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SOME RELATIONSHIPS BETWEEN SYSTEMATICS AND TROPHIC ECOLOGY IN NEARCTIC AQUATIC INSECTS, WITH SPECIAL REFERENCE TO TRICHOPTERA[1]

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Abstract. Based on the general premise that the genus represents an ecological, as well as a morphological type, a number of generalizations are developed concerning the use of food resources in fresh waters by Trichoptera and some other aquatic orders of the Nearctic fauna.

There are more genera of the Nearctic order Trichoptera (144) than in the orders Ephemeroptera (59), Odonata (84), or Plecoptera (88). Trichoptera have a wide range of habitats and a broader range of trophic categories than any of these other wholly aquatic orders. This relatively high ecological diversity is attributed to the many uses of silk by trichopteran larvae.

Genera of 3 families of filter-feeding Trichoptera show differences in distribution which are correlated with the type of food particle. Most of these genera are found in the eastern deciduous forest biome and all sizes of organic particles are filtered. In the western montane forest biome, generalist filter feeders are absent or underrepresented; predacious genera or those filtering very fine particles have been more successful. Possibly there are differences in the quality and quantity of fine particulate detritus between eastern and western forests which account for the above distributions.

In the trichopteran family Limnephilidae, genera of detritivorous shredders have exploited lotic, lentic, and even terrestrial habitats; grazer genera are mostly confined to cool lotic habitats. Grazers in other families of Trichoptera are also more diverse in upstream areas, and grazer genera are particularly well-represented in the western montane forest biome.

In streams of the eastern deciduous forest biome, the relative proportions of feeding categories shown by trichopteran genera appear to agree with a general trophic model of benthic invertebrate communities in that dominance of shredder–collector genera in upstream sections gives way to grazer–collector dominance downstream. In western montane streams, trichopteran generic distributions conform to the model downstream, but show relatively more grazers than the model would predict for upstream areas. Periphyton growth, and thus food for grazers, may be more abundant in the western coniferous forest than in the shaded streams of the eastern deciduous forest.

In general, an ecological analysis of Nearctic Trichoptera at the generic level appears to provide a reasonable indication of the energy resources available in aquatic habitats.

Key words: aquatic habitats; biomes; Ephemeroptera; Nearctic; Odonata; organic matter; periphyton; Plecoptera; stream continuum; Trichoptera; trophic categories.

INTRODUCTION

Ecological studies of animal communities in fresh water have frequently resulted in little more than lists of taxa in various habitats. Cummins (1974) pointed out that such "taxonomic inventories" did not lead to an understanding of the structure and function of stream ecosystems and urged a more enquiring approach to aquatic ecology. Cummins' own review (1973) of trophic categories (shredders, collectors, grazers and predators) directed attention to the ecological roles of aquatic insects, and recently a first summary of functional categories for genera of Nearctic aquatic insects has appeared (Merritt and Cummins 1978).

In this paper we use data on Nearctic Ephemeroptera, Odonata, Plecoptera, and Trichoptera as a basis for some ecological generalizations concerning genera and higher taxa. Our analysis is limited to Nearctic genera of these 4 wholly aquatic orders because their general ecology and taxonomy are moderately well known. North America includes a sufficiently large portion of the earth's fresh waters to allow some generalizations to be made about evolutionary patterns; our objective is to improve understanding of the ways in which insects have evolved and dispersed to use the energy resources of fresh waters. We adopt the premise that the genus is an ecological as well as a morphological type. In terms of trophic category and broad habitat requirements, the genus has a particular theme, while congeneric species have subtle variations on this theme. Although there are certainly exceptions to the ecological uniformity of the genus in these orders, it is our view that they do not seriously affect our generalizations.

Numbers of Nearctic genera for the 4 orders discussed are based on the most recent summaries available to us, supplemented by additional information in some cases: Ephemeroptera 59 genera (Edmunds et al. 1976), Odonata 84 (Westfall 1978), Plecoptera 88 (Baumann 1976), and Trichoptera 144 (Wiggins 1977). Habitat data were drawn from these same sources.

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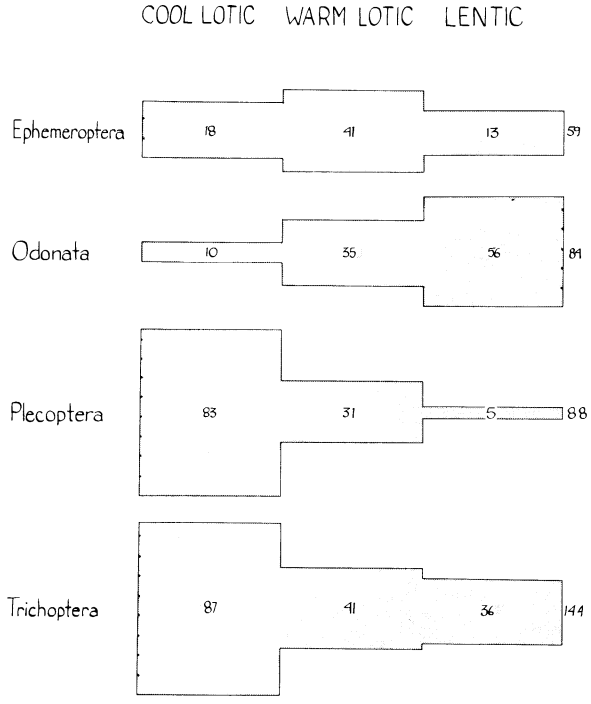

FIG. 1. Habitats of Nearctic genera in 4 orders of aquatic insects. Total number of Nearctic genera per order are shown on the right of the figure. Number of genera per habitat is shown within each block; the sum of these numbers exceeds the number on the right because a few genera are represented in >1 habitat type.

Data for trophic categories of genera are taken mainly from the recent summaries in Merritt and Cummins (1978); where information was not available for a genus, we have assigned it to the general trophic category of closely related genera.

DISCUSSION

Comparison of habitats

The simplest classification of aquatic habitats depends on temperature and current velocity, reflecting the availability of dissolved oxygen. Figure 1 compares the 4 orders on the basis of habitat type for genera. Most Ephemeroptera occur in warm lotic habitats, most Odonata in lentic habitats. Plecoptera have not been able to adapt successfully to still water, presumably because they lack an effective means of generating their own respiratory current—a problem solved by different means in each of the other 3 orders. Although most Trichoptera are restricted to cool lotic waters, the order is well represented in lotic and lentic habitats.

Comparison of feeding habits

Based on Cummins' (1973) classification of trophic categories in aquatic insects, grazers can be defined as animals which nibble and scrape periphyton and fine organic materials on rocks and vegetation; collectors are filter feeders and gatherers of suspended or loosely deposited fine organic particles; shredders feed on decomposing vascular plant tissue, filamentous algae or living vascular plants; and predators are carnivores whose main food items are animal prey, although this category does not include omnivores feeding mainly as shredders or collectors.

All Odonata are predators; in many lentic sites they are the dominant carnivores, rivalling aquatic Hemiptera and Coleoptera. Figure 2 represents an analysis of trophic categories for Nearctic genera of the other three orders. Ephemeroptera appear to be mostly collectors and grazers; a few genera are predators and even fewer are shredders. Plecoptera are basically shredders or predators but may be opportunistic, shredders ingesting some animal material and predators some plant material (Richardson and Gaufin 1971, Shapas and Hilsenhoff 1976). Also, several species of Plecoptera are grazers or fine particle feeders during

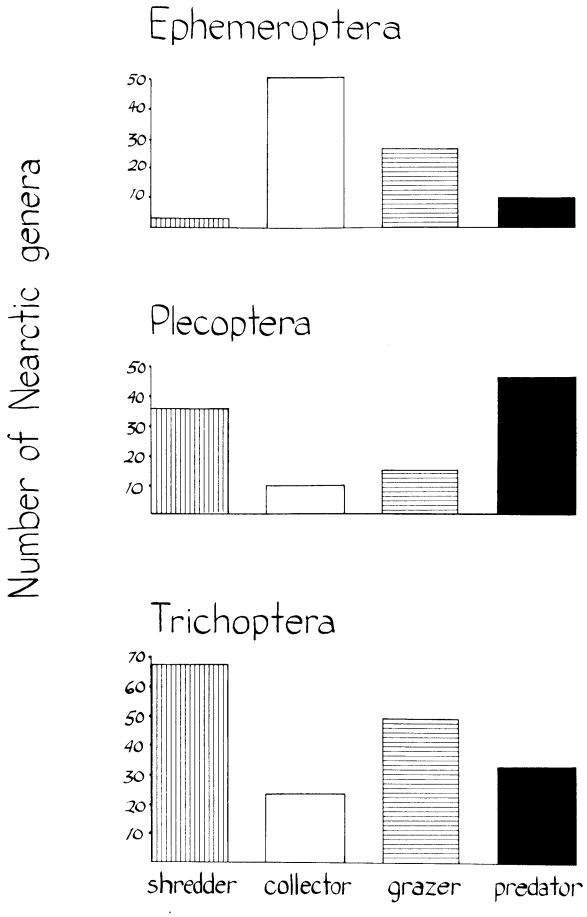

FIG. 2. Trophic categories of Nearctic genera in 3 orders of aquatic insects. Sum of habitat totals exceeds the total number of Nearctic genera in the order because some genera are assigned to >1 trophic category.

their early instars (Richardson and Gaufin 1971, Fuller and Stewart 1977 *in press*), changing their diet when suitable food such as dead leaves or prey organisms become available, or when predator or prey reach a certain size. Few Plecoptera, however, are grazers throughout development. Thus, Plecoptera and Ephemeroptera each appear to be using food resources that are largely unexploited by the other. This relationship suggests that coevolution of Ephemeroptera and Plecoptera in lotic habitats reflects complementary feeding habits, especially as most predacious Ephemeroptera occur in warm lotic habitats where there are few Plecoptera (Fig. 1). Moreover, trophic complementarity between Ephemeroptera and Plecoptera is probably an important yet unappreciated component of community structure in lotic waters.

In contrast to the other 3 orders, Trichoptera are far more diversified (Fig. 2). All methods of feeding are used, and each by a substantial number of genera.

Generic and ecological diversity in aquatic insects

In the Nearctic fauna there are 144 genera of Trichoptera compared with 59 Ephemeroptera, 84 Odonata, and 88 Plecoptera (Fig. 1). If we are correct in equating the genus to an ecological type, ecological diversity in the Trichoptera is much greater than in any of the other 3 orders. This diversity has already been demonstrated in habitat and feeding categories (Figs. 1 and 2). When habitats are examined on a finer scale, for example the various surfaces of a rock in a stream riffle, the Trichoptera are also found to be distributed in more microhabitats than the Ephemeroptera or Plecoptera. For example, larvae of some genera of Trichoptera roam freely all over the rock, some are in fixed retreats on the exposed surface, others in fixed retreats on the underside. Larvae of most genera of Trichoptera make portable cases: some fix the case temporarily on exposed surfaces while filtering particles from the current; some move over the exposed surface while grazing on diatoms; some are found only in attached filamentous algae; some are only in the underlying gravel; and some are in deadwater areas behind the rock. Most lithophilous Ephemeroptera and Plecoptera are more mobile, less likely to be found on one particular part of a rock, and hence have fewer morphological or trophic specializations which might confine them to particular microhabitats.

We believe that a fundamental, and perhaps dominant, factor underlying the evolution of trichopteran ecological diversity was the silk produced by larvae. There are 5 general trophic strategies in which silk is used:

1. To construct nets of different mesh sizes for filtering fine particulate organic matter (FPOM) from the water and to build a fixed retreat (Hydropsychoidea: Philopotamidae, Hydropsychidae, and some Polycentropodidae);
2. To build fixed tubular retreats from which larvae graze adjacent surfaces (Psychomyiidae, some Hydroptilidae) or capture moving prey (some Polycentropodidae);
3. To build portable cases for shelter while moving over rock surfaces seeking periphyton or epilithic FPOM (Glossosomatidae, Helicopsychidae, some Limnephilidae, some Hydroptilidae);
4. To use the tubular case or retreat to maintain a ventilatory current; resulting respiratory independence from stream current allows larvae to exploit lentic habitats, feeding on coarse particulate organic material (CPOM) (most Limnephiloidea) or other organisms (some Polycentropodidae);
5. To provide an anchor line for free-living predators, (Rhyacophilidae, Ross 1964*a*), enabling them to roam freely over all surfaces of a rock with added resistance to strong currents.

In evolutionary terms, silk production is therefore a major factor increasing diversity of Trichoptera; in comparison with other wholly aquatic insect orders, silk has led to finer partitioning of the same habitat and trophic resources by Trichoptera. Our conclusion concerning fine partitioning has two important corollaries:

a) Finer partitioning of resources by Trichoptera has important applications for applied ecology. If each genus is finely adapted to particular environments, and the various species have even more specialized requirements, then Trichoptera have strong potential as indices of environmental perturbations.

b) Finer partitioning of resources by Trichoptera could increase the probability for survival of more of the transitional types that have lead to apomorph groups, e.g., those discussed by Ross (1964*a,b*) and Wiggins (1962, 1973*b,c*, 1976). Hence on theoretical grounds the Trichoptera ought to be especially appropriate for phylogenetic reconstruction, as has been done extensively by Ross (1956, 1967, etc.).

Aquatic Diptera have not been treated above because larvae of many families respire atmospheric oxygen in contrast to the apneustic aquatic orders considered here. Considering only the Chironomidae which do have apneustic aquatic larvae, the number of Nearctic genera is approximately equal to the Trichoptera (Coffman 1978). Our view that silk is ecologically advantageous is borne out by the fact that most chironomid subfamilies except Tanypodinae use silk to construct a shelter or dwelling tube, and ecological diversity in Nearctic Chironomidae will probably prove to be greater than in any other aquatic insect group.

Diversity in Trichoptera and Chironomidae may be

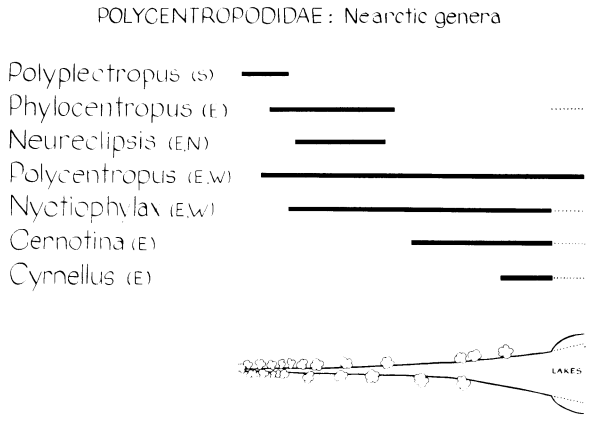

FIG. 3. Distribution of Nearctic genera of Polycentropodidae along the stream continuum. Schematic representation of the continuum modified from Cummins (1975) to include lentic habitats and rocky lakeshores (dotted lines); broad regional distribution in North America indicated by E (east), W (west), N (north), S (south).

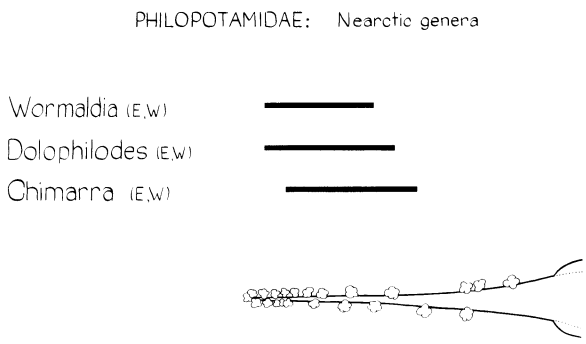

FIG. 4. Distribution of Nearctic genera of Philopotamidae along the stream continuum. (Schematic diagram and regional abbreviations as in Fig. 3.)

augmented by complete metamorphosis which appears to give ecological advantages to most endopterygote insects. Because hazards of pupation are substantially reduced by shelters made from silk, silk production seems almost a prerequisite for success of holometabolous apneustic aquatic insects.

Distribution of Trichoptera

Relationships between Trichoptera and resources of broad geographic areas were first discussed by Ross (1963) who correlated the distribution of certain stream-living genera and species-groups with conditions imposed by different terrestrial biomes. We have extended Ross' analysis by considering how various resources might have favored the evolution and dispersal of genera in different trophic categories. Our hypothesis is that abundant supplies of a particular resource (such as CPOM) have supported increased diversification of the functional group (such as shredders) using and partitioning that resource. This diversification is indicated by an increased number of genera, assuming the genus represents an ecological type.

The stream ecosystem has been modelled as a continuum of changing habitats and food resources rather than a series of zones (Cummins 1975). Contributions of allochthonous organic material and autochthonous plant growth change as a stream becomes wider and the influence of bankside vegetation is reduced. In the upper, tree-shaded reaches, the major energy source is CPOM from riparian vegetation; resources for shredders are predicted to be higher than those for grazers. Farther downstream as the relative shading effect of trees diminishes, autochthonous periphyton and vascular plants increase, thus providing more food for grazers, while allochthonous CPOM decreases proportionally. In all areas FPOM is produced when CPOM is broken down by physical, chemical and biological processes. The larger the stream or river, the more dependent it is on FPOM imported from upstream areas; and in very large rivers, which are often turbid and hence have poor light penetration, FPOM is usually the major food resource.

The distribution of Nearctic genera of Trichoptera along the stream continuum or across North America depends principally on habitat type and food. Warm rivers and lentic habitats occur across the continent; filamentous algae and animal food for predators are similarly widespread. Small cool streams and certain types of plant detritus or periphyton are more local. From this distribution of resources it follows that predators and larvae of warm lotic and lentic habitats will become more widespread than grazers or detritivores with specialized food and larvae of cool lotic habitats, assuming that dispersal is not markedly limited by other factors.

We shall examine the ecology of some Trichoptera in more detail by referring to resource partitioning along the stream continuum in different areas of North America. To illustrate the full range of trichopteran habitats, we have extended the Cummins (1975) model to include lentic habitats (Figs. 3–6). For the sake of brevity we shall refer to the western montane forest biome as the West, and to the eastern deciduous forest biome as the East.

Partitioning of FPOM resources by filter feeders

Several families of Trichoptera spin silken nets which filter particles of a certain diameter depending on mesh shape and size.

Polycentropodidae.—Most Nearctic genera of this family (Fig. 3) feed by filtering FPOM from the current; a few are largely if not entirely predacious. The family is widespread and abundant throughout eastern, central, and northern sections of the continent,

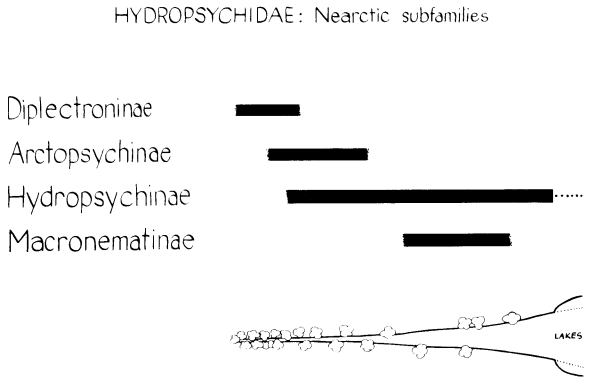

FIG. 5. Distribution of Nearctic subfamilies of Hydropsychidae along the stream continuum. (Schematic diagram as in Fig. 3.)

but sparse in the West. The 2 genera which are established in the West, *Polycentropus* and *Nyctiophylax*, are mainly predacious, and by their ability to exploit most of the stream continuum (Fig. 3), are clearly the ecological generalists of the Nearctic Polycentropodidae. Therefore, in this family there are indications that genera largely dependent on FPOM resources are not as readily accommodated in the West as they are in other parts of the continent.

Philopotamidae.—In this family there is little difference in the habitats of the 3 Nearctic genera (Fig. 4). All 3 are well represented in eastern and western areas of North America, and in fact species richness is greater for the family in the West.

Wallace and Malas (1976) have shown that the nets of philopotamid larvae have the finest meshes of all filter feeders and collect the finest particles. The rather even distribution of philopotamid genera suggests that this very fine particle resource is not limited in the West.

Hydropsychidae.—Figure 5 shows that 3 of the 4 subfamilies of the filter-feeding family Hydropsychidae have rather restricted distributions in the stream continuum. The success of the Macronematinae in large rivers is clearly related to the fine mesh of their nets which can filter the tiny particles in suspension (Sattler 1963*b*, Wallace 1975*b*). In contrast, the coarse meshes of the Arctopsychinae are suitable for animal prey and some CPOM in rapid mountain streams (Wallace 1975*a*). The Diplectroninae are confined to headwater streams; *Diplectrona felix* in Europe is unable to tolerate high temperatures, and grows less efficiently at temperatures >10°C (Edington and Hildrew 1973). Although feeding habits of this subfamily have not been studied, nets spun by *Diplectrona* in Europe are similar to those of the Hydropsychinae (Sattler 1963*a*). The Hydropsychinae are clearly the generalists of the family, occupying almost the entire spectrum of moving water habitats, even to lake margins, and spinning nets with meshes intermediate in size between the Arctopsychinae and Macronematinae. Hydropsychinae are also more generalized feeders since they are known to graze periphyton and to eat other insects as well as the particles caught in their nets. *Hydropsyche* and *Cheumatopsyche*, by far the dominant genera of Nearctic Hydropsychinae in number of species, are represented by ≈3 times as many species in the eastern, northern and central regions of North America as in the West.

Summary of filter feeding.—When the generic distributions of these 3 families of filter-feeding Trichoptera in North America are compared, regional uniformity for the Philopotamidae through eastern and western parts of the continent suggests that streams in the West differ little from streams in other areas in supplies of very fine organic particles. But in the Polycentropodidae, genera with larvae feeding on coarser FPOM are few in the West although widespread and abundant in most other parts of the continent. This suggests that FPOM in western montane forest streams differs in some way from FPOM in streams in other parts of the continent. The possibility of such differences in the FPOM resources of western montane streams is also inferred from distributional patterns in the Hydropsychidae, for the dominant genera of Hydropsychinae have fewer species and are far less abundant in the West than in the East. This regional discrepancy suggests that the FPOM resources on which the Hydropsychinae depend are not sufficient in Western streams to support the degree of partitioning and larval densities that are found in Eastern streams. Therefore, we suggest that FPOM resources in the West are quantitatively or qualitatively different from those in the East.

The FPOM used by Polycentropodidae and Hydropsychidae is probably derived from the feeding actions and feces of shredders (Hynes 1970, Cummins 1974). As will be shown below, trichopteran shredders seem to be fewer in proportion to other feeding categories in the West than in the East. Furthermore, the retention time of organic matter in the ecosystem by "spiralling" through the various detritivores (Wallace et al. 1977) may be shorter in Western streams because autumn freshets and generally steeper gradients tend to flush CPOM out of the system (Anderson and Lehmkuhl 1968). Thus, there could be less processing of the organic matter and less production of FPOM. It is also possible that the rather different physical structure of CPOM in western streams, which includes more wood and coniferous needles than deciduous forest leaves (Sedell et al. 1975, N. H. Anderson *personal communication*), may not be broken down to the same sort of particle as are softer leaves. We can only speculate on the composition of FPOM as no studies have yet traced the origin of naturally occurring fine particles. The very fine particles trapped by Philopotamidae may be produced by precipitation and flocculation

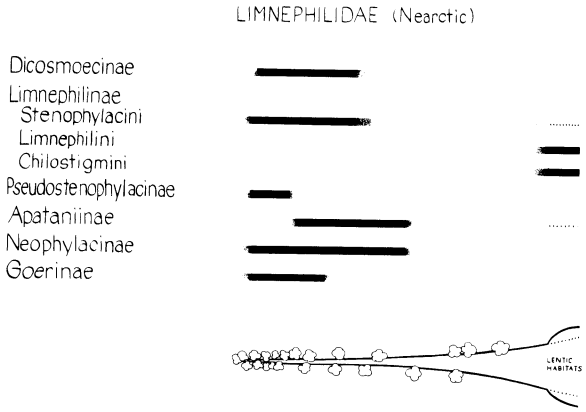

FIG. 6. Distribution of Nearctic subfamilies and tribes of Limnephilidae along the stream continuum. Stippled bars represent few genera, dark bars majority of genera. (Schematic diagram as in Fig. 3.)

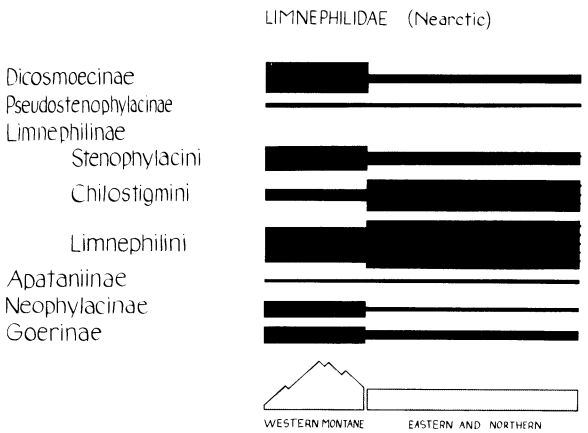

FIG. 7. Numbers of Nearctic genera of Limnephilidae occurring in western montane and eastern/northern regions of North America.

of dissolved organic matter (Lush and Hynes 1973) rather than by CPOM fragmentation.

Partitioning of food resources by Limnephilidae

More than one-third of the Nearctic genera of Trichoptera are members of the family Limnephilidae. The ecological implications of this fact are important, for no fewer than 18 families of Trichoptera are represented in North America. Much of the generic and hence ecological diversity of the Trichoptera as a whole must be due to successful partitioning of resources within this single family.

Feeding methods divide the limnephilid genera into two groups. One, comprising the subfamilies Dicosmoecinae, Apataniinae, Neophylacinae, and Goerinae, are mostly grazers or scrapers feeding on periphyton and fine organic particles on rock surfaces. The Dicosmoecinae have toothed mandibles; a few genera are shredders feeding on CPOM such as leaves, but the rest evidently function as scrapers. Most genera in the other 3 subfamilies have lost the mandibular teeth and have bladelike mandibles obviously well adapted for scraping. The second group, comprising the 2 remaining subfamilies, Limnephilinae and Pseudostenophylacinae, are shredders and have toothed mandibles. Therefore, partitioning of food is one major factor accounting for the large size of this family.

Scrapers (Fig. 6) occur only in running water habitats except for the dicosmoecine genus *Ironoquia* which occurs in temporary pools and streams. Other grazing Trichoptera such as the Glossosomatidae and Helicopsychidae are also confined to smaller streams and rivers or wave-washed shores. It appears that grazing imposes certain restrictions in terms of habitat requirements because grazers have had little success in lentic habitats.

By contrast, the detritivorous shredders have shown considerable diversification in both lotic and lentic habitats (Fig. 6). Pseudostenophylacinae are found mainly in cool streams. The Limnephilinae are represented in all lotic and lentic waters including spring seepage areas and even damp terrestrial habitats (Fig. 6). Within the Limnephilinae, the tribes Limnephilini and Chilostigmini, which have many genera in lentic habitats, account for a large proportion of the total genera in the family. Thus, feeding by shredding detritus appears to provide more potential for the exploitation of lentic habitats than does grazing periphyton. Another reason for the success of the Limnephilini in warm water might be their adaptation for transient waters through a combination of diapause and drought-resistant egg matrices (Wiggins 1973*a*).

Grazing Limnephilidae are represented by more genera in the West than in the rest of North America (Fig. 7). Another family of lotic grazers, the Glossosomatidae, has more species in the West than elsewhere. This uneven distribution of grazers suggests that their food resources also are uneven—a point we raised above when discussing filter feeders. The higher number of western grazers may mean that periphyton is capable of supporting a higher degree of partitioning in the West than in the East. We have no data on relative periphyton production, but richer growths seem possible, at least in summer, in streams bordered by the Western coniferous forest because coniferous trees overhang and shade less stream-bottom than deciduous trees.

Longitudinal changes in food resources of streams

Cummins' (1975) model of the stream continuum predicts that predators form a small and relatively constant part of the macro-invertebrate fauna in all zones of the stream ecosystem, but that changing proportions of collectors, shredders, and grazers reflect the changing availability of plant-derived energy sources. In upstream benthic communities shredders and col-

TABLE 1. Trophic categories of trichopteran genera in streams of 2 North American biomes

A. Eastern Deciduous Forest Biome
(including Great Lakes–St. Lawrence transitional forest)

Cool lotic

shredders	collectors	grazers	predators
Adicrophleps	*Aphropsyche*	*Agapetus*	*Oligostomis*
Agarodes	*Arctopsyche*	*Apatania*	*Polycentropus*
Anisocentropus	*Cheumatopsyche*	*Cheumatopsyche*	*Ptilostomis*
Beraea	*Chimarra*	*Glossosoma*	*Pseudogoera*
Chyranda	*Diplectrona*	*Goera*	*Rhyacophila*
Fattigia	*Dolophilodes*	*Goerita*	$N = 5$
Frenesia	*Hydropsyche*	*Hesperophylax*	
Heteroplectron	*Oropsyche*	*Hydropsyche*	
Hydatophylax	*Parapsyche*	*Lype*	
Hydroptila	*Phylocentropus*	*Matrioptila*	
Lepidostoma	*Wormaldia*	*Micrasema*	
Micrasema	*Xiphocentron*	*Neophylax*	
Oligostomis	$N = 12$	*Ochrotrichia*	
Onocosmoecus		*Onocosmoecus*	
Palaeagapetus		*Psychomyia*	
Pseudostenophylax		$N = 15$	
Psilotreta			
Psychoglypha			
Pycnopsyche			
Stactobiella			
Theliopsyche			
$N = 21$			

Warm lotic

Agarodes	*Brachycentrus*	*Brachycentrus*	*Nyctiophylax*
Dibusa	*Cheumatopsyche*	*Ceraclea*	*Oecetis*
Hydroptila	*Chimarra*	*Cheumatopsyche*	*Polycentropus*
Ironoquia	*Cyrnellus*	*Culoptila*	*Ptilostomis*
Lepidostoma	*Hydropsyche*	*Helicopsyche*	*Setodes*
Nectopsyche	*Macronema*	*Hydropsyche*	$N = 5$
Pycnopsyche	*Neureclipsis*	*Ithytrichia*	
Setodes	*Potamyia*	*Leucotrichia*	
Triaenodes	$N = 8$	*Mayatrichia*	
$N = 9$		*Neophylax*	
		Neotrichia	
		Ochrotrichia	
		Protoptila	
		$N = 13$	

B. Western Montane Forest Biome

Cool lotic

shredders	collectors	grazers	predators
Amphicosmoecus	*Arctopsyche*	*Agapetus*	*Atopsyche*
Chyranda	*Cheumatopsyche*	*Allocosmoecus*	*Himalopsyche*
Clostoeca	*Chimarra*	*Amiocentrus*	*Polycentropus*
Desmona	*Diplectrona*	*Anagapetus*	*Polyplectropus*
Eobrachycentrus	*Dolophilodes*	*Apatania*	*Rhyacophila*
Goereilla	*Homoplectra*	*Cheumatopsyche*	*Yphria*
Heteroplectron	*Hydropsyche*	*Cryptochia*	$N = 6$
Homophylax	*Parapsyche*	*Dicosmoecus*	
Hydatophylax	*Wormaldia*	*Ecclisocosmoecus*	
Hydroptila	$N = 9$	*Ecclisomyia*	
Lepania		*Farula*	
Lepidostoma		*Glossosoma*	
Micrasema		*Goera*	
Mosleyana		*Goeracea*	
Namamyia		*Hesperophylax*	
Nerophilus		*Hydropsyche*	
Onocosmoecus		*Imania*	
Palaeagapetus		*Manophylax*	
Parthina		*Micrasema*	
Philocasca		*Neophylax*	
Phylloicus		*Neothremma*	
Psychoglypha		*Ochrotrichia*	

TABLE 1. Continued

B. Western Montane Forest Biome

shredders	collectors	grazers	predators
Psychoronia *Rossiana* *Stactobiella* $N = 25$		*Oligophlebodes* *Pedomoecus* *Psychomyia* *Tinodes* $N = 26$	
		Warm lotic	
Gumaga *Hydroptila* *Lepidostoma* *Nectopsyche* *Pseudostenophylax* *Triaenodes* $N = 6$	*Brachycentrus* *Cheumatopsyche* *Chimarra* *Hydropsyche* *Oligoplectrum* *Smicridea* $N = 6$	*Alisotrichia* *Brachycentrus* *Ceraclea* *Cheumatopsyche* *Culoptila* *Helicopsyche* *Hydropsyche* *Leucotrichia* *Neotrichia* *Ochrotrichia* *Oligoplectrum* *Protoptila* *Zumatrichia* $N = 13$	*Marilia* *Nyctiophylax* *Oecetis* *Polycentropus* $N = 4$

lectors are the major consumers, whereas grazers and collectors become more important as streams widen; farther downstream in very large rivers, the benthos consists mainly of collectors. Proportions of the several trophic categories in the benthos of any one part of the stream continuum reflect the components of the food supply in that area.

Nearctic Trichoptera occur in all parts of the stream continuum with many genera in each trophic category (Figs. 1 and 2). We have suggested above that the number of genera per trophic category reflects the richness of the corresponding food resource. Therefore, genera of Nearctic Trichoptera provide an appropriate set of data with which to test the downstream change in resource exploitation predicted by the Cummins model.

Table 1 lists lotic genera of Nearctic Trichoptera by trophic category for the eastern deciduous forest biome (including the ecotone or transitional forest of the Great Lakes–St. Lawrence area) and for the western montane forest biome; in general, genera listed as cool lotic are characteristic of cool, headwater areas, and warm lotic genera of warmer, wider rivers. The proportions of genera in each category are shown in the appropriate sectors of the circle graphs in Figure 8.

In the East, our results (Table 2) show that shredder genera predominate in upstream habitats in relation both to grazers (3:2) and collectors (2:1), but that in downstream sections the proportion of shredder genera becomes markedly smaller in relation to grazers (2:3) and to collectors (1:1). These changes are consistent with the prediction of the Cummins model. Since our generic analysis agrees well with the model

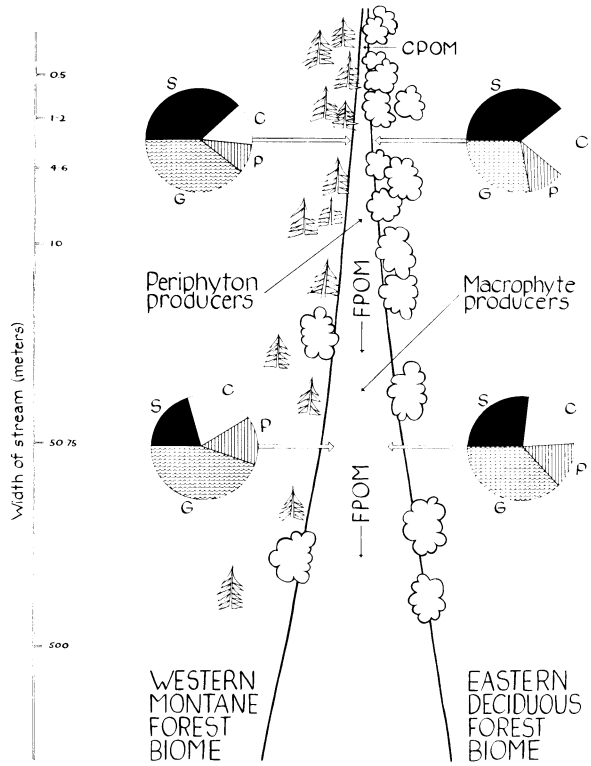

FIG. 8. Trophic categories of stream-living Nearctic Trichoptera in the western montane forest biome and the eastern deciduous forest biome (including the ecotonal Great Lakes–St. Lawrence forest). Circle graphs are based on the number of trichopteran genera in each category: S = shredder, C = collector, P = predator, G = grazer. (Modified from Cummins [1975].)

TABLE 2. Proportional relationships between trophic categories of trichopteran genera in streams of 2 North American biomes; actual numbers of genera in parentheses

	Trophic categories	Western Montane Forest Biome	Eastern Deciduous Forest Biome
Upstream sections	shredders:grazers	≈1:1 (25:26)	≈3:2 (21:15)
	shredders:collectors	≈3:1 (25:9)	≈2:1 (21:12)
Downstream sections	shredders:grazers	≈1:2 (6:13)	≈2:3 (9:13)
	shredders:collectors	≈1:1 (6:6)	≈1:1 (9:8)

which was based on data drawn chiefly from the East (Cummins 1974, 1975), we conclude that the distribution of trichopteran genera does indeed reflect resources available in the stream continuum.

Results for the West (Table 2) show that the upstream dominance of shredders over collectors (3:1) is reduced downstream (1:1) as in the East. But an anomaly arises in the ratio of shredders to grazers in upstream sections because their 1:1 relationship suggests that resources for grazers are proportionally much greater in the West than in the East. This same general conclusion was reached above in our consideration of Nearctic distributional patterns of the Limnephilidae and Glossosomatidae.

The differences are probably caused by the forest vegetation of the two areas. In the western mountains, coniferous forests predominate; streams receive more light in summer and probably support more diatoms than streams in deciduous forests. Conifer leaves (needles) fall regularly through the year and differ in texture from autumn-shed deciduous leaves. These differences in food resources coupled with other factors (e.g., temperature, substrate) related to high altitudes contribute to the development of a characteristic montane fauna. Similar observations were made on invertebrates in an English mountain stream by Minshall and Kuehne (1969) who attributed upstream faunal anomalies to differences in the type and nutritive quality of detritus.

We therefore suggest that the generally accepted model of a stream ecosystem based on theories of structure and function developed by Hynes (1970) and Cummins (1975) is too narrowly defined in that it is largely dependent on a deciduous forest in upstream areas. Headwater sections of streams in the western montane areas of North America depart somewhat from the existing model; and we suspect that streams in other parts of the world also may not fit this model, depending on the characteristics of the watershed, the vegetation in particular. These views are foreshadowed in a general way by Hynes (1975) with his concept of the stream and its valley.

CONCLUSIONS

We have shown that Trichoptera comprise more genera and have exploited a broader range of habitats and food materials than any of the other 3 wholly aquatic insect orders in North America. Clearly, Trichoptera have had great evolutionary potential and ecological success. They have adapted to cool and warm, fast and slow, seepage and temporary waters; even terrestrial habitats have been invaded. Trichoptera use all feeding methods commonly found in benthic invertebrates. The most widespread Trichoptera are usually those whose food and preferred habitat are also widely available; e.g., the continent-wide predacious Polycentropodidae which can tolerate warm water with little or no flow, and the detritus-eating Limnephilinae which are represented in every type of lentic habitat in North America. Similar general statements could be made about certain Leptoceridae (omnivorous in mainly lentic habitats) and Hydroptilidae (feeding on widespread filamentous algae in warm lotic or lentic habitats).

We have proposed the hypothesis that differences in food resources in the western montane forest biome of North America, especially reduced supplies of CPOM and all but the finest particles of organic matter, limited the radiation of certain genera of Trichoptera. We have shown that filter-feeding Polycentropodidae and Hydropsychinae are underrepresented in the West; since the Hydropsychinae have been particularly successful elsewhere in terms of numbers of species, their relatively poor showing in the West seems unlikely to be due to weak adaptive potential. On the other hand, grazers appear to be relatively more successful in the western montane region.

Our thesis obviously depends on how well the genera of Trichoptera mirror the resources available; and although there is much information on Trichoptera, ecological data at the generic level are inevitably based on those species whose larvae are known. However, in spite of such limitations we offer these general ideas with the intention of stimulating a constructive exchange of ideas between ecologists and systematists studying aquatic insects.

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