ECOLOGY OF THREE CONGENERIC SPECIES OF CADDIS FLIES

ABSTRACT OF Ph.D. THESIS

The life cycle and ecology of Pycnopsyche gentilis (McLachlan), P. luculenta (Betten), and P. scabripennis (Rambur), (Trichoptera:Limnephilidae) in West Creek, Mont St. Hilaire, Quebec

by Rosemary Joan Mackay

Biology Department, McGill

Three species of Pycnopsyche occur in West Creek. The life history of P. scabripennis is distinct from P. gentilis and P. luculenta which are contemporaneous and similar in size. Adult males of each species differ in the peak time of arrival at light when active on the same night. Field studies and laboratory experiments show that the populations of P. gentilis and P. luculenta overlap but are proportional to the amount of preferred habitat space. P. gentilis uses leaves for case materials and habitat; P. luculenta can utilize leaves or twigs, but remains near twigs. Both species feed preferentially on fungally-infected leaves; P. luculenta ingests less leaf material if twigs are available. Larval habitat is uninfluenced by mineral substrates except during case-construction by 5th-instar P. gentilis and aestivation by P. scabripennis. Larvae and leaves are washed downstream during the spring thaw. Subsequent crowding in the reduced habitat space may result in competitive interactions. Factors contributing to the coexistence of related species are discussed.

The life cycle and ecology of *Pycnopsyche gentilis* (McLachlan), *P. luculenta* (Betten), and *P. scabripennis* (Rambur), (Trichoptera:Limnephilidae) in West Creek, Mont St. Hilaire, Quebec

by

Rosemary Joan Mackay, M.Sc.

A Thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Biology
McGill University
Montreal

April 1972

PREFACE

In keeping with the newly-accepted regulations for thesis style that have been authorized by the Graduate Training Committee of the Biology Department at McGill, Parts I and II of this thesis have been written in the form of papers suitable for publication (Part II will be shortened before submission). The thesis also includes a General Introduction and some overall Conclusions, each section having its own bibliography.

ACKNOWLEDGMENTS

I wish to thank the following for their contributions to this thesis:

Dr. Jaap Kalff for his direction and encouragement,

Dr. Fernand Schmid, Entomology Research Institute, Ottawa, for identification of adult *Pycnopsyche* specimens;

Mr. Harry McCandlish and the workshop staff of the Biology Department, McGill, for making the sampling traps and laboratory stream systems;

M. Raymond Lahaye and his staff on the Gault Estate of Mont St. Hilaire for erecting and wiring the black-light trap, and other assistance;

The Faculty of Graduate Studies and Research of McGill for financial support in the form of a David Stewart Memorial Fellowship, 1968-69, and a McConnell Fellowship, 1969-72.

LIST OF CONTENTS

Part I

Part II

LIST OF FIGURES AND PLATES

LIST OF TABLES

GENERAL INTRODUCTION

The genus Pycnopsyche is a large, yellow-brown, limnephilid caddis fly of eastern North America where it is the only important nearctic representative of the tribe Stenophylacini (Schmid 1955). Fourteen species are known in the adult stage (Betten 1950). Although the larvae when fully grown are large (up to 25 mm long) aquatic insects, carrying characteristic cases, only a few scattered and incomplete descriptions (Vorhies 1909, Lloyd 1921, Sibley 1926, Betten 1934) had appeared in the literature before Flint (1960) described the terminal larval instars of 7 species. Flint included notes on the habits and cases of P. gentilis (McLachlan), P. luculenta (Banks), and P. scabripennis (Rambur); but no detailed information on the microhabitats, feeding behaviour or life histories of these species was available before the present study. Only 2 other Pycnopsyche species out of this conspicuous genus have been studied from an ecological aspect (Cummins 1964, Feldmeth 1970).

In view of the widespread distribution of Pycnopsyche species, and the fact that the larvae can be found in streams and small rivers from September through July, the only explanation for the paucity of information is that the larvae spend most or all of their lives in slow-flowing water along stream margins or pool bottoms. Nearly all studies of stream-living insects have concentrated on those in riffle areas, and particularly their distribution in relation to trout and other sport fish. In fact the emphasis placed on insects in terms of fish food has often overshadowed the roles the insects themselves play as consumers, and thus their positions in the ecosystem relative to lower trophic levels. However, increasing interest in energy relationships within aquatic ecosystems has recently directed attention to other components of energy flow in streams, especially the importance of allochthonous organic material as a potential food source (e.g. Jones 1950, Teal 1957, Nelson and Scott 1962, Hynes 1963, Darnell 1964, Egglishaw 1964, Minshall 1967, 1968, Kaushik and Hynes 1968, 1971). *Pycnopsyche* larvae feed on allochthonous organic material in the form of submerged leaves and other detritus that have fallen from riparian trees. As the range of the genus coincides remarkably with that of the sugar maple (*Acer saccharum* Marsh) and the eastern temperate deciduous forest (Ross 1963) the dense shade (restricting autotrophic plants) and heavy autumnal leaf fall in the forest probably favoured the evolution of species able to use allochthonous matter as a primary food source (Ross 1963, Hynes 1963).

Not only are the 14 species of *Pycnopsyche* distributed within one forest biome, but 2 or 3 species are commonly found together in one stream. Similar species are often found in broadly similar environments (Williams 1947, 1964, Freeman 1968) unless speciation has been unusually divergent. But as Mayr (1963) has pointed out, closely related species persisting in sympatry must have those properties that initiated speciation: a) mechanisms guaranteeing reproductive isolation and b) the ability to resist competition from other species using the same resources. Many investigations have concerned the ecological relationships of sympatric congeneric species (e.g. Elton 1946, Brian 1956, Broadhead 1958, MacArthur 1958, Hutchinson 1959, Kohn 1959, Miller 1964, 1968, Inger 1969). The variously named principles underlying these relationships (see Gilbert *et al* 1952, Hardin 1960, DeBach 1966) all conclude that where 2 (or more) species co-occur indefinitely, they must be occupying different niches (*sensu* Hutchinson 1957).

The following study was undertaken to examine the niches of three related caddis flies, and the extent of overlap of respective niche spaces, with special emphasis on the way *Pycnopsyche* larvae exploit the resources of allochthonous organic material in a small stream.

REFERENCES

Betten, C. 1934. The caddis flies or Trichoptera of New York State. N.Y. State Mus. Bull. 292: 1-576.

Betten, C. 1950. The genus Pycnopsyche (Trichoptera). Ann. ent. Soc. Amer. 43: 508-522.

Brian, M.V. 1956. Segregation of species of the ant genus Myrmica. J. Anim. Ecol. 25: 319-337.

Cummins, K.W. 1964. Factors limiting the microdistribution of the caddis flies (Pycnopsyche lepida (Hagen) and Pycnopsyche guttifer (Walker) in a Michigan stream (Trichoptera:Limnephilidae). Ecol. Monogr. 34: 271-295.

Broadhead, E. 1958. The psocid fauna of larch trees in northern England — an ecological study of mixed species populations exploiting a common resource. J. Anim. Ecol. 27: 217-263.

Darnell, R.M. 1964. Organic detritus in relation to secondary production in aquatic communities. Verh. internat. Verein. Limnol. 15: 462-470.

DeBach, P. 1966. The competitive displacement and coexistence principles. Ann. Rev. Ent. 11: 183-212.

Egglishaw, H.J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. J. Anim. Ecol. 33: 463-476.

Elton, C. 1946. Competition and the structure of ecological communities. J. Anim. Ecol. 15: 54-68.

Feldmeth, C.R. 1970. The influence of acclimation to current velocity on the behaviour and respiratory physiology of two species of stream Trichoptera larvae. *Physiol. Zool.* 43: 185-193.

Flint, O.S. 1960. Taxonomy and biology of Nearctic limnephilid larvae (Trichoptera) with special reference to species in eastern United States. *Entomol. Amer.* 40: 1-120.

Freeman, B.E. 1968. Studies on the ecology of adult Tipulidae (Diptera) in Southern England. *J. Anim. Ecol.* 37: 339-362.

Gilbert, O., T.B. Reynoldson, and J. Hobart. 1952. Gause's hypothesis: an examination. *J. Anim. Ecol.* 21: 310-312.

Hardin, G. 1960. The competitive exclusion principle. *Science*. 131: 1292-1297.

Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symp.* on *Quant. Biol.* 22: 415-427.

Hutchinson, G.E. 1959. Homage to Santa Rosalia *or* why are there so many kinds of animals? *Amer. Nat.* 93: 117-125.

Hynes, H.B.N. 1963. Imported organic matter and secondary productivity in streams. *Proc. Internat. Congress Zool.* 16: 324-329.

Inger, R.F. 1969. Organization of communities of frogs along small rain forest streams in Sarawak. *J. Anim. Ecol.* 38: 123-148.

Jones, J.R.E. 1950. A further ecological study of the River Rheidol: the food of the common insects of the main stream. *J. Anim. Ecol.* 19: 159-174.

Kaushik, N.K., and H.B.N. Hynes. 1968. Experimental study on the role of autumn-shed leaves in aquatic environments. J. Ecol. 56: 229-243.

Kaushik, N.K., and H.B.N. Hynes. 1971. The fate of dead leaves that fall into streams. Arch. Hydrobiol. 68: 465-515.

Kohn, A.J. 1959. The ecology of Conus in Hawaii. Ecol. Monogr. 29: 47-90.

Lloyd, J.T. 1921. The biology of North American caddis fly larvae. Bull. Lloyd Libr. 21, Ent. Ser. 1: 1-124.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology. 39: 599-619.

Mayr, E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, Mass.

Miller, R.S. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. Ecology. 45: 256-272.

Miller, R.S. 1968. Conditions of competition between Redwings and Yellow-headed blackbirds. J. Anim. Ecol. 37: 43-61.

Minshall, G.W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology. 48: 139-149.

Minshall, G.W. 1968. Community dynamics of the benthic fauna in a woodland springbrook. Hydrobiologia. 32: 305-339.

Nelson, D.J., and D.C. Scott. 1962. Role of detritus in the productivity of a rock-outcrop community in a Piedmond Stream. *Limnol. Oceanogr.* 7: 396-413.

Ross, H.H. 1963. Stream communities and terrestrial biomes. *Arch. Hydrobiol.* 59: 235-242.

Schmid, F. 1955. Contribution à l'étude des Limnophilidae. *Mitt. schweiz. ent. Ges.* 28: 1-245.

Sibley, C.K. 1926. Trichoptera, *in* A preliminary biological survey of the Lloyd-Cornell Reservation. *Bull. Lloyd Libr.* 27, *Ent. Ser.* 5: 102-108, 185-221.

Teal, J.M. 1957. Community metabolism in a temperate cold spring. *Ecol. Monogr.* 27: 283-302.

Vorhies, C.T. 1909. Studies on the Trichoptera of Wisconsin. *Trans. Wisc. Acad. Sci.* 16: 647-738.

Williams, C.B. 1947. The generic relations of species in small ecological communities. *J. Anim. Ecol.* 16: 11-18.

Williams, C.B. 1964. Patterns in the balance of Nature and related problems in Quantitative Ecology. Academic Press, London and New York.

PART I

INTRODUCTION

A general survey of the aquatic insect fauna of West Creek, Mont St. Hilaire, Quebec (Mackay 1969) revealed several genera represented by more than one species. In most cases the commonly occurring congeneric species were ecologically segregated (Grant and Mackay 1969), either occupying different habitats or developing at different times of the year. If extensive temporal overlap did occur, then the species differed markedly in size. The only obvious exceptions to this pattern were three species of the caddis fly Pycnopsyche (Limnephilidae: Stenophylacini) but the small numbers collected, and uncertain identification of small larvae at the time of the survey, prevented detailed analysis. Certainly P. gentilis, P. luculenta and P. scabripennis had nearly contemporaneous larval periods lasting 9-10 months, and were the same size. All three species were found in slow-flowing areas of the stream, in packets of fallen hardwood leaves and in leaf and twig detritus. Their longitudinal distribution in West Creek (Mackay 1969) was found to agree fairly well with the notes on habits given by Flint (1960) in that P. gentilis was the only species found near the spring-fed source, and all species occurred at lower, wider sampling stations. However, P. gentilis was the most abundant species even where the stream was 2-4 m wide (and hence in a bigger stream than Flint's "spring-fed brooklets only 1 or 2 feet wide"). P. luculenta in West Creek was not, as in Flint's study, most commonly found with larvae of scabripennis because P. scabripennis was relatively rare. Yet the ranges of the 2 species were similar. The type of larval case built by terminal instars of each species had been described briefly (Flint 1960), but excluding these case materials, little was known about individual species requirements in the stream. The limited literature on the behaviour of *Pycnepsyche* adults shows only that collection records range from July to November (Betten 1950).

Therefore to elucidate the ways *P. gentilis*, *P. luculenta* and *P. scabripennis* share the resources of a woodland stream environment, an intensive field sampling programme was carried out coupled with laboratory experiments in model streams. Part I of this study describes the life history (including growth rates) and general biology of all stages of each species. Details of microhabitat choice and the effects of catastrophic drift, species interactions, and feeding behaviour appear in Part II.

STUDY AREA

West Creek is a small, cool, woodland stream on Mont St. Hilaire, Rouville County, Quebec. As the stream has been described in detail before (Mackay 1969, Mackay and Kalff 1969) only a brief summary is given here. The stream is 1.7 km long and 30 cm to 2 m wide for most of the year. It is generally slow flowing, the lowest recorded rate being 1 litre/sec in September, but melting snow in April increases the discharge to a recorded high of 360 litre/sec, and may double the width of the stream for 2-3 weeks. The stream bottom is mainly sandy with patches of gravel, interrupted by short riffles over boulders, cobbles and pebbles. The water temperature ranges from 0°C in January, when much of the stream is covered by ice and snow bridges, to 17-18°C in August.

An important characteristic of the stream is the large amount of allochthonous organic matter it contains: fallen logs, twigs, bud scales, catkins, seeds, and an annual increment of autumn-shed leaves, all in various stages of decomposition.

METHODS

1. Collections of *Pycnopsyche* larvae and pupae.

Pycnopsyche larvae were collected for 3 years between September 1968 and July 1971. Five samples of organic substrate in West Creek (leaves, leaf and twig detritus, or mixtures of leaves and detritus) were taken at approximately weekly intervals from September 1968 through May 1969, and at 10-day intervals from September 1969 through May 1970. The sampling procedures used during these 2 periods were designed to investigate microhabitat selection as well as other features of larval biology and are described in more detail in Part II. During the 1969-1970 season, samples were also taken from sand and gravel; and logs and stones were examined for aestivating larvae and pupae during the summer. Collections in the 1970-71 season (made frequently during September and October 1970, then at monthly intervals until August 1971) were taken from areas in West Creek where *Pycnopsyche* larvae or pupae were known to be abundant so that large numbers were available for weight measurements.

Two Surber-type samplers were used, having Nitex nets of mesh size 0.5 mm and 2 mm respectively. As the minimum diameter of encased *Pycnopsyche* larvae is more than 0.5 mm, the fine net retained all the early instars. It was used throughout the first sampling season to detect any late-hatching or slow-growing larvae. During the 2 following seasons, the fine net was used until the end of January, by which time all larvae were large enough to be caught in the coarse net.

After transportation to the laboratory (1-2 hours) the samples were reimmersed in dechlorinated tap-water kept at temperatures similar to those in the field. Larvae were sorted live within 24 hours of collection, identification being confirmed by rearing individuals to the adult stage. Larval head width was measured across the eyes with a micrometer eye piece in a binocular microscope. Freshly caught representatives of each instar were persuaded to leave their cases by gently prodding the anal region with a blunt probe. Naked pupae and larvae were killed in a 100°C oven where they died within 15 seconds. They were then dried at 60°C for 24 hours, and weighed immediately on a Cahn electrobalance (model G) to the nearest 0.001 mg (instars I to III) or 0.01 mg (instars IV and V).

2. Collections of *Pycnopsyche* adults

A preliminary study of adult behaviour in the field was conducted in 1970. The attractant was a butane pressure lantern (Camping Gaz International: model Lumogaz C) hung near the upstream side of a vertical white cotton sheet 2.8 m x 1.3 m. The sheet was erected at various points along the stream, either on the bank or across the stream, 30 cm above the water. When caddis flies settled on the sheet they were flicked into a jar of 80% ethanol. Collections were made on every 2nd and 3rd night from 27 July - 10 September, and on 17, 30 September and 13 October 1970. The catch on each collection night was separated into 15-minute catch-periods beginning at sunset and continuing for at least 10, and up to 18, periods. During daytime, a sweepnet was used in the streamside vegetation, and crevices in tree trunks and fallen logs were searched for resting adults.

In 1971 when 110V a-c electricity was available at the streamside, long-wave UV light (black-light) was used as the attractant in a modified Pennsylvanian funnel trap (Southwood 1966). The trap was suspended 2 m above water level on the bank, 150 m from the mouth of West Creek at a point where pupae of all 3 Pycnopsyche species were present. The light was produced by two 4 w fluorescent black-light lamps (General Electric F4T5 BL) fixed vertically over an aluminum funnel leading to a removable plastic bag. Caddis flies falling into the bag could settle on, or hide under crumpled cardboard. The lamp was turned on at sunset and the bags were changed every 15 minutes over 2½ hours. The bags were subsequently left undisturbed overnight. The following morning, each bag-catch was lightly anaesthetized with ether while Pycnopsyche species were counted and sexed. Recovery took place within 5-15 minutes in a box provided with dilute honey solution and cardboard retreats. Some females were dissected for egg counts; other females and males were placed in cages (1 per species) in West Creek. Each cage covered flowing and still water, damp gravel, and an overhanging bank to provide a choice of egg-laying sites.

The light trap was operated every 2nd night from 9 August to 14 September, then every 3rd or 4th night until the end of September; a final collection was made on 6 October. Readings of air temperature and relative humidity were taken by a sling-psychrometer every half hour during collection periods, and notes were made on wind speed, cloud cover and moonlight.

The lantern-and-sheet trap was used on 27 July, 2 August and 11, 13 September to compare the efficiency of the 2 trapping methods.

RESULTS

1. Life cycle and growth

Measurements of head widths of *Pycnopsyche* larvae fell into 5 non-overlapping groups in each species (Table 1) indicating 5 larval instars.

First-instar larvae of *P. scabripennis* appear in West Creek in September, about one month ahead of *P. gentilis* and *P. luculenta*. The instar development of each species during 3 growing seasons is shown in Figs 1 and 2. As total numbers per collection during 1968-69 were variable and often small, the data are presented (Fig 1) as combined pairs of collections at approximately 2-week intervals.

Every autumn, *P. scabripennis* larvae pass rapidly through 1st, 2nd and 3rd instars so that 4th-instar and sometimes 5th-instar larvae were collected in October. A few 4th-instar larvae were collected as late as January in 1969 and 1971, but most *P. scabripennis* larvae complete the 4th moult before winter, which they spend in the 5th instar.

The autumn moults of *P. gentilis* and *P. luculenta* are less frequent; the larvae overwinter every year in the 3rd and 4th instars, with the percentage in the 4th instar gradually increasing between January and March (Figs 1, 2). No 5th-instar larvae of either species appear before the end of February. The frequent collections made in 1968-69 and 1969-70 showed that instar development in these 2 species is similar, *P. luculenta* larvae usually moulting only slightly in advance of *P. gentilis*.

Table 1 Range and mean larval head width (mm) of *Pycnopsyche* larvae in West Creek

Instar	*P. scabripennis*	*P. gentilis*	*P. luculenta*
I	0.3 -0.4 (0.35)	0.3 -0.4 (0.35)	0.26-0.3 (0.27)
II	0.52-0.58 (0.55)	0.5 -0.6 (0.55)	0.45-0.5 (0.48)
III	0.8 -0.9 (0.85)	0.75-0.85 (0.8)	0.7 -0.8 (0.75)
IV	1.2 -1.5 (1.4)	1.2 -1.5 (1.35)	1.0 -1.2 (1.05)
V	1.8 -2.2 (2.0)	1.8 -2.0 (1.85)	1.4 -1.7 (1.6)

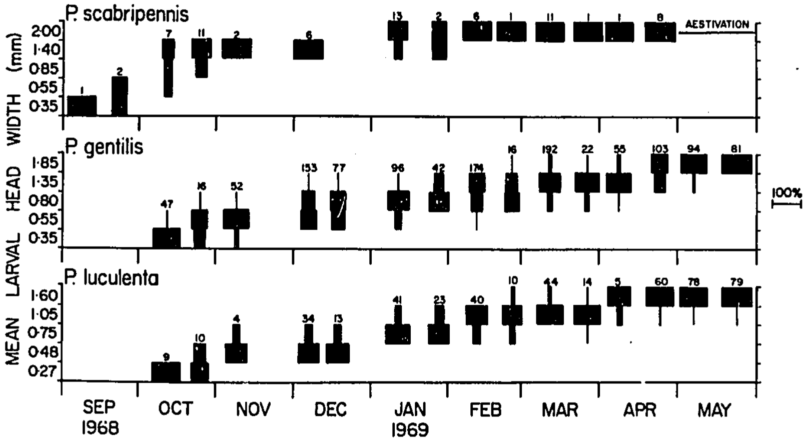


Figure 1. Instar development of *Pycnopsyche* larvae in West Creek, 1968-69. Each histogram shows the total number of larvae collected (in figures) and the percentage/instar (black).

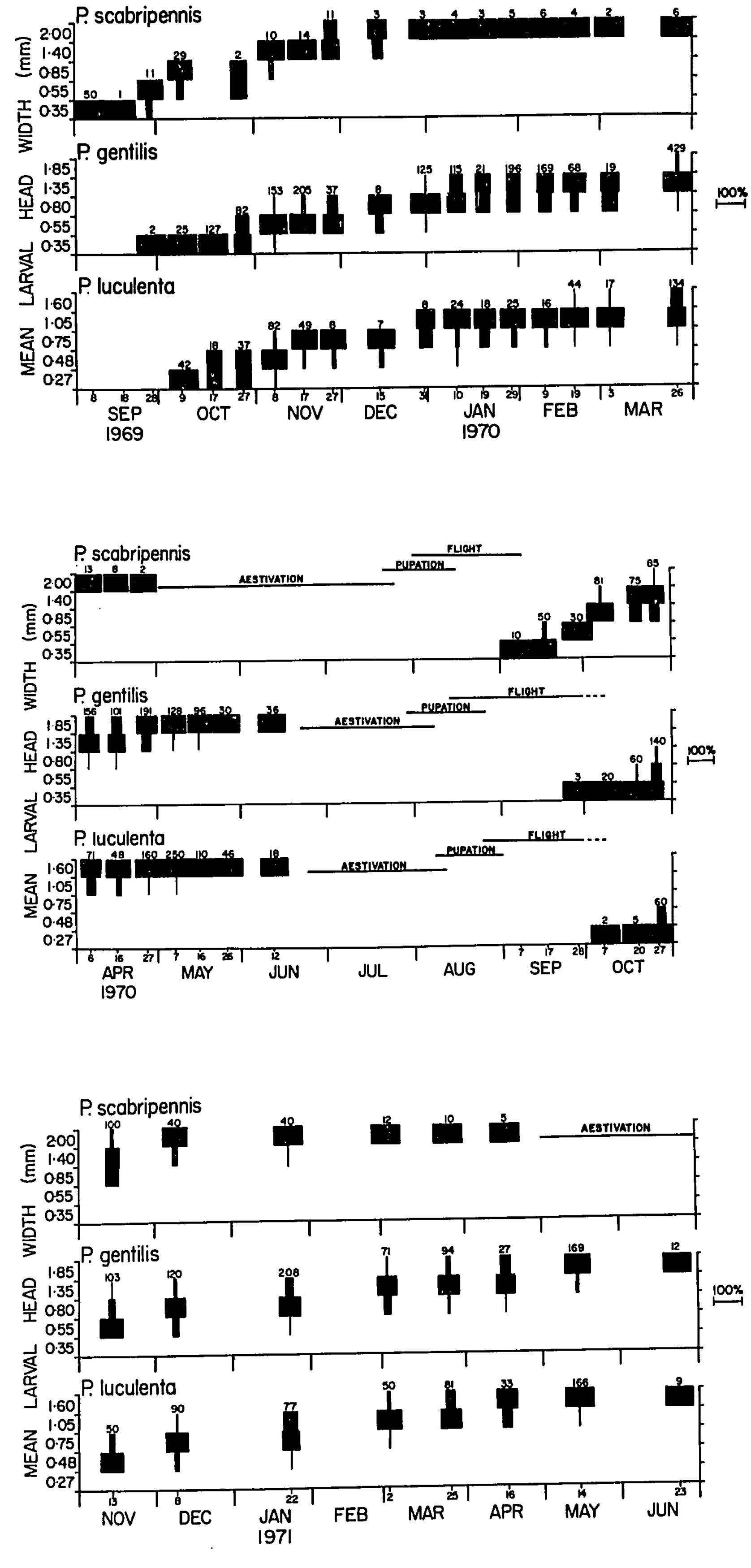


Figure 2. Life history stages and instar development of Pycnopsyche species in West Creek, 1969-71. (Histograms as in Fig 1).

In spite of the early appearance of 5th-instar _P. scabripennis_, it begins to pupate only at the end of July, while _P. gentilis_ and _P. luculenta_ begin in August. The pupal period lasts 10-14 days with the adults emerging in early August (_P. scabripennis_), or late August and September (_P. gentilis_ and _P. luculenta_). Flight continues for 2-4 weeks after emergence.

Collections in 1970-71 were less frequent than earlier years but included more specimens for weighing so that separate weight/time curves could be drawn for the 5 instars of each _Pycnopsyche_ species (Fig 3). Each instar gains weight rapidly at first, then less quickly and, towards the end, may begin to lose weight. _P. scabripennis_ shows its greatest weight increase during the first 3 instars. _P. gentilis_ and _P. luculenta_ both gain weight quickly during the 1st instar; further weight changes within instars are relatively gradual until the marked increase in the 5th instar of both species between mid-May and the end of June. All species lose weight during prepupal aestivation, and again when they pupate (Fig 3).

The developmental patterns of the 3 species can be more closely compared by considering the mean individual weight (MIW) of a species at any one time (Fig 4);

$$\mathrm{MIW} = \Sigma\, \bar{x}_i\, p_i$$

where $\bar{x}_i$ is the mean weight of the i th instar and p_i is the proportion of the i th instar in the population.

An instantaneous growth rate (IGR) was calculated with the formula

$$IGR = \frac{\log_e W_t - \log_e W_o}{t}$$

where W_t is the mean individual weight (mg) of a species at the end of time t, and W_o is the weight at the beginning of the period.

The IGR during the first month of growth is higher in *P. scabripennis* than in *P. gentilis* or *P. luculenta* (Fig 5), giving *P. scabripennis* a further initial advantage in addition to its earlier hatching, thus making larvae of this species the largest in West Creek at any one time. The MIW of *P. scabripennis* larvae rose steeply between September and December 1970 (Fig 4) then levelled off due to completion of the 4th larval moult and to the small weight gain of 5th-instar larvae during winter. This flattening of the weight curve (Fig 4) is reflected in the low IGR (Fig 5) during the same period. *P. scabripennis* shows little change in weight with the coming of spring; a slight increase in growth rate in March is followed by a steady decrease until pupation.

In contrast, the MIW curves of *P. gentilis* and *P. luculenta* (Fig 4) after rising steadily through the autumn do not level off in winter although the slopes are less steep from December to April. The IGR of both species decreases during autumn (although not as much as the IGR of *P. scabripennis*) and increases the following spring. Continuous recordings of water temperature were not kept in 1970-71, but data from previous years suggest that the IGR begins to increase as water temperatures rise. The flattening of the IGR curves of *P. gentilis* and *P. luculenta* at the end of April 1971 (Fig 5) may be caused by the disruptive effects of the spring thaw **on** larval habitats and food supplies.

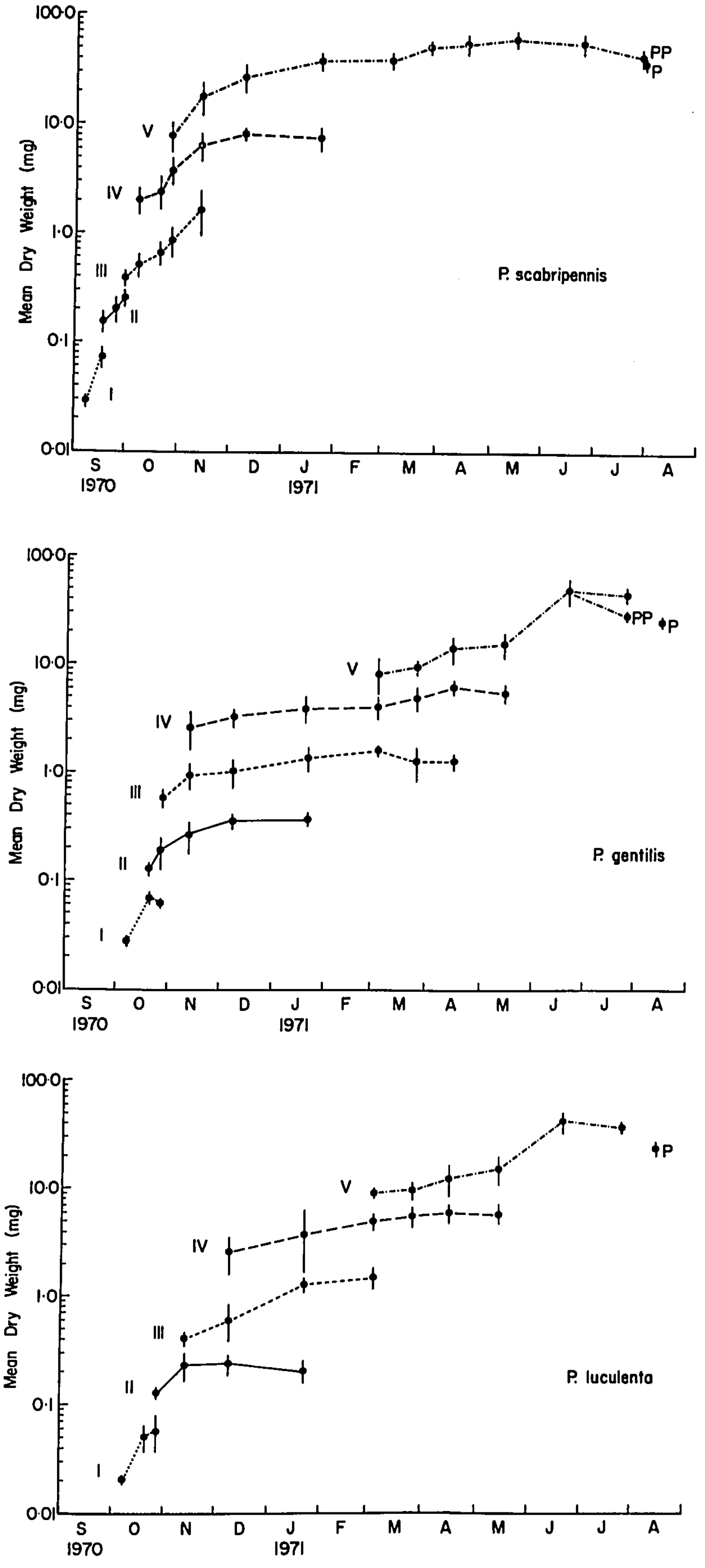


Figure 3. Changes in mean dry weight per instar during larval instars I-V, prepupae (PP) and pupae (P) of Pycnopsyche species in West Creek, 1970-71. (Vertical lines represent 95% confidence limits).

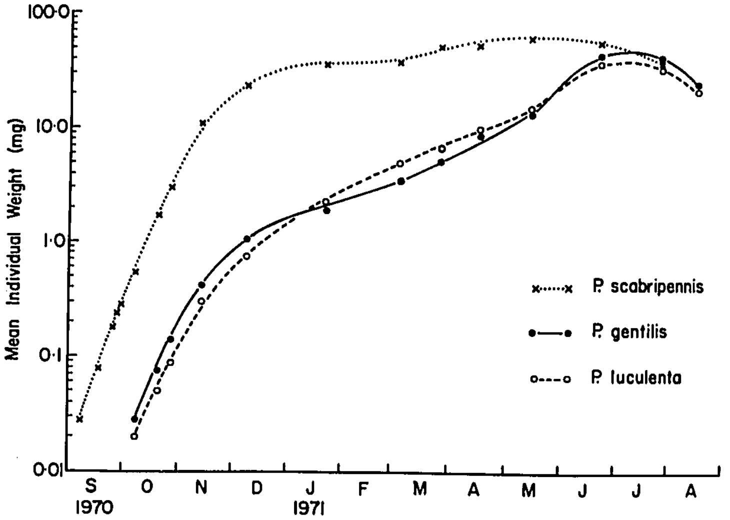


Figure 4. Changes in mean individual weight of Pycnopsyche species in West Creek, 1970-71. (Curves fitted by eye).

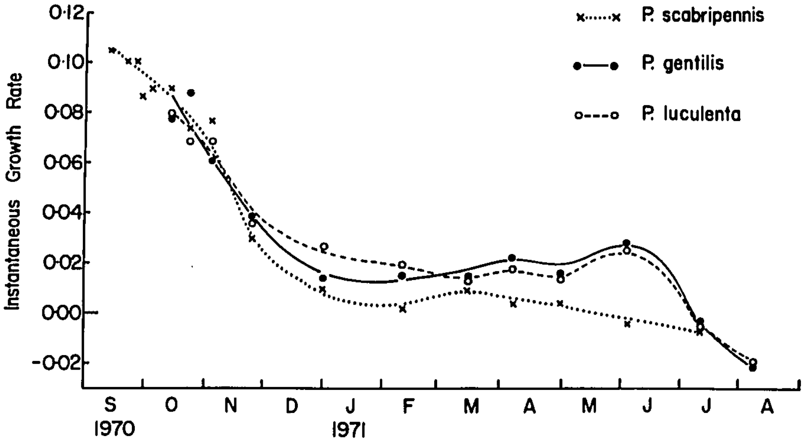


Figure 5. Instantaneous growth rate ($\log_e$ mg/day) of Pycnopsyche species in West Creek, 1970-71. (Curves fitted by eye).

Although P. luculenta larvae always have narrower head capsules than equivalent instars of P. gentilis (Table 1), differences in weight are less consistent and could only be detected at the beginning of the 1970-71 growing season, and just before pupation. From October to December 1970, the mean weight per instar of P. luculenta was usually significantly less than equivalent instars of P. gentilis (Table 2). There was no significant difference between equivalent instars from January through June 1971; but owing to the slightly advanced moult of P. luculenta, its MIW exceeded that of P. gentilis during winter and spring. As the proportion of larvae in the 5th-instar increased, the smaller absolute size of P. luculenta again became apparent, but the weight difference between the 2 species did not become significant until the end of July 1971 (Table 2).

2. Larval and pupal habitats

As details of larval habitat selection are given in Part II, only the general habitat will be described below.

P. gentilis larvae are found chiefly among fallen hardwood leaves and occasionally in leafy detritus. During the spring thaw when much leafy material is washed downstream, up to two-thirds of the P. gentilis population enter the drift passively through habitat displacement. Those larvae that survive the drift, or drop to the stream bottom, are subsequently found in any remaining allochthonous detritus until the end of June when they crawl under large stones or submerged logs. They remain hidden and relatively inactive for a month, at some stage fastening the case to the underside of the covering, before passing into the prepupal stage.

Table 2 Differences between the mean dry weight per instar of equivalent instars of *Pycnopsyche gentilis* (G) and *P. luculenta* (L), 1970-1971 (significance determined by "t" tests)

Date	Instars				
	I	II	III	IV	V
October 7	G>L***				
October 20	G>L***				
October 27	n.s.	G>L***			
November 13		G>L*	G>L**		
December 8		G>L**	G>L*	G>L*	
January 22			n.s.	n.s.	
March 2			n.s.	n.s.	n.s.
March 25				n.s.	n.s.
April 16				n.s.	n.s.
May 14				n.s.	n.s.
June 23					n.s.
July 27					G>L*

***$P<0.001$ **$P=0.001-0.01$ *$P=0.01-0.05$ n.s. $P > 0.05$

P. luculenta larvae live in patches of leaf and twig detritus near the stream bottom, and sometimes in piles of fallen leaves. Like *P. gentilis*, larvae in leafy habitats are displaced by the spring thaw, but the *P. luculenta* population as a whole is less affected. At the end of June the larvae aestivate for 4-6 weeks under stones and logs, but before pupation are more likely to fix their cases to the sides of these structures, head up, than to the underside like *P. gentilis*.

P. scabripennis larvae live in leaves and in detritus. The large 5th-instar larvae appear to select areas of woody detritus during the spring thaw, and are seldom carried in the drift. At the beginning of May the larvae burrow 2-3 cm into coarse gravel (4-16 mm diameter) in swift flowing areas, where they spend a 3-month aestivation period. Near the end of July the front of the case is attached to 1-4 gravel particles, but remains buried in the substrate during pupation.

3. Case construction

Newly hatched larvae of *Pycnopsyche* in West Creek make a roughly tubular covering of leaf fragments, sometimes incorporating fine sand grains (*P. gentilis*). After 7-10 days, the case is improved and consists of an inner cylinder of leaf or bark fragments and silk, covered by larger pieces of organic or mineral materials characteristic of each species (Fig 6). The specific case types depend on habitat (*P. luculenta*) or age (*P. gentilis* and *P. scabripennis*), as shown diagrammatically in Fig 7.

P. gentilis covers the inner cylinder with leaf discs (usually beech) so that the case is triangular in cross section (Fig 6a). Fifth-

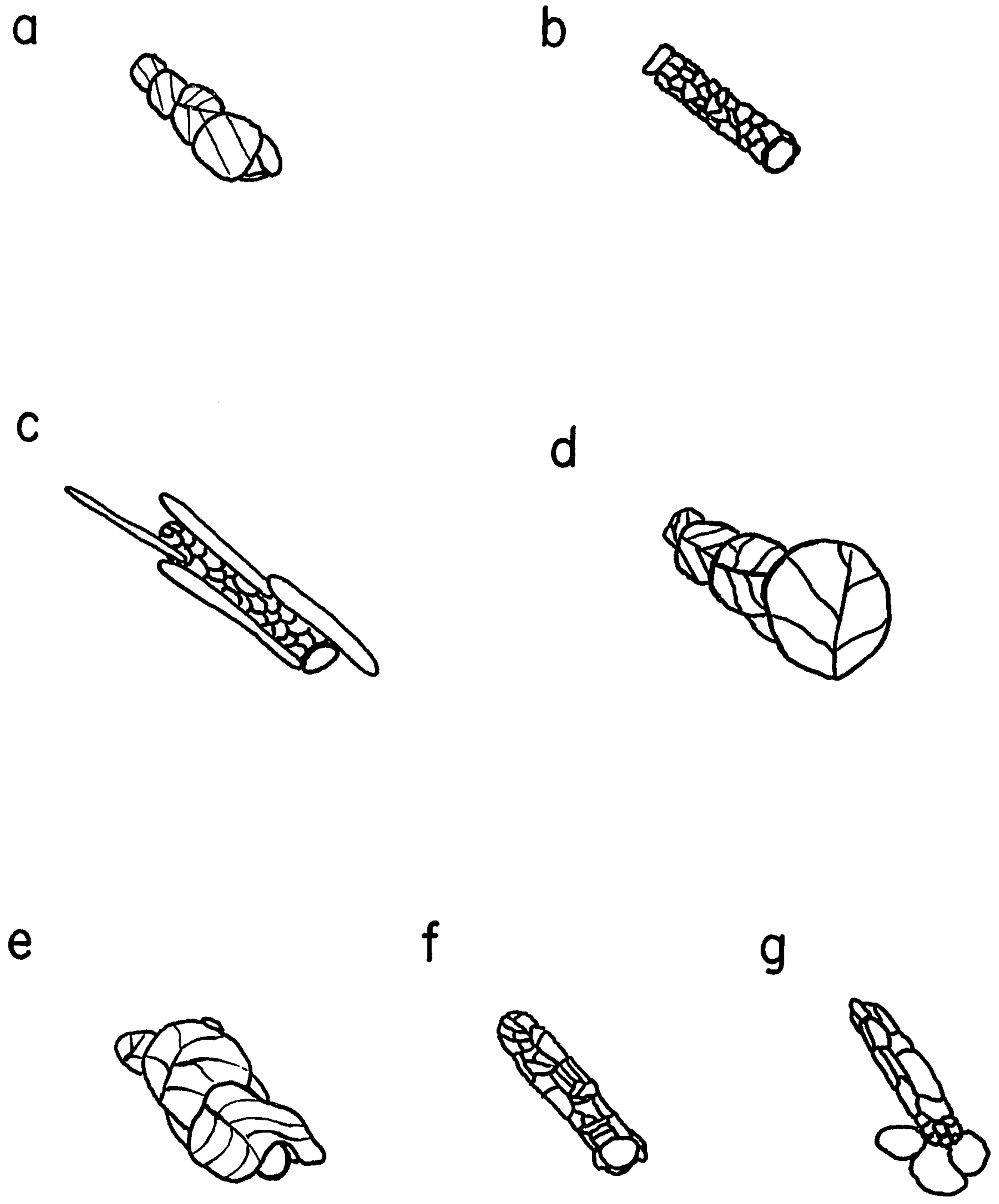


Figure 6. *Pycnopsyche* cases: a) leaf-disc case and b) sand-grain case of *P. gentilis*; c) stick case and d) leaf-disc case of *P. luculenta*; e) leaf-disc case, f) bark case and g) pupal case of *P. scabripennis*.

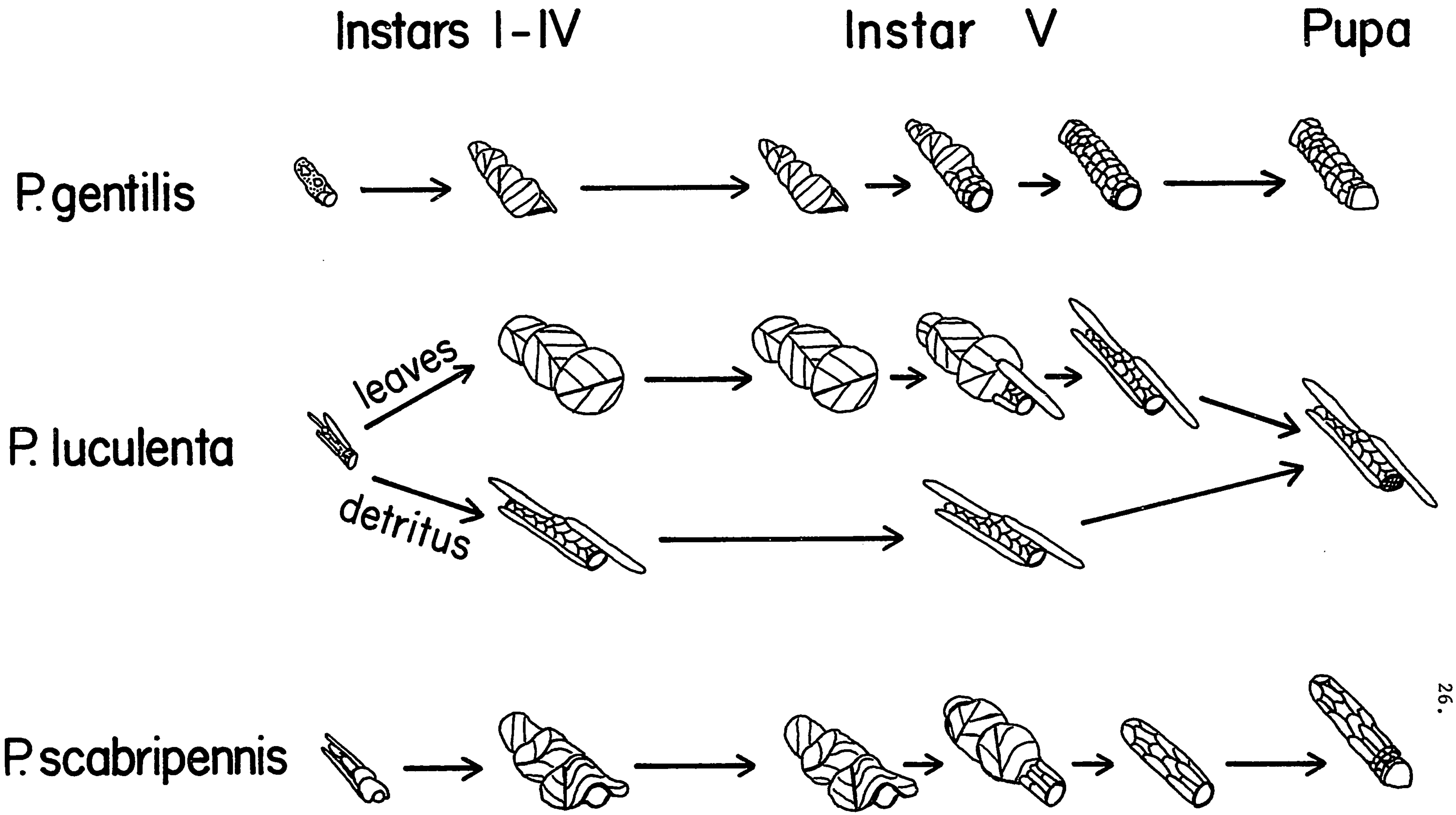


Figure 7. *Pycnopsyche* cases: changes in case type with age and habitat.

instar larvae gradually convert this case to a sand-grain cylinder (Fig 6b; Table 3), finally closing the openings with silk gratings and pieces of gravel before pupation.

P. luculenta usually adds leaf stalks or smooth sticks to a bark-chip cylinder (Fig 6c), or adds hemlock needles when available (instars II and III). Larvae in predominantly leafy habitats add large overlapping leaf discs to the top and bottom of the cylinder instead of sticks (Fig 6d), but convert this case to the stick type if detritus becomes available, or at least during the 5th instar. Before pupation, the stick case is closed by a silk grating.

P. scabripennis first makes a leaf-and-stick case intermediate in type between those of *P. gentilis* and *P. luculenta*. By the 3rd instar, the case is typically dorsoventrally flattened with large beech discs slightly curved around the central leafy cylinder (Fig 6e). This case is changed to a smooth cylinder of bark chips (Fig 6f) early in the 5th instar. Just before pupation a rim of sand grains is added to the case which is then closed with a silk grating and a piece of gravel (Fig 6f).

P. scabripennis was the only species that frequently vacated its case during transportation from stream to laboratory. It was also the only species with any marked ability to reconstruct a new case in the laboratory after losing the old one, when the naked larva would build a soft, tubular covering of irregularly shaped leaf bits.

None of the 3 species of *Pycnopsyche* showed any case-recognition behaviour by naked larvae in the presence of their own empty cases.

Table 3 Percentage of case types of 5th-instar *P. gentilis* larvae in West Creek during 1970

Date	leaf-disc case	intermediate case	sand-grain case
March 26	100	—	—
April 6	100	—	—
April 16	100	—	—
April 27	98	2	—
May 7	71	24	5
May 16	51	29	20
May 26	17	33	50
June 12	—	8	92
June 30	—	—	100

4. Pycnopsyche adults

Lantern-and-sheet collections in 1970 indicated that *P. scabripennis* flew during 4-5 weeks from the beginning of August, overlapping the flight periods of *P. gentilis* (beginning in mid-August) and *P. luculenta* (beginning near the end of August). *P. gentilis* and *P. luculenta* continued flying until at least the end of September, but were not collected on 13 October (Fig 2). The lantern attracted more males than females, highest numbers being collected on cloudy nights especially during or just after thunderstorms. *Pycnopsyche* began to settle on the sheet about 1 hour after sunset (earlier on cloudy nights) and continued to arrive for another 1-2 hours. By dividing the catch into 15-minute periods it was apparent that when 2 or more species were caught on the same night, *P. scabripennis* arrived significantly earlier than *P. gentilis* and *P. luculenta* (Table 4). Table 4 indicates that *P. luculenta* usually arrived later than *P. gentilis*; however numbers of *P. luculenta* were small and irregular so that the apparent difference is not statistically significant.

In 1971, the seasonal overlap between *P. scabripennis* and *P. gentilis* was shorter than in 1970, the species occurring together on only 4 collection nights, but again *P. scabripennis* males arrived at the light trap significantly earlier ($P = 0.01-0.05$) than *P. gentilis* (Fig 8). It was also clear that whereas before 20 August (and the first *P. gentilis* of the season) *P. scabripennis* males arrived most frequently in the 5th and 6th periods after sunset, after this date they came in the 3rd and 4th periods. With the last appearance of *P. scabripennis*

Table 4 Mean arrival times (coded in terms of 15-minute periods after sunset) of Pycnopsyche males at a lantern-and-sheet trap in 1970. (Differences between species tested by 2-way Analysis of Variance)

Date	P. scabripennis	P. gentilis[a]	P. luculenta[b]
August 4	6.0		
5	6.5		
6	6.1		
9	(♀ only)		
11	6.0		
13	6.0	7.5	
17	6.1	(absent)	
20	3.8	5.1	
23	5.8	7.9	
25	6.6	7.2	5.0
27	(absent)	8.5	11.0
30	5.0	6.7	9.5
September 4	4.5	5.4	13.0
7	5.0	7.8	12.0
10		5.4	6.4
17		7.0	7.0
30		8.2	(♀ only)

[a] P. gentilis time > P. scabripennis time ($P < 0.01$)

[b] P. luculenta time > P. scabripennis time ($P < 0.01$)

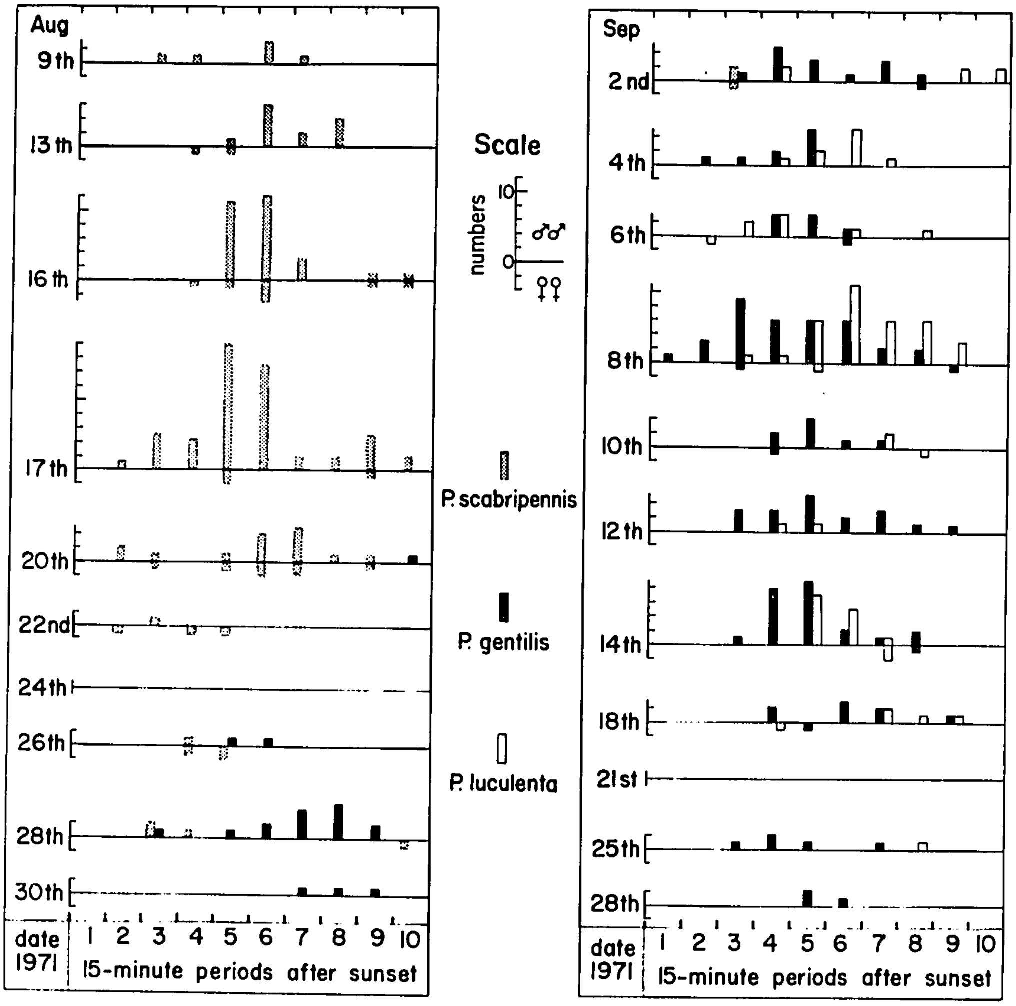


Figure 8. Frequencies and arrival times (in terms of 15-minute catch-periods after sunset) of *Pycnopsyche* species at a black-light trap in 1971.

on 2 September, P. gentilis began to arrive earlier, the peak periods being the 4th and 5th. This change in timing also coincided with the first appearance of P. luculenta, which continued to fly on the same nights as P. gentilis during September. More P. luculenta were collected per night in 1971 than in 1970, and the mean time of arrival at the black-light was significantly later ($P = 0.01-0.05$) than P. gentilis (Fig 8) thus confirming the indications of the previous year. The abundance of P. luculenta in 1971 was not simply the result of black-light because comparable numbers were also caught on 11, 13 September 1971 using the lantern-and-sheet method.

All three species of Pycnopsyche showed the same sexual bias in their behaviour towards black-light as they did in 1970 towards the butane lantern, mainly males being attracted. The true sex ratio is close to 50 percent as shown by rearing larvae at various temperatures in the laboratory (Tables 5 and 6). At the extreme temperatures of 5°C and 18°C, few adults emerged as pupal mortality was high, but even pupae still covered by larval exuviae could be sexed according to the number of segments in the maxillary palps.

Females that did approach the black-light trap usually settled first on the trap support or on the trunks of 2 nearby trees, and were found when the trees were inspected at the end of each 15-minute catch period. When randomly selected females were dissected, there was no correlation between the arrival of females and the appearance of the reproductive system (stages according to Gower 1965, 1967). Some had neither ovulated nor been impregnated; some had ovulated but still had tightly packed eggs in the oviducts; and others had partially or

Table 5 Emergence of Pycnopsyche gentilis and P. luculenta in a flowing-water aquarium (12 ± 2°C) in 1968

Date	Number of adults			
	P. gentilis		P. luculenta	
	male	female	male	female
August 6	4			
8	4	2		
14	2	0		
14-21	4	8	4	1
21-24	5	2	1	3
26	2	7	0	2
27-31	0	9	0	2
TOTALS	21	28	5	8

Table 6 Sex ratio of pupae and adults reared from full-grown larvae in laboratory streams

Water Temperature (°C)	Species	No. of larvae	No. of pupae and adults	
			males	females
18 ± 2	*P. scabripennis*	8	3	3
18 ± 2	*P. gentilis*	30	12	12
18 ± 2	*P. luculenta*	30	12	11
5	*P. scabripennis*	16	4	8
5	*P. gentilis*	20	9	8
5	*P. luculenta*	20	8	10

completely oviposited. No one type was more attracted to light than others. When the oviducts were tightly packed, the total numbers of eggs per female were: P. scabripennis - 240-250 (5 specimens), P. gentilis - 240-270 (4 specimens), P. luculenta - 360-390 (2 specimens). Unfortunately, most of the females placed in the field cages were drowned in the heavy rain that was frequent in August and September 1971. No egg masses were found in the cages nor under banks or stones along the length of West Creek. Spot sampling of suitable habitats in September and October 1971 indicated that larval numbers were lower than previous years, so the egg masses appear to have suffered from the rain.

Total numbers per catch night in 1971 (Fig 9) were usually high on warm, cloudy nights, although numbers of P. scabripennis were not obviously correlated with air temperature. Numbers were low on nights of full moonlight, particularly when the moon rose early and when air temperatures were also low (e.g. August 30th). Wind in the sheltered stream valley was a negligible factor as only occasional gusts reached 11-16 kph and all Pycnopsyche species appear to be strong fliers. Relative humidity was usually high (Fig 9) during the collection periods.

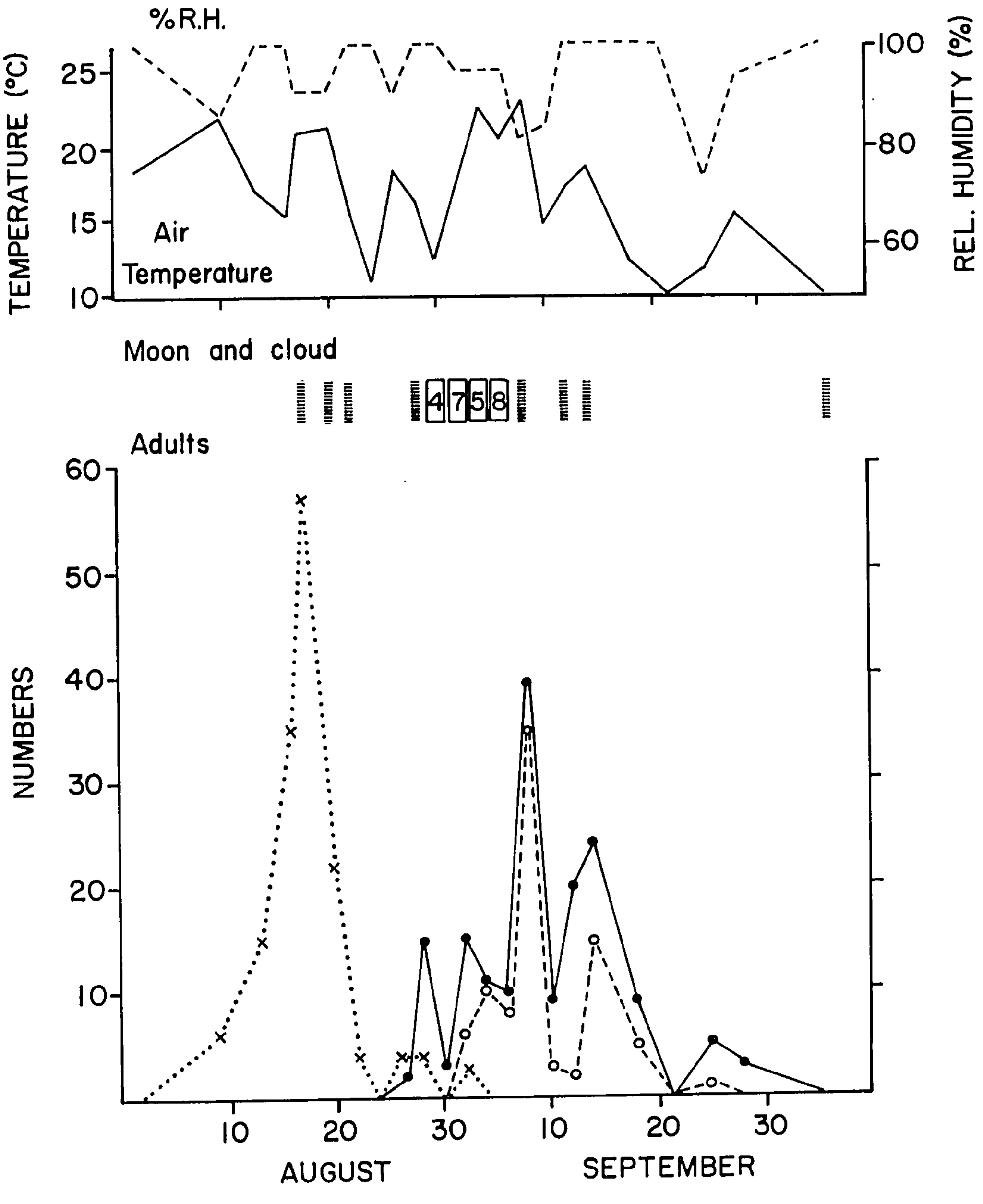


Figure 9. Total numbers of adult Pycnopsyche scabripennis (x....x), P. gentilis (●——●) and P. luculenta (○——○) per catch night in 1971 in relation to the air temperature and relative humidity recorded one hour after sunset, to cloud cover (striped bars), and to moonlight (open bars, time of appearance indicated by catch-period number).

DISCUSSION

As 2 or 3 Pycnopsyche species are commonly found together in one stream (K.W. Cummins, F.O. Howard, and F.F. Sherberger, personal communications), and as successful sympatry depends on reproductive isolation and non-competitive use of environmental resources (Mayr 1963, Ross 1967), the life cycles and behaviour of P. gentilis, P. luculenta and P. scabripennis show how segregation may be effected.

Many related species of aquatic insects are thought to avoid interspecific conflicts over mates and other requirements because they differ in their times of emergence (Corbet 1964). However comparatively little attention has been given to the extent of overlap of total flying periods with later or earlier emerging species. In West Creek, the emergence of P. scabripennis preceeds P. gentilis by at least 2 weeks (Figs 2, 8, 9). But whereas the female P. scabripennis most likely were impregnated before the emergence of P. gentilis, the continued flight of P. scabripennis males and females into September might interfere with P. gentilis and P. luculenta. The 2 latter species have overlapping emergence periods and seasonal flying periods, for teneral specimens of both species were often collected on the same night. As the genitalia of the above 3 species appear quite different, interspecific copulation is unlikely but in any case is considered by many to be prevented by behavioural rather than mechanical barriers (Mayr 1963). The mating behaviour of Pycnopsyche is unknown although the strong odour of many limnephilids including Stenophylax (Betten 1934) suggests that scent production may be involved. The males of many nocturnal moths of the related order Lepidoptera actively track down the odours secreted by females which often do not attempt to fly, especially if they have not mated (Edwards 1962). Yet Schneider (1962) found that the sexual attractants of 7 related Saturniidae were not all species-specific. If this were the case in Pycnopsyche, indistinct chemical stimuli could result in attempted interspecific copulation, or at least time-wasting confusion, unless the males of each species were active only at different times of the night.

Although light traps may be unsuitable for some insect studies in that they rely on an unnatural phototactic response and do not sample randomly, the responses of limnephilid caddis flies, especially autumn fliers, have been particularly well examined (Crichton 1961, 1965; Ulfstrand 1970). Crichton (1965) found that a suction trap and a light trap shielded by trees and 70 m from water caught 100 percent and 97.1 percent limnephilids respectively, with a 2:1 ratio of males to females, indicating that the caddis flies were probably in the immediate area of each trap and not attracted from the water. As Pycnopsyche species at West Creek were collected only during certain limited periods even when the lamp was left on all night, the periods of peak collection probably represent the true activity patterns of males at least.

Other studies have considered nightly activity of non-biting insects at light traps (e.g. Williams 1935, Robertson 1939, Nimmo 1966) but have not discussed the ecological significance of different arrival times of closely related species. Nimmo's (1966) study of the arrival of St. Lawrence River caddis flies at a light trap near Montreal considered only one pair of congeneric species, and the difference between them (based on 10-minute catches on 10 nights) was slight. Further examination of Nimmo's unpublished data from the same study showed that none of the common congeneric species flying on the same night (4 genera) differed significantly in the time of collection ($\underline{P} > 0.05$).

The differences observed between specific peak activity periods of Pycnopsyche males at West Creek could be behavioural adaptations reducing interspecific interference during mating. As similar temporal segregation is not found among nearby riverine species, it may be typical only of species sharing limited flight space or oviposition sites. The St. Lawrence River species, which mostly lay their eggs under water, have access to relatively more flight space and oviposition sites than species in a small wooded stream valley, especially limnephilids which usually lay their eggs out of water.

Several authors have questionaed the unequal sex ratios of limnephilids in light traps (Crichton 1960, Ulfstrand 1970) and have suggested that it may result from a stronger phototactic response or higher activity of males. This suggestion is supported by the present study, assuming that sex ratios in the field and laboratory are the same.

The seasonal flight period must be timed to coincide with environmental conditions favouring mating and egg development as many limnephilids, even those emerging earlier in the year, do not mature or lay eggs until autumn (Novak and Sehnal 1963, Gower 1967). Crichton (1960) proposed that the more frequent rain in autumn acts as a releasing stimulus for mating and egg laying, possibly connected with the limnephilid habit of laying eggs out of water. In the present study the greatest activity also occurred during or following rain, and at least *Pycnopsyche scabripennis* is known to lay its eggs on land (F.O. Howard, personal communication). In West Creek, autumn also provides an abundant food supply for developing *Pycnopsyche* larvae, and the different seasonal flight periods of each adult species subject the eggs and larvae to different physical and biotic environments that determine their future development. Based on the first and last appearances of gravid females and of 1st-instar larvae, the eggs probably hatch within 3-4 weeks of oviposition. The earlier flight period of *P. scabripennis* exposes both eggs and larvae to higher water temperatures than those experienced by early stages of *P. gentilis* and *P. luculenta*, and probably accounts for the higher IGR of young *P. scabripennis* larvae (Fig 5). These larvae also encounter the soft, rapidly decaying leaves of ironwood (*Ostrya virgincana* (Mill) K. Koch), one of the more palatable species in the stream, (see Part II) which begin to fall about one month earlier than other species of autumn-shed leaves.

Both food and temperature were probably important factors in the evolution of life history patterns in *Pycnopsyche*, small differences in the rates of development having decided effects on the numbers of species able to exploit one particular habitat. The rapid autumn development of *P. scabripennis* means that its larvae are always larger than *P. gentilis* and *P. luculenta* (Figs 3, 4) and can probably exploit space and materials unsuitable for the smaller species. During winter, *P. scabripennis* has a low IGR and makes fewer demands on the resources at a time when *P. gentilis* and *P. luculenta* are still growing relatively fast. The 2 latter species are similar in size and have almost identical growth rates (Figs 4, 5), but they differ in their use of allochthonous matter. *P. gentilis* uses leafy material for case materials, food, and habitat, with only 10% of the population occupying detritus areas; *P. luculenta* can make its case from leaves or sticks, but feeds preferentially on twigs (in the laboratory), and lives in or near detritus (see Part II). The resources in West Creek appear to be ample for 3 *Pycnopsyche* species during autumn and winter. When leaves and detritus are flushed out of the stream during the spring thaw, potential competitive pressure is relieved by the beginning of an aestivation period by *P. scabripennis*. At this time of food shortage, increased interactions have been observed between *P. gentilis* and *P. luculenta* (see Part II). In extreme conditions, *P. luculenta* feeds on the leaf case of *P. gentilis*, sometimes evicting the inhabiting larva. This behaviour may explain the evolution of the sand-grain case of *P. gentilis*. The change to this latter case (Table 3) begins after the increased spring discharge and so is contrary to the general observation that a stone case is an adaptation to fast current (Webster and Webster 1943, Hynes 1970). The delayed change in construction can only mean that in the evolutionary history of *P. gentilis*, vulnerability to drift has been less important than the attacks of competing detritivors, and therefore sand and gravel cases are protective clothing rather than ballast. In this respect the burrowing habit of *P. scabripennis* during aestivation may have arisen as an additional way of avoiding interspecific conflicts when food and shelter are scarce, and when a larva in a bark case is vulnerable to detritivors. Although many species of stream insects are known to aestivate and avoid warm periods of the year, *P. scabripennis* does not fit the conventional explanation as summer temperatures in West Creek are relatively low and the pupa emerges when the water temperature is maximum. The distribution of the genus *Pycnopsyche* within the eastern deciduous forest of North America (Ross 1963), and the theory that caddis flies evolved in small cool streams (Ross 1956) suggest that the ancestral habitat of the genus probably resembled West Creek, having allochthonous detritus as the primary food source. During spring and summer, food supplies would diminish rapidly as a result of rising temperatures and increasing rates of decay; some streams, like West Creek, probably suffered from the flushing effects of spring spates. The burrowing behaviour of *P. scabripennis* may have evolved through being the most efficient way of avoiding the unfavourable effects of diminishing organic substrates. It also would ensure that the remaining resources were shared between fewer *Pycnopsyche* species and so contribute to coexistence. The ability of *P. scabripennis* to live in West Creek with 2 more abundant species of *Pycnopsyche* is probably due to its distinctive life history. The coexistence of *P. gentilis* and *P. luculenta* relies on specific habitat and food preferences which are considered further in Part II.

REFERENCES

Betten, C. 1934. The caddis flies or Trichoptera of New York State. *N.Y. State Mus. Bull.* 292: 1-576.

Betten, C. 1950. The genus *Pycnopsyche* (Trichoptera). *Ann. ent. Soc.* Amer. 43: 508-522.

Corbet, P.S. 1964. Temporal patterns of emergence in aquatic insects. *Can. Ent.* 96: 264-279.

Crichton, M.I. 1960. A study of captures of Trichoptera in a light trap near Reading, Berkshire. *Trans. R. ent. Soc. Lond.* 112: 319-344.

Crichton, M.I. 1961. Observations on the longevity and dispersal of adult Limnephilidae (Trichoptera). *Internat. Kong. Ent. Wein.* 1: 366-371.

Crichton, M.I. 1965. Observations on captures of Trichoptera in suction- and light-traps near Reading, Berkshire. *Proc. R. ent. Soc. Lond.* (A) 40: 101-108.

Edwards, D.K. 1962. Laboratory determinations of the daily flight times of separate sexes of some moths in naturally changing light. *Can. J. Zool.* 40: 511-530.

Flint, O.S. 1960. Taxonomy and biology of Nearctic limnephilid larvae (Trichoptera) with special reference to species in eastern United States. *Entomol. Amer.* 40: 1-120.

Gower, A.M. 1965. The life cycle of *Drusus annulatus* Steph. (Trich., Limnephilidae) in watercress beds. *Entomologist's Mon. Mag.* 101: 133-141.

Gower, A.M. 1967. A study of *Limnephilus lunatus* Curtis (Trichoptera: Limnephilidae) with reference to its life cycle in watercress beds. *Trans. R. ent. Soc. Lond.* 119: 283-302.

Grant, P.R., and R.J. Mackay. 1969. Ecological segregation of systematically related stream insects. *Can. J. Zool.* 47: 691-694.

Hynes, H.B.N. 1970. The ecology of running waters. Liverpool Univ. Press.

Mackay, R.J. 1969. Aquatic insect communities of a small stream on Mont St. Hilaire, Quebec. *J. Fish. Res. Bd. Canada.* 26: 1157-1183.

Mackay, R.J., and J. Kalff. 1969. Seasonal variation in standing crop and species diversity in a small Quebec stream. *Ecology.* 50: 101-109.

Mayr, E. 1963. Animal species and evolution. Harvard Univ. Press. Cambridge, Mass.

Nimmo, A. 1966. The arrival pattern of Trichoptera at artificial light near Montreal, Quebec. *Quaest. ent.* 2: 217-242.

Novak, K., and F. Sehnal. 1963. The development cycle of some species of the genus Limnephilus (Trichoptera). *Čas. čsl. Spol. ent.* 60: 68-80.

Robertson, A.G. 1939. The nocturnal activity of crane-flies (Tipulinae) as indicated by captures in a light trap at Rothamsted. J. Anim. Ecol. 8: 300-322.

Ross, H.H. 1956. The evolution and classification of the mountain caddis flies. Univ. Illinois Press, Urbana, Ill.

Ross, H.H. 1963. Stream communities and terrestrial biomes. Arch. Hydrobiol. 59: 235-242.

Ross, H.H. 1967. The evolution and past dispersal of the Trichoptera. Ann. Rev. Ent. 12: 169-206.

Schneider, D. 1962. Electrophysiological investigation on the olfactory specificity of sexual attracting substances in different species of moths. J. Insect. Physiol. 8: 15-30.

Southwood, T.R.E. 1966. Ecological methods with particular reference to the study of insect populations. Methuen, London.

Ulfstrand, S. 1970. Trichoptera from River Vindelälven in Swedish Lapland. Entomol. Tidskr. 91: 46-63.

Webster, D.A., and P.C. Webster. 1943. Influence of water current on case weight in larvae of the caddis fly Goera clacarata Banks. Can. Ent. 75: 105-108.

Williams, C.B. The times of activity of certain nocturnal insects, chiefly Lepidoptera, as indicated by a light trap. Trans. R. ent. Soc. Lond. 83: 523-555.

PART II

INTRODUCTION

Larvae of the caddis fly genus *Pycnopsyche* (Limnephilidae: Stenophylacini) live in streams and small rivers in the temperate deciduous forest biome of eastern North America (Ross 1963) where they are usually found among deposits of allochthonous organic material. Typically more than one species of *Pycnopsyche* is present in any one stream. *P. gentilis* (McLachlan), *P. luculenta* (Betten) and *P. scabripennis* (Rambur) occur in West Creek on Mont St. Hilaire, Quebec, where they are members of the insect communities in fallen leaves and detritus that were first studied between 1966 and 1967 (Mackay 1969, Mackay and Kalff 1969). The data obtained at that time were insufficient to indicate the precise requirements or life histories of the *Pycnopsyche* species. Later work has shown that *P. scabripennis* has a distinctive life history pattern, temporally separated from *P. gentilis* and *P. luculenta*, but that these latter species have contemporaneous larval periods and are similar in size (see Part I).

The ways in which sympatric congeneric species avoid competition have been studied in many habitats, but in spite of the current interest in allochthonous organic materials in streams (see references in Kaushik and Hynes 1971), little is known about the distribution of related species within organic substrates.

The only other ecological study of *Pycnopsyche* species in the field was on *P. lepida* (Hagen) and *P. guttifer* (Walker) (Cummins 1964). These species are found in larger, warmer streams, less dependent on allochthonous material as potential food than the small forest streams described by Ross (1963) of which West Creek is a typical example. Cummins' (1964) study was therefore more concerned with mineral substrate selection by _P. lepida_ and _P. guttifer_ than with their impact on organic detritus. He also found that any interaction between these 2 species was diminished by temporal separation of larval periods, and the selection of different habitats.

The present study was undertaken, therefore, with the aim of determining how _Pycnopsyche_ species exploit allochthonous organic material and other resources in the environment, and to what extent the species in West Creek interact competitively. An intensive study of microhabitats in the field and of the effects of catastrophic drift was accompanied by laboratory experiments designed to test the field data, and to investigate habitat selection and feeding behaviour.

STUDY AREA

Detailed descriptions of West Creek have been given elsewhere (Mackay 1969, Mackay and Kalff 1969); only a brief summary will be given here. The stream flows 1.7 km through thick deciduous forest into Lac Hertel. The lower third of the stream (where larval collections for the present study were made) is 1-2 m wide during most of the year although melting snow may double the width during April. Flow rates recorded range from 1 litre/sec in September to 360 litres/sec at peak discharge during the spring thaw. The stream bottom consists of extensive sand and gravel interrupted by short riffles over boulders, cobbles and pebbles. Water temperatures range from 0°C in January and February to 17-18°C in August.

Leaves falling from riparian trees or blown in from the forest floor are principally sugar maple (*Acer saccharum* Marsh) and beech (*Fagus grandifolia* Ehrh.) with smaller numbers of red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), and ironwood (*Ostrya virginiana* [Mill] K. Koch); rare species are white ash (*Fraxinus americana* L.) and basswood (*Tilia americana* L.). Twigs, bud scales, catkins and various seeds and fruits also accumulate in the stream. Fallen leaves choke the stream every October until late autumn rains wash them into bays and pools, and behind fallen trees and branches. The network of fallen branches, plus ice formation on these barriers in winter, prevent any large-scale flushing of leaves until the spring thaw. Between November and March, Mont St. Hilaire receives 200-300 cm of snow, which may be more than 1 m deep, packed, when the thaw begins. The marked increase in discharge as the snow melts flushes intact leaves as well as much leaf detritus into Lac Hertel.

METHODS

1. Collecting methods

The 1966-67 survey of West Creek showed that *Pycnopsyche* species are most common in the lower half of West Creek, in allochthonous organic material lying on coarse to fine sand in slow-flowing water. Intensive sampling of *Pycnopsyche* populations was therefore confined to such habitats, beginning in September 1968. Collections were made at approximately weekly intervals through May 1969, and at 10-day intervals from September 1969 through May 1970. Further occasional collections were made of maturing larvae and pupae during the summer.

As each sample was collected, the organic substrate was assigned according to its appearance to one of 4 categories as follows:

1. DETRITUS: finely divided leaf material, twigs, bud scales, seeds, bark chips etc.
2. DETRITUS (& LEAVES): detritus with a thin, loosely-packed covering of leaves
3. LEAVES (& DETRITUS): detritus with a thick covering of leaves
4. LEAVES: leaves with little or no accompanying detritus

These 4 categories, when printed as above, will refer to specific habitats and are distinct from the general terms "leaves" or "detritus". Habitats were categorized throughout each year of sampling except during the period from mid-March to mid-May when the procedure was made impossible by the disruptive effects of the spring thaw. Quantitative data on habitat selection will be described only for the pre-thaw season up to mid-March of each year.

During the pre-thaw seasons of 1968/69 and 1969/70, the 4 habitat types were more or less evenly distributed through the sampling area of West Creek (100-400 m from Lac Hertel), each covering approximately equal areas of stream bottom. The total number of samples taken from the 4 habitats was 150, 75 in each pre-thaw season.

The organic substrates were collected with 2 Surber-type samplers, mesh sizes 0.5 mm and 2 mm respectively. The fine net was used throughout the first season (it retained the smallest encased larvae); the coarse net was used during the latter part of the 1969-70 pre-thaw season after life history studies had established that the minimum diameter of encased larvae at this time exceeded the mesh size. Both samplers had side screens that could be pushed down into the stream bottom ahead of the net opening so that water and leaves were directed into the net. The area sampled was 0.2 m^2. On each collection date, 5 samples were netted, drained, and placed in plastic bags. The volume (drained) of leaves and/or detritus per 0.2 m^2 was extremely variable, ranging from 1-4 litres, samples of LEAVES and LEAVES (& DETRITUS) usually being greater than samples of DETRITUS or DETRITUS (& LEAVES).

After transportation to the laboratory (1-2 hours) the samples were reimmersed in dechlorinated water kept at temperatures similar to those in the field. Within 24 hours of collection, *Pycnopsyche* larvae were sorted live and kept in flowing water in a refrigerated room, with leaves and detritus for food, before being used in experiments.

On March 23, 1971, 5 drift traps were placed side by side across West Creek to measure the quantities of leaves, detritus and Pycnopsyche larvae washed downstream during the spring thaw. The traps were situated 300 m from the mouth of the stream at a point where high banks channelled the entire surface flow through the traps. Square-ended Nitex nets, 1 m long, with mesh size 1050 μ, were supported at the front by rectangular brass frames 30 cm wide and 20 cm high. The traps were held in position by side rings on the frames that passed over vertical steel rods driven into the gravel substrate. The nets were emptied daily March 23-April 6, 1971, and twice daily April 6-10. The nets then began to fill so quickly that only samples of drift could be taken; the length of sampling period and number of samples per day were variable. The nets were raised above water level between sampling periods. Samples were taken daily until April 18, every 4th or 5th day until May 14, and for 24 hours May 27-28, 1971.

When the nets were emptied, Pycnopsyche larvae were sorted and counted, then were either dried and weighed or were returned within 2-3 hours to West Creek downstream of the drift nets. Leaves and leaf detritus from the nets were tightly packed into a 2.5 litre beaker and the packed volume measured to the nearest half litre. At intervals, samples of leaves and detritus were dried at 60°C to constant weight.

Discharge (D) was calculated by the formula

$$D = \frac{lwda}{t}$$

where l = length of an unobstructed straight channel of the stream (5 m in this case)

w = average width (measured at 1 m intervals along l)

d = average depth (measured at 30 cm intervals across transects corresponding with each width measurement)

t = average time in seconds for a wooden float to travel distance l (10 timings)

a = substrate coefficient (0.8 according to Hynes (1970)).

2. General Experimental Methods

All experiments were conducted in a thermostatically-controlled refrigerated room where air temperatures were adjusted to match water temperatures in West Creek from September to April. In May and June, the room temperatures were up to 5°C cooler than maximum temperatures recorded at this time in West Creek.

Except for occasional observations, all experiments were carried out under natural day-length conditions, light from a small window being supplemented by ceiling lamps controlled by a time-switch.

Experiments concerning habitat selection and interspecific reactions were carried out in laboratory streams (Fig 10) based on the system described by Feldmeth (1970). Four plexiglass troughs (hereafter called streams) were supported side by side on dexion racks over a lower reservoir made of plywood lined with 6 mille plastic sheeting. Water was pumped through neoprene pipes from the lower reservoir to an upper reservoir made of fibreglassed plywood. The pump was

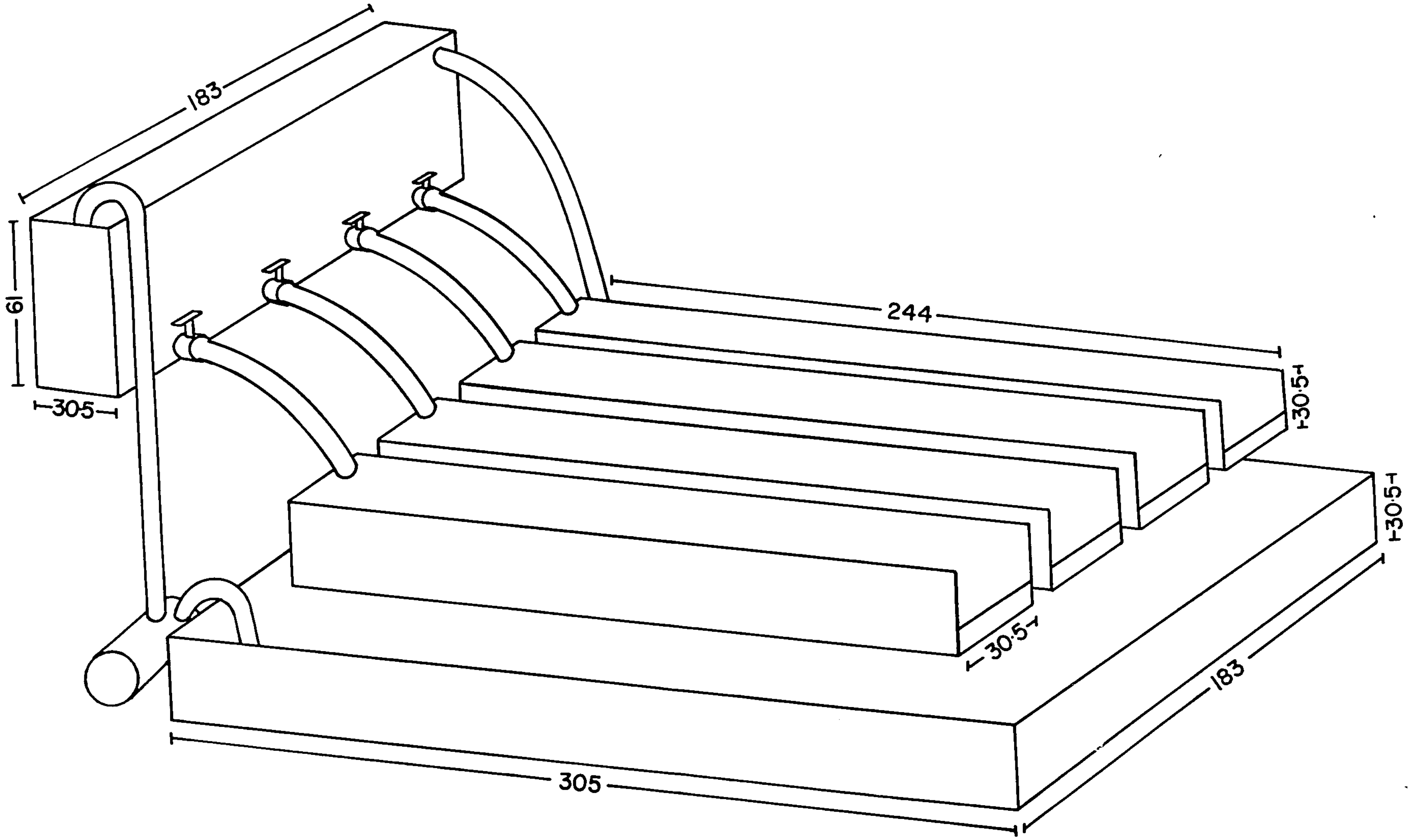


Figure 10. The laboratory stream system (dimensions in cm). The supports under troughs and upper reservoir are not shown.

non-submersible and magnetic (Little Giant model 5-MD) and delivered about 1 litre/sec at a 1.8 m head. An overflow pipe led from the upper to the lower reservoir. At the base of the upper reservoir, 4 brass gate valves controlled the discharge of water through short neoprene pipes, each pipe directing the water into a stream from a height 20 cm above stream water level. By timing the collection of a known volume of water and using the known cross sectional area of each stream it was possible to compute the very low current speeds that were suitable for most experiments. Except where specifically mentioned, current speeds were maintained at approximately 0.3 cm/sec. Turbulence was reduced by a series of Nitex screens across the upstream portion of each trough. Downstream, the water flowed over the 10 cm-high end-wall into the lower reservoir.

The experimental section of each stream followed the design of Lauff and Cummins (1964). Mineral substrates (sand, gravel, pebbles) were placed in plexiglass trays (15.25 x 30.5 x 2.5 cm) that exactly fitted the width of the stream. At each end of a series of 8 substrate trays an empty tray was reversed to act as a neutral zone between the substrate zone and the filter boxes that marked the upstream and downstream limits of the experimental area. The plexiglass on the reversed trays was roughened with sand paper to enable the larvae to grip the surface. The filter boxes, made of Nitex on a plexiglass frame (15.25 x 30.5 x 15.25 cm), contained replaceable glass wool or crumpled cheese cloth; they reduced the circulation of feces and kept larvae and food materials within the experimental area. After each experiment, the valves were closed while the water and organic detritus in the streams were siphoned out of the system to prevent accumulation of waste products, and then replaced by clean water.

Mineral substrates were taken from West Creek, washed, and sorted into a geometric series of 8 particle sizes according to Cummins (1962), ranging from medium sand particles 0.25-0.5 mm diameter (called ¼ mm) to small pebbles 16-32 mm diameter (called 16 mm). Organic substrates consisted of leaves and detritus from West Creek.

Feeding experiments considered the weight of leaf material ingested by an individual larva. Most leaves were collected from West Creek a few days before an experiment began and were kept in cold aerated water, but some were dried for use later in the season when few entire leaves remained in West Creek. Larvae were offered leaf discs 1-2.5 cm in diameter, cut from water-soaked leaves. As different leaves of any one species varied in texture and weight depending on the parent tree and the amount of leaching or decomposition that had occurred before collection, all replicates per experiment were set up with discs cut from one leaf. When the food requirements per larva exceeded the amount supplied by one disc, but not enough large discs could be cut from one leaf to supply all replicates, then each larva received a small disc cut from each of 2 or 3 leaves.

Two methods were used to determine the weight of leaf material ingested. Either the discs were dried at 60°C and weighed individually before and after the experiment; or each disc was cut in half (along a line that divided the veins as evenly as possible), one half being offered to larvae while the other was used as a control. Both halves were dried and weighed after the experiment and the difference in weight between matching halves was assumed to be due to ingestion. The second method ensured that the leaf material and associated microflora remained wet and relatively unaltered before feeding the larvae, but an accurate division of a disc (< 5% error) was only possible if the diameter exceeded 2 cm. Pycnopsyche larvae do not drop material that their mandibles have cut from a leaf so that McDiffett's (1970) warning against the use of before-and-after gravimetric techniques to measure ingestion did not apply here. Occasionally P. gentilis larvae cut case-building discs from the food disc but again the cuts were clean, no material was dropped, and the new addition to the case was always obvious and could be removed and weighed with the remains of the food disc. In all experiments additional control discs were cut to account for leaching and microbial activity during experiments, and to provide correction factors accounting for changes in relative humidity in the laboratory between weighings. A Cahn electrobalance (model G, accurate to 0.001 mg) was used to weigh discs, and also larvae after some experiments.

As the feeding experiments involved batches of replicate larvae and food materials, petri dishes containing dechlorinated tapwater were used to maintain uniform conditions between replicates, with one larva per dish. Pycnopsyche gentilis and P. luculenta larvae survived on leaves in cold, still, dechlorinated water for several months, but no experiments lasted more than 48 hours. Details of individual experimental procedures will be described with the results in a later section.

RESULTS

A. Larval distribution in the field and effects of catastrophic drift

This section is concerned mainly with Pycnopsyche gentilis and P. luculenta as they are more abundant in West Creek than P. scabripennis.

Mean numbers of P. scabripennis were less than one larva per sample ($< 5/m^2$) in all types of organic substrate during the 1968/69 and 1969/70 sampling seasons.

Mean numbers of P. gentilis per sample (Table 7) ranged from 7.7 ($38.5/m^2$) in DETRITUS 1968/69 to 32.4 ($162/m^2$) in LEAVES 1969/70. Mean numbers of P. luculenta per sample (Table 7) ranged from 0.7 ($3.5/m^2$) in LEAVES 1968/69 to 8.7 ($43.5/m^2$) in DETRITUS 1969/70. Total numbers of larvae per sample were highest in the more leafy habitats because of increased numbers of P. gentilis; numbers of P. luculenta tended to decrease as the proportions of leaves to detritus increased. Total numbers were higher in 1969/70 because unusually heavy rain in November 1969 had concentrated the organic deposits. Numbers of P. gentilis per sample were plotted against numbers of P. luculenta per sample (Fig 11) to show the relative proportions of the 2 species in each habitat. Regression lines were drawn using the method of least squares. As "t" test calculations showed no significant differences ($P > 0.05$) between the 1968/69 and 1969/70 data, the regression lines were calculated from the combined data. Further "t" tests between regression coefficients (Simpson et al 1960) showed that the slopes of the 4 regression lines in Fig 11 were all significantly different

Table 7 Number of samples and number of larvae/sample taken from 4 habitats in West Creek between early October and mid-March 1969/70, with corresponding data for 1968/69 in brackets

	DETRITUS	DETRITUS (& LEAVES)	LEAVES (& DETRITUS)	LEAVES
No. of samples	17 (18)	23 (19)	19 (18)	16 (20)
Mean no. ± Std. Error of total larvae/sample	15.5 ± 3.4 (12.6 ± 1.9)	16.4 ± 4.3 (13.3 ± 3.0)	36.4 ± 7.3 (17.3 ± 3.7)	33.5 ± 6.3 (15.4 ± 4.3)
Mean no. ± Std. Error of _P_. _gentilis_/sample	6.8 ± 1.7 (7.7 ± 1.4)	11.1 ± 3.0 (8.8 ± 2.0)	29.7 ± 6.1 (15.1 ± 3.3)	32.4 ± 6.1 (14.3 ± 4.1)
Mean no. ± Std. Error of _P_. _luculenta_/sample	8.7 ± 2.1 (4.9 ± 0.7)	5.3 ± 1.5 (4.6 ± 1.2)	6.7 ± 1.3 (2.2 ± 0.6)	1.1 ± 0.8 (0.7 ± 0.7)

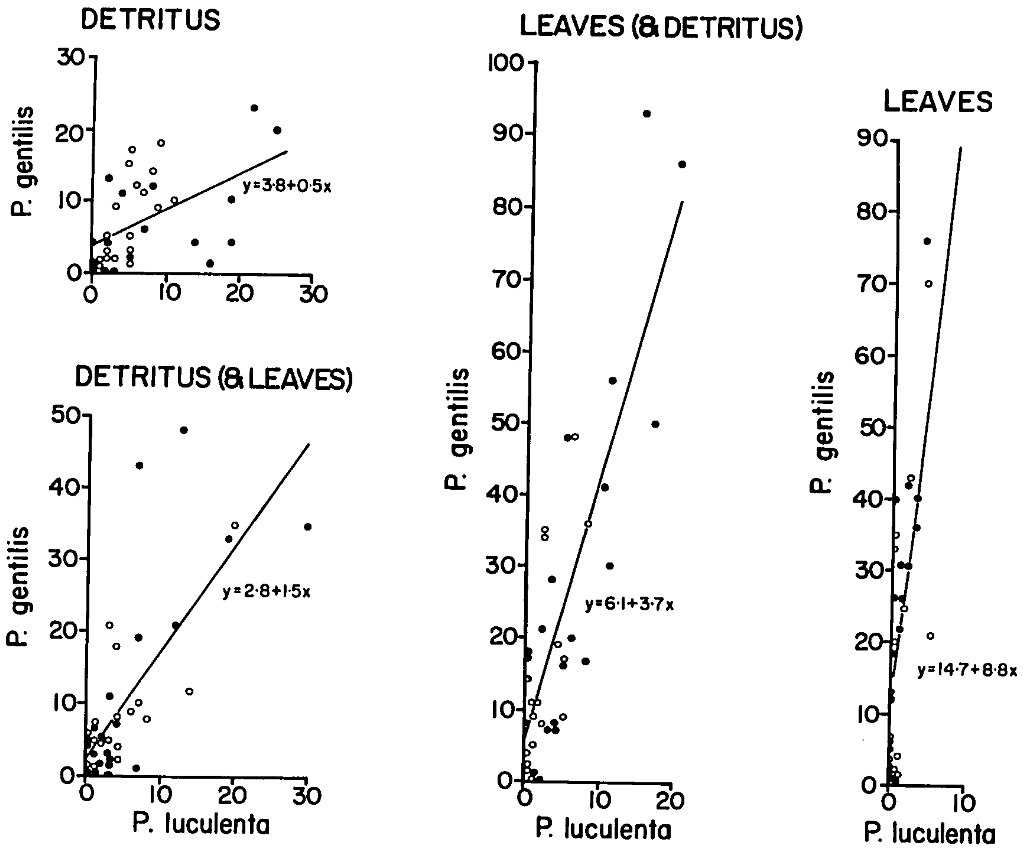


Figure 11. The relationship between numbers of *Pycnopsyche gentilis* per sample and *P. luculenta* per sample from 4 habitats in West Creek between October and March, with calculated regression lines (1968/69 data, o; 1969/70 data,).

Table 8 Regression coefficients of numbers of _P. gentilis_/sample on numbers of _P. luculenta_/sample from 4 habitats in West Creek, showing the differences between habitats

Habitat	b_{yx}	Difference
DETRITUS	0.51	
		0.94***
DETRITUS (& LEAVES)	1.45	
		2.73***
LEAVES (& DETRITUS)	3.68	
		5.16*
LEAVES	8.84	

*_P_ = 0.02-0.01 ***_P_ < 0.001

from each other (Table 8) indicating that the particular ratio of P. gentilis to P. luculenta in each habitat is due to real differences in species distribution. During each pre-thaw season, the proportions of the 2 species in each habitat remained relatively constant, no apparent change occurring with age. However, the increased spring discharge resulting from melting snow in 1969 and 1970 changed the composition and quantities of organic substrates so that larval distributions were greatly altered. The magnitude of this catastrophic drift with respect to Pycnopsyche larvae and allochthonous organic matter was therefore monitored in 1971.

During the last week in March, 1971, West Creek was still covered by ice and snow bridges for most of its length, although the water was still flowing. The drift traps were in one of the occasional clear areas that was 4 m long (Plate Ia). While the snow barriers remained intact, less than 10 larvae were collected per day (24 hours) and less than 1 litre of organic matter/day. By the end of March the snow was beginning to melt, and drift began to increase (Fig 12). During this period all the P. luculenta in the drift had cases made of leaf discs, whereas at least half of the population in West Creek had cases made of bark chips and small, longitudinally arranged sticks (see Part I). All P. gentilis larvae make leaf-disc cases at this time of year. In March and early April, the dry weights of drifting P. gentilis and P. luculenta were significantly different from the weights of larvae collected by hand (Table 9) but similar comparisons on April 16 showed no significant differences.

Plate Ia. Drift nets in front of snow bridge in West Creek, March 30, 1971 (50 cm bar in foreground).

Plate Ib. Drift nets during thaw in West Creek, April 17, 1971.

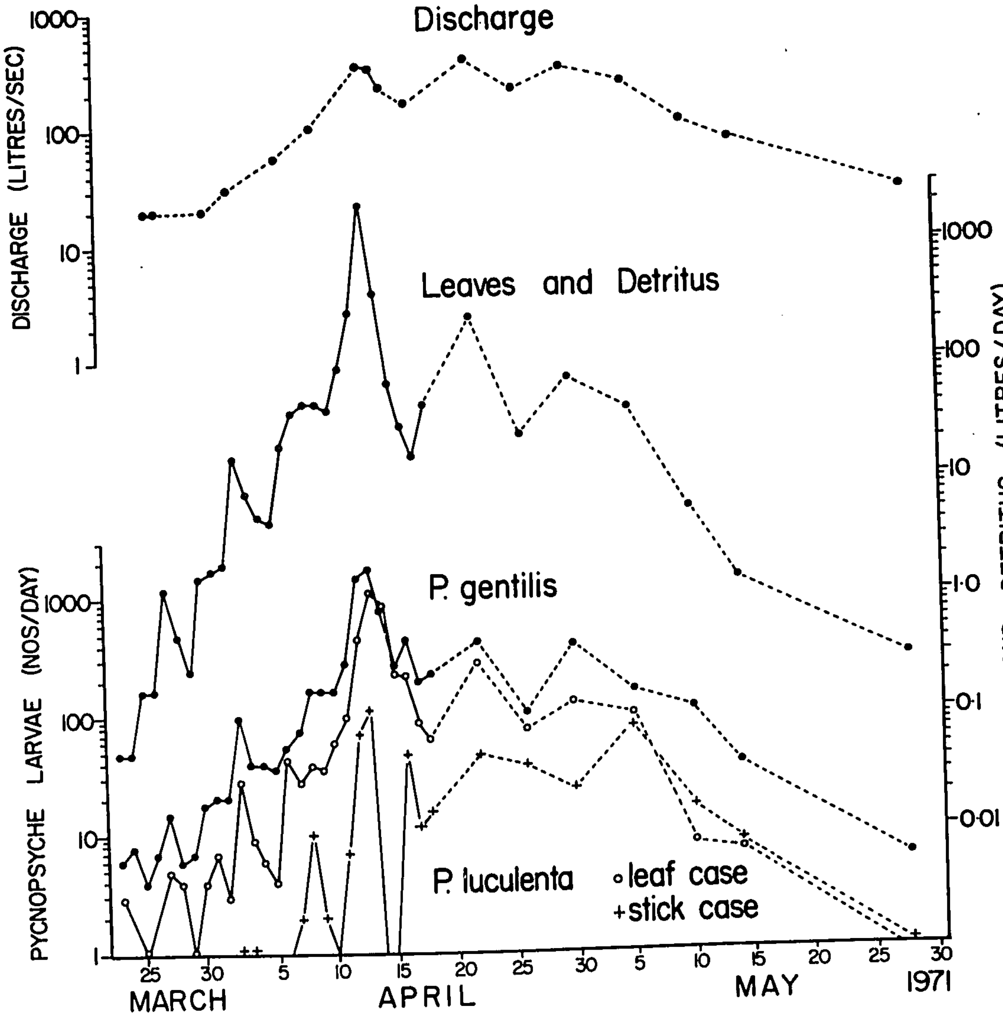


Figure 12. Stream discharge and 24-hour drift of Pycnopsyche larvae and allochthonous organic matter in West Creek during the spring thaw of 1971. (Unbroken lines join consecutive daily measurements, dashed lines join less frequent measurements).

Table 9 Dry weights of drifting _P_. _gentilis_ and _P_. _luculenta_ larvae compared with non-drifting larvae in West Creek during March and April, 1971

Date	Species, instar (and case type)	Mean dry weight (mg) Drift (D)	Mean dry weight (mg) Non-drift (N)	Difference[a]
Mar 25-Apr 1	_P_. _gentilis_ III (leaf)	0.97	1.26	N>D*
"	" IV "	3.26	4.81	N>D*
"	" V "	6.93	9.26	N>D***
"	_P_. _luculenta_ IV (leaf)	3.23	5.81	N>D***
"	" V "	absent	9.23	
Apr 16	_P_. _gentilis_ III (leaf)	1.26	1.26	n.s.
"	" IV "	5.39	6.00	n.s.
"	" V "	9.77	13.72	n.s.
"	_P_. _luculenta_ IV (leaf)	5.01	6.05	n.s.
"	" IV (stick)	3.86	5.58	n.s.
"	" V (leaf)	8.06	8.27	n.s.
"	" V (stick)	absent	11.88	

[a] Significance levels calculated by "t" test

***$P < 0.001$; *$P = 0.01\text{-}0.05$; n.s. = not significant, $P > 0.05$

During the first half of April, the stream discharge increased (to a marked peak on April 13), with corresponding increases in the drift of organic matter and *Pycnopsyche* larvae including very irregular collections of stick-case *P. luculenta*. Subsequent rises in discharge rate on April 22 and 30 were accompanied by much lower peaks in drift rates. By this time, all snow bridges had collapsed (Plate Ib) and no large accumulations of leaves remained in the stream. When correlation was measured between discharge and the separate drift components, it was not significant between discharge and organic matter (Table 10), but was significant between discharge and *Pycnopsyche* larvae. However the correlation was much higher between drift rates of organic matter and *Pycnopsyche* larvae in leaf-disc cases (Table 10). Correlation between organic matter and stick-case larvae was not significant. Stream discharge and drift rates returned to pre-thaw levels at the end of May. Even during periods of peak discharge, *P. scabripennis* larvae were rarely collected, and the estimated total number drifting during the 9-week spring thaw period was about 60 compared with about 12,100 *P. gentilis* and 7,300 *P. luculenta* (80% leaf case, 20% stick case). During the same period, the nets collected nearly 4700 litres (360 kg dry weight) of organic matter. Observations upstream during May showed that whereas some larvae, mostly *P. luculenta* in stick cases, were still present, very few leaves remained and detritus was reduced to occasional patches of twigs and bark.

Most of the drift was carried into Lac Hertel where the larvae presumably died because 10 Ekman grab samples along a transect from the stream mouth into Lac Hertel failed to recover any larvae although

Table 10 Correlation between stream discharge and drift rates of organic matter of _Pycnopsyche_ larvae, and between drift rates of organic matter and _Pycnopsyche_ larvae during the spring thaw, 1971

Data compared	Correlation coefficient
Discharge with organic matter	$0.47^{n.s.}$
Discharge with _P. gentilis_	0.67^{**}
Discharge with _P. luculenta_ (leaf case)	0.68^{**}
Discharge with _P. luculenta_ (stick case)	0.61^{**}
Organic matter with _P. gentilis_	0.82^{***}
Organic matter with _P. luculenta_ (leaf case)	0.86^{***}
Organic matter with _P. luculenta_ (stick case)	$0.31^{n.s.}$

$^{***}P < 0.001$; $^{**}P = 0.001\text{-}0.01$; $^{n.s.}P > 0.05$

empty cases, leaves, and twigs were picked up. However some larvae remained in West Creek, 150 m below the drift traps, where flooding had reduced the current in the main stream and allowed *P. gentilis* and *P. luculenta* to resettle on the bottom. On May 14, 1971, samples of the woody detritus remaining in this area contained approximately equal numbers of *P. gentilis* and *P. luculenta* at a density of about 600 larvae/m^2. Between the flooded area and Lac Hertel (average annual area of 450 m^2) the total area of detritus remaining in May was estimated to be 5 m^2, with 1500 *P. gentilis* and an equal number of *P. luculenta*. As the discharge decreased, these concentrations of larvae attracted flocks of grackles (*Quiscalus quiscula* (L)) whose feeding may have accounted for much of the further reduction in larval numbers, as many empty cases were found on the banks, and 2 birds (observed over two 5-minute periods) ate an average of 3 larvae per minute. Samples taken on June 23, 1971 indicated that both organic matter and larvae were more widely scattered, but that only one third of the May numbers of *P. gentilis* and *P. luculenta* were left in the stream. *P. scabripennis*, which by the beginning of May had burrowed into gravel substrates (see Part I), did not apparently suffer the same reduction in numbers; the June density was only a little less than pre-thaw levels.

B. Experimental procedures and results

1. Mineral substrate selection

Experiments were designed to test the reactions of larvae to different particle sizes in the absence of food. To minimize the growth of micro-organisms specific to certain substrates and their effect on the subsequent selection of particles by larvae, substrates were dried at 250°C for 12 hours immediately before each experiment which were limited to 24 hours.

In the experimental area of each laboratory stream the substrate trays were arranged in graded series with the coarsest particles either upstream (streams 1 and 3) or downstream (streams 2 and 4), and the substrates were smoothed over to cover the partitions between trays. Each experiment used all 4 streams, providing 2 replicates for each tray arrangement. Nine experiments were run in flowing water (current 1 cm/sec or 2 cm/sec) and 7 were in still water.

At the beginning of each flowing-water experiment, 16 larvae (2 per tray) were placed in each stream and their positions were noted after 3, 6, 21 and 24 hours. These 4 readings were pooled with those of the replicate stream to give 8 values per tray arrangement. The results are summarized in Table 11). There was a marked reaction by all larvae to the current even when only 1 cm/sec, observations during the first 3 hours showing that initially this reaction resulted in downstream movement. Third-instar *P. gentilis* larvae remained mainly in the lower half of the stream for 24 hours. Fourth-instar and 5th-instar larvae of *P. gentilis* had moved upstream after 3 hours, although young 4th-instar larvae (2nd column in Table 11) did not show the obvious selection for the upstream end that was shown by older larvae. This upstream movement was particularly noticeable when coarse substrates were upstream, especially in the case of *P. luculenta*, larvae occupying the 32 mm and 16 mm substrate trays as well as the end zones.

Table 11 Percentage of *Pycnopsyche* larvae (instars III-V) on different sizes of substrate particles and in end zones in laboratory streams with 2 arrangements of substrate trays (+++, 51-75%; ++, 26-50%; +, 1-25%; mean of 8 values per tray arrangement)

Particle size and tray arrangement	*P. gentilis*						*P. luculenta*	
	III[a]	IV[a]	IV[a]	V[a]	V[a]	V[b]	V[a]	V[b]
Upstream end		+	++	+++	+++	+++	++	++
32 mm		+	++[c]		+	+	++[c]	++[c]
16 mm	+	+	+	+		+	+	+
8 mm	+	+	+	+	+			
4 mm	+	+	+		+			
2 mm	+	+	+		+	+		
1 mm	+	+	+		+	+		+
½ mm	+	+	+					+
¼ mm	++[c]	+		+	+			+
Downstream end	++	++	+	+	+	+	+	+
Upstream end		+	++	+++	+++	+++	+++	+++
¼ mm			+[c]	+	+	+	+	+
½ mm	+	+	+	+			+	+
1 mm	+	+	+	+		+	+	+
2 mm	+	+	+			+	+	
4 mm	+	+	+	+	+		+	+
8 mm	+	+	+	+	+		+	+
16 mm	+	+	+		+		+	+
32 mm	++[c]	+	+			+	+[d]	+
Downstream end	++	++	+	+	+	+	+	+

[a] Current speed 1cm/sec, [b] Current speed 2 cm/sec,

[c] Significant substrate selection (1% level), (tested by one-way analysis of variance)

[d] Significant substrate selection (5% level)

When fine substrates were upstream, many larvae were in the upstream end zone but fewer selected the adjacent ¼ mm particles. Any significant selection for a particular substrate particle size is indicated in Table 11.

The reactions of P. gentilis and P. luculenta to current alone were tested by replacing the mineral substrates by reversed, roughened plexiglass trays. Both species moved upstream against a current of 1 cm/sec (4 replicate experiments per species) but were distributed randomly in still water (2 replicates per species).

The next set of experiments therefore considered the behaviour of P. gentilis and P. luculenta on mineral substrates in still water to avoid the bias introduced by current. All larvae were now in the 5th instar although some had only recently moulted. As P. gentilis larvae make a leaf-disc case until about 1 month after they have entered the 5th instar, they automatically carry potential food with them. While they were never seen eating their own cases, they often fed on each others cases during substrate selection experiments. So the streams were again used in pairs to compare

a) the effects of different densities on the behaviour of leaf-case P. gentilis;

b) the substrate selection behaviour of leaf-case larvae with older P. gentilis larvae that had made sand-grain cases;

c) the substrate selection behaviour by sand-grain case P. gentilis with that of P. luculenta.

One case type or species was placed in each pair of streams and readings of larval distribution were taken as in earlier experiments. The results of these single-species experiments (Table 12) showed that P. gentilis significantly selected 1 mm or 2 mm particles which they added to the fronts of their cases (either type). This behaviour was particularly noticeable among the high-density leaf-case larvae whose reciprocal feeding had resulted in very ragged remnants of their cases. The only difference between leaf-case and sand-grain-case larvae was in the selection of 2 mm particles that were favoured more by larvae already in sand-grain cases than by those beginning the transformation. P. luculenta showed an overwhelming preference for 32 mm pebbles and the 16 mm particles and plexiglass tray on either side, and a less marked selection of the plexiglass tray at the opposite end of the stream. Larvae of both species (except for those P. gentilis that were case-building) were restless, moving up and down the streams, usually along the edges of the plexiglass trays at the sides of the stream with occasional trips over the substrate particles.

Two further experiments in still water (4 replicates each) combined P. luculenta with either leaf-case or sand-grain-case P. gentilis. The distribution was noted 18, 21 and 24 hours after the beginning of each experiment. The mean of the 12 readings from each experiment (Table 12) showed that selection for 1 mm particles (and case building) by P. gentilis was more marked by leaf-case larvae than by sand-grain-case larvae, the latter being distributed randomly. P. luculenta again showed a significant selection for 32 mm pebbles, and a lesser selection for the adjacent substrates.

P. scabripennis was not used in the above experiments because few larvae were available at the time. A year later, 16 5th-instar

Table 12 Percentage of 5th-instar *Pycnopsyche* larvae on different sizes of substrate particles in still water (++++, 31-40%; +++, 21-30%; ++, 11-20%; +, 1-10%; mean of 8 values per single-species experiment, 12 values per combined-species experiment)

Substrate type or particle size	Single species experiments				Combined species experiments			
	P. gentilis[a] (leaf case)	*P. gentilis*[b] (leaf case)	*P. gentilis*[b] (sand case)	*P. luculenta*[b]	*P. gentilis*[a] (leaf case)	*P. luculenta*[a]	*P. gentilis*[a] (sand case)	*P. luculenta*[a]
Rough plexiglass	+	+	+	++	+	++	+	++
¼ mm	+	+	+	+	+	+	+	
½ mm	+	+	+	+	+	+	+	+
1 mm	++	+++[c]	++[c]	+	++++[c]		++	
2 mm	++	++	++[c]	+	++		++	
4 mm	+	+	+	+	+		++	+
8 mm	+	+	+	+	+	+	++	+
16 mm	+	+	+	++	+	++	++	++
32 mm	+	+	+	+++[c]	+	+++[c]	+	+++[c]
Rough plexiglass	+	+	+	++	+	++	+	++

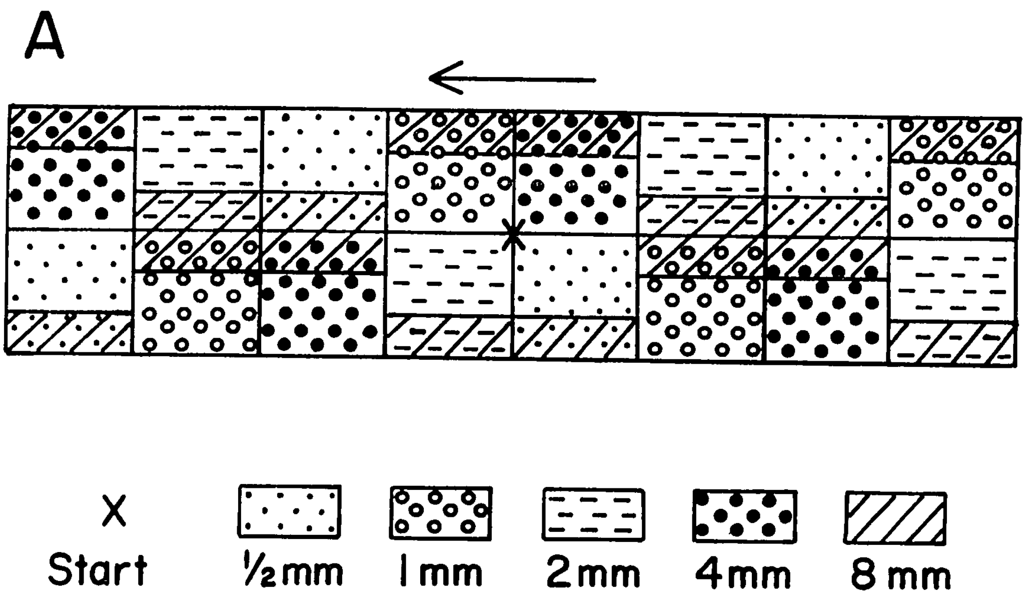
[a] 8 larvae per experiment, [b] 16 larvae per experiment

[c] Significant substrate selection (1% level, tested by analysis of variance)

P. scabripennis, collected just before aestivation, were offered a choice of sand and gravel particles placed directly on the bottom of a laboratory stream to allow random burrowing without the confines of substrate trays. The substrates were arranged in a checker-board pattern (Fig 13a) of ½, 1, 2 and 4 mm particles (5 cm deep) with overlying bands (3 cm deep) of 8 mm particles. The larvae were placed in a group at the centre of the stream; all began to burrow within 2 hours. After 24 hours they were uncovered, counted, and replaced at the starting point. This procedure was repeated 4 times. The resulting burrows (total of 80 sites, Fig 13b) were confined to 4 mm and 8 mm particles; P. scabripennis showed a significant preference ($P < 0.001$) for the 8 mm gravel (actual size 8-16 mm). Only one larva in 5 experiments burrowed deeper than 2.5 mm below the surface; this larva burrowed beyond the 8 mm-gravel overlay into the underlying 4 mm-gravel.

2. Organic substrate selection

Samples of organic substrates from West Creek indicated that P. gentilis were more abundant in leafy habitats while numbers of P. luculenta decreased as the proportion of leaves to detritus increased. Experiments were designed to determine whether the field distributions were due to habitat preferences or to interspecific interactions. Laboratory streams were first set up to offer a choice between DETRITUS and LEAVES. The substrate trays were filled with 1 mm sand that was smoothed over the transverse partitions. A layer of DETRITUS 1-3 cm thick and 8 cm wide was placed down one side of the stream and a



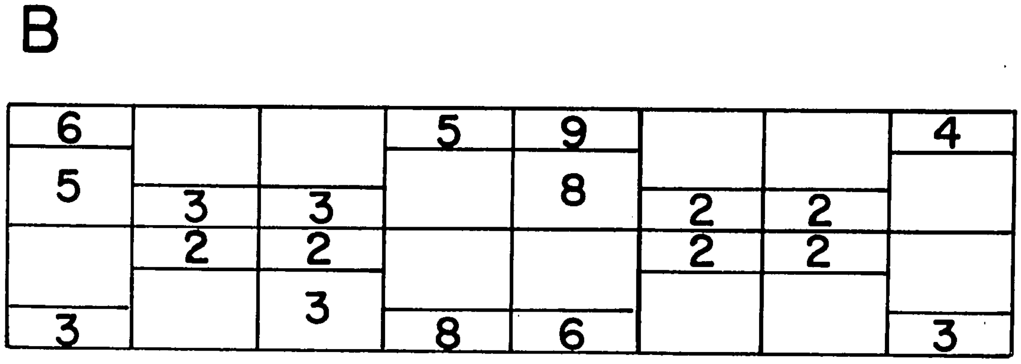


Figure 13a. Arrangement of substrate particles in Pycnopsyche scabripennis burrowing experiments. (Arrow indicates direction of current).

Figure 13b. Total number of burrowing sites per substrate in 5 replicate experiments.

similar layer of LEAVES down the other, leaving a central strip of bare sand about 15 cm wide. Seven groups of experiments were performed, with at least 5 replicates per experiment. *P. gentilis* and *P. luculenta* were each tested alone at 2 densities (50 or 200 per stream), and combined at 3 densities (50:50, 80:20, 20:80). All larvae were in the 3rd, 4th or 5th instars. Some *P. luculenta* had leaf-disc cases, others had the more usual stick-case. *P. gentilis* cases (leaf-disc or sand-grain) depended on larval age. Larvae were evenly distributed down the central strip of sand at the beginning of each experiment, facing in random directions, and allowed to disperse during 24 hours. A few 5th-instar *P. gentilis* larvae building sand-grain cases were seen on bare sand, and one or two larvae often were in the end zones of the streams. The mean numbers/substrate/experiment (expressed as percentages in Table 13) showed that about 90% of *P. gentilis* had a significant preference for LEAVES. The 10% in DETRITUS included several larvae that had fixed their cases to twigs while moulting. *P. luculenta* showed no significant preference for LEAVES or DETRITUS. The behaviour of each species did not differ at the various densities tested ($P > 0.05$). No significant differences were found between instars although young *P. luculenta* tended to select DETRITUS more than LEAVES. The type of case carried by the experimental larvae did not affect their choice of substrate.

In a second series of experiments, 4 types of organic substrates were prepared to simulate the 4 categories in West Creek. DETRITUS, DETRITUS (& LEAVES), LEAVES (& DETRITUS), and LEAVES were placed over

Table 13 Mean numbers (%) of *P. gentilis* and *P. luculenta* in 2 organic substrates in laboratory streams

Species	No. larvae /species	No. of replicates	% in DETRITUS	% in LEAVES	Difference between substrates[a]
P. gentilis	50[b]	9	7.0	93.0	$P < 0.001$
P. luculenta	50	12	51.8	48.2	n.s. $P>0.05$
P. gentilis	200[b]	7	12.6	87.4	$P < 0.001$
P. luculenta	200	6	48.0	52.0	n.s. $P.>0.05$
P. gentilis	50[b]	12	12.1	87.9	$P < 0.001$
P. luculenta	50		53.0	47.0	n.s. $P>0.05$
P. gentilis	80[b]	5	11.1	88.9	$P < 0.001$
P. luculenta	20		62.8	37.2	n.s. $P>0.05$
P. gentilis	20[b]	5	11.4	88.6	$P < 0.001$
P. luculenta	80		60.8	39.2	n.s. $P>0.05$

[a] Significance levels calculated by "t" test

[b] Difference between experiments tested by analysis of variance after the arcsin transformation (Sokal and Rohlf 1969)

sand in 8 transverse strips (2 of each type), each the width of the stream (30 cm) and 10 cm long, with a 5 cm-strip of sand between each. *P. gentilis* and *P. luculenta* were tested singly or combined, using 48 larvae per stream placed initially as 6 larvae per strip. They were allowed to disperse for 24 hours. The behaviour of *P. gentilis* (4th instar), with and without *P. luculenta*, towards the 4 substrates (Table 14) differed little from the field data, larvae selecting chiefly the leafy habitats. *P. luculenta* larvae were more numerous in habitats with detritus than in leafy habitats but a significant difference in selection behaviour between habitats was only shown by 4th-instar larvae (Table 14).

3. Interspecific interactions

Severe catastrophic drift in West Creek during the spring thaw greatly reduces the amount of organic substrate available to *P. gentilis* and *P. luculenta* larvae and results in highly concentrated aggregations of both species. In a laboratory stream the behaviour of both species under such crowded conditions was compared with situations where the larvae were able to disperse from an area of high density.

Ten substrate trays (total length 1.5 m) were filled with sand (1 mm particles) and covered with detritus taken from West Creek in May 1971. Nitex screens enclosed an area 30 x 50 cm (0.15 m^2) in the centre of the stream. One hundred larvae of one species, or 50 each of *P. gentilis* (leaf case or sand-grain case) and *P. luculenta* (stick case) were placed in the enclosure for 24 hours. Then, after counting and dislodging any larvae on the screens, and noting the condition

Table 14 Mean numbers (%) of _P. gentilis_ and _P. luculenta_ in 4 organic substrates in laboratory streams

Species	Instar	No. of replicates	DETRITUS	DETRITUS (& LEAVES	LEAVES (& DETRITUS)	LEAVES
P. gentilis	IV	3	11.5*	16.5	36.2	35.8
P. luculenta	IV		35.6	36.3	24.1	3.9*
P. gentilis	IV	3	10.0*	16.5	39.5	34.0
P. luculenta	IV	3	46.9	31.4	13.6	8.1*
P. luculenta	V	4	29.5	27.5	25.1	17.9

*Selection significantly different
(5% level, tested by analysis of variance)

of all larval cases, the screens were lifted. After another 24 hours, numbers per tray were counted and removed. Between experiments the stream discharge was usually increased to aerate the water and remove waste materials, but the detritus was only changed after groups of experiments. Single species were introduced to fresh detritus and to detritus conditioned by the second species.

In the high-density enclosures, *P. luculenta* was more active than *P. gentilis*, more larvae were crawling about, and they often climbed the screens; their cases did not appear damaged and no naked larvae were found. *P. gentilis*, whether alone at high density or with *P. luculenta*, suffered considerable damage to leaf cases and frequently has been evicted from their cases.

The results of dispersion from high density areas (Table 15) are expressed as numbers (percent) in the upstream or downstream half of the extended area. Dispersal was random by each species when alone; however in combined-species experiments more *P. gentilis* were upstream and more *P. luculenta* were downstream. These species-specific distributions resulted only from the presence of actual larvae and not from conditioned detritus.

4. Feeding experiments

Most feeding experiments compared the amount of leaf material ingested by equivalent instars of *Pycnopsyche gentilis* and *P. luculenta* Replicate discs of each leaf species were distributed between randomly selected larvae, and control dishes. Usually only one leaf species was considered per experiment; if mixtures were used then unless stated

Table 15 Mean numbers (%) of _P. gentilis_ and _P. luculenta_ upstream and downstream after dispersing from high-density enclosures

Species	No. of larvae	No. of replicates	% Upstream	% Downstream
P. gentilis	100	6	49.1	50.9
P. luculenta	100	6	43.4	56.6
P. gentilis	50	8	60.9**	39.1
P. luculenta	50		32.0	68.0**

**Distribution along the stream significantly different from random at 1% level (tested by analysis of variance) otherwise, the total amount ingested was calculated. The mean dry body weight of larvae was calculated by weighing the experimental larvae (instars I-III) or by weighing equivalent control larvae.

P. gentilis usually ingested more leaf material than P. luculenta (in terms of mg material ingested per larva) but differences between species were not always significant (Table 16). When the amount ingested was expressed as percentage of larval body weight (100 x mean weight ingested/mean body weight) the difference between young instars (I to III) of the respective species was usually smaller or even reversed (Table 16, sugar maple A, red maple B). One experiment (sugar maple D) compared 2nd-instar P. gentilis with 3rd-instar P. luculenta, because these were the stages most common in West Creek at the time; there was no specific difference in the amount of leaf ingested in terms of percent of body weight.

The preferred leaf species were sugar maple, red maple, and ironwood. First-instar larvae and early 2nd instars ingested significantly more ironwood (up to 64% of body weight). By the time P. gentilis and P. luculenta had entered the 3rd instar, few entire ironwood leaves remained in West Creek. Both sugar maple and red maple were readily ingested by 4th and 5th instars of both species, especially when the leaf discs had not been predried. In some cases the amounts ingested by P. gentilis exceeded the body weight (sugar maple F, red maple C).

Beech and oak leaves were very rarely ingested; the results of 2 beech disc experiments are included in Table 16 for comparison.

Table 16 Summary of feeding experiments comparing mean dry weights of leaf material ingested per 24 hours by *P. gentilis* and *P. luculenta* larvae (expressed as mg ingested per larva[a], and as the percentage of mean dry body weight of larva)

Leaf species		*P. gentilis*			*P. luculenta*	
	Replicates /instar	Mean dry wt (mg) leaf ingested/24 hrs /larva (±95% limits)	% body wt	Replicates /instar	Mean dry wt (mg) leaf ingested/24 hrs /larva (±95% limits)	% body wt
Ironwood A	I - 19	0.045 (±0.009)**	64.3	I - 19	0.028 (±0.005)	63.6
B	II - 20	0.102 (±0.034)**	51.0	II - 20	0.074 (±0.022)	50.0
C	III - 19	0.270 (±0.076	28.0	III - 19	0.354 (±0.086)$^{n.s.}$	59.5
D	III - 10	0.503 (±0.132)$^{n.s.}$	63.0	III - 10	0.378 (±0.143)	63.0
Sugar maple A	I - 9	0.022 (±0.007)$^{n.s.}$	38.6	I - 10	0.018 (±0.005)	38.0
A	II - 10	0.088 (±0.012)**	32.6	II - 8	0.045 (±0.022)	35.7
B	II - 20	0.080 (±0.044)**	35.0	II - 20	0.034 (±0.014)	24.0
C	II - 17	0.087 (±0.020)$^{n.s.}$	46.8	II - 6	0.053 (±0.027)	21.8
D	II - 20	0.230 (±0.051)	62.0	III - 28	0.371 (±0.061)*	61.4
E	III - 20	0.416 (±0.072)$^{n.s.}$	42.0	III - 20	0.356 (±0.100)	59.3
F[b]	IV - 5	6.784 (±3.005)$^{n.s.}$	113.0	IV - 4	4.160 (±2.694)	71.7

continued ....

(Table 16 continued)

Leaf species		*P. gentilis*			*P. luculenta*		
		Replicates /instar	Mean dry wt (mg) leaf ingested/24 hrs /larva (±95% limits)	% body wt	Replicates /instar	Mean dry wt (mg) leaf ingested/24 hrs /larva (±95% limits)	% body wt
Sugar maple	F^{b}	V - 14	10.886 (±1.195)$^{n.s.}$	72.6	V - 8	8.960 (±2.427)	60.6
Red maple	A	II - 20	0.064 (±0.022)*	32.0	II - 20	0.044 (±0.014)	29.0
	B	III - 20	0.407 (±0.093)*	55.3	III - 20	0.285 (±0.124)	57.0
	C^{b}	IV - 10	5.120 (±1.221)*	95.0	IV - 5	3.328 (±0.870)	76.5
	C^{b}	V - 14	15.269 (±2.580)**	100.8	V - 14	10.468 (±1.424)	80.8
Mixed maples	A^{b}	IV - 9	3.800 (±1.572)$^{n.s.}$	63.3	IV - 6	3.333 (±1.683)	57.5
	A^{b}	V - 8	7.584 (±2.149)$^{n.s.}$	58.3	V - 8	6.624 (±2.359)	55.2
Beech	A	II - 20	0.005 (±0.002)$^{n.s.}$	2.5	II - 20	0.002 (±0.003)	1.5
	B	III - 10	0.030 (±0.015)$^{n.s.}$	4.0	III - 10	0.017 (±0.007)	3.0

[a] Significance of greater mean calculated by "t" test

[b] Leaves not pre-dried)

**$\underline{P}$ = 0.001-0.01 *$\underline{P}$ = 0.01-0.05 $^{n.s.}$$\underline{P}$ > 0.05

Two other factors affecting feeding behaviour were considered:

a) the effects of offering twigs with leaf discs;

b) the effects of bacteria and fungi on the leaf discs.

a) The effects of additional twigs

Fine twigs collected from West Creek were cut into 1 cm lengths and distributed between half the replicate larvae of *P. gentilis* and *P. luculenta*. All larvae received similar replicate leaf discs. In 2 experiments, *P. gentilis* ingested the same amount of leaf material whether or not twigs were available (Table 17). The behaviour of *P. luculenta* was very different. When only leaf discs were available, the amounts ingested in each experiment were similar to those ingested by *P. gentilis*. When twigs were added, *P. luculenta* ingested significantly less leaf material and appeared to rasp the twigs.

b) The effects of bacteria and fungi

Two experiments compared the ingestion of leaf discs that had been incubated in a fungal culture, with leaf discs from a bacterial culture, and with sterile leaf discs (autoclaved). Fungi and bacteria were obtained from leaves collected in West Creek that were cut into several discs. Half the number of discs were rinsed in distilled water and drained (3 times) to wash off surface bacteria; each of these discs was then placed on the edge of a sterile nutrient agar plate (cornmeal agar with added dextrose and peptone). The remaining number of discs was homogenized in distilled water, filtered, and single drops of filtrate were plated on identical agar. All plates were incubated at room temperature for 90 hours, when bacterial colonies had developed from the filtrate and fungal hyphae had spread

Table 17 Mean dry weights of leaf material ingested per 24 hours by P. gentilis and P. luculenta larvae under different experimental conditions[a] (expressed as mg ingested per larva, and as the percentage of mean dry body weight of larva)

Leaf type	Conditions	Replicates /instar /species	P. gentilis		P. luculenta	
			Wt (mg) leaf ingested/24 hrs /larva (±95% limits)	% body wt	Wt (mg) leaf ingested/24 hr /larva (±95% limits)	% body wt
Wet sugar maple	leaf discs only	IV - 9	2.880 (±0.853)	76.4	2.806 (±0.898)	78.2
	leaf discs + twigs	IV - 9	2.930 (±1.093)$^{n.s.}$	77.7	0.808 (±0.726)**	22.6
Wet mixed maples	leaf discs only	IV - 8	3.585 (±0.900)	95.1	3.336 (±0.819)	83.4
	leaf discs + twigs	IV - 8	3.987 (±1.049)$^{n.s.}$	105.8	1.899 (±0.765)**	47.5
Mixed wet and predried maples	fungal culture	V - 11	20.451 (±6.520)	130.0	9.460 (±3.801)	72.8
	bacterial culture	V - 11	11.080 (±4.551)**	73.9	1.761 (±1.472)**	13.6
	sterile	V - 11	0.491 (±0.528)**	3.0	0.073 (±0.162)**	0.6
Mixed predried maples	fungal } choice	V - 18	15.726 (±3.252)	105.0	11.690 (±2.190)	90.0
	bacterial		0.135 (±0.180)**	0.7	0.051 (±0.081)**	0.3
	sterile		---------	----	-----------	----

[a] Differences between conditions tested by analysis of variance

$^{**}P < 0.01$ $^{n.s.}P > 0.05$

out from the leaf discs. The innoculating discs and underlying agar were then cut out of the plates. The 2 types of culture plates plus a 3rd set of sterile agar plates served as treatment chambers for the experimental food discs. The food discs were cut from a number of maple leaves (sugar and red), mostly predried. Each leaf was cut into 6 food discs that were autoclaved, then incubated in the 3 treatment chambers (2 discs per treatment) for 48 hours and in sterile water for 24 hours. Three discs (1 from each treatment) were then offered to *P. gentilis*, the other 3 to *P. luculenta*. In Experiment 1, each larva received one leaf disc and therefore only one of the 3 treatments. In Experiment 2, each larva received 3 discs, one from each treatment, and so was offered a choice. (In this experiment the discs intended for different treatments were cut in slightly different shapes so that they could be identified at the end of the feeding period).

The incubating procedures and sources of microflora were identical in the 2 experiments, and all plating and transferring was done in a sterile room. The experiments were carried out in covered dishes, to prevent contamination, at normal experimental temperatures, and lasted only 4 hours to avoid the depletion of preferred food.

The results (Table 17) were obvious even before the discs had been dried and weighed. When a choice of discs was available, *P. gentilis* and *P. luculenta* fed almost exclusively on the fungal discs, and sterile discs were not ingested. Without a choice, larvae receiving fungal discs had again ingested the most leaf material. However, the bacterial discs were apparently not distasteful to either species, and *P. gentilis* ingested an amount representing over 70%

of the body weight. Even small amounts of sterile discs were ingested when no choice was available.

DISCUSSION

The habitats of stream organisms living in well oxygenated water are characterized by the types of mineral substrate (which usually reflect current regimes) and the overlying allochthonous organic materials or aquatic vegetation. Most of the organic substrates in West Creek lie over coarse sand and gravel, but apart from the period of sand-grain case construction in *P. gentilis* neither this species nor *P. luculenta* showed any definite preference for a particular substrate in the laboratory that could be related to their natural habitats. As the rough plexiglass trays as well as 16 mm and 32 mm particles were attractive to *P. luculenta*, the larvae were probably selecting a suitable firm texture underfoot more like the submerged logs and twigs they crawl on in West Creek.

Pycnopsyche scabripennis (when burrowing) was the only species that selected 4 mm and 8 mm particles exclusively. The coarsest particles selected are probably the largest that the larvae can handle in order to burrow; the lower limit may be dependent on the interstitial spaces and the amount of oxygen reaching the larva during the 3-month aestivation period. Eriksen (1964) has shown that substrate particle size selection by burrowing mayflies is determined by their oxygen requirements.

The substrate selection by burrowing *P. scabripennis* is similar to that of burrowing *P. lepida* larvae (Cummins 1964) although *P. lepida* chooses a wider range of substrates (2 mm through 16 mm). An important difference between *P. scabripennis* and *P. lepida* lies in their pupation sites. P. lepida returns to the surface before pupating whereas P. scabripennis remains buried, forcing the unprotected pupa to make its way through the gravel before emergence. The substrates selected by burrowing P. scabripennis may therefore be dictated by more complex factors than simply size.

As P. gentilis and P. luculenta appear relatively unaffected by the distribution of mineral substrates for most of the larval period, the nature of the organic substrates is a critical factor in determining habitat.

Allochthonous organic matter has usually been considered as just one type of stream habitat, contrasting with mineral substrates and living vegetation; however, the non-random distribution of P. gentilis and P. luculenta within allochthonous matter in West Creek suggests that it should be considered as a mozaic of microhabitats probably differing in the relative amounts of leaves and detritus and associated microflora.

The chief question raised by the data from West Creek was whether the respective distributions of P. gentilis and P. luculenta reflected specific habitat preferences or whether the presence of one species excluded the other. Laboratory stream experiments offering a choice of LEAVES and DETRITUS showed that the small percentage of P. gentilis in DETRITUS was not due to interference from P. luculenta in this habitat, therefore the pre-thaw field distribution of P. gentilis is probably in the preferred habitat.

P. luculenta in the laboratory entered LEAVES in unexpectedly high numbers, but lack of interference by P. gentilis in similar combined-species experiments made the possibility of exclusion an unlikely explanation for the small number of P. luculenta in LEAVES in West Creek. The high numbers in laboratory LEAVES might have been caused by some reduction in the food quality of DETRITUS as a result of handling and abrasion. However, the consistently even distribution between LEAVES and DETRITUS in several experiments and even at high densities suggests that P. luculenta larvae were not avoiding DETRITUS but were dispersing randomly within the model streams. In West Creek, although P. luculenta was usually found in habitats including detritus, some larvae were seen on clean leaf surfaces where they were feeding or cutting discs to add to their cases. In fact this species appears to be partly facultative in its use of the 2 main types of allochthonous material but it seldom moves far from a source of detritus. In laboratory experiments, the longitudinal strips of LEAVES were within the critical distance of DETRITUS so that larvae dispersed randomly. When 4 types of substrate were arranged in horizontal strips, then LEAVES and DETRITUS were further apart and at least the younger larvae selected habitats with detritus. Very little work has been done on the nutritional value of woody detritus in streams, but Willoughby (1971) has shown that twigs can support vigourous fungal growth. During a 24-hour experiment, P. luculenta fed preferentially on twigs, and possibly the micro-organisms specific to woody substrates form an important part of the diet. Small sticks are also the preferred case building material, and leaf-case larvae were only found in thick piles of LEAVES or LEAVES (& DETRITUS) that were at least 3 m from DETRITUS. Larvae in these situations probably had been trapped in accumulating leaf packets as these were washed into bays or behind logs in autumn, especially as many leaf-case larvae were collected in 1969/70 when LEAVES had been concentrated by heavy rain in November 1969.

If the organic substrates in West Creek are considered as islands of DETRITUS merging into more leafy substrates, with _P. luculenta_ dispersed randomly up to a critical distance from the DETRITUS island, then the apparent differences between field and laboratory distributions can be reconciled. In either situation, half the population is in DETRITUS; the other half is in the more leafy substrates.

In the part of West Creek where most sampling was done (100-400 m from Lac Hertel) the area covered by DETRITUS before the spring thaw was one quarter of the whole area of organic substrates. The total number of _P. luculenta_ collected during the pre-thaw period was one quarter of the number of _P. gentilis_. These similar proportions between habitats and numbers may not be coincidental, and the overlapping distributions of the 2 species must now be considered.

If the total area of organic substrates is pictured as a square containing, for example, 100 _Pycnopsyche_ larve (80 _P. gentilis_, 20 _P. luculenta_), then one quadrant of this square represents DETRITUS containing 50% of the _P. luculenta_ population (10 larvae) and 10% of the _P. gentilis_ population (8 larvae), a total of 18 larvae. The remainder of the large square can be considered as representing the 3 leafy habitats containing another 10 _P. luculenta_ and 72 _P. gentilis_.

Thus the density per unit area in the leafy habitats is higher than in DETRITUS but can be explained by the greater volume of leafy material. Numbers of P. luculenta are probably limited by the amount of DETRITUS available in the immediate area. More detritus would support more larvae provided that sufficient amounts of the more leafy habitats were also available to accommodate half of the population. Numbers of P. gentilis are in proportion to the area of leaves, but because of the variable volume of samples from West Creek, only estimates can be made of the total amounts of leaves available. Probably they exceed the amounts required as several samples of LEAVES did not include Pycnopsyche larvae.

However, the distribution of Pycnopsyche on leaves is dependent on more than the absolute area or volume of leaves. Aquatic detritivors are known to feed preferentially on different leaf species (Wallace et al 1970, Kaushik and Hynes 1971) and similar conclusions can be drawn from the feeding experiments described in the present study. The palatability of ironwood leaves in early autumn can be related to their soft texture and rapid rate of decay, and to the relatively warm water temperatures in September when these leaves begin to fall. Maple leaves also decay fast (although later and slower than ironwood) and are known to decay faster than beech and oak (Coldwell and DeLong 1950, Slack and Feltz 1968, Kaushik and Hynes 1971). Rapid decomposition indicates high microbial activity (Hynes and Kaushik 1969) so that leaf preferences found in the present study probably result from the presence or effects of micro-organisms. Kaushik and Hynes (1971) have shown that fungi are more important in the initial period of leaf decay than bacteria, and that fungi retain or increase the nitrogen and protein content of leaves, improving their food quality. They also found that leaves supporting microbial growth were preferred by leaf-feeding invertebrates. Feeding experiments in which *Pycnopsyche* larvae fed preferentially on leaves supporting fungi have been done by 2 other workers (Sedell 1970, Triska 1970) but no details have been published to date.

In experiments where *P. gentilis* and *P. luculenta* were offered leaf discs from fungal and bacterial cultures, no attempt was made to identify the micro-organisms, and probably only a few of the normal stream species were represented since only one culture medium was used. However the clear preference for fungal discs when a choice was availalbe strongly suggests that similar behaviour is normal in the stream environment, and that most larvae live on the rapidly decaying leaves and associated micro-organisms. The only exceptions are individuals cutting beech discs for case construction. It is not surprising in view of the greatly delayed decomposition of beech leaves that they should be selected as case material, and until spring, when beech decay is beginning and food supplies are diminished, they are not attacked by other leaf-feeders.

The large amounts of leaves remaining in West Creek through the winter partly reflect the low winter temperatures and slow rate of decomposition; they may also be affected by the low calcium hardness of West Creek (Mackay 1969) for Egglishaw (1968) has shown that plant material decomposes more quickly in streams with high calcium concentrations.

When the leaves are concentrated by autumn rain, there must also be some downstream drifting of larvae although the distances travelled cannot be great owing to the many barriers formed by fallen branches. Several species of limnephilids have been reported in drift (usually as a result of habitat displacement) especially young instars with cases of plant material (Anderson 1967, Bishop and Hynes 1969, Elliott 1971), but autumn drift rates were not monitored in West Creek.

The greatest factor affecting distributions of *P. gentilis* and *P. luculenta* in West Creek is the increased discharge during the spring thaw. Although several cases of catastrophic drift have been studied (e.g. Anderson and Lehmkuhl 1968, Elliott 1971) none of the spates described removed so high a percentage of allochthonous organic matter as the 1971 thaw in West Creek. The drift of *Pycnopsyche* larvae was also higher than previously published drift rates of Trichoptera. The high correlation between organic matter and leaf-case larvae (Table 10) strongly suggests that they entered the drift passively through habitat displacement. Weight differences between drifting and non-drifting larvae (Table 9) indicate that in March small larvae were predominant in the drift, possibly because they could not resist displacement nor move against the current. (Laboratory experiments showed that young *P. gentilis* did not move against a current of 1 cm/sec). While discharge was relatively low, bigger larvae could cling to stationary objects, or sink to the bottom and then (as in experiments) migrate upstream. Increasing flow carried larger packets of leaves with more enclosed, trapped larvae, so the mean weight of drifting larvae increased.

The high numbers of leaf-case _P_. _luculenta_ larvae in the early drift confirms the observation that such larvae live in leaves. Stick-case larvae in detritus were not affected until the swirling currents at peak discharge began to disturb the heavier substrates. The stick case is also more streamlined and therefore more stable than the broad leaf-disc case.

Approximate estimates of the upstream populations based on unpublished data from earlier years were 19,000 _P_. _gentilis_, and 15,000 _P_. _luculenta_ (of which about 10,000 would have stick cases in March). On a stream-wide basis, these population densities of _P_. _gentilis_ and _P_. _luculenta_ are equivalent to $11/m^2$ and $9/m^2$ respectively. Assuming similar population sizes in 1971, then over 65% of the _P_. _gentilis_ population and all the leaf-case _P_. _luculenta_ were in the drift, but only 13% of the stick-case _P_. _luculenta_. The numbers of larvae remaining upstream in May 1971 were in agreement with these estimates of displacement. Such severe upstream depopulation only seems to occur during years of heavy snow followed by a rapid thaw and was not as extensive in 1966 or 1967 during the first study of West Creek.

Renewal of upstream insect populations is generally assumed to result from the upstream flight of gravid females and has been observed in many species of Trichoptera (Ross 1957, Elliott 1971); but this aspect of flight was not studied at West Creek. Upstream migrations of limnephilid larvae have been studied by Hynes (1968) after a severe spate, and by Hultin _et_ _al_ (1969) just before pupation and after high water. It is therefore interesting that _P_. _gentilis_, the species most affected by drift in West Creek, migrates upstream away from areas crowded with *P. luculenta* in experiments simulating post-thaw conditions. Such behaviour would help to restore upstream numbers as well as removing *P. gentilis* from competitive situations. *P. gentilis* is at a disadvantage in such situations because as well as being vulnerable in its leaf-disc case and so suffering directly from *P. luculenta*, it is in the least preferred range of its habitat and it does not feed preferentially on twigs.

Competition in adverse seasons has been observed between other insect species that normally coexist (Broadhead 1958), usually because changes in the environment have altered the differences in niche space that allowed coexistence (Mayr 1963, Hutchinson 1965). During most of the year, *P. gentilis* uses mainly leaves for food, case-building, and habitat. It is therefore a specialist and its niche space is relatively small. *P. luculenta* is facultative, indicating a larger niche space. These niches overlap completely in time and to a certain extent in food and habitat, but normally the overlap is tolerated because no shared resources are in short supply. Any competitive interactions between the species occur only when the habitat and food of *P. gentilis* are violently disrupted by catastrophic drift, and the harmful effects of such interactions are probably less than the effects of drift itself.

REFERENCES

Anderson, N.H. 1967. Biology and downstream drift of some Oregon Trichoptera. Can. Ent. 99: 507-521.

Anderson, N.H., and D.M. Lehmkuhl. 1968. Catastrophic drift of insects in a woodland stream. Ecology. 49: 198-206.

Bishop, J.E., and H.B.N. Hynes. 1969. Downstream drift of the invertebrate fauna in a stream ecosystem. Arch. Hydrobiol. 66: 56-90.

Broadhead, E. 1958. The psocid fauna of larch trees in northern England — an ecological study of mixed species populations exploiting a common resource. J. Anim. Ecol. 27: 217-263.

Coldwell, B.B., and W.A. DeLong. 1950. Studies of the composition of deciduous forest tree leaves before and after partial decomposition. Sci. Agric. 30: 456-466.

Cummins, K.W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. Amer. Midl. Nat. 67: 477-504.

Cummins, K.W. 1964. Factors limiting the microdistribution of the caddis flies *Pycnopsyche lepida* (Hagen) and *Pycnopsyche guttifer* (Walker) in a Michigan stream (Trichoptera:Limnephilidae). Ecol. Monogr. 34: 271-295.

Egglishaw, H.J. 1968. The quantitative relationship between bottom fauna and plant detritus in streams of different calcium concentrations. J. Appl. Ecol. 5: 731-740.

Elliott, J.M. 1971. Life histories and drifting of three species of Limnephilidae (Trichoptera). Oikos. 22: 56-61.

Eriksen, C.H. 1964. The influence of respiration and substrate upon the distribution of burrowing mayfly naiads. Verh. internat. Verein. Limnol. 15: 903-911.

Feldmeth, C.R. 1970. A large volume laboratory stream. Hydrobiologia. 35: 397-400.

Hultin, L., B. Svensson, and S. Ulfstrand. 1969. Upstream movements of insects in a South Swedish small stream. Oikos. 20: 553-557.

Hutchinson, G.E. 1965. The ecological theatre and the evolutionary play. Yale Univ. Press, New Haven and London.

Hynes, H.B.N. 1968. Further studies on the invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 65: 360-379.

Hynes, H.B.N. 1970. The ecology of running waters. Liverpool Univ. Press.

Hynes, H.B.N., and N.K. Kaushik. 1969. The relationship between dissolved nutrient salts and protein production in submerged autumnal leaves. Verh. internat. Verein. Limnol. 17: 95-103.

Kaushik, N.K., and H.B.N. Hynes. 1971. The fate of dead leaves that fall into streams. Arch. Hydrobiol. 68: 465-515.

Lauff, G.H., and K.W. Cummins. 1964. A model stream for studies in lotic ecology. Ecology. 45: 188-191.

Mackay, R.J. 1969. Aquatic insect communities of a small stream on Mont St. Hilaire, Quebec. J. Fish. Res. Bd. Canada. 26: 1157-1183.

Mackay, R.J., and J. Kalff. 1969. Seasonal variation in standing crop and species diversity in a small Quebec stream. Ecology. 50: 101-109.

Mayr, E. 1963. Animal species and evolution. Harvard Univ. Press. Cambridge, Mass.

McDiffett, W.F. 1970. The transformation of energy by a stream detritivor, *Pteronarcys scotti* (Plecoptera). Ecology. 51: 975-988.

Roos, T. 1957. Studies on upstream migration in adult stream-dwelling insects. Rept. Inst. Freshwater Res. Drottningholm. 38: 167-193.

Ross, H.H. 1963. Stream communities and terrestrial biomes. Arch. Hydrobiol. 59: 235-242.

Sedell, J.R. 1970. Detritus and the stream system (Abstract). Bull. Ecol. Soc. Amer. 51(4):30.

Simpson, G.G., A. Roe, and R.C. Lewontin. 1960. Quantitative Zoology. Harcourt Brace and World, Inc. New York.

Slack, K.V., and H.R. Feltz. 1968. Tree leaf control on low flow water quality in a small Virginia stream. Environ. Sci. and Tech. 2: 126-131.

Sokal, R.R., and F.J. Rohlf. 1969. Biometry. W.H. Freeman and Company. San Francisco.

Triska, F.J. 1970. Seasonal distribution of aquatic hyphomycetes in relation to the disappearance of leaf litter from a woodland stream. Unpublished Ph.D. Thesis, Univ. Of Pittsburgh.

Wallace, J.B., W.R. Woodall, and F.F. Sherberger. 1970. Breakdown of leaves by feeding of *Peltoperla maria* nymphs (Plecoptera:Peltoperlidae). *Ann. ent. Soc. Amer.* 63: 562-567.

Willoughby, L.G. 1971. Observations on some aquatic Actinomycetes of streams and rivers. *Freshwat. Biol.* 1: 23-27.

CONCLUSIONS

The extensive areas of allochthonous organic material in West Creek are able to support the immature stages (detritivors) of 3 Pycnopsyche species because the generally slow rate of decomposition ensures abundant supplies of food, case-building materials and habitat-space, at least until the spring thaw.

Pycnopsyche scabripennis differs from P. gentilis in its life cycle and rate of growth. As it is always the largest species, it probably exploits different resources and is therefore less likely to conflict with the smaller species. P. gentilis and P. luculenta have contemporaneous larval periods and are also similar in size.

The habitats of P. gentilis and P. luculenta overlap to the extent that 10% of the P. gentilis population share detritus areas with approximately equal numbers of P. luculenta, and 50% of the P. luculenta population enter leafy areas occupied mainly by P. gentilis. But P. luculenta seems to select only leafy areas within a certain critical distance of detritus and therefore does not extend over the entire habitat of P. gentilis. Within these habitats the 2 species may select different foods as P. luculenta in the laboratory fed preferentially on twigs, whereas P. gentilis ignored twigs and usually ingested more leafy material than P. luculenta. However, both species, when feeding on leaves, appear to select leaves that decay rapidly, especially leaves bearing fungi.

A further difference in the use of allochthonous materials lies in specific case-building materials. P. gentilis uses only leaf discs (usually beech) until the 5th instar when the case is changed to a sand-grain cylinder. P. luculenta usually uses bark and small sticks, but can make a leaf-disc case if twigs are not available.

P. gentilis can therefore be considered as having a narrow niche space in terms of habitat, food, and case materials, but in the area of West Creek that was under study, this species had a larger population because of greater amounts of the preferred resources. The population size of P. luculenta appeared to be limited by the amount of detritus available, although this species had a wider niche space than P. gentilis.

As long as sufficient leaves and leafy detritus remain in West Creek, the niche spaces of P. scabripennis, P. gentilis and P. luculenta are sufficiently different to allow the 3 species to coexist. But the fundamental niche spaces are considerably altered by catastrophic drift which reduces organic substrates to patches of woody detritus. P. scabripennis, by burrowing during aestivation, avoids the unfavourable period following the spring thaw. P. gentilis is forced to inhabit the woody detritus and thus becomes involved in competitive interactions with P. luculenta. Such interactions may be reduced by the subsequent upstream migration of P. gentilis.

Larval adaptations to the different niches available in an environment such as West Creek may have resulted from the aggregation of Pycnopsyche species as they evolved in the primitive woodland stream environment, which was probably a cool stream in the temperate forest biome. As long as the adult stages remained segregated during mating, they probably had little effect on each other. Studies of adult flight at West Creek indicate that specific flight periods of _Pycnopsyche_ males are temporally separated within one night. This behaviour may prevent interspecific copulation or confusion during mating and thus preserve specific identity and contribute further towards the coexistence of 3 related species of caddis fly.