.0 (54.9)
SEP	A	187	170	0
	B	221	219	60
	C	31	99	30
	D	1	1	1

(contd.)

MONTH	STAT.	Cheumatopsyche pettiti	Neureclipsis crepuscularis	Chimarra aterrima
OCT	A	421	147	12
	B	149	100	90
	C	19	29	44
	D	0	4	18
NOV	A	390	295	18
	B	153	131	42
	C	63	137	140
	D	1	0	3
DEC	A	364	223	16
	B	274	237	806
	C	9	4	11
	D	3	1	33

MONTH	STAT.	Hydropsyche sparna	Hydropsyche betteni	Hydropsyche slossonae
JAN	A	7	67	0
	B	59	15	34
FEB	A	4.5 (3.5)	83.0 (24.0)	0
	B	57	10	37
	C	18	0	17
	D	2	1	8
MAR	A	0.7 (0.6)	91.3 (88.0)	3.3 (4.9)
	B	24.3 (10.4)	7.3 (4.0)	37.0 (20.7)
	C	31.3 (19.9)	1.0 (1.7)	66.0 (74.1)
	D	9.3 (5.8)	0	13.0 (14.7)
APR	A	1.7 (1.5)	158.0 (133.1)	1.7 (2.9)
	B	11.7 (9.6)	0.7 (0.6)	14.7 (13.0)
	C	4.7 (4.6)	0	14.7 (6.6)
	D	4.3 (2.3)	0	2.0 (1.7)
MAY	A	0	36.7 (27.3)	2.7 (0.6)
	B	23.7 (27.1)	12.3 (17.0)	53.7 (55.6)
	C	5.7 (5.7)	0.3 (0.6)	16.3 (17.9)
	D	1.0 (1.0)	1.0 (1.0)	4.0 (1.0)
JUN	A	1.0 (1.7)	20.0 (29.5)	0.7 (0.6)
	B	7.3 (12.7)	4.7 (7.2)	20.7 (34.1)
	C	5.3 (0.6)	0.3 (0.6)	16.3 (3.5)
	D	0.3 (0.6)	0	0.7 (0.6)
JUL	A	0	6.3 (2.1)	0
	B	15.7 (16.0)	4.0 (3.6)	7.7 (5.8)
	C	1.0 (1.0)	0.3 (0.6)	11.3 (11.0)
	D	4.0 (2.6)	0	0.7 (0.6)

(contd.)

MONTH	STAT.	Hydropsyche sparna	Hydropsyche betteni	Hydropsyche slossonae
AUG	A	20.3 (24.1)	33.0 (36.4)	1.7 (1.5)
	B	6.7 (7.0)	0.7 (1.2)	1.7 (2.1)
	C	57.0 (56.2)	1.0 (1.0)	37.3 (43.7)
	D	10.0 (8.9)	0	8.7 (14.2)
SEP	A	3	66	2
	B	195	4	155
	C	55	0	50
	D	1	0	0
OCT	A	18	40	5
	B	88	1	68
	C	20	0	24
	D	2	0	3
NOV	A	15	55	6
	B	62	14	50
	C	77	3	79
	D	4	0	0
DEC	A	6	84	3
	B	81	11	103
	C	7	0	4
	D	7	0	15

FIGURE 8. Life history profiles for Cheumatopsyche pettiti and Hydropsyche betteni in Axes Brook. Larvae are represented as relative proportions of each instar, totalling 100 percent. (Note: P = pupae)

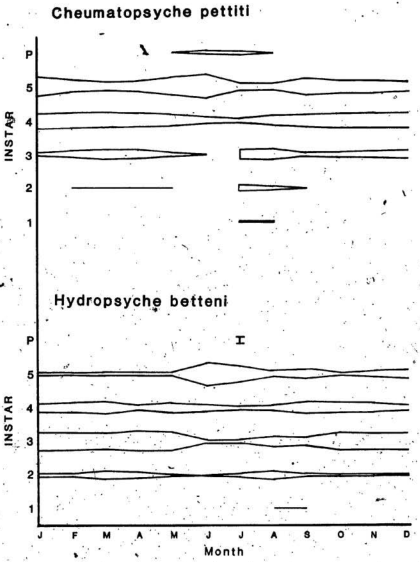

Cheumatopsyche pettiti
P
5
4
3
2
1
INSTAR
Hydropsyche betteni
P
5
4
3
2
1
INSTAR
J F M A M J J A S O N D
Month

TABLE 5. Mean head capsule width values (mm) for the larval instars of six net-spinning caddisflies found in Axes Brook. The values of MacKay (1978) are presented for comparison with the Hydropsychidae.

NAME	INSTAR	N	RANGE	MEANS(S.D.)	MACKAY (1978) RANGE	MACKAY (1978) MEAN
Cheumatopsyche pettiti	V	605	0.83-1.13	0.97(0.07)	0.89-1.05	0.96
	IV	677	0.55-0.78	0.65(0.04)	0.59-0.69	0.64
	III	307	0.38-0.50	0.43(0.02)	0.43-0.49	0.45
	II	23	0.28-0.33	0.31(0.02)	0.29-0.34	0.31
	I	33	0.18-0.23	0.20(0.01)	0.19-0.22	0.20
Hydropsyche sparna	V	106	1.08-1.25	1.16(0.04)	0.87-1.13	1.00
	IV	161	0.70-0.85	0.77(0.03)	0.61-0.80	0.69
	III	165	0.45-0.58	0.51(0.02)	0.41-0.54	0.46
	II	55	0.33-0.43	0.36(0.03)	0.28-0.35	0.32
	I	4	0.20-0.25	0.22(0.02)	0.20-0.23	0.22
Hydropsyche slossonae	V	26	1.15-1.43	1.29(0.07)	1.01-1.30	1.16
	IV	93	0.75-0.98	0.90(0.04)	0.70-0.93	0.80
	III	287	0.50-0.65	0.58(0.02)	0.47-0.59	0.53
	II	99	0.33-0.40	0.38(0.01)	0.34-0.36	0.35
	I	1	0.23	0.23	0.23-0.25	0.24
Hydropsyche betteni	V	52	1.35-1.58	1.44(0.05)	1.11-1.41	1.26
	IV	160	0.85-1.00	0.92(0.03)	0.76-0.92	0.84
	III	332	0.53-0.65	0.59(0.02)	0.49-0.61	0.53
	II	112	0.33-0.40	0.38(0.02)	0.34-0.38	0.36
	I	1	0.23	0.23	0.25	0.25
Chimarra aterrima	V	91	0.85-1.10	0.98(0.06)		
	IV	336	0.65-0.85	0.74(0.04)		
	III	245	0.43-0.60	0.52(0.03)		
	II	13	0.28-0.35	0.33(0.02)		
	I	19	0.18-0.20	0.19(0.01)		
Neureclipsis crepuscularis	V	326	0.90-1.15	1.02(0.05)		
	IV	592	0.60-0.78	0.67(0.03)		
	III	560	0.38-0.50	0.43(0.02)		
	II	22	0.25-0.30	0.28(0.02)		
	I	64	0.18-0.20	0.18(0.01)		

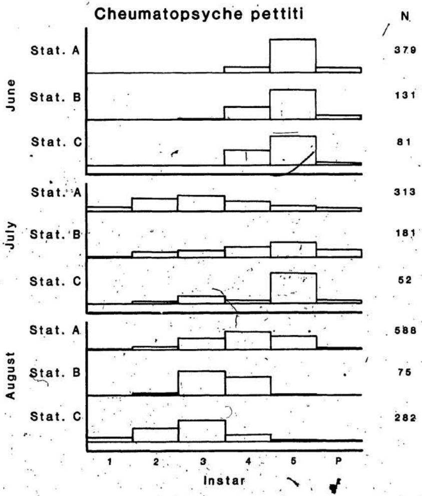
was strongly correlated with the log of mean wet weight (Log Y = -1.80 + 3.88 X; r^2 = 0.955). Little larval growth was seen in the population throughout the winter months of 1983. The most abundant overwintering instar was the fourth. Development was rapid between April and May as fifth instars began to predominate and pupae were present. Adults emerged from late June to late July. Instar I was found in July and August and larvae grew rapidly until September at which time the population became static with large numbers of fourth instar larvae present. The population at this point was virtually identical in composition to that seen in January-April. Instars III-V were present at all times although they varied in the proportion of the population they represented at various times of the year which may indicate a certain proportion of the population is semivoltine (ie eggs laid in late summer require 2 years to complete their life cycle).

There was a significant (Chi-square $P<.05$) lag in development time during the summer between station 'A' and station 'C', with earlier appearance of first and second instar larvae at station 'A' (Figure 9).

b) Hydropsyche betteni

Hydropsyche betteni was the largest hydropsychid encountered during the study. Like C. pettiti, H. betteni was most common at the outlet (station A) and numbers declined rapidly as sampling progressed further downstream.

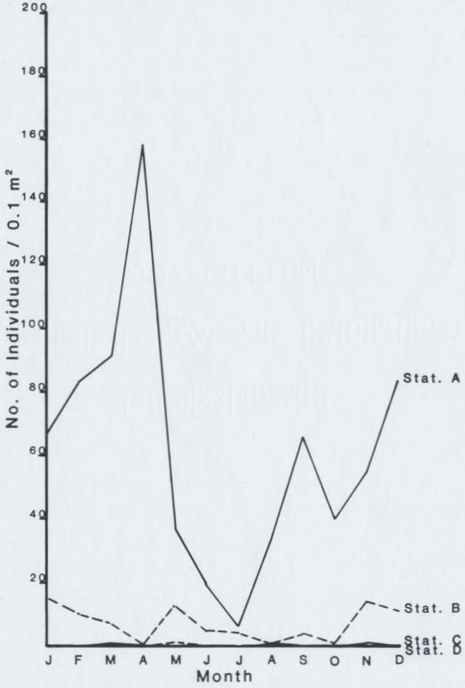
FIGURE 9. Frequency histogram of <u>Cheumatopsyche pettiti</u> larval instars collected in Axes Brook, stations 'A' - 'C', over a three month period (June - August, 1983). (Note: P = pupae)


Cheumatopsyche pettiti
N
June
Stat. A
379
Stat. B
131
Stat. C
81
July
Stat. A
313
Stat. B
181
Stat. C
52
August
Stat. A
588
Stat. B
75
Stat. C
282
1
2
3
4
5
P
Instar

In fact, H. betteni was largely confined to the outlet (Figure 10; Table 4).

H. betteni exhibited a largely univoltine life cycle (Figure 8) consisting of 5 instars with a mean proportional increase in head capsule width between successive instars of 1.582 ± .05 S.D. per instar. Mean head capsule width of instars III-V was strongly correlated with the log of mean wet weight (Log Y = -1.37 + 3.40 X; r^2 = 0.998). Little change in the relative abundance of instar cohorts was observed throughout the winter. The most abundant overwintering stage was instar III with substantial numbers of instar IV larvae also present. Slow larval growth occurred in April but growth was very rapid in May and June. Adults of this species and the two other species of Hydropsyche were difficult to capture due to their nocturnal habits but they were found in late July although earlier emergence may have occurred. Instar I was found in August and September although the relatively large number of instar II larvae found in August would indicate they were probably present in late July as well. Larval growth ended by late September, leaving large numbers of instar III and some instar IV larvae to overwinter. Instars II-V were present at all times although not always in the same relative proportions. As with C. pettiti, this may indicate that a certain proportion of the population is semivoltine.

FIGURE 10. Abundance profile for Hydropsyche betteni at Axes Brook, stations 'A' - 'D', during 1983. (Note: Only stations 'A' and 'B' were sampled in January)


200
180
160
140
120
100
80
60
40
20
No. of Individuals / 0.1 m²
Stat. A
Stat. B
Stat. C
Stat. D
J F M A M J J A S O N D
Month

c) Hydropsyche slossonae and d) Hydropsyche sparna

In contrast with the two previous hydropsychids, Hydropsyche slossonae and Hydropsyche sparna showed peak densities below the outlet (Figures 11 and 12 respectively; Table 4). Both species were abundant at stations 'B' and 'C' and were commonly found at station 'D'.

Hydropsyche slossonae exhibited a strictly univoltine life cycle (Figure 13) consisting of 5 instars with a mean proportional increase in head capsule width between successive instars of 1.54 ± .09 S.D. per instar. Mean head capsule width of instars III-V was strongly correlated with the log of mean wet weight (Log Y = -1.88 + 3.83 X; r^2 = 0.958). The larvae showed little or no growth over winter until May. The most abundant overwintering instar was the third with smaller numbers of instar IV also present. While larval growth increased in May, instar V larvae were not seen in large numbers until late June and pupae were not seen until late July at which time the population was composed almost exclusively of instar V larvae. Instar I larvae were not seen until August and continued to be present until late September. Larval growth continued then until late October at which time the same overwintering population profile seen the previous winter was reached and remained static for the duration of the year. Instar III-V larvae were always present but at very low numbers during certain times of the year.

FIGURE 11. Abundance profile for Hydropsyche slossonae at Axes Brook, stations 'A' - 'D', during 1983. (Note: Only stations 'A' and 'B' were sampled in January)

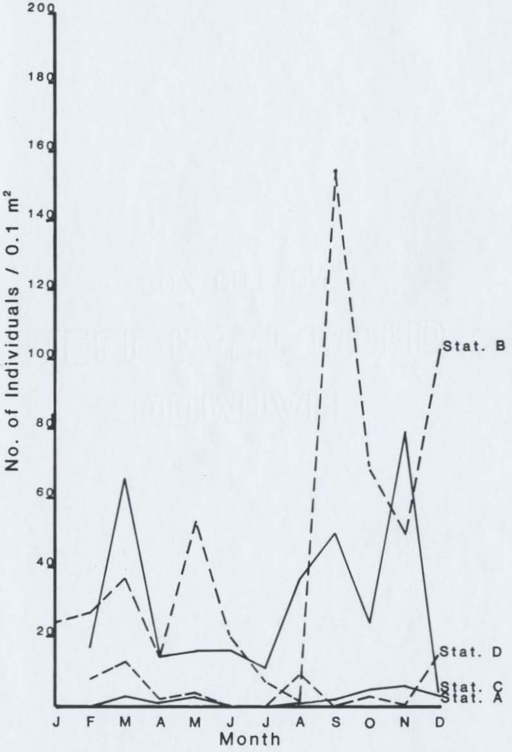

200
180
160
140
120
100
80
60
40
20
No. of Individuals / 0.1 m²
Stat. B
Stat. D
Stat. C
Stat. A
J F M A M J J A S O N D
Month

FIGURE 12. Abundance profile for <u>Hydropsyche sparna</u> at Axes Brook, stations 'A' - 'D', during 1983. (Note: Only stations 'A' and 'B' were sampled in January)

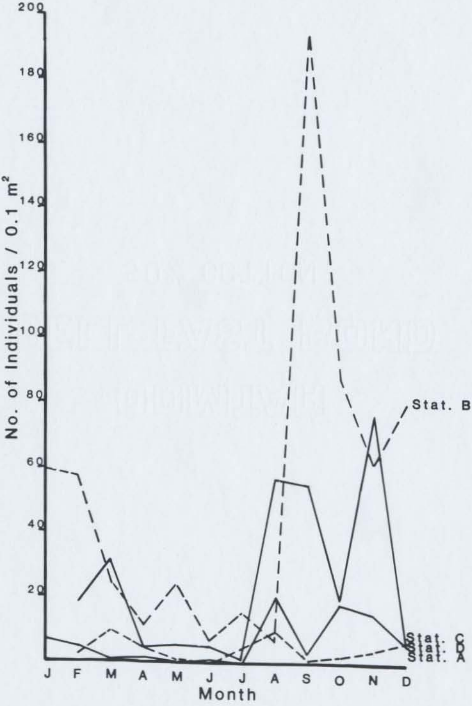
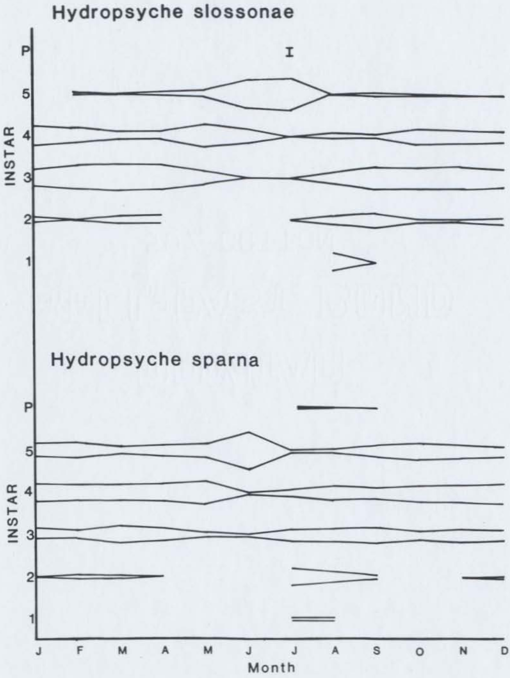

200
180
160
140
120
100
80
60
40
20
No. of Individuals / 0.1 m²
Stat. B
Stat. C
Stat. D
Stat. A
J F M A M J J A S O N D
Month

FIGURE 13. Life history profiles for <u>Hydropsyche slossonae</u> and <u>Hydropsyche sparna</u> in Axes Brook. Larvae are represented as relative proportions of each instar, totalling 100 percent. (Note: P = pupae)


Hydropsyche slossonae
P
5
4
3
2
1
INSTAR
I
Hydropsyche sparna
P
5
4
3
2
1
INSTAR
J F M A M J J A S O N D
Month

Hydropsyche sparna exhibited a largely univoltine life cycle (Figure 13) consisting of 5 instars with a mean proportional increase in head capsule width between successive instars of 1.52 ± .09 S.D. per instar. Mean head capsule width of instars III-V was strongly correlated with the log of mean wet weight (Log Y = -1.94 + 3.94 X; r^2 = 0.997). The larvae showed little or no development until May. The most abundant overwintering instar was the fourth followed by third and fifth instars which existed in roughly equal numbers. Larval growth was most rapid during June and by late June the population was almost exclusively composed of instar V larvae. Instar I larvae were first seen in late July, although the relatively large numbers of instar II larvae in July would indicate they were probably present in late June. Instar I larvae continued to be present through late August. Larval growth then continued until late September at which time the same overwintering population profile was reached as observed the previous winter and this remained static for the duration of the year. Instar III-V larvae were always present in appreciable numbers which may indicate a certain proportion of the population was semivoltine.

There was a modest increase in numbers of both _H. slossonae_ and _H. sparna_ at station 'A' during the late summer and fall, but their numbers gradually declined as winter set in.

e) Neureclipsis crepuscularis

Neureclipsis crepuscularis exhibited a life cycle (Figure 14) and distributional pattern (Figure 15; Table 4) similar to C. pettiti with a mean proportional increase in head capsule width between successive instars of 1.54 $\pm$ .02 S.D. per instar. Mean head capsule width of instars III-V was strongly correlated with the log of mean wet weight (Log Y = -2.04 + 4.31 X; r^2 = 1.000). The only notable difference was related to distribution. N. crepuscularis had a broader range (ie. stations 'A', 'B', and 'C') than C. pettiti which appeared to be more restricted to the immediate outlet area (ie. stations 'A' and 'B'). In addition, N. crepuscularis also demonstrated the lag in development time between stations described earlier for C. pettiti ($P<.05$) (Figure 16).

f) Chimarra aterrima

Chimarra aterrima also exhibited a life history pattern (Figure 14) similar to C. pettiti with a mean proportional increase in head capsule width between successive instars of 1.51 $\pm$ .18 S.D. per instar. Mean head capsule width of instars III-V was strongly correlated with the log of mean wet weight (Log Y = -3.92 + 5.85 X; r^2 = 1.000). Again, the only notable difference was distributional (Figure 17; Table 4). C. aterrima was largely confined to stations 'B' and 'C'. Its sporadic appearance in large numbers (Figure 17) indicated that the population was clumped.

FIGURE 14. Life history profiles for _Neureclipsis crepuscularis_ and _Chimarra aterrima_ in Axes Brook. Larvae are represented as relative proportions of each instar, totalling 100 percent. (Note: P = pupae)

2

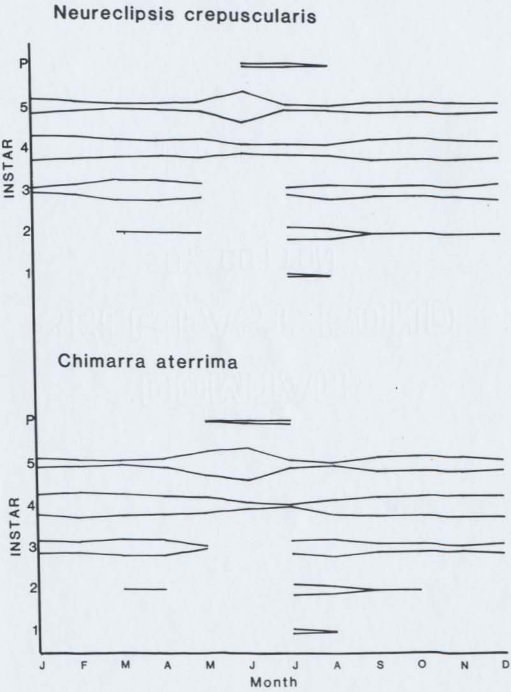

Neureclipsis crepuscularis
P
5
4
3
2
1
INSTAR
Chimarra aterrima
P
5
4
3
2
1
INSTAR
J F M A M J J A S O N D
Month

FIGURE 15. Abundance profile for Neureclipsis crepuscularis at Axes Brook, stations 'A' - 'D', during 1983. (Note: Only stations 'A' and 'B' were sampled in January)

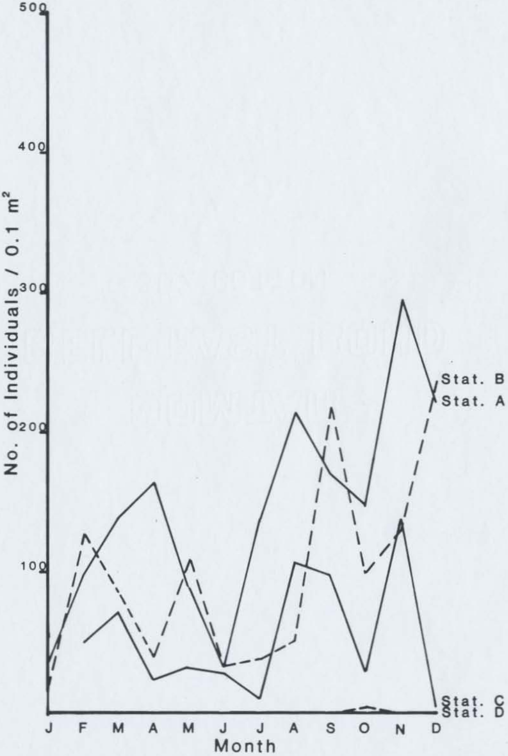

500
400
300
200
100
No. of Individuals / 0.1 m²
Stat. B
Stat. A
Stat. C
Stat. D
J F M A M J J A S O N D
Month

FIGURE 16. Frequency histogram of Neureclipsis crepuscularis larval instars collected in Axes Brook, stations 'A' - 'C', over a three month period (June - August, 1983). (Note: P = pupae)

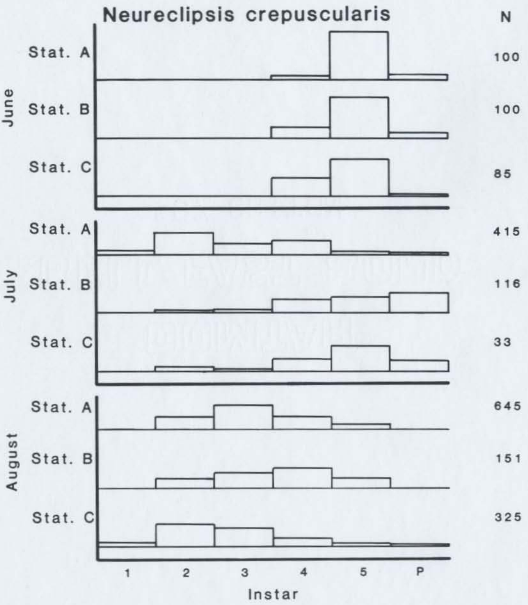
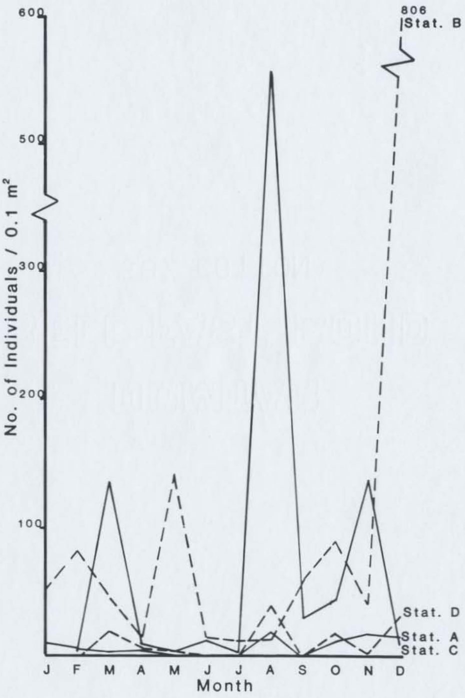

Neureclipsis crepuscularis
N
June
Stat. A
100
Stat. B
100
Stat. C
85
July
Stat. A
415
Stat. B
116
Stat. C
33
August
Stat. A
645
Stat. B
151
Stat. C
325
1
2
3
4
5
P
Instar

FIGURE 17. Abundance profile for Chimarra aterrima at Axes Brook, stations 'A' - 'D', during 1983. (Note: Only stations 'A' and 'B' were sampled in January)



806
Stat. B
600
500
300
200
100
No. of Individuals / 0.1 m²
Stat. D
Stat. A
Stat. C
J F M A M J J A S O N D
Month

Feeding Ecology

Feeding ecology appears to be similar for all species except C. aterrima which is a detritivore (Table 6). Much of the ingested material was planktonic in nature (ie. drifting). Each of the other species appears to be omnivorous, with tendencies towards carnivory, H. betteni being the most carnivorous, followed by H. slossonae and H. sparna and finally C. pettiti and N. crepuscularis. This latter distinction is based solely on the size of the animal food particles found ingested rather than total animal food ingested which may in fact be very similar (as illustrated in Table 6).

Seston

There is some indication that diurnal patterns exist in the amount of lake-derived plankton which enters the outlet. Two peaks in zooplankton numbers were observed over a 24 hour period: during late morning and shortly after sunset (Figure 18). This diurnal pattern may have been part of the cause for the highly variable results obtained for the phytoplankton cell counts (Table 7), zooplankton total counts (Table 8) and total seston ash-free dry weights (Table 9). From this data the only observable trend was that, plankton, while relatively abundant during the spring, summer and fall, is very scarce in the winter. Total seston showed no seasonal trend at all. It is true, however, that these findings are far from conclusive, based on the diurnal

TABLE 6. Gut content analysis for final instar, net-spinning caddisfly larvae collected from Axes Brook (June 1984).

FOOD TYPE

NAME	filamentous algae	free-swimming algae	desmids	diatoms	crustacean	other arthropods	detritus
Cheumatopsyche pettiti	+++	+	+	+	+	++	+
Hydropsyche sparna	+++	+	+	++	+	++	+
Hydropsyche slossonae	+++	+	+	++	+	++	+
Hydropsyche betteni	+++	+	+	+	++	++	+
Chimarra aterrima	-	+	+	-	-	-	+++
Neureclipsis crepuscularis	+++	+	+	++	+	++	+

+++ - > predominant food item ingested
++ - > found in large amounts
+ - > present but not occupying a large volume of the forgut

FIGURE 18. Zooplankton drift at Axes Pond outlet (station 'A') over 24 hours (July 16-17, 1983). (Broken lines indicate missing values at 2300 and 0100 hours)

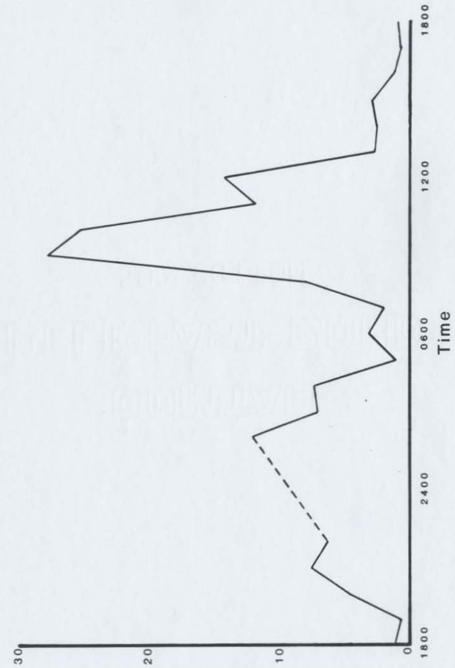

No. Zooplankton / m³ x 1000
0
10
20
30
1800
2400
0600
1200
1800
Time

TABLE 7. Total phyplankton count for Axes Brook stations 'A' - 'D'. Cell count per ml is equal to the table value x 30.

DATE	TIME	TOTAL CELL COUNT A	B	C	D
27/05/83	1000	223	169	114	136
27/05/83	1400	307	213	219	263
29/06/83	1300	251	217	219	-
15/07/83	1900	311	-	-	227
15/07/83	2000	262	-	-	172
15/07/83	2100	249	-	-	176
15/07/83	2300	179	-	-	115
15/07/83	2400	281	-	-	143
16/07/83	0900	207	232	244	158
16/07/83	1100	291	-	-	124
16/07/83	1200	190	-	-	212
16/07/83	1300	259	271	153	175
16/07/83	1400	286	-	-	216
16/07/83	1500	268	-	-	206
16/07/83	1600	324	-	-	213
16/07/83	1700	208	239	275	314
16/07/83	1800	227	-	-	180
16/07/83	1900	258	-	-	133
16/07/83	2000	209	-	-	179
16/07/83	2100	-	169	181	118
16/07/83	2200	257	-	-	147
16/07/83	2400	204	-	-	207
21/09/83	1300	308	-	275	343
12/10/83	1300	-	227	143	289
22/10/83	1300	331	403	200	268
08/11/83	1300	181	163	172	175
21/11/83	1300	156	103	159	96
22/01/84	1300	44	38	43	44

TABLE 8. Total number of copepods per cubic meter for Axes Brook station 'A' - 'D'.

DATE	TIME	TOTAL COUNT A	B	C	D
27/05/83	1000	1477	416	167	35
27/05/83	1400	1542	561	167	0
29/06/83	1300	325	65	39	11
15/07/83	1800	5964	-	-	0
15/07/83	1900	3173	-	-	140
15/07/83	2000	4557	-	-	655
15/07/83	2100	6727	119	0	111
15/07/83	2200	6298	-	-	167
15/07/83	2300	8254	-	-	529
15/07/83	2400	6393	-	[illegible]	1002
16/07/83	0200	3006	239	143	28
16/07/83	0900	7347	1631	179	0
16/07/83	1000	7160	-	-	28
16/07/83	1100	3149	-	-	28
16/07/83	1200	2863	-	-	0
16/07/83	1300	859	159	72	0
16/07/83	1400	1861	-	-	0
16/07/83	1500	1957	-	-	0
16/07/83	1600	3626	-	-	0
16/07/83	1700	3912	239	0	0
16/07/83	1800	1050	-	-	0
16/07/83	1900	716	-	-	84
16/07/84	2000	4819	-	-	0
16/07/83	2100	7681	557	0	0
16/07/83	2200	6298	-	-	0
16/07/83	2400	9017	-	-	557
17/07/83	0200	12023	-	-	1002
17/07/83	0300	7061	-	-	278

(contd.)

DATE	TIME	A	TOTAL COUNT B	C	D
17/07/83	0400	7347	-	-	2227
17/07/83	0500	1050	597	143	139
17/07/83	0600	3340	-	-	891
17/07/83	0700	2242	-	-	445
17/07/83	0800	7920	-	-	28
17/07/83	0900	27614	3222	143	56
17/07/83	1000	25012	-	-	56
17/07/83	1100	11855	-	-	0
17/07/83	1200	14313	-	-	28
17/07/83	1300	2602	756	215	58
17/07/83	1400	2313	-	-	251
17/07/83	1500	2747	-	-	0
17/07/83	1600	1301	-	-	84
17/07/83	1700	431	80	36	0
17/07/83	1800	811	-	-	0
21/09/83	1300	0	0	32	0
12/10/83	1300	0	0	32	0
22/10/83	1300	1288	334	215	0
08/11/83	1300	0	0	0	0
21/11/83	1300	0	32	0	0
22/01/84	1300	0	0	0	0

TABLE 9. Ash free dry weight of total seston per liter for Axes Brook stations 'A' - 'D'.

DATE	TIME	ASH-FREE WEIGHT (mg/l) A	B	C	D
19/03/83	1300	1.00	2.00	0.75	0.84
19/05/83	1300	2.66	1.96	1.85	2.14
27/05/83	1000	0.29	0.36	0.57	0.54
27/05/83	1400	1.97	1.03	1.14	0.95
29/06/83	1300	1.12	1.19	1.22	--
15/07/83	2100	1.39	1.30	1.58	1.29
16/07/83	1600	2.35	2.44	2.64	2.79
16/07/83	2000	1.22	1.62	1.63	0.79
17/07/83	0200	1.72	--	3.04	2.78
17/07/83	0600	1.68	1.64	1.17	0.90
17/07/83	1000	1.07	0.86	0.70	1.21
17/07/83	1400	0.94	2.08	0.75	0.98
17/07/83	1800	3.13	1.61	1.49	3.60
22/10/83	1300	1.35	1.25	--	1.21
08/11/83	1300	--	0.97	0.96	0.66
22/01/84	1300	1.55	1.50	1.69	--

pattern observed for a single 24 hour period. A sampling program involving longer intervals (48 or 72 hours), at several different times during the year, is needed to obtain a definitive result for the relative abundance (and consequent importance) of each potential food source during different parts of the year.

Examination of the data from Tables 7-9 using the Sign test (Table 10) showed no significant difference ($P<0.10$) in total seston per liter between adjacent stations or between the outlet (station A) and the furthest removed station (station D). Phytoplankton showed no significant difference ($P<0.10$) in numbers between adjacent stations but did show a significant decrease in numbers between the outlet and downstream ($P<0.05$). Zooplankton showed a significant downstream decrease ($P<0.05$) in numbers between all sets of adjacent stations.

TABLE 10. Sign test values for suspended organic matter contrasts between sampling stations on Axes Brook

	N	S+	S-	P
SESTON				
A - B	14	7	7	.6047
B - C	14	9	5	.2120
C - D	13	5	8	.2905
A - D	13	6	7	.5000
PHYTOPLANKTON (>30um)				
A - B	6	4	2	.3438
B - C	9	5	4	.5000
C - D	9	3	6	.2539
A - D	19	13	6	.0835*
PHYTOPLANKTON (<30um)				
A - B	8	4	4	.6367
B - C	10	4	6	.3770
C - D	10	3	7	.1719
A - D	23	19	4	.0018**
ZOOPLANKTON				
A - B	15	14	1	.0000**
B - C	17	15	2	.0000**
C - D	14	13	1	.0000**
A - D	44	44	0	.0000**

*SIGNIFICANT AT P<.10

**SIGNIFICANT AT P<.05

DISCUSSION

LIFE HISTORY

Mackay (1979) described the life history patterns of three of the species covered in this study: H. betteni; H. slossonae; and H. sparna. In southern Ontario each of these species is capable of bivoltine life histories in certain locations but is univoltine in others. The reasons for the difference in development rates seem to revolve around average stream temperature and stream enrichment due to runoff from surrounding farmland. Warmer waters and high enrichment tend to promote bivoltine life histories. In Axes Brook both of these factors are obviously less than optimal resulting in a single generation or less per year.

Peak abundance of H. betteni in southern Ontario, as in Newfoundland, occurred below an impoundment. From May through to oviposition in July, the life history patterns of the univoltine populations described for Ontario were comparable with a large proportion of any given population observed in this study. However, the Ontario populations of

H. betteni developed rapidly in late summer through September and overwintered largely as instar V larvae while at Axes Pond development was slower and the dominant overwintering stage was instar III. The substantial numbers of instar IV and V larvae present in Axes Brook during late summer and winter, were suspected to be passing through their second winter. The reasoning behind this being that later instar larvae occurred in the system too quickly to have been derived from eggs laid that summer. It is much more likely that these larvae are the result of the instar II, and some of the instar III, larvae observed during the previous winter and spring (January - May). Furthermore, these later instar larvae did not pupate during the late summer and fall. Instead, the population maintained a fairly constant proportion of these later instar larvae throughout late summer, fall and winter.

The high densities of H. betteni observed at the Axes Pond outlet reflect more than the general pattern of high densities of filter feeders below a lentic outflow. H. betteni is resricted to lentic outflows and the few specimens encountered downstream were probably the result of "catastrophic" drift.

Hydropsyche sparna and H. slossonae were similar in their distributions and occurred in similar numbers within Axes Brook but H. sparna developed faster and emerged earlier than H. slossonae (Figure 13). Both occurred at all stations but were found predominantly just downstream from the outlet. However, at the outlet they occurred only as early instar larvae during the late summer. Both species have been reported to have two generations in some streams in southern Ontario (Sprules 1947, Mackay 1979) but there is no evidence of this occurring in Newfoundland. H. slossonae was strictly univoltine, while H. sparna appears to be both univoltine and semivoltine for similar reasons as described for H. betteni. In addition, these species overwintered in earlier instar larvae than those recorded from southern Ontario (Mackay 1979).

C. pettiti was the smallest of the hydropsychids encountered and most numerous. Its larvae lived predominantly at the outlet and generally co-occurred with larvae of H. betteni. However, C. pettiti larvae also lived in relatively large numbers short distances below the outlet and consequently partially overlapped in distribution with those of H. sparna and H. slossonae. Mackay (1979) suspected that bivoltine life histories were related to the size of the final instar larvae (ie. species with small final instar larvae are more likely to have bivoltine life histories than those with large final instar larvae). Since C. pettiti is smaller than any of the hydropsychids described thus far, it is the most likely species, given the right conditions, to have multiple generations. Fremling (1960) reported Cheumatopsyche campyla has two generations a year but to date this has not been observed in C. pettiti and certainly is not true for those individuals living in

Axes Brook, which were either univoltine or semivoltine for the same reasons as given for H. betteni.

The larvae of C. aterrima were found most often under stones in shallow, fast flowing, shaded areas of the stream. Larvae were found in localized aggregations in the portion of the stream below the outlet. Instead of possessing individual nets such as those of the hydropsychids, larvae occurred in complexes of nets in which nets were attached to one another. Within these complexes, any or all of C. aterrima's five instars might be found. When such aggregates were found other net-spinning caddisflies were notably absent. This was one of the first caddisflies to emerge in the spring (June) at which time adults were seen actively running around on various stream side vegetation. Williams and Hynes (1973) reported instar I larvae were present as early as late June in an Ontario stream but locally they were not seen until late July. C. aterrima, was either univoltine or semivoltine again for the same reasons as given for H. betteni. Other members of the genus have been reported to be bivoltine (eg Chimarra mosleyi (Cudney and Wallace 1980)).

Wiggins (1977) has suggested that due to the large size of the nets produced, N. crepuscularis is probably restricted to areas of fairly slow current. Apparently, the current speeds found in Axes Brook were within a suitable range for N. crepuscularis as larvae were found in relatively large numbers as far downstream as station 'C'.

N. crepuscularis has been studied and found to be bivoltine in South Carolina and Georgia (Cudney and Wallace 1980). During the study at Axes Brook it displayed either a univoltine or semivoltine life cycle, the reasoning being the same as that given for H. betteni.

What are the implications of a semivoltine life history in Newfoundland net-spinning caddisflies? Net-spinning caddisflies with bivoltine life histories have now been reported for several species, generally from areas of fairly warm climates (eg southern Ontario and further south) (Sprules 1947, Fremling 1960, Mackay 1979, Cudney and Wallace 1980). Prior to these studies, Trichoptera were generally considered to be univoltine. Neither a bivoltine nor univoltine life history pattern satisfactorily explains the observations at Axes Brook. While there is no doubt that the univoltine life history is present and commonly adopted by the Newfoundland net-spinning caddisflies, it is apparent that some proportion of the population is semivoltine.

Adult caddisflies which emerged early in the summer or late spring laid eggs which were able to develop and grow into intermediate instar (III or IV) larvae before the winter set in. The following spring they continued to grow and emerged as adults that summer. Total time required-- 1 year. As flight periods for many of these caddisflies are fairly long (generally from early June through late August, as evidenced by adult collection dates given by Marshall and

Larson (1982) and specimens in the insect collection of Memorial University), many eggs were probably laid during the late summer and early fall. Since instar II larvae were found in early spring, it might be presumed that these eggs hatched during the fall but development was retarded. These larvae would then grow rapidly during the summer but not reach instar IV or V until late summer. As no pupae were found in late summer, it is assumed these larvae did not pupate until the following spring, emerging shortly afterwards. Total time required-- 1.5 years.

Apparently the life histories of these insects are highly flexible. During the winter a diapause may exist or growth may be slowed due to the slowed metabolism of the larvae combined with a shortage of lake-derived plankton. Fuller and Mackay (1980) have observed grazing behaviour in <u>H.</u> <u>betteni</u>, <u>H.</u> <u>slossonae</u> and <u>H.</u> <u>sparna</u> during the winter months which indicates that slow growth may indeed occur. The only event in the life histories which appeared to be very synchronous was the onset of pupation.

Why pupation occurs only during early summer and not in late summer or early fall is not certain. As pupation appears to occur over a short period of time, it seems likely that a diapause exists in the instar V larvae which remains in effect until a given set of environmental factors become acceptable for the onset of pupation. What are these factors? It is difficult to say. Temperature would seem an obvious choice. When the water becomes warm enough in early summer, instar V larvae pupate. However, due to the existence of a semivoltine life history, many instar V larvae exist during August and September when temperatures are still high but no pupae were found. Increasing day length during late spring and early summer might result in some photoperiod response but then why would species on the mainland have a second generation in late summer while the same species in Newfoundland do not. A food shortage might reduce the energy reserves of instar V larvae, thus prolonging the onset of pupation. Given the oligotrophic nature of the system this might be held to be true. However, since very rapid growth was observed between August and September, it would seem that ample food was available for the mature larvae to proceed on to pupation.

CO-EXISTENCE

The high densities of net-spinning caddisflies at the lake outlet indicates that this location is very suitable for certain species of filter-feeders (notable in their absence were the blackflies). Co-existence of several species in lake outlets suggests that some means of reducing competition for food and space must exist. Therefore, it would be expected that divergence in life history patterns, food requirements, and/or habitat preference may exist as mechanisms reducing competitive pressure.

a) Life History

How may life history play a role in reducing either inter- or intraspecific competition? Interspecific differences in size-class frequencies of co-occuring larvae is one of several ways available. Larvae of different instars may consume different foods and/or size-classes of foods (Grant and Mackay 1969, Fuller and Mackay 1980). Williams and Hynes (1973) found the nets of older instar larvae of Hydropsyche had larger mesh sizes than nets of smaller larvae. Similarly, Wallace (1975a) found large mesh sizes in nets of later instar larvae of Arctopsyche. Furthermore, he found carnivory (and food particle size) increased in larvae of instars III-V. Temporal divergence in life histories may lessen competition by separating periods of high energy demand in each species' life history. Also, differences in life history patterns may provide a means of reproductive isolation between closely related sympatric species.

~~Separation in time is a likely strategy~~ of ecological segregation in congeneric species. For example, larval net-spinning caddisflies are limited in the habitats they can occupy by rather stringent requirements for water velocity and substrate type (Malas and Wallace 1977, Wallace et al. 1977). Separation, strictly by food type, is difficult given the filtration methods of feeding and homogeneous nature of the food (seston and benthic diatoms). Divergence of life history patterns allows larvae of different instars to partition available resources, remaining trophically distinct (such as the case of H. sparna and H. slossonae described above), (Fuller 1980). Intraspecific competition could promote asynchrony in development even within species thus permitting larger populations to occupy a single location.

b) Food

Analysis of food consumption in aquatic insects is beset with difficulties (reviewed by Cummins 1973). Composition of gut contents does not necessarily indicate proportionate utilization of food types although, as Cummins pointed out, evolutionary processes should lead to a close correspondance between food ingested and food assimilated. For example, Bjarnov (1972) in a survey of carbohydrase activity in a variety of Trichoptera, Chironomus and Gammarus, found chitinase activity only in carnivorous or omnivorous animals. Furthermore, it is not clear as to what extent ingested detrital material serves as a substrate for microflora which is the food source, to what extent living plant materials, particularly diatoms and filamentous algae, are utilized and what importance enteric symbionts have in breakdown of particularly refractory material (eg. chitin and cellulose). Foods vary considerably in nutritional quality, particularly in protein contents.

Extensive gut content determinations are exceedingly time consuming, limiting possible replication of study in time and space. For this reason, gut contents which were collected in 1984 during late spring (June 20) were analyzed only for the occurrence and relative abundance of various food types in the guts of larvae (Table 6). Detailed information on the feeding habits of several hydropsychids have been reported by Fuller (1980) (including many of the species studied in this work) and Oswood (1976).

All species consumed considerable quantities of detrital particles, in fact C. aterrima has been reported (Williams and Hynes 1973) and was observed to feed almost exclusively on this material. This corroborates the generalization that detritus is an important dietary component of net-spinning caddisflies (eg Egglishaw 1964, Malmqvist et al. 1978, Ross and Wallace 1983, Drake 1984). However, there do appear to be interspecific differences in the relative degree of carnivory (Table 6). H. betteni larvae were found to contain large pieces of animal remains (ie. chironomid larvae, copepods, mites and terrestrial insects) in relatively large amounts while H. slossonae and H. sparna larvae had smaller pieces and considerably less animal material. Animal remains were rare in the guts of C. pettiti and N. crepuscularis while C. aterrima had none whatsoever. The predominant ingested material in all cases, except C. aterrima, was filamentous green algae but since this was found to be intact even in the hind gut, it was considered to be undigested and ingested largely as a means of keeping the filter net clean. Also found in large numbers in all species except C. aterrima were large numbers of benthic diatoms and numerous small flagellate algae. This was particularly true for C. pettiti and N. crepuscularis. While every species ingested large amounts of detritus, there appears to be a spectrum of relative importance of each potential food source between the various species in much the same way as reported by Oswood (1976). The larvae of H. betteni consumes large amounts of animal material and relatively few diatoms. Those of H. sparna and H. slossonae were somewhat less carnivorous (ie. more omnivorous). Larvae of C. pettiti and N. crepuscularis were even less carnivorous, almost herbivorous and C. aterrima appeared to be a detritivore although algae has been reported to compose a large proportion of its diet (Coffman et al. 1971).

These interspecific differences in feeding raise a couple of questions. What are the implications for resource partitioning (ecological divergence)? How does partitioning take place? Interpretation must be tempered by the theoretical and methodological difficulties discussed previously. However, it seems that, as Grant and Mackay (1969) predict, life history patterns may combine with species and instar specific feeding patterns to produce considerable ecological divergence. H. betteni is a consumer of large particles and is relatively carnivorous as has been pointed out several times before. C. pettiti, which was the principal co-occurring species, consumes smaller particles including large numbers of diatoms. Both species were found predominantly at the immediate outlet. In this location, the caddisfly larvae have first choice of the inflowing lake-derived seston. While seston alone may not be important in determining the large build-up of larvae at the outlet (Carlsson et al. 1977), the components within the seston may be vital. At the outlet any large drifting insect or plankter may be readily caught by H. betteni. C. pettiti gets first choice of phytoplankton as well as any drifting animals entrained in the water. H. sparna and H. slossonae may be eliminated from the immediate outlet by the larger and more carnivorous H. betteni and thus are found predominantly just below the outlet. While larvae of H. sparna and H. slossonae are comparable in diet and size, their developmental times differ. During any one generation the larvae of H. sparna were in a higher instar number than those of H. slossonae. Furthermore, Fuller and Mackay (1980) have shown that early instar larvae of Hydropsyche are generally much less carnivorous than older larval instars. Consequently, H. sparna would tend to eat more large particles, while H. slossonae would feed primarily on phytoplankton and detritus for much of their overlapping larval lives. By living in close proximity to the outlet, H. slossonae and H. sparna still benefit from the lake-derived plankton and large seston particles, even though this material is reduced in abundance, without encountering the severe competitive pressures which probably occur at the outlet itself. C. aterrima, being a detritivore, probably depends on considerable amounts of dead allochthonous material. Since the pond would tend to act as a 'sink' for allochthonous material it might be expected that detritus levels at the immediate outlet would be lower than those found further downstream. Consequently, C. aterrima larvae occur in largest numbers just below the outlet where lake-derived phytoplankton, pre-conditioned plankton (as a result of the filter-feeders upstream) and allochthonous input from the stream banks would be most abundant. N. crepuscularis larvae showed very similar distribution patterns and feeding ecology to that of C. pettiti. However, N. crepuscularis larvae occur for some distance downstream of the outlet and tend to produce nets on any available surface (Wiggins 1977), which in turn seem to deter other net-spinning caddisflies. C. pettiti larvae tend to construct nets on the sides of, or under stones primarily at the immediate outlet and very short distances downstream.

The apparently simple guild of filter-feeders at the lake outlet turns out to be quite complex. It would seem that the outlet has a broad system of biological filters. The components of the system are life history stages of species. The system is thus dynamic and will change components with seasonal life history changes. Such niche divergence would seem to produce a very efficient seston filter. Wallace et al. (1977) and Oswood (1976) concluded that larger seston loads may engender even more efficient filtering communities by increasing interspecific competition which in turn increases niche divergence such that the resource base is effectively expanded (ie. specific components of the seston are more efficiently utilized by specialists).

By what means does partitioning of food resources take place? Differences in capture net structure offer one possibility (eg Malas and Wallace 1977). As already discussed, mesh size of capture nets often increases with instar number. In addition, Cheumatopsyche mesh size is smaller than that of Hydropsyche (Wallace 1975b, Oswood 1976) while Chimarra (Williams and Hynes 1973) and Neureclipsis probably have still smaller mesh sizes. The literature values for the mesh sizes may not be completely applicable to this study as the Newfoundland species are, generally, larger than their mainland counterparts (Table 5). This phenomenon of relatively large body size of Newfoundland insects was observed earlier by Lindroth (1963) in carabid beetles.

Microhabitat differences in net placement may influence both size and type of filtered particles. Wallace (1975b) found intergeneric differences among three hydropsychids in distribution of nets on single rocks. He suggests that placement of nets in microhabitats of relatively slow current velocity (sides and bottoms of rocks) leads to a decrease in particle sizes carried by water and hence available as food. This may help to explain C. aterrima's behaviour as a detritivore as its nets are found on the undersides of rocks (Wiggins 1977, personal observations).

Feeding methods which increase carnivory are more difficult to envision. Perhaps there are behavioural adaptations such as rapid capture of organisms contacting the capture net or increased activity during high rates of insect drift.

c) Habitat

A major niche dimension by which ecological segregation may take place ~~is~~ space. Utilization of space by net-spinning larvae was investigated based on longitudinal changes in density over a length of the stream -- macrohabitat patterns.

Net-spinning caddisflies reached very high densities at the lake outlet. However, densities declined dramatically downstream. This rapid longitudinal decrease in benthic filter-feeder densities is a common feature of lake outlets. Oswood (1976) found a relationship between the logarithmic transformation of both larval densities and downstream distances from the lake outlet that could be described mathematically as a power function but he did admit that species-specific patterns (ie. macrohabitats) may vary widely. Similar to Oswood's (1976) findings with Cheumatopsyche gracilis, I found C. pettiti densities declined very rapidly with distance (Figure 7). But even more dramatic were the findings for <u>H. betteni</u> which lived almost exclusively at the outlet (Figure 10). As the sampling sites were chosen to minimize the physical differences between them, it would appear that the faunal changes observed over longitudinal distance are the direct result of presence of the outlet. The only non-outlet related physical feature which differed to a great extent between sites was the amount of shade. The relative importance of this parameter, specifically as it relates to oviposition in net-spinning caddisflies, is uncertain.

Stability, although a difficult parameter to measure, is one of the few physical differences that exist between sampling sites which may be directly related to the outlet. The pond acts as a buffer to rapid changes in temperature, water chemistry and current velocity. In addition, outlets are generally free of ice even during the coldest winter months. As the current nearest the outlet is usually quite slow, scouring as a result of rolling stones and suspended material is greatly reduced. Even the ice during the spring break-up tends to float over the immediate outlet before stream turbulence causes the large pans of ice to break into smaller chunks which, along with snow which may fall off overhanging vegetation, become suspended in the water column and act to scour areas further downstream.

Since the lake outlet provides such a stable environment, those species which are best adapted would tend to flourish in great numbers. In fact, Spence and Hynes (1971) compared the fauna of an outlet with an area receiving mild organic enrichment or pollution due to the high density but relatively low diversity of the fauna. The scouring and fluctuations in physical parameters of the areas downstream make it difficult for any net-spinning caddisfly to form a monopoly (McAuliffe 1984) and thus diversity would be expected to be much greater than that seen at the outlet while total numbers are reduced.

It might be speculated that, because C. pettiti and N. crepuscularis exist further downstream as well as at the outlet, while H. betteni appears to be restricted to the outlet, these caddisflies are more eurytopic or less specialized than H. betteni. In fact, it may simply be that H. betteni has the largest and most aggressive larvae and, therefore, these are least likely to be dislodged from their preferred sites. The other caddisflies populate the outlet until the carrying capacity is reached (ie density is at a maximum). Beyond that point any new arrivals are actively dislodged or voluntarily drift downstream, possibly as a result of stridulatory warnings (Jansson and Vuoristo 1979, Johnstone 1964, Silver 1980), to a less favorable but less crowded location producing density dependent drift (Muller 1955, Waters 1965, Dimond 1967, Mackay and Wiggins 1979). This drift could result in the apparent lag in development time observed in specimens in downstream stations as these stations are colonized later than the outlet area (Figures 9 and 16). A similar lag was observed for several blackfly species in a Swedish lake outlet (Carlsson *et al.* 1977). This may, in turn, explain some of the reports of female caddisflies flying upstream to deposit their eggs (eg. Roos 1957). Certain features of the lake outlet may act as oviposition cues to the adult females. Adults emerging from the outlet itself would probably remain in that area while those resulting from the 'victims' of density dependent drift would be observed flying in search of oviposition sites. While this density dependence appears to contradict Peckarsky's (1979) results which indicated the distributions of *Hydropsyche* species were generally density independent, it must be kept in mind that the densities encountered at the Axes Pond outlet were much greater than those of her study.

ESTABLISHMENT OF A LAKE OUTLET COMMUNITY

Having considered how these species are able to exist together in spite of their overlap in food capture technique, the question of how they actually establish themselves at the outlet still remains. The actual recognition of a lake outlet by adult caddisflies is probably not difficult and those which have specifically evolved to inhabit outlet regions could well be expected to use very specific outlet cues for oviposition. As this is a very restricted region along the stream, the density of eggs laid in this small area by these caddisflies is probably quite high. H. betteni eggs are laid later than most of the other outlet species so it might be expected that these eggs and early instar larvae would be readily removed by larger instar larvae of H. sparna and perhaps N. crepuscularis and C. pettiti. However, since densities during mid summer are quite low and early instar hydropsychid larvae are generally not very carnivorous (Fuller and Mackay 1980), it may be possible that, for a short time, H. sparna and H. betteni can co-exist at the outlet. This in spite of the fact that H. sparna arrived first and both tend to occupy similar locations on the substrate. By the time densities become critical H. betteni larvae would be comparable in size with those of H. sparna even though H. betteni larvae exist, predominantly in an earlier instar. At this point a difference in aggressive behaviour or carnivory may be the deciding factor which determines the dominance of H. betteni at the outlet. C. pettiti adults emerged early and laid eggs early enough that hatching larvae could establish nets prior to the hatching of Hydropsyche larvae. Also, C. pettiti nets may occur in locations which are largely unsuitable for Hydropsyche and thus avoid competition. Personal observations indicated that C. pettiti nets were built more towards the sides of substrates rather than the front or top of them (the preferred location for Hydropsyche). Also, nets were sometimes found over crevices too small for mature Hydropsyche larvae to inhabit. However, sheer numbers alone seem to insure existence of *C. pettiti* larvae at the outlet. *N. crepuscularis* is so general in its habitat requirements that it is probably the best equipped to avoid competition by existing in areas unsuitable for other species. In addition, the large billowing nets which it produces seem to interfere with hydropsychid nets so substrates with attached, abandoned *Neureclipsis* nets from the spring are often still free of hydropsychids in late summer. Consequently, pre-conditioned sites sometimes exist for young *N. crepuscularis* larvae.

PRODUCTION IMPLICATIONS

While precise production estimates are not within the scope of this study, several factors involved in obtaining them have been mentioned. It is obvious that any biomass estimates derived from summer sampling programs will be small since large numbers of larvae are in the smallest instar or still in the egg stage, making them difficult to collect, and peak standing crops occur from late fall to spring. In turn this generalization must be tempered with the knowledge that production estimates can not be transferred from one study to another because life history patterns, even within the same species, differ with geographical location. Any attempt at deriving a production value for a given system must be based on an independent study of the faunal life history patterns of that self same system.

The reduced production found in Axes Pond outlet, relative to mainland outlets can only be examined superficially by comparing the peak standing crops for the different systems. Cushing (1963) found 3,340 campodeiform Trichoptera per square foot (3591 / 0.1 square meters) below a series of lakes on the Montreal River, Saskatchewan. Oswood (1979) observed a maximum density of 5555 hydropsychid larvae per 0.2 square meters (2777 / 0.1 square meters) at Owl Creek, Montana. Axes Pond outlet could boast a peak density for all net-spinning caddisflies studied (Hydropsychidae, Philopotamidae and Polycentropodidae) of 1285 per 0.1 square meters. A higher peak was observed further downstream (1999 per 0.1 square meters) due to a large aggregation of <u>C. aterrima</u> (See Figure 6; Dec., Stat. B). In addition, the existence of a semivoltine life history in some of the Newfoundland net-spinning caddisflies creates a further complication in that even these low estimates may overestimate the actual annual production.

SESTON

The precipitous decline in seston usually observed at a lake outlet is thought to be due largely to ingestion by filter-feeding organisms (Maciolek and Tunzi 1968). Researchers who have studied seston dynamics have often found only one filter-feeder group. This may be due to seston quality or unsuitable habitat for other groups (Ladle <u>et al</u>. 1972, Maciolek and Tunzi 1968, Ulfstrand 1968). Occasionally, a mixed filter-feeder community is encountered (eg. Oswood (1976) observed both Hydropsychidae and Simuliidae in large numbers at an outlet) which usually corresponds with a much more drastic decline in seston at the lake outlet than that observed for a single filter-feeder group. In contrast, there was no significant change in total seston between any of the sampling stations on Axes Brook. This may be due, in part, to the scarcity of fine particle filter-feeders at the outlet (ie blackflies).

Within the seston are several components. These include the drifting arthropods, phytoplankton and detritus. Drifting arthropods were generally found in small numbers in seston samples. However, a series of drift samples taken over 24 hours at the lake outlet showed a distinct peak in drifting organisms shortly after dark (Figure 18). Such large increases in drift at night are common (Hynes 1970). Most of the nocturnal increase in drift at the Axes Pond outlet was due to lake derived plankters (Cladocera and Copepoda). This contrasts with Oswood (1976), who saw large numbers of larval and adult insects in the seston. Downstream export of lake plankters at night is certainly related to vertical migration of Cladocera and Copepoda in the lake water column (Wetzel 1975). The existence of this pulse of lake plankters entering the outlet stream indicates availability of a qualitatively and quantitatively different food source that is unique amongst flowing water systems. This food source was utilized to varying degrees by all of the net-spinning caddisflies present in the Axes Pond outlet. This was the only component of the seston to show a dramatic decline over a short distance indicating some settling of plankton on the substrate and its selective removal from the seston by outlet filter-feeders were taking place. Furthermore, since the disappearance of zooplankton from the outlet corresponded roughly with the distribution of *H. betteni*, there may be a close relationship between the two (ie *H. betteni* larvae had a large component of animal remains in their guts).

Similarly, phytoplankton would be expected to show a diurnal pattern of vertical migration but to a lesser extent than zooplankton. There is, however, no strong evidence for this in the Axes Pond data. While phytoplankton was eaten by the filter-feeders, its removal from the water column was much slower with significant differences in abundance observed only between the outlet and the station furthest downstream (station 'D'). This may indicate that the bulk of the filter-feeders have nets with mesh sizes too large to efficiently filter these small, largely unicellular plankton. *C. aterrima* has the finest mesh size of any of the nets encountered but its preferred net location (under stones) would remove it from areas of faster, more turbulent flow and thus away from areas of higher sieving rates. *C. aterrima*'s method of feeding would seem to rely heavily on sedimentation and chance to make food available to it.

Detritus was abundant at all locations along the stream. In all probability, it increased in abundance downstream from the outlet. This assumption is based on the fact that zooplankton and phytoplankton numbers were shown to decrease significantly as they progressed downstream while total seston was unchanged (ie detritus replaced the plankton which was removed). The importance of detritus in the diet of the outlet net-spinning caddisfly larvae may have been masked by the preponderance of filamentous algae present in the guts examined. In previous studies, although many authors have classified the organisms as carnivorous, omnivorous or herbivorous, the bulk of the material ingested has generally been detritus (Cudney and Wallace 1980, Fuller and Mackay 1980). Is this detrital material acting as a substrate for microflora which is used, in turn, by the filter-feeders? This is still unclear. Only C. sterrima appeared to be specialized for detritus feeding and its presence in relatively large numbers at all locations below the outlet indicates that detritus is readily available at all sites.

Although appreciable amounts of non-planktonic arthropods and periphyton (ie. benthic diatoms) were observed in the caddisfly gut contents, they were not a significant component of the seston. This indicated grazing may also be involved in the feeding of filter-feeding caddisflies. Grazing behaviour has been reported previously by Fuller and Mackay (1980). This may be an important feeding behaviour during the winter months when plankton abundance was low.

Seston concentrations have traditionally been assumed to decrease downstream from the lake outlet to some steady state value. However, Oswood (1976) found a rapid decline in seston directly below the lake outlet followed by a recovery then subsequent decline. A similar finding was made by Maciolek and Tunzi (1968). It was proposed that this phenomenon was a result of periphyton production. Heterotrophs ingested lake seston and converted it into nutrients useful to the periphyton. The periphyton, consequently, increased production below the area of peak heterotroph activity. As periphyton production reached a peak, available nutrients became limiting and periphyton production further downstream declined. The result of this chain of events would be a pattern such as that observed by Oswood (1976). Furthermore, Oswood (1976) demonstrated that, as with phyto- and zooplankton, periphyton abundance has a seasonal pattern. Periphyton was more abundant in the spring/summer than in winter. This seasonality was attributed to differing regimes of light and temperature. As no such overall patterns were observed in this study, it was assumed that the longitudinal distance involved was too short (eg. Oswood's study site was nearly 20 times longer).

CONCLUSIONS

1) Zonation exists in the abundance and distribution of species of net-spinning caddisflies within short distances from an outlet. Highest densities and biomass of net-spinning larvae were found in the stations closest to the outlet with attenuation of numbers downstream.

2) Hydropsyche betteni was found almost exclusively at the immediate outlet. Hydropsyche slossonae and Hydropsyche sparna were found, predominantly, just below the outlet but were also found in smaller numbers further downstream. Cheumatopsyche pettiti was most abundant at the outlet but existed in large numbers for some distance below the outlet. Neureclipsis crepuscularis was also most abundant at the outlet and present in large numbers for some distance downstream but did not show as marked a preference for the immediate outlet as did C. pettiti. Chimarra aterrima was found below the outlet and in relatively large numbers for a distance of at least 335 meters.

3) Biomass of net-spinning caddisfly larvae varied throughout the year and between stations. Minimum values were obtained between June and August. Maximum values were observed during the late spring and during the late fall and early winter. Maximum observed biomass of 4.7 gm wet weight / 0.1 square meters was observed at station 'B' (December), but on most sampling dates, highest values were observed for station 'A'. The most downstream station (station 'D') had, consistently, the lowest biomass of any of the stations.

4) Life history patterns of the net-spinning caddisflies are not necessarily comparable with those described for the same species on the mainland. Newfoundland populations tend to overwinter in earlier instars than mainland populations. Furthermore, Newfoundland net-spinning caddisflies are univoltine and/or semivoltine. Semivoltine life cycles have not been recognized for these net-spinning caddisflies previously.

5) Larvae of most species of hydropsychids tend to be larger than those of the respective mainland populations.

6) Density dependent drift resulted in a developmental gradient within the densest populations at the outlet. Larvae of a given generation which were observed at the outlet were generally found in later instars than those found in stations further downstream. This is thought to be due to the high densities of net-spinning caddisflies at the outlet and the resulting competitive displacement of smaller

instar larvae to locations further downstream.

7) Production estimates require year round study of the system and must not be confined to one location. Seasonal variations, longitudinal variation in relation to position of lakes in the drainage system, and the occurrence of semivoltine life cycles in local populations which produces high standing crops with relatively low annual production are all important variables which must be addressed in future estimates of production in Newfoundland streams.

8) Large particles of lake-derived seston tend to be removed from the stream faster than smaller particles.

9) Zonation in species and total biomass tends to exist along a gradient in food quality and food particle sizes. The carnivorous larvae of Hydropsyche betteni are found at the outlet where large food particles are readily available (eg copepods). Less carnivorous species, such as Hydropsyche slossonae and Hydropsyche sparna exist further downstream where the abundance of large food particles is reduced but intermediate food size particles (eg diatoms) are readily available. As these intermediate food size particles are very abundant for some distance downstream from the outlet, some of the net-spinning caddisflies (eg Cheumatopsyche pettiti and Neureclipsis crepuscularis), which feed predominantly on this food type, exist at the outlet as well as further downstream. The larger food particle sizes are quickly removed from the water column

within a short distance from the outlet, the remaining available food material consisting largely of detritus and small unicellular phytoplankton. Chimarra aterrima, a detritivore, is abundant in such areas.

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APPENDICIES

APPENDIX 1. Larval mean wet weight for instars III - V. Standard deviation was determined for instar V larvae because they have the largest influence on total biomass estimates.

INDIVIDUAL MEAN WET WEIGHT (mg)

NAME	III	(N)	IV	(N)	V (SD)	(N)
C. pettiti	0.79	14	2.49	26	6.65 ± 2.51	22
H. betteni	1.82	22	6.15	26	33.27 ± 16.80	28
H. slossonae	1.24	18	6.05	17	19.31 ± 8.72	28
H. sparna	1.04	14	3.19	14	13.65 ± 5.75	23
N. crepuscularis	0.82	11	2.37	32	10.46 ± 6.20	29
C. aterrima	0.42	12	1.48	29	6.20 ± 1.81	32

APPENDIX 2. Physical measurements taken in conjunction with plankton samples for Axes Brook stations 'A' - 'D'.

DATE	MEAN DEPTH (cm) A	B	C	D	MEAN VELOCITY (cm/sec) A	B	C	D
19/03/83	18.0	20.0	18.0	24.0	20.0	20.0	24.0	24.0
27/05/83	24.0	23.0	25.0	27.0	27.4	21.6	20.2	31.7
04/06/83	20.2	20.8	19.8	18.9	20.0	22.0	26.0	32.7
29/06/83	10.0	10.0	13.0	14.0	7.2	5.4	9.0	12.6
16/07/83	18.0	20.5	24.0	25.0	20.0	24.0	26.7	34.3
21/09/83	26.0	20.5	20.5	20.5	24.0	24.0	30.0	24.0
12/10/83	14.0	19.0	17.0	17.0	24.0	24.0	30.0	24.0
22/10/83	35.5	34.0	40.0	33.5	24.0	40.0	40.0	40.0
08/11/83	19.5	23.5	23.5	23.0	20.0	30.0	24.0	30.0
21/11/83	31.5	34.0	32.5	32.5	20.0	30.0	24.0	40.0
05/12/83	18.0	24.0	22.5	27.5	20.0	24.0	20.0	24.0
20/12/83	19.0	18.0	22.0	25.5	20.0	20.0	30.0	24.0
11/01/84	35.0	37.0	38.0	41.5	26.7	40.0	40.0	60.0
22/01/84	20.0	23.0	22.0	27.0	30.0	30.0	24.0	30.0

APPENDIX 3. Kruskal-Wallis test values for <u>Cheumatopsyche pettiti</u>. This particular test is a modification of the usual Kruskal-Wallis test as described by Gibbons (1976) which allows for large numbers of ties in the data.

	MONTH											
	1	2	3	4	5	6	7	8	9	10	11	12
CLASS												
P + V	139	286	470	503	345	324	60	188	91	172	158	141
IV	90	324	638	641	201	54	30	230	72	183	145	160
I + II + III	21	112	409	411	76	0	223	180	24	66	87	63
TOTALS	250	722	1517	1555	622	378	313	598	187	421	390	364

CLASS TOTALS	
P + V	2877
IV	2768
I + II + III	1673

MONTH	SUM OF RANKS	N	MEAN RANK
1	719678	250	2827.7
2	2518264	722	3487.9
3	6046305	1517	3985.7
4	6119540.5	1555	3935.4
5	1845648.5	622	2967.3
6	702839	379	1854.5
7	1659671	313	5302.5
8	2417437	598	4042.5
9	593345	187	3173.0
10	1455174.5	421	3456.5
11	1409213.5	390	3613.4
12	1293105	364	3552.5

CORRECTION FACTOR FOR TIES (CALCULATED AS DESCRIBED BY GIBBONS (1976) = 1974.16

CONTRAST	OBSERVED VALUE	CRITICAL VALUE (P<.05)
(1+2) - (9+10+11+12)	-156.9	235.2
(1+2) - (3+4)	-629.0	206.2*
3 - 4	50.3	202.2
(3+4) - 5	992.9	246.3*
(3+4) - 6	2105.7	305.0*
(3+4) - 7	-1342.3	332.4*
(3+4) - 8	-82.3	250.4
5 - 6	1112.8	365.1*
6 - 7	-3448.0	427.9*
7 - 8	1260.0	390.9*
8 - 9	869.5	469.4*

*SIGNIFICANT AT P<.05