GUT CONTENT ANALYSIS OF AQUATIC INSECTS FROM WOOD SUBSTRATES[1]

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ABSTRACT

The contents of the guts from 108 taxa of aquatic and semi-aquatic insects collected on or within woody debris in streams were examined for the primary dietary components. Contents were identified as fungi, diatoms, animal material, and detritus including wood. Leaf materials and filamentous algae were noted. The results were used in part to indicate the types of utilization of the wood habitat, and in particular to identify those taxa that may contribute by their feeding habits to particle-size reduction of wood. At least 45 taxa of detritivores contained significant amounts of wood. Many of the surface associates were scrapers that fed on periphyton and aufwuchs.

INTRODUCTION

Wood debris is the most refractory type of organic material in streams. Because of its large size and long-term residency, it can have a major impact on channel morphology and in creating habitat for the aquatic biota (Keller and Swanson, 1979; Anderson and Sedell, 1979). However, because of its refractory nature and because few invertebrates possess the appropriate enzymes to digest lignin or cellulose (Monk, 1976), the direct exploitation of stream wood as a food source would seem to be minimal. Though a considerable fauna has been shown to be associated with wood (Dudley and Anderson, 1982), it remains to be documented how many of these are actually ingesting wood and the associated microbes. Thus, the objective of this study was to complement their survey results by examination of gut contents of insects from wood substrates and in this way to assess the relative importance of the xylophilous taxa in the degradation of wood debris in streams.

Dudley and Anderson (1982) emphasized the importance of texture as a factor in utilization of wood by the fauna. This is largely related to the decay class, or degree of microbial conditioning of the substrate. Fungi are the major decomposer group able to penetrate into wood and to cause significant decay. They may invade the wood prior to its entry into the water or inoculate it after submergence. Through fungal conditioning, wood is both mechanically softened and nutritionally enhanced (Anderson *et al.*, 1978; Triska and Cromack, 1980).

Cummins (1973) pointed out that even those animals that select micro-habitat on a non-food basis will automatically be exposed to a narrow range of nutritive materials. For this investigation the range of materials available for ingestion was divided into 5 categories: (1) fungal mycelia and spores; (2) diatoms, plus filamentous algae; (3) animal material; (4) detritus; and (5) wood (as a component of detritus).

METHODS

Invertebrates collected from the field survey of wood debris were preserved in 70% ethyl alcohol. Specimens were dissected and the contents of the foregut were mounted on slides in Hoyer's medium. The preparations were examined under a compound microscope at a magnification of 450X. An estimate of the frequencies of the various food types was obtained by examination of the entire food bolus. This enabled us to classify ingested materials into abundance categories although it does not provide quantitative comparisons. Specimens with nearly empty guts were excluded from the results.

The major difference between this study and most other studies of gut contents (e.g. Muttkowski and Smith, 1929; Coffman *et al.*, 1971; Fuller and Stewart, 1977; Gilpin and Brusven, 1970; Malas and Wallace, 1977) is in a further breakdown of the "detritus" category. We were particularly looking for woody material and associated fungi as components of the ingested material. The latter were recognized as spores or, as mycelia, by the brown color of the thickened cell wall and by the clamp connections. Wood particles were identified by the presence of lignified fibrous tissue, spiral thickenings, pits and entire or portions of tracheids. Where leaf material was recognized, it is identified as (L) in the detritus column. However, most of the detritus was amorphous and could have originated from fine particulates, leaves, or wood.

Wood consumption in Table 1 is meant as a comparison between taxa. It is listed separately because its relative abundance is difficult to compare with the other categories. Identifiable fragments were large in comparison with most other items and sporadic in occurrence. Also, some of the amorphous detritus is likely of wood origin. All xylophages are listed as ingesting a major component of detritus but detritivores are not always wood consumers.

The restricted scope of the gut content study should be emphasized. Basically, we were surveying a large number of taxa to determine whether they were ingesting wood and the associated microbes. Thus, we examined relatively few individuals in many taxa, opting instead to include as diverse a series as possible. It should also be noted that the resources available for insect feeding depend on the season of collection. Because of the small numbers of specimens examined, some seasonal bias may be reflected in the results. Except for Diptera, emphasis was on the surface-associated taxa, as opposed to the tunnelling or boring species, because the latter would be expected to ingest wood as a natural part of their behavior.

RESULTS

EPHEMEROPTERA

The data for gut contents are summarized from an intensive study in which monthly collections of wood-associated mayflies were examined (Pereira, 1980; Pereira and Anderson, 1982). Of the 10 genera listed in Table 1, all except *Heptagenia* and some of the Ephemerellidae were from the study site at Berry Creek, near Corvallis, Oregon. The number of specimens examined was roughly proportional to prevalence of a taxon on wood compared with other substrates. Thus, *Cinygma integrum* Eaton was the most thoroughly studied as 76% of the larvae were collected from wood. *Baetis* spp. was the numerically dominant genus on wood but it was equally abundant on other substrates and showed no preference for the wood debris.

All of the genera ingested some wood, though only a trace was recorded from *Rhithrogena. Cinygma integrum, Ironodes nitidus* (Eaton) and *Paraleptophlebia* spp. are listed in Table 1 as ingesting abundant amounts of wood. Only *C. integrum* is closely associated with wood debris; *I. nitidus* and *Paraleptophlebia* are common on other substrates as well. However, these three genera are potentially important in effecting particle-size reduction when their population density is high.

Most of the mayflies examined are classified as scrapers or collector-gatherers by Merritt and Cummins (1978). On a wood surface they scrape the aufwuchs film ingesting the fine particles entrained therein. Fine-particulate detritus was abundant in guts of all taxa, though somewhat less so in *Baetis* and *Cinygma* than in the others. As *Baetis* larvae are especially vagile, the gut contents likely include material ingested from the benthos even though all the specimens examined were from wood.

C. integrum and *I. nitidus* were mostly collected from firm wood. The fungal hyphae in their guts tended to be loosely associated with the wood fibers. That is, it appeared as a mat on the surface of wood particles, indicating that the scraping action of the labial palps removed the soft outer layer of wood along with the mycelia. *Paraleptophlebia* larvae occurred in backwater areas often on, or in, quite rotten wood. Although the gut contents were mostly fine particles, their collector-gathering type of feeding also resulted in removal of some soft woody detritus.

The genus *Ephemerella* merits subdivision into several subgenera. Hawkins (1982) indicates that several species are differentiated both by habitat and feeding habits. A portion of our data is based on some of his collections from wood. *E. (Drunella)* is largely predaceous, especially in its later stages, but still ingests some wood in its capacity as a scraper. *E. (Caudatella)* and *E. (Serratella)* may be diatom specialists, while *E. (Ephemerella)* is basically detritivorous and ingests considerable amounts of wood, the gut contents sometimes being over 50% wood material. None is a wood specialist, however, as all feed on other materials in different microhabitats.

PLECOPTERA

Traces of wood were found in representatives of all families of stoneflies examined, but only in peltoperlids, some nemourids and pteronarcids was wood classed as abundant. These families are basically detritivores that scrape or shred the surface layers of leaf or wood debris. Though the sample size is small, the gut analysis data suggest that pteronarcids are less xylophagous than peltoperlids or the nemourids. Pteronarcid feeding behavior may be more suited to shredding leaf material than to ingesting wood and the associated mycelia.

Trace amounts of wood particles in the predaceous perlids and perlodids may be either from gut contents of their prey or from incidental ingestion of detritus. Significant amounts of detritus in *Skwala* indicate omnivorous feeding by this genus.

TRICHOPTERA

As caddisflies are a diverse component of the wood-associated fauna, we examined gut contents of individuals from 25 genera. At least 16 genera contained more than a trace of wood fragments. As expected, the dominant functional group was shredders, but taxa classified by Wiggins and Mackay (1978) as grazers (scrapers) and predators also ingested some wood. Most of the shredders with wood in the guts were limnephilids (8 genera) but brachycentrids, calamoceratids, lepidostomatids and sericostomatids also included xylophages. Though some taxa listed as grazers by Wiggins and Mackay (1978) may be partially shredders (e.g. *Cryptochia, Ecclisocosmoecus),* other definite scrapers such as *Neophylax* and *Ecclisomyia,* have a role in fragmentation via their feeding activities.

A number of these caddisflies are intimately associated with wood debris in ways other than feeding. For example, wood is used in case construction, as an oviposition and emergence site, and several species bore into soft wood for pupation. However, the major point from the gut analysis studies is the documentation that feeding activities of about two-thirds of the taxa examined would result in fragmentation of wood debris. Larvae in some of these genera attain a large size (e.g. *Hydatophylax, Psychoglypha),* so the impact of individuals in shredding the soft surface wood can be significant simply due to their size.

COLEOPTERA

The elmid beetle, *Lara avara* LeConte has been previously demonstrated to be an obligate xylophage (Anderson *et al.,* 1978). The other elmids examined and the psephenids and hydraenid were primarily scrapers or collectors. The preponderance of diatoms in guts indicates a scraping behavior. Fungi were found in all *Optioservus* larvae and in the one *Heterlimnius* larva examined which suggests some impact on the wood surface by their feeding.

Except for *L. avara,* the beetles listed by Dudley and Anderson (1982) were a minor component of the wood-associated fauna in aquatic habitats with limited effect in the degradation process. Ptilodactylid larvae are listed by Merritt and Cummins (1978) as shredders sometimes associated with wood substrates but none was available for gut analysis.

DIPTERA

The comprehensive study of Teskey (1976) includes 47 families of flies associated with wood and many of these are aquatic or semiaquatic. Gut analysis was done for most of the families included by Dudley and Anderson (1982) in their "closely associated" category.

The families with identifiable wood fragments in the gut were Axymyiidae, Chironomidae, Pachyneuridae, Pelecorhynchidae, Sciaridae and Tipulidae. Most of the listed genera in these families are borers in soft, sodden wood. Taxa with fungi, but no wood fragments, included surface associates *(Dixa, Pericoma)* and burrowers *(Myxosargus, Hexatoma).* Several of the burrowers were at least partially predaceous *(Symmerus, Myxosargus, Hexatoma* and *Pedicia).* Practically all of the flies examined contained a major component of unidentifiable detritus. In the syrphids *Pocota* and *Xylota* this was an amorphous substance with no fibrous material. As syrphids have a specialized cibarial filter (Roberts, 1970) they would be expected to ingest only liquid or fine particles. Consequently, wood or fungus would not be detectable in their guts. Likewise, *Xylophagus* is a predator restricted to wood, but contained no identifiable material because its cone-shaped head capsule is not designed for ingestion of intact prey (Teskey, 1976).

The family Chironomidae is of interest because it contains nearly all the functional feeding groups found in streams within the single family. Analysis of the gut contents of a representative sample of chironomid midges from western Oregon showed resource use patterns similar to those found among the whole community. A relatively small number of the taxa were clearly xylophagous. Their guts contained wood and little else, save for small amounts of organic material from the wood surface. This extraneous material would be acquired through the wood ingestion process, and may provide an important nutritional component to the diet. The xylophagous taxa include *Brillia spp., Stenochironomus,* and two undescribed genera of the subfamily Orthocladiinae. Some species of *Polypedilum* are wood feeders

(D. R. Oliver, pers. comm.), but the specimens that we examined did not contain wood, implying that xylophagy may be a species-level trait.

Another group of midges apparently ingests some wood material in the course of feeding on surface-associated organic material. Such opportunistic detritivory was exhibited by *Eukiefferiella, Paraphaenocladius,* and *Phaenopsectra* which were otherwise fine-particle feeders, and by an undescribed genus near *Paracladius* which contained diatoms. While the impact per individual may be low, the total impact of the community may be significant given the ubiquitous occurrence of some of these generalists.

The majority of the chironomids analyzed could not be implicated with wood mineralization. These groups primarily used wood as a substrate on which to collect aufwuchs, capture prey, or take refuge. Many may not possess mouthparts which could remove wood fibers, and indeed most of the genera are listed by Coffman (1978) as collector-gatherers. Some predatory genera of the subfamily Tanypodinae also had FPOM in the guts. *Procladius* was an algal feeder; diatoms occurred in 5 of 6 guts examined. It is considered to be a collector-gatherer in some seasons (Coffman, 1976).

DISCUSSION

This project supplements the survey by Dudley and Anderson (1982) in documenting wood ingestion by a diverse assortment of aquatic insects associated with wood debris. Though behavior such as case building and boring for pupation are significant nonfood related activities that cause particle-size reduction, we believe that feeding is the main process effecting fragmentation.

The most important insects in the degradation process are probably the borers and gougers rather than the surface associates. However, compared with terrestrial situations, the diversity and density of the subsurface xylophages is low. For example, *Lipsothrix* spp. are the dominant wood boring aquatic tipulids (Dudley, 1982), and *Lara avara* is a common surface gouger but abundance or impact of these species is orders of magnitude less than that of terrestrial xylophages such as termites, carpenter ants, or buprestid and cerambycid beetles. This is in large part due to the fact that aquatic wood borers are limited to the outer portion of wood because of anaerobic conditions within, while terrestrial animals are able to colonize the internal portions as well (Triska and Cromack, 1980).

From terrestrial studies of wood decomposition (e.g. Swift, 1977; Ausmus, 1977), it is apparent that fungi are primarily responsible for the biochemical breakdown of lignin and cellulose, and that exploitation by invertebrates is usually via symbionts in the hindgut (Wigglesworth, 1972). Symbiotic relationships in aquatic xylophages have received little attention and our analysis did not explore this possibility because we examined contents of the foregut where there was the best chance of indentifying wood fragments.

Some inferences on the interrelationships between the invertebrate fauna and the microbial flora emerge from examination of gut contents. Hyphae and spores in the guts of scrapers and collector-gatherers were more loosely associated with wood particles than in the borers or gougers. In the latter the mycelia were found to ramify between the cells of the wood. The scrapers utilized the mat of hyphae in the aufwuchs or organic layer that builds up on stone or wood surfaces (Karlström, 1978), and ingestion of wood particles occurred by scraping this layer plus the wood surface that was loosened by microbial attack. Martin (1978) has suggested that xylophages not only benefit by digestion of fungi but that they may sequester extracellular enzymes from fungi that also make the wood particles digestible.

Quantification of the impact of invertebrate feeding in wood degradation will require controlled feeding experiments, along with field estimates of population density of the xylophilous fauna. This study and the survey by Dudley and Anderson (1982) provide a framework for selecting taxa in various functional groups for further study. The current status of our understanding of wood degradation in aquatic habitats is that it is a slow process influenced by both biotic and abiotic factors. The microbiota account for most of the biochemical degradation while the macrobiota are instrumental in physical breakdown and in dispersal of microbes to fresh sites.

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Table 1. Gut contents of insects collected from wood substrates in streams. ++ = major component; + = present; T = trace; - = absent; (S) = also spores; (F) = also filamentous algae; ? = questionable presence; A = abundant component of detritus; C = common; O = occasional; * = known wood associates.

	No.	Fungi	Diatoms	Detritus	Animal	Wood
EPHEMEROPTERA						
Baetidae						
Baetis	34	+	+	++	-	O
Ephemerellidae						
E. (Caudatella)	4	-	++	+	-	C
E. (Drunella) 4 spp.	21	T	+	+	+	C
E. (Ephemerella)	14	T	+	++	T	A
E. (Serratella)	1	+	++	+	-	O
E. (Timpanoga)	1	-	+	+	-	-
Heptageniidae						
* Cinygma	>100	++	+	++	-	A
Cinygmula	22	+	++(F)	+	-	C
Heptagenia	1	T	+	+	-	O
Iron	10	+	+(F)	++	-	C
* Ironodes	>100	++	+	++	-	A
Rhithrogena	4	T	T(F)	+	-	O
Leptophlebiidae						
Paraleptophlebia	38	+	T	++(L)	-	C
Siphlonuridae						
Ameletus	10	+	+	++	-	O
PLECOPTERA						
Capniidae						
Capnia	5	+	+(F)	++	-	O
Nemouridae						
Malenka	4	+	-	T	-	C
Soyedina	3	-	+	+	-	C
Visoka	6	-	-	++	-	A
Zapada	6	+	-	+	-	A
Peltoperlidae						
* Yoraperla	6	T	-	++	-	A
Perlidae						
Hesperoperla	2	T	-	T	++	O
Calineura	2	-	T	T	++	O
Perlodidae						
Skwala	3	T	-	+	++	O
Pteronarcidae						
Pteronarcella	3	+	-(F)	+	-	C
Pteronarcys	3	+	-	+(L)	-	C
Taeniopterygidae						
Taenionema	3	-	-	++	-	O?
TRICHOPTERA						
Brachycentridae						
Brachycentrus	1	T	++	+	T	-
Micrasema	6	+(S)	+(F)	++	-	C
Calamoceratidae						
* Heteroplectron	7	+	+?	+	-	A
Glossosomatidae						
Glossosoma	4	+(S)	+(F)	++	-	O
Lepidostomatidae						
Lepidostoma 2 spp.	11	+(S)	+	++(L)	-	C
Limnephilidae						
Apatania	4	T	+	+	-	-
Asynarchus	2	T	T	-	-	C
Chyranda	2	+	-	++	T	C
Cryptochia	4	+(S)	+(F)	+(L)	T	O?
Ecclisocosmoecus	1	T	+	+	T	C

Table 1. Continued (pg. 2)

	No.	Fungi	Diatoms	Detritus	Animal	Wood
Ecclisomyia	5	T	+	+(L)	-	A
Glyphopsyche	2	+	+	++	-	A
Hesperophylax	1	-	+	++	-	-
Homophylax	1	T	-	+	-	A
Hydatophylax	4	-	T	+	T	C
Limnephilus	1	+	+	+	-	0
Neophylax	4	+(S)	+(F)	+	-	C
Neothremma	3	+	++	+	T	0
Onocosmoecus	4	T(S)	-	++	+	C
Psychoglypha	5	+	+(F)	+	-	A
Polycentropodidae						
Polycentropus	5	T	T(F)	++	-	0
Psychomyiidae						
Psychomyia	2	-	-	++	-	-
Tinodes	1	+	+(F)	+	+	-
Rhyacophilidae						
Rhyacophila (acropedes gr.)	7	+	T(F)	+	T	C
R. (blarina gr.)	4	-	-	++	-	C
Rhyacophila (3 spp.)	4	T	+	+	+	0
Sericostomatidae						
Gumaga	2	+	+(F)	+	+	0
COLEOPTERA						
Elmidae						
Heterlimnius-larva	2	+	+(F)	+	-	0
Heterlimnius-adult	1	T	+	+	-	-
* Lara-larva	6	+	+	++	-	A
Optioservus-larva	5	+	+	++	-	-
Hydraenidae						
Hydraena-adult	2	T	++	T	-	0

	No.	Fungi	Diatoms	Detritus	Animal	Wood
Psephenidae						
Acneus-larva	4	T	++(F)	++	-	0
Eubrianax-larva	1	-	++	+?	-	-
DIPTERA						
Axymyiidae						
* Axymyia	1	T	-	++	-	A
Chironomidae						
Chironominae						
Paratendipes	3	-	-	++	-	-
Phaenopsectra	4	-	T(S)	++	-	0
* Polypedilum	4	-	-	++	-	-
Rheotanytarsus	7	-	-	++	-	-
* Stenochironomus	2	-	-	++	-	A
Tanytarsus	6	-	-	++	-	-
Orthocladiinae						
* Brillia	7	T	T	++	-	A
Corynoneura	17	T	T	++	-	-
Cricotopus-Orthocladius	10	T	+	+	T	-
Eukiefferiella	22	-	T	++	-	0
Heterotrissocladius	2	-	-	+	-	-
Orthocladius	2	-	+	+	-	-
O. (Euorthocladius)	3	-	++	T	-	-
"Parakiefferiella"	4	-	-	++	-	-
Parametriocnemus	4	-	T	++	-	-
Paraphaenocladius	2	-	-	+	-	0
Rheocricotopus	18	+	T	++	-	-
Synorthocladius	11	-	++	T	-	-
Thienemanniella	4	-	+	+	-	-
* n. gen. nr. O. acutilabis	7	T?	-	++	-	A
n. gen. nr. Paracladius	2	-	+	+	-	C

Table 1. Continued (pg. 3)

	No.	Fungi	Diatoms	Detritus	Animal	Wood
* n. gen. nr. Limnophyes or Tokunagaia	6	T?	-	++	-	A
Tanypodinae						
Larsia	4	-	T	T	+	-
Macropelopia	3	-	T	+	+	-
Procladius	6	-	++	+	T	-
Thienemannimyia	13	-	-	++	+	-
Zavrelia	2	-	-	+	+	-
Dixidae						
Dixa	1	+	+(F)	+	-	-
Dolichopodidae	1	T	-	T?	+	-
Mycetophilidae						
*(?)Symmerus	2	+	T	+	T	O?
Pachyneuridae						
* Cramptonomyia	1	+	-	+	-	C
Pelecorhynchidae						
Glutops	1	+	-	+	-	C
Psychodidae						
Pericoma 2 spp.	3	+	+	+	-	-
*(?)Sciaridae	4	+	T	+	T?	C
Stratiomyidae						
*(?)Myxosargus	1	+	-	+	+	-
Syrphidae						
*(?)Pocota	2	T	T	+	-	-
*(?)Xylota	1	T	-	+	-	-
Tipulidae						
Antocha	2	-	+(F)	+	-	-
* Austrolimnophila	>10	+	-	++	-	A
Dicranota	2	+	T	+	+	C
Hexatoma	1	+	-	+	+	-
* Limonia 4 spp.	8	+	+	+(L)	-	C
* Lipsothrix 5 spp.	>10	+	-	++	-	A
Ormosia	2	-	+	+	-	O
Pedicia	1	-	-(F)	+	+	-
*(?)Tipula 2 spp.	3	+	+	++	-	A
Thaumaleidae						
Thaumalea	2	-	T	+	T?	-
Xylophagidae						
* Xylophagus	4	-	-	+	?	-