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Functional Analysis of Stream Macroinvertebrates

Kenneth W. Cummins

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Abstract

The worldwide study of stream ecosystems remains a topic of great interest, impacting methods and concepts critical to the preservation and management of global freshwater resources. Stream macroinvertebrates, especially aquatic insects, have served as one of the main pillars of inquiry into the structure and function of running water ecosystems. Stream macroinvertebrates have been used so extensively for over 100 years because they are universally present and abundant, can be readily observed with the unaided eye, (unlike algae and microbes) and are much less mobile than fish which can easily move to totally new locations. Although taxonomic identification has been the basis of analysis of stream macroinvertebrates, functional analysis now offers an additional tool that allows much more rapid analysis that can be accomplished in the field using simpler methodology.

Keywords: streams, macroinvertebrates, functional feeding groups, foods of stream invertebrates, surrogates for ecosystem attributes

1. Introduction

In 1970, Robert Pennak, the preeminent freshwater invertebrate biologist, held that the basic unit of all stream ecology studies should be species level taxonomy (personal communication). This view was shared by essentially all stream ecologists of the day. Given the condition of many stream ecosystems and the taxonomy of aquatic insects then and now [1] that was, and is, a severe impediment to the advancement of research on streams. An alternative approach, based on macroinvertebrate functional analysis, coupled with higher order taxonomy (family or, if possible, genus) was proposed to facilitate addressing stream ecosystem research questions [2, 3]. This functional analysis focuses on adaptations used by freshwater macroinvertebrates to acquire their food. In this approach, seven functional feeding groups

Functional feeding groups (FFG)	Examples of taxa	Adaptations for acquiring food resources
Scrapers (SC)	Ephemeroptera: Heptageniidae, Ephemerellidae <i>Drunella</i> Trichoptera: Uenoidae, Glossosomatidae Helicopsychidae, Psychomyiidae Hemiptera: Corixidae Coleoptera (larvae): Psephenidae, Elmidae Gastropoda	Mandibles with knife-like leading edge in aquatic insects, and file-like radula in Mollusca that removes attached algae; in Ephemeroptera, alga removal may be assisted by front legs
Algal piercers (APR)	Trichoptera: Hydroptilidae	Piercing mouth parts that suck contents from individual algal cells
Detrital shredders (DSH)	Plecoptera: Pteronarcyidae, Nemouridae, Capniidae, Peltoperlidae, Leuctridae, Taeniopterygidae Trichoptera: Limnephilidae, Calamoceratidae, Lepidostomatidae Tipulidae: <i>Tipula</i> Crustacea: Amphipoda, Isopoda, Decapoda	Chewing mouthparts, selection for softest portions of conditioned (colonized by microbes, especially aquatic hyphomycete fungi) vascular plant tissue
Gathering collectors (GC)	Ephemeroptera: Baetidae, Leptophlebiidae, Ephemerellidae, Tricorythidae, Caenidae Trichoptera: Leptoceridae, Odontoceridae Coleoptera: Elmidae (larvae), Hydrophilidae (adults) Diptera: Chironomidae Chironomini, Orthocladiinae Oligochaeta	Non-specialized mouth part morphology that facilitates sweeping fine FPOM into the mouth
Filtering collectors (FC)	Ephemeroptera: Isonychiidae Trichoptera: Hydropsychidae, Philopotamidae, Polycentropidae Diptera: Simuliidae, Chironomidae, Tanytarsini Mollusca: Sphaeriidae, Unionidae	Filtering fans or setae on front legs or silk nets or strands that trap FPOM from the passing water column

Functional feeding groups (FFG)	Examples of taxa	Adaptations for acquiring food resources
Herbivore shredders (HSH)	Lepidoptera: Crambidae, Noctuidae Coleoptera: Cocinellidae <i>Galerocella</i>	Chewing moth parts and crochets (Lepidoptera) that hold plant in place while feeding
Predators (P)	Plecoptera: Perlidae, Perlodidae Trichoptera: Rhyacophilidae Odonata: Anisoptera, Zygoptera Megaloptera: Corydalidae, Sialidae Hemiptera: Belastomatidae, Naucoridae, Coleoptera: Dytiscidae, Hydrophilidae (larvae), Dytiscidae (adults) Diptera: Tipulidae, Tabanidae, Empididae, Chironomidae, Tanypodinae	Crushing, piercing or grasping moth parts and/or front legs; active, with large eyes or ambush predators; with swimming hind legs, crawling legs or welts or prolegs

Categories based on morphological and behavioral adaptations for acquiring specific food categories [1, 3–5].

Table 1. Macroinvertebrate functional feeding groups (FFG).

(FFG) usually are coupled with their seven food categories. The relative abundance of the food categories matches with the relative abundance of the FFGs that utilize those food categories (**Table 1**) [1, 3–6].

Therefore, by identifying a limited number of food categories supporting stream macroinvertebrates it is possible to arrive at the morphological and behavioral adaptations generally shared by groups of taxa (FFG) that are adapted to acquire each of the food resource categories [7].

2. Functional groups (FFG) and food categories

Stream macroinvertebrate FFGs are listed below and summarized in **Table 1**.

1. Scrapers (SC) have morphological-behavioral adaptations that enable them to scrape non-filamentous attached algae from substrates (coarse sediments, wood, or stems of rooted aquatic vascular plants) in streams or lake littoral zones.
2. Detrital shredders (DSH) are adapted to feed on terrestrial plant litter (coarse particulate organic matter (CPOM), primarily leaves or needles that have been entrained in the stream and conditioned (colonized by) microbes, especially aquatic hyphomycete fungi.
3. Gathering collectors (GC) have very generalized adaptations used to feed on fine particulate organic matter (FPOM) of particle size less than 1 mm FPOM) which they sweep up

from depositional areas or crevices in flowing or turbulent where it has settled or been entrained.

4. Filtering collectors (FC) have adaptations that allow them to capture FPOM from the passing water in streams or resuspension by turbulence in lakes using morphological structures or silk capture nets.
5. Herbivore shredders (HSH) are adapted to feed on live rooted aquatic plants, primarily the leaves.
6. Herbivore piercers (HPCR) are adapted to pierce individual filamentous algal cells and suck out the cell contents (primarily Trichoptera, Hydroptilidae).
7. Predators (P) are adapted to catch and consume live prey by engulfing the prey or piercing and extracting the prey hemolymph.

Most genera of North American aquatic insects have been assigned to FFG categories in tables that appear after each taxonomic chapter in [1].

Parallel or convergent evolution has endowed differing taxonomic groups with similar morphological (e. g. mandible structure) and behavioral (e. g. net spinning and case construction) adaptations for acquiring a given food resource.

An example is the similar mandible structure found in larvae of four different scrapers (SC); three caddisfly (Trichoptera) genera representing three different families and one beetle

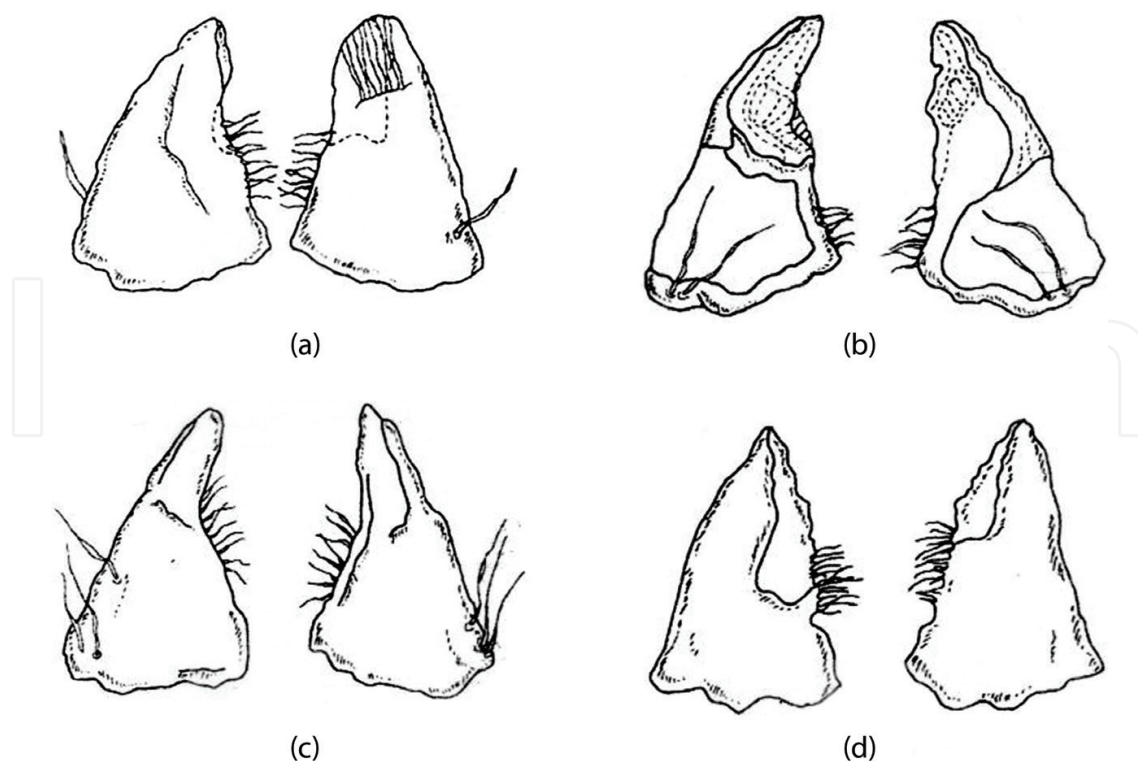


Figure 1. Mandible structure of algal scrapers (SC) in four different taxa: Three Trichoptera genera: (A) *Glossosoma*, (B) *Helicopsyche*, (C) *Neophylax* in different families and a Coleoptera genus (D) *Psephenus*. All have scraper leading edges and basal setae to aid in retention and passage into the mouth of the removed algae. Modified from [8].

(Coleoptera) genus, *Psephenus*, in the Family Elmidae are shown in **Figure 1** [8]. All the mandibles have a knife-like leading edge which, when drawn across a rock or wood surface towards the mouth and remove attached algae. This material is contained and directed into the mouth by basal setae **Figure 1**. A further example is found in the mandibles of wood gouging detrital shredders (HSH) shown in **Figure 2** [9]. Three different genera in three different families and orders are represented. The mandibles of these wood shredder aquatic insects are all three-toothed, scooped-shaped with basal setae. The mandibles are used to gouge grooves in the surface of wood entrained in a stream, ingest it and digest the microbes present that are the source of their nutrition. This poor quality food resource results in longer

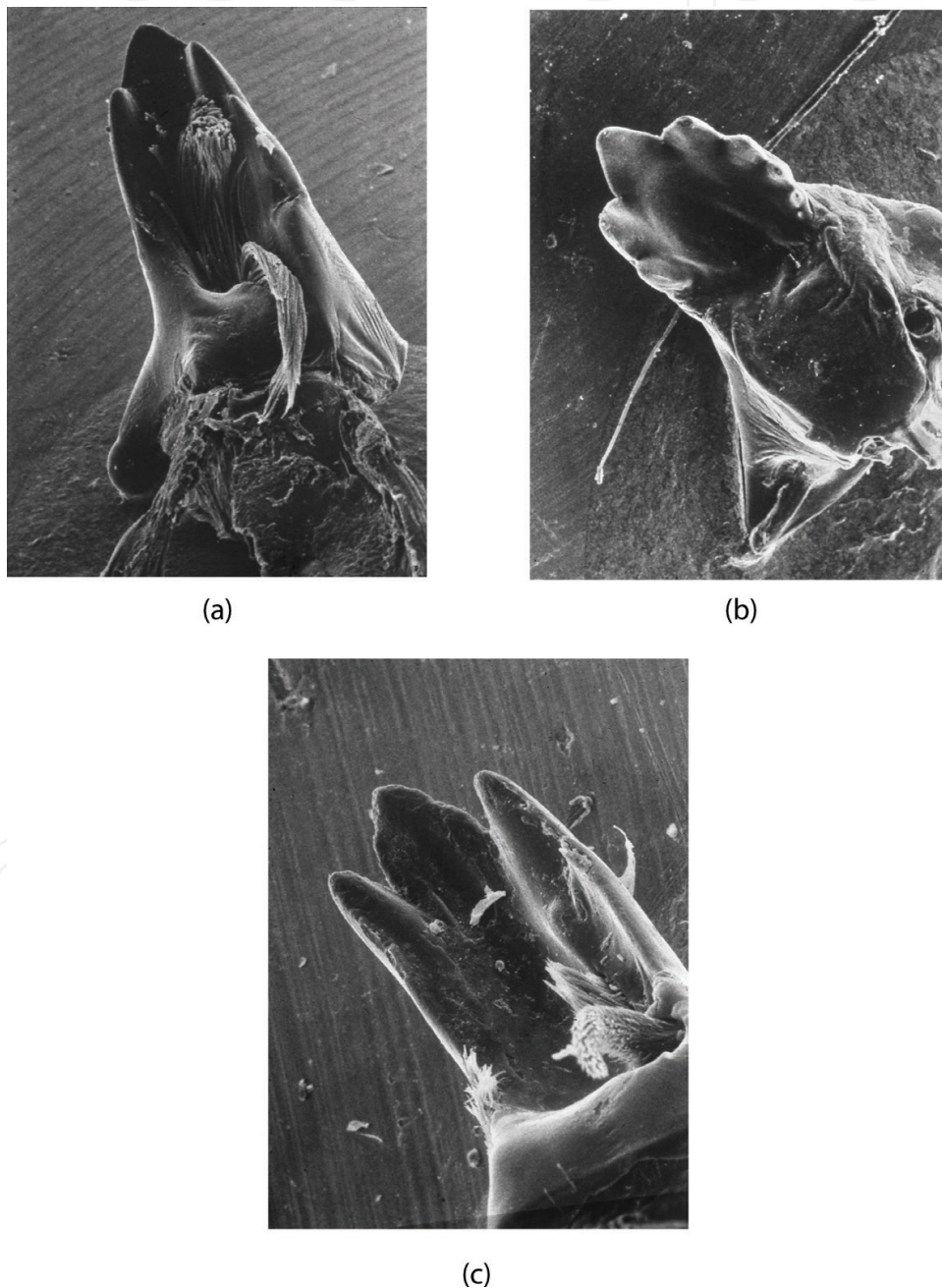


Figure 2. Mandible structure of three wood gouger shredders (DSH) genera representing three different insect orders. (A) Trichoptera Heteroplecton, (B) Coleoptera *Lara*, (C) Diptera Lipsotrix. All have three teeth and are scoop-shaped with basal setae that aid in retention and passage into the mouth of the removed wood fragments and contained microbes [9].

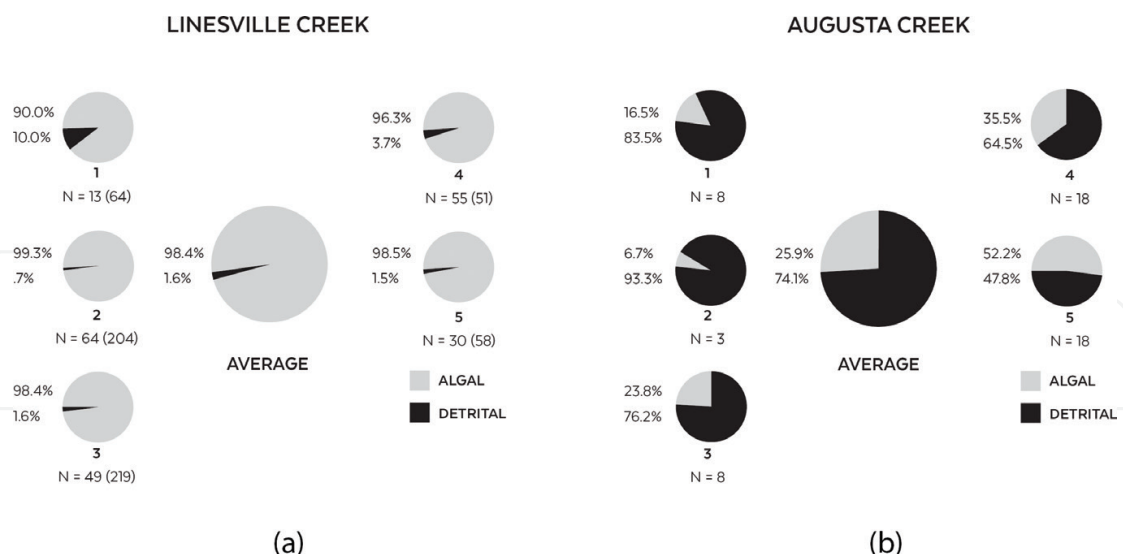


Figure 3. Gut analyses of each of the five instars, and the overall average of larvae of the Trichoptera species *Glossosoma nigrion* from two different streams. (A) Linesville creek, a second order stream in Pennsylvania, USA, with diatom dominated periphyton (average of all five instars = 98.4% algae) and (B) Augusta creek, a second order stream in Michigan, USA, with a detritus dominated periphyton (average of all five instars = 74.1% detritus) [9].

life cycles, especially the larvae of the beetle *Lara* that requires 5 years to mature. Often, *Lara* is found on long term stable large wood habitat in northwest, old growth conifer bordered streams [10, 11].

Many FFGs are restricted to a single mode of feeding. These obligate taxa maintain the same FFG mode of feeding, independent of the quality of the food being harvested [12]. A measure of the match between the FFG and the harvested food resource can be described by the efficiency of the conversion of food ingested to growth [4]. An example is the caddisfly *Glossosoma nigrion* (Trichoptera Glossosomatidae) [12]. Analysis of gut contents of two populations of *G. nigrion* occurring in two different streams, where they both fed as FFG scrapers, revealed that the ingested food differed significantly through all five instars of the growth period (**Figure 3**) [9]. The *G. nigrion* population in the stream that provided good non-filamentous algal periphyton had gut contents totally dominated by algae. The pre-pupae in this population achieved significantly higher final dry biomass than the other population which had gut contents dominated by detritus. This second stream was in a canopy closed forest in which the rock surfaces were covered with fine detritus with little or no algal periphyton. The gut analysis method involving the use of Millipore™ filters is described in [13].

Facultative FFG taxa are not as fixed with regard to adaptations for acquiring food. The added flexibility in feeding allows for survival in a wider range of habitats that offer more food types but the conversion of ingested food to growth is less efficient than in obligate taxa. In their early instars, the majority of taxa are facultative generalists feeding on detritus, even predators like the megalopteran *Nigronia* [14].

A picture key to stream macroinvertebrate FFGs appears as an Appendix in [5].

Stream macroinvertebrate FFG food categories are listed below and described in **Table 2** [4, 5].

Functional feeding groups (FFG)	Foods and descriptions	Typical habitats
Scrapers (SC)	Periphyton: single cells or colonies of non-filamentous algae, especially diatoms, attached to the substrate with loosely associated FPOM, microbes, and/or micro-arthropods	Stream riffles and runs, lake wave-swept shore lines, or rooted vascular aquatic plant beds
Algal piercers (APR)	Filamentous algae: green, blue green, or red algae	Riffles, pools, stream margins or back waters where ever filamentous algae occurs.
Detrital shredders (DSH)	CPOM: riparian vascular plant litter conditioned in the water (colonized by aquatic hyphomycete fungi and bacteria). Micro-arthropods may be present	Plant litter accumulations against obstructions in the current (leaf packs) or settled in pools and on the bottom in lake plant beds
Gathering collectors (GC)	FPOM: organic particles surface colonized by bacteria or mineral particles with organic coating	Pools and other depositional areas in streams and lakes
Filtering collectors (FC)	FPOM: same as above	Particles suspended in the current or by wave action
Herbivore shredders (HSH)	Plant beds: live rooted aquatic vascular plants	Any stream or lake habitats where plant beds grow
Predators (P)	Prey: live aquatic invertebrates in the size range that can be captured by a predator	Essentially all stream and lake habitats where prey are found

After [4, 5]. FPOM is fine particulate organic matter of particle size <1 mm. CPOM is coarse particulate organic matter of particle size >1 mm.

Table 2. Macroinvertebrate functional feeding groups (FFG) food categories they are adapted to acquire and typical habitats where the food resources will be found.

1. Attached non-filamentous algae, primarily diatoms but also green or red algae.
2. Terrestrial plant litter (CP)M) entrained in the stream and colonized and conditioned by microbes.
3. Depositional FPOM on fine sediments in pools, stream margins or under or in crevices in coarse sediments in the current.
4. Suspended FPOM transported in the water column or suspended by turbulence.
5. Living rooted vascular aquatic plants.
6. Filamentous green algae.
7. Live prey.

3. Similar FFG adaptations in different taxa

Noel Hynes, arguably the premier stream ecologist of the last 60 years, observed that he could “turn over a rock in any clean stream the world over and recognize familiar aquatic

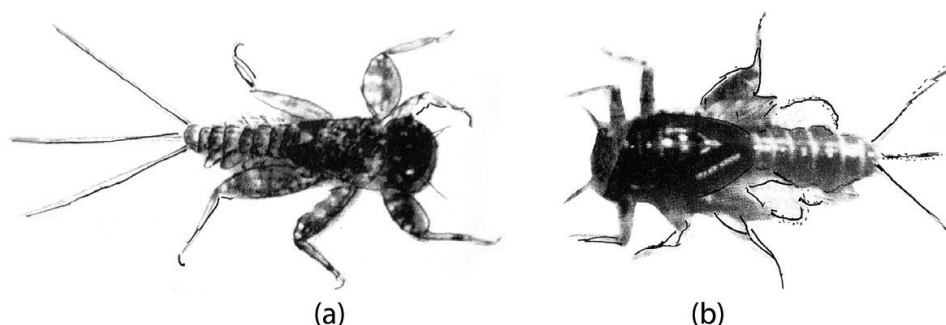


Figure 4. Two scraper (SC) mayfly nymphs from two different families from two continents. Ephemeroptera: (A) Heptageniidae from North America and (B) Ephemeroptera Leptophlebiidae from Brazil. Both nymphs are dorsoventrally flattened with the eyes and antennae located dorsally and the scraper mouth parts ventrally positioned on the head including the scraper mouth parts [9, 15].

insects, but they were all in different families” (personal communication). An example is the very similar dorsal-ventrally flattened body form of a North American scraper mayfly (Ephemeroptera, Heptageniidae) and a Brazilian mayfly (Ephemeroptera, Leptophlebiidae) (**Figure 4**) [9, 15]. Both these scrapers primarily use the mandibles to remove attached periphytic algae from rock surfaces. The mandibles of different taxa functioning as scrapers are similar: a cutting ventral edge with basal setae that keep the algae confined as it is moved into the mouth (**Figure 1**). Another example of similar feeding structures was described above for wood-gouging shredders belonging to different taxa (**Figure 2**). All these examples represent parallel or convergent evolution resulting in differing taxa being adapted to acquire the same food resource type.

The FFG of a given taxon can vary with age (instar in aquatic insects). There is evidence that essentially all aquatic insects are gathering collectors in the first (and second in some) instars. For example, Petersen [14] documented through gut analysis that the first instar of the predaceous megalopteran *Nigronia serricornis* (Corydalidae) fed on FPOM as a gathering collector. Taxa can also switch FFG as they progress through the growth period. The limnephilid caddisfly (Trichoptera) *Pycnopsyche lepida* switches from feeding on conditioned CPOM leaf litter as a detrital shredder in the first four instars to a scraper in the fifth (final) instar. This transition is readily discernable because in the first four instars the larvae construct an organic case made of leaf sections and fine sticks that are readily available in the litter accumulations where the larvae occur. In the fifth instar the larvae move into fast water where they feed by scraping periphytic algae from cobbles in flowing water. At that time, the larvae convert to heavier mineral cases [15, 16].

4. Benefits of FFG analysis

There are two significant benefits in the FFG approach. First, it allows stream macroinvertebrates collected live in benthic or drift samples to be placed in ecologically relevant categories using only the level of taxonomy needed to separate them [6]. Simple examples would be: all Odonata dragonfly and damselfly nymphs are predators (P) and stone case-bearing Trichoptera (caddisfly) larvae are scrapers (SC) while those in organic cases (leaf and stick/stem material) are detrital shredders (DSH). These examples, in which ordinal taxonomy is

all that is required, are used in the key given in Merritt et al. [5]. Clearly, the more taxonomic resolution the better, but the FFG allows typical volunteer or class groups to gather useful data on aquatic ecosystems of local concern. And, importantly, the data can be taken on site using live specimens that allow behavioral and color pattern traits, that are lost or fade in preservation, to be used in the evaluation. Furthermore, the collected organisms can be preserved and returned to a laboratory, if accessible, when detailed taxonomic determinations are required, for example to calculate diversity indices (e. g. see ecological tables in [1]).

The FFG detrital shredders (DSH) are reliably linked to the inputs plant litter from the riparian zone [17] that can be studied easily with the use leaf or needle packs which accurately mimic how plant litter is naturally processed by fungi and detrital shredders (DHS) in streams [18]. These are prepared using leaves or needles of trees that are present in the riparian zone of a stream under study (**Figure 5**) [8, 18]. Dry leaves or needles are weighed into 10 g amounts (to nearest 0.01 g) and soaked in warm water until soft (5–10 minutes). When the leaves are soft enough to handle so that they do not break, they are gathered into a pack and stapled together with the plastic Ts using a Buttoneer™ gun. The needles are threaded into a chain on monofilament fishing line (**Figures 5 and 6**). Each leaf or needle pack is fastened to an elastic band of sufficient size so that it can be attached to a common brick (**Figure 6**). The packs, one or two to a brick (**Figure 6**), are placed in the stream facing into the current to simulate the obstructions against which plant litter accumulates in streams in the current. It is important that some flow occurs across the surface of the leaves or needles to maintain dissolved oxygen levels required by the obligate aerobic aquatic Hyphomycete fungi that colonize the plant material and constitute the major source of the nutrition for detrital shredders (DHS) [19]. The leaf pack shown in **Figure 6** are hickory leaves that were incubated in a third order woodland Michigan stream in October for 2 weeks at 10°C. The effect of the shredder feeding is evident. The softer, most heavily fungal colonized portions of the leaf have been used [20, 21]. The detrital shredders (DSH) select portions of the leaves or needles that are most heavily colonized by aquatic hyphomycete fungi. Specific polyunsaturated lipids of the fungi attract the shredders [19].

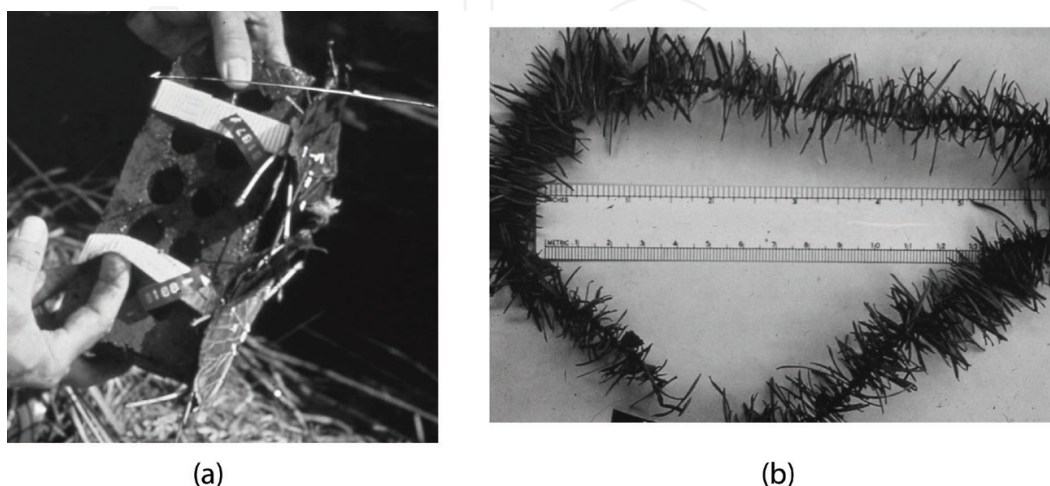


Figure 5. Leaf packs stapled together with plastic Ts using a Buttoneer™ gun and fastened to an elastic band and attached to a common brick prior to placement in a stream (A). The conifer needles are strung on fishing monofilament line prior to fastening to an elastic band and attachment to a common brick for placement in a stream (B). Such leaf and needle packs can be used as a bioassay for microbial-shredder (DSH) processing of CPOM in a stream ecosystem.

The second benefit of using the FFG approach is that ratios of the number of specimens collected in each FFG category can be used to describe a stream reach and compare it to other reaches and other streams (Table 3) [5, 8]. Because these ratios are dimensionless numbers, they are relatively independent of sample size. For example, it has been demonstrated that the *relative* number of scrapers collected from one rock in a given stream riffle is not statistically different from the collection from five rocks in the same riffle [9]. Some FFG ratios that can serve as surrogates for stream ecosystem attributes are summarized in Table 4. Threshold ratio values (percentages) have been proposed based on field evaluations that can serve as



Figure 6. Deciduous leaf pack after 2 weeks at 10°C in a woodland stream in Michigan. The effect of detrital shredder (DSH) feeding is evident. The softer leaf tissues with the greater biomass of aquatic Hyphomycete fungi have been consumed before the more lignified leaf veins. The plastic Buttoner™ Tees that held the leaves together are visible.

Stream ecosystem attributes	Name of FFG surrogate ratio	Definition of FFG surrogate ratio
Autotrophic vs. heterotrophic energetics	P/R: autotrophy to heterotrophy index	Gross primary production compared total community respiration (primary production/respiration or P/R)
CPOM vs. FPOM	Shredder index	CPOM riparian plant litter compared to riparian FPOM + FPOM generated within the stream (e. g. macroinvertebrate feces, mechanical fragmentation microbes, DOM flocculation)
Suspended vs. storage FPOM	Filtering collector index	Suspended FPOM transported in the current compared to FPOM in storage (entrained) in or on the sediments
Stable vs. unstable sediments	Habitat stability index	Coarse sediments + large wood + bed rock + rooted vascular plants compared to small easily moved sediments + FPOM
Top down vs. bottom up macroinvertebrate communities	Predator top down index	Predator regulation of macroinvertebrate communities as compared to regulation by in stream primary production + detritus support of macroinvertebrate communities

Based on [5, 8]. FPOM is fine particulate organic matter of particle size <1 mm, CPOM is coarse particulate organic matter of particle size >1 mm, DOM is dissolved organic matter.

Table 3. Use of functional feeding groups (FFG) as surrogates for stream ecosystem attributes.

Ratio name	FFG surrogate ratios	Proposed thresholds and explanations	Interpretations
Autotrophy-heterotrophy index	SC + HSH + APC to DSH + GC + FC	FFG ratio of >0.75 corresponds to a directly measured P/R = 1.00. Represents in stream plant (algae and vascular) production > than riparian plant litter inputs (or total respiration of microbes + plants and animals)	Stream energetics driven by periphytic algal + any vascular plant production as compared to riparian plant litter inputs
Shredder index	DSH + HSH to GC + FC	FFG ratio of >0.50 in fall-winter or >0.25 in spring-summer. Represents CPOM shredder food availability > FPOM collector food availability	CPOM food support for shredders > than FPOM for Collectors. Fall-winter litter inputs usually > spring-summer and condition more rapidly
Filtering collector index	FC to GC	FFG ratio of >0.50 indicates suspended FPOM load > storage (entrained) FPOM	FPOM food for collectors at higher density and/or better quality than storage FPOM
Habitat stability index	FC + SC + HSH to DSH + GC	FFG ratio of >0.50 indicates that stable locations for scraping and attachment are in greater abundance than shifting unstable substrates	Filtering collectors require stable locations for attachment and construction of capture nets and scrapers require surfaces that remain in a stable position facing up
Top down predator index	P to total FFGs	Predator to prey ratio 0.10–0.20 to total macroinvertebrate population	This level of predator population density (or biomass) allows for sufficient prey to support them. If predators >20% probably indicates populations of rapid turnover (polyvoltine prey populations present)

Proposed thresholds after [22–25]. SC = scrapers, HSH = herbivore shredders, DSH = detrital shredders, GC = gathering collectors, FC = filtering collectors, APC = algal piercers, P = predators.

Table 4. FFG surrogate ratios for stream ecosystem attributes, proposed surrogate ratio thresholds and resulting interpretations.

surrogates to ecosystem attributes such as the classification of a stream reach as autotrophic (i.e. dependent on in-stream primary production as the primary energy source) vs. heterotrophic (dependent on riparian out of stream primary production as the primary energy source) (Table 4) [22–25]. This particular ratio (SC + HSH/DSH + SC + FC) is a surrogate for directly measured P/R, which is the ratio of gross primary production to total community respiration (i. e. including autotrophs). P/R, which is measured by monitoring oxygen levels over time across a stream reach or in enclosed *in situ* chambers [26]. The FFG surrogate P/R ratio is strongly influenced by season and like other FFG ratios might require a different threshold for spring-summer vs. fall-winter (Table 4).

In the case of detrital shredders (DSH), their presence and abundance depends on the type of plant litter inputs and season. If the riparian zone is dominated by deciduous hard woods, the inputs are in the fall–winter period. Hardwoods, except oaks, are conditioned rapidly by aquatic hyphomycetes and fed on by shredders. Conifers (evergreens) shed foliage primarily in the spring–summer and conditioning by fungi is much slower and shredder feeding is

delayed. Prairie Creek in Redwood National Park, California provides an example from an old growth conifer forest stream with slow fungal conditioning and delayed detrital shredder (DSH) activity (Table 5 [27]). The riparian derived CPOM is largely wood and conifer needles which require along conditioning times before shredders begin feeding. This suggests that samples taken in December were too early to detect the major shredder activity. The shredder caddisfly larvae (Trichoptera: *Lepidostoma* and *Gumaga*) and stonefly Nymphs (Plecoptera: Peltoperlidae, Capniidae, Leuctridae) that were collected were quite small. The mean dry mass per individual, of the 34 individuals collected was 6.6 mg (caddisflies 111 mg, stoneflies 75 mg) indicating very early instars. The ratio was low because the biomass of the GC (0.061 mg) plus FC (3.35 mg) was much greater. The recommended threshold for conifer old growth forest streams should be based samples for February or March. The general 0.50 threshold was based on data from deciduous forest streams taken in the fall when the conditioning of the riparian litter was sufficient to accommodate expected shredder populations [18].

There is an extensive literature using FFG analyses, for example the numerous references cited in the ecological tables that accompany each aquatic insect order in [1]. FFG analyses and the ratio method, including proposed thresholds have been used to evaluate Florida Rivers. FFGs were used to characterize the un-dammed reach of the Kissimmee River as a model for general restoration of the 100 miles of the channelized River [22]. The ratio method was employed to characterize the remnant oxbows of the Caloosahatchee River according to their ecological attributes and to provide recommendations for preservation and restoration of the River's oxbows [25]. Floodplain (marsh) habitats of the St. John's River were also evaluated relative to hydrological influences using FFG surrogate ratios to predict the effects of water withdrawal from the river [25]. The method also was used to characterize the ecological conditions in a wide range of Brazilian streams and rivers [24].

Stream FFG ratios	Calculated ratios		Proposed thresholds	Stream ecosystem interpretations
	Numbers	Dry biomass (mg)		
P/R index: (SC + HSH/DSH = GC = FC)	0.96	0.55	Ratio > 0.75 (autotrophic)	SC numbers indicate a significant algal periphyton based autotrophic stream ecosystem (significant biomass of stonefly and caddisfly shredders indicate heterotrophic system supported by riparian plant litter inputs)
CPOM shredder index: (DSH/GC = FC)	0.15	0.04	Ratio > 0.50 (predicted fall–winter shredder component)	The predicted range for fall–winter shredder populations not met. (supply of sufficiently conditioned [colonized by microbes] riparian plant litter inputs, not adequate)

Stream FFG ratios	Calculated ratios		Proposed thresholds	Stream ecosystem interpretations
	Numbers	Dry biomass (mg)		
FPOM suspended load index: (FC/DSH + GC + FC)	0.14	0.28	Ratio > 0.50 (sufficient FPOM to support filtering collectors, assuming sufficient quality)	The amount, or quality (e.g. organic content) of FPOM in suspension and transport below typical levels to support FC populations (this old growth conifer forest stream dominated by slowly processed wood and litter likely generated only primarily low amounts of poor quality FPOM; rapid turnover deciduous litter from big leaf and vine maple probably absent)
Channel stability index: (SC + FC + HSH/DSH + GC)	1.09	0.96	Ratio > 0.50 (sufficient stability to support SC and FC populations)	Stable substrates, coarse sediments and large wood, well above levels predicted to support surfaces required scraping and filtering macroinvertebrates (large wood in old growth forest streams observed to provide a long term stable habitat)
Top down predator index: (P % of total)	0.15	0.21	Ratio > 0.10 < 0.20 (predicted predator top down control of macroinvertebrate populations)	Both numerical and biomass estimates of predators fall within the expected % of the macroinvertebrate community (all the expected predators present; stoneflies, especially the large Perlidae, Tipulidae [except <i>Tipula</i>], and <i>Tanypodinae</i> midges)

Modified from [27].

Table 5. FFG ratio analysis of macroinvertebrate benthic summer samples taken in Prairie Creek winter (December).

5. Conclusions

Proposed in this chapter is the use of the FFG method of analysis to gain rapid and efficient insight into macroinvertebrate community composition and its function in freshwater ecosystems. The method should be compatible with a broad level of expertise, from beginner to

advanced, and can be conducted stream-side allowing live animals to be released or preserved and returned to the lab. If the FFG ratio method is to be used, at least some qualitative observational data should be recorded: riparian information about the dominant vegetation cover (e. g. percent deciduous vs. evergreen) and the % canopy closure; dominant stream habitat (riffles vs. pools, coarse vs. fine sediments, % accumulation plant litter such as leaf packs); discharge level relative to bank full (the permanent vegetation line) and general land use observations (e. g. agricultural or live stock grazing, timber harvest or other human disturbances). When conducting FFG analysis it is most useful to collect, and keep separate, samples from three types of habitat: Riffles (coarse sediments), pools (fine sediments), and plant litter accumulations. Samples can be taken with timed (e. g. 15 s) D-frame or aquarium net samples. The data can be combined later into a “composite” sample, but the relative importance of each habitat can be assigned based on the qualitative evaluation of the % stream bottom cover of each habitat type. Most importantly, The FFG analysis technique does not foreclose on any traditional use of taxonomic analysis of the samples in the laboratory.

Acknowledgements

Thinking back to 1973, I first became fascinated with adaptations of freshwater macroinvertebrates, especially in streams. Herb Ross (Illinois Natural History Survey) invited me to submit a contribution to the Annual Review of Entomology. He said there were rarely any papers on aquatics and suggested I consider ecological adaptations of aquatic insects as a topic. At about the same time, Noel Hynes (University of Waterloo, Canada) told me he could turn over a rock in any stream in the world and recognize the mayfly nymphs, but they were all in the “wrong family.” This example of convergent or parallel evolution formed the basis for the functional feeding group approach. During the intervening years, a monumental array of colleagues has been instrumental in my understanding of freshwater macroinvertebrates. George Lauff (at the University of Michigan) directed my PhD work and Rich Merritt (Michigan State University) and Peggy Wilzbach (Humboldt State University, CA) have provided ideas and encouragement for decades.

Author details

Kenneth W. Cummins

Address all correspondence to: kc8161@gmail.com

Fisheries Biology, Humboldt State University, Arcata, CA, USA

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