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ORIGINAL ARTICLE

Combining taxonomy and function in the study of stream macroinvertebrates

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ABSTRACT

*Over the last fifty years, research on freshwater macroinvertebrates has been driven largely by the state of the taxonomy of these animals. In the great majority of studies conducted during the 2000s macroinvertebrates have been operationally defined by investigators as invertebrates retained by a 250 μ mesh in field sampling devices. Significant advances have been and continue to be made in developing ever more refined keys to macroinvertebrate groups. The analysis by function is a viable alternative when advances in macroinvertebrate ecological research is restricted by the level of detail in identifications. Focus on function, namely adaptations of macroinvertebrates to habitats and the utilization of food resources, has facilitated ecological evaluation of freshwater ecosystems (Functional feeding groups; FFG). As the great stream ecologist Noel Hynes observed, aquatic insects around the world exhibit similar morphologies and behaviors, even though they are in very different taxonomic groups. This is the basis for the FFG analysis that was initially developed in the early 1970s. FFG analysis applies taxonomy only to the level of detail that allows assignment to one of six FFG categories: scrapers adapted to feed on periphyton, detrital shredders adapted to feed on coarse (CPOM) riparian-derived plant litter that has been colonized by microbes, herbivore shredders that feed on live, rooted aquatic vascular plants, filtering collectors adapted to remove fine particle detritus (FPOM) from the water column, gathering collectors adapted to feed on FPOM where it is deposited on surfaces or in crevices in the sediments, and predators that capture live prey. The interacting roles of these FFGs in stream ecosystems were originally depicted in a conceptual model. Thus, there are a limited number of adaptations exhibited by stream macroinvertebrates that exploit these habitats and food resources. This accounts for the wide range of macroinvertebrate taxa in freshwater ecosystems found in different geographical settings that are represented by a much smaller number of FFGs. An example of the generality of the functional group concept is the presence of detrital shredders that are dependent upon riparian plant litter inputs being found in essentially all forested streams world-wide (*e.g.*, across the USA and Canada, Chile, Brazil, West Africa, New Zealand, Australia, Japan, Thailand; Cummins,* unpublished*). Freshwater macroinvertebrate taxonomic determinations, especially at the species level, may be the best basis for developing specific indices of pollution (tolerance values in ecological tables). However, the FFG method appears to provide better indicators of overall freshwater ecosystem condition.*

Key words: Stream macroinvertebrates; freshwater macroinvertebrate functional groups; stream ecosystem attributes; stream P/R ratio.

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INTRODUCTION

For over 50 years, the study of stream macroinvertebrates has followed two separate but related paths. One path focused on taxonomy, that is, the assignment of names to macroinvertebrates; the other path focused on their ecology, that is, their adaptation to habitats and in feeding behavior. During the 50-year period, the two approaches have been coming closer together. The time has come to recognize a full integration of the two paths.

In the 1950s the renowned North American freshwater invertebrate biologist, Robert Pennak, argued that freshwater ecosystem principles could be determined only if macroinvertebrate taxonomy was determined at the species level. Given the primitive state of the taxonomy of aquatic insects (the dominant forms in streams) at the time, this was highly discouraging to stream ecologists interested in establishing basic principles of stream ecosystem structure and function. This led Merritt and Cummins and colleagues to commit intensive effort on moving the taxonomy of North American aquatic insects forward. The first edition of the 'Introduction to the Aquatic Insects of North America' was published in 1978. This edition provided keys to families of aquatic and semi-aquatic North American forms. Significantly, for each order, a table giving referenced information on the taxonomy and ecology of each family was linked. Included in these tables was an estimate of the dominant functional feeding group for each family (FFG: Cummins, 1964; Cummins and Klug, 1979; Merritt *et al*., 2008). The 1978 edition of the aquatic insect book was the first comprehensive attempt to merge taxonomy and a functional classification of freshwater North American aquatic insects.

THE FUNCTIONAL FEEDING GROUP APPROACH

The Functional feeding group (FFG) method originated from a defining statement made by Noel Hynes, arguably the greatest stream ecologist ever. He stated: *if I* *turn a rock over in the riffle in any stream in the world, I see old friends* (Hynes, 1970; personal communication). The concept was that aquatic insects with similar morphology and behavior allow them to maintain their position in fast water where they feed on attached algae. Although the macroinvertebrates appear morphologically the same, their taxonomy is often different. An example is shown in Fig. 1 of a Heptageniidae mayfly nymph from the USA compared to a Leptophlebiidae mayfly nymph from Brazil. These nymphs have similar morphology and behavior. They live in fast water and feed by scraping attached algae from rock surfaces. That is, they occupy similar habitats and have the same morphological and behavioral adaptations, but are in different taxonomic families of mayflies.

The FFG classification (Cummins, 1964, 1988, 1993; Cummins and Klug, 1979; Merritt *et al*., 2008) assigns freshwater macroinvertebrates to groups based on their morphology and the behavior used to acquire one of five food categories: periphytic algae, terrestrial plant litter from the riparian zone, fine particulate organic matter, live rooted aquatic vascular plants, and prey for predators. The FFGs that match the food resources are: scrapers (periphyton), detrital shredders (microbial conditioned riparian plant litter); filtering collectors (fine particulate organic matter transported in the water column); gathering collectors (fine particulate organic matter deposited on the stream bottom); herbivore shredders (live rooted vascular aquatic plants), and predators (capture live prey). It is important to emphasize that the FFG categorization is based on the morphology and behavior that enables the acquisition of a given food resource by stream/river macroinvertebrates. Therefore, analysis of gut contents is a poor predictor of FFG assignment. For example, two populations of the caddisfly *Glossosoma nigrior* observed in two different streams exhibited the same feeding behavior, namely scraping attached periphyton from rock surfaces in flowing water, but they had distinctly different gut contents. In one stream, which had an open canopy where green algae dominated the periphyton, algae were the major items in the gut contents of all five larval instars. This would be consistent with a classification as a scraper. However, in the other stream, which had a closed canopy, the periphyton consisted of some diatoms but was dominated by detritus that had settled out on rock surfaces in the periphyton. In this stream, detritus dominated the gut contents of all five larval instars. This would be consistent with a classification as a gathering collector. Larvae with the same feeding strategy in the same general habitat type but in two different streams had greatly different gut contents. Further, in the detritus-dominated stream, the resulting adult females were significantly smaller and carried fewer eggs than those from the algal-dominated stream (Anderson and Cummins, 1979).

The relationship between the FFGs and their roles in

Fig. 1. Example of two mayfly FFG scraper nymphs in different taxonomic groups. Ephemeroptera: Heptageniidae from the USA (original); Leptophlebiidae from Brazil (modified from Hamada *et al.*, 2014). Both nymphs share the same habitat type and feeding adaptations.

stream ecosystems that was proposed in 1973 (see also Cummins, 1974; Cummins and Klug, 1979; Merritt *et al*., 2008) is shown in Fig. 2. Two general pathways of energy flow are highlighted. In one, the energy of is converted to algal (and rooted aquatic plants not shown) biomass through photosynthesis. In the other, the energy source is from terrestrial plants growing in the riparian (stream side) zone. The algal biomass, and detritus and associated organisms, such as protozoans and bacteria, constitute the periphyton that is fed upon by scrapers.

Scrapers have adaptations that allow them to maintain their position in the current on surfaces where the periphyton is attached where they feed by scraping off the algae and associated material and into the mouth. The major scraper taxa in North America are mayflies in the family Heptageniidae and mineral (stone) case-bearing caddisflies in the order Trichoptera (Merritt *et al*., 2008). The efficiency of scraping by a stone case caddisfly larva (Glossosomatidae) is shown in Fig. 3.

It is likely that some Mexican mayflies in the family Leptophlebiidae may be scrapers, as they are in Brazil (Cummins *et al*., 2005; Fig. 1). In North America, the genius *Drunella*, in the mayfly family Ephemerellidae, has scraper species (Merritt *et al*., 2008). There may be some genera in that family that occur in Mexico that are scraper species. Determining which Mexican mayfly taxa are scrapers awaits further research.

The processing of terrestrial plant litter that enters a

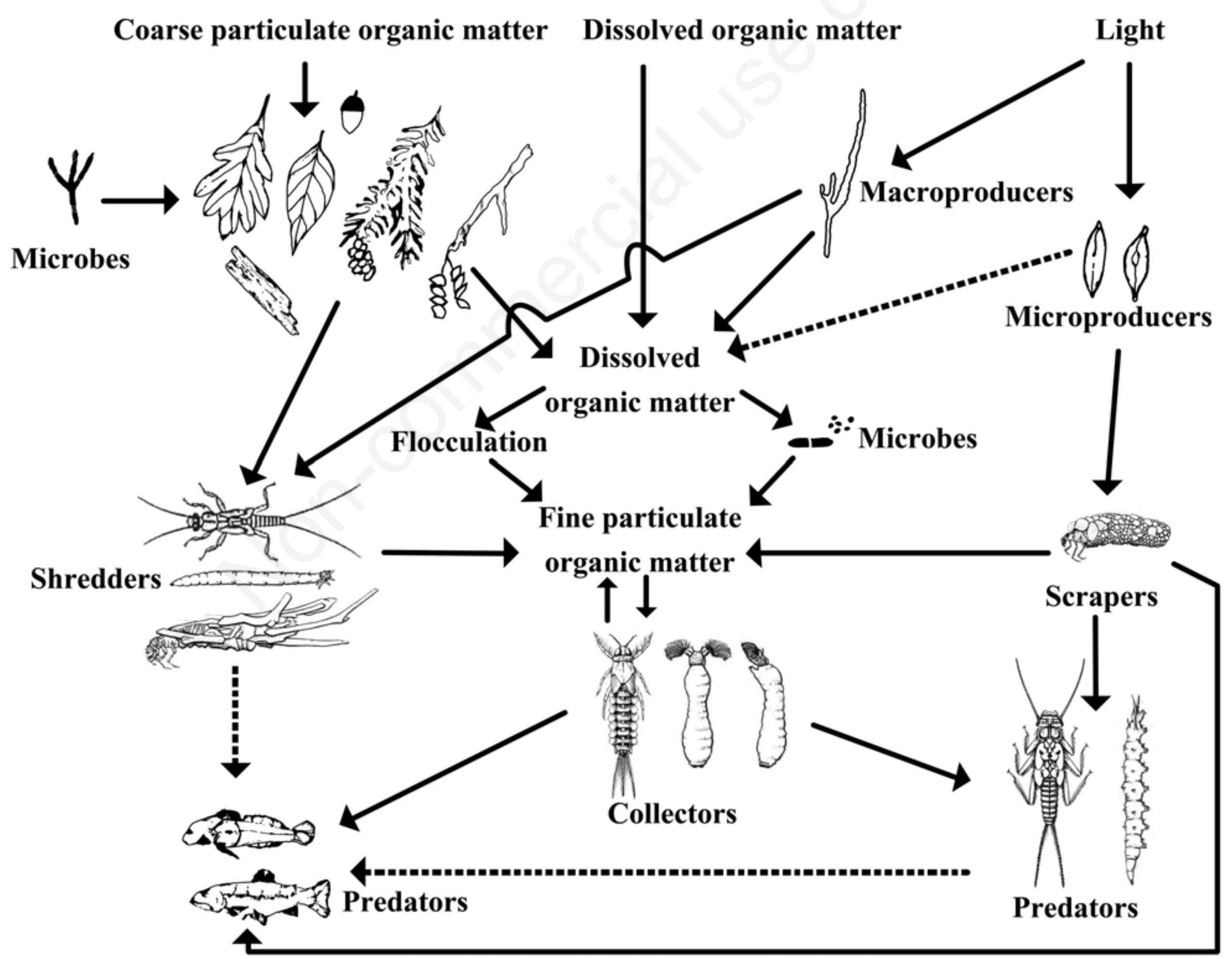

Fig. 2. Stream ecosystem conceptual model of energy sources and transfers through the macroinvertebrate community. On the right, the energy of sunlight drives in-stream primary production (algae and rooted vascular aquatic plants) that is utilized by scrapers. On the left, the energy source is the input of plant tissue (CPOM) from the riparian zone and utilized by shredders once it is conditioned by hyphomycete fungi and bacteria. Shredders convert this coarse plant tissue to FPOM that is transferred to collectors. Predators feed on all FFGs (from Cummins, 1974).

stream begins with the leaching of the litter. Plant material can lose up to 40% of its dry weight in 24 to 48 hours, even at temperatures below 5°C (Petersen and Cummins, 1974; Cummins *et al*., 1989). This dissolved organic matter (DOM) can be converted to fine particulate organic matter (FPOM) by complexing with the divalent cations Ca or Mg, or by being assimilated by stream bacteria (Fig. 2; Petersen and Cummins, 1974; Cummins *et al*., 1989). When this plant material enters the stream and is entrained, very soon after leaching the plant litter is colonized by freshwater microorganisms, especially aquatic hyphomycete fungi. The rate of colonization is determined by the thickness and wax layer of the cuticle of the plant tissue and the types of organic chemical leachates that are released, such as phenolic compounds that can be fungal inhibitors (Cummins *et al*., 1989). The invasion of the plant litter termed conditioning renders the plant tissue suitable for ingestion by shredders. The presence and density of aquatic hyphomycete fungi in the plant litter tissue controls feeding by the shredders (Suberkropp *et al*., 1975; Cargill *et al*., 1984, 1985; Hanson *et al*., 1985). Thus, differences in colonization of plant litter by hyphomycete fungi (conditioning), determines which plant species and which tissues of a given plant species are fed upon by detrital shredder macroinvertebrates. These differences in shredder feeding allow riparian plant species to be classified as *fast* or *slow* with regard to the rate of disappearance of the plant litter biomass and conversion to fine particulate organic matter (FPOM; Cummins *et al*., 1989; Grubs and Cummins, 1996). The term shredder refers to their feeding mode in which they eat through the material because the biomass of the microbes is primarily in the matrix of the plant tissue (Suberkropp *et al*., 1975; Cummins *et al*., 1989). Feeding by shredders on the litter causes some fragmentation and yields significant fecal material. The fragments and feces are all FPOM, defined as organic particles less than 1 mm in diameter (Cummins, 1974; Cummins *et al*., 1989). In streams with rooted aquatic vascular plants, herbivore shredders feed directly on the live plant tissue producing holes in the leaves of the plants. Common herbivore shredder taxa include aquatic moths (Lepidoptera), beetles (Coleoptera), and a few Diptera and Trichoptera (Merritt *et al*., 1996, 2008). In North America, the genus *Lipsothrix* (Diptera, Tipulidae) and *Lara* (Coleoptera, Elmidae) are shredders of wood in streams (Merritt *et al*., 2008).

The FPOM from shredder feeding, complexing of DOM with cations, and uptake by microbes constitutes the food resource for macroinvertebrate collectors. Filtering collectors capture FPOM from the passing water column. The particles are captured by morphological filtering structures such as the pre-mandibular fans of black flies (Diptera, Simuliidae) or in silk nets such as those spun by caddisfly larvae in the family Hydropsychidae (Cummins and Klug, 1979; Fig. 4).

Fig. 3. Scraping (grazing) track (white) of a stone case-baring caddisfly larva (Trichoptera: Glossosomatidae, *Glossosoma*) on a white ceramic tile. The tile was colonized by periphyton (dark color) in a North American woodland stream placed in a laboratory flume and a caddis larva introduced.

Fig. 4. Filtering collector, blackfly larva (left, Simuliidae) and the capture net of a filtering collector, net-spinning caddisfly (right, Hydropsychidae). The blackfly larva spins a layer of silk on the substrate surface and attaches a circle of hooks at the terminus of the bulbous abdomen to the silk to maintain its position in the current. FPOM is removed from the passing water column with the mucous-coated filaments on their pre-mandibular fans. The fans are stuffed into the mouth in rapid succession where the FPOM is combed from the fans by spines that border the mouth. Net spinning filtering collector caddis larvae.

Gathering collectors browse FPOM from locations where it settles out in pools or crevices in bottom sediments. They have little specialized morphology or behavior for acquiring the FPOM. They move from place to place and brush the loose particles into the mouth or simply eat their way through the deposits of FPOM detritus (Cummins and Klugg, 1979). A majority of the non-biting midges in the family Chironomidae (Diptera) are gathering collectors in which a thoracic proleg moves the particles into the mouth (Fig. 5). Gathering collector families of mayfly nymphs have a streamlined body shape and are good swimmers (*e.g.*, Baetidae). Other mayfly gathering collector families, such as Caenidae and some Ephemerellidae, are not active swimmers but have the first pair of gills modified as opercula that cover the remaining gills to protect them from settling FPOM in slow water (Merritt *et al*., 2008).

EVALUATING STREAMS USING A COMBINATION OF TAXONOMY AND FUNCTIONAL GROUPS

Characterization of stream ecosystem condition through a combination of macroinvertebrate taxonomic identifications and their adaptations to habitat and food resources is highlighted in Merritt *et al*. (2008). The summary tables that appear at the end of each ordinal and selected family chapters provide FFG for each taxon. This approach involves making those taxonomic macroinvertebrate determinations that allow for their assignment to a functional group. In some cases, this can be at the order level, for example, all Odonata are predators.

A key for separating most mayfly nymphs into scrapers and gathering collectors, stoneflies into predators and shredders, and all dragonflies and damselflies as predators is given in Fig. 6. The mayfly genus *Isonychia* is a filtering collector and an exception to the general pattern shown in Fig 6.

The combination of taxonomy and functional feeding groups (FFG) can be used to provide insight into the condition of any given stream ecosystem. This is based on the contention that the relative proportions (ratios) of the functional groups can serve as surrogates for stream ecosystem attributes. Most of these ecosystem attributes are difficult to measure over seasonal or annual time periods and/or on a stream reach or watershed spatial scale. Most often, direct measures of stream ecosystem conditions are only an instantaneous spatially limited snap shop. Recording probes have increased longer-term data gathering for some selected chemicals but even multiple probes do not totally solve the problem. However, every stream has an in-place monitoring system that integrates the needed time and space data acquisition requirements for evaluating stream ecosystem condition. This monitoring system is the macroinvertebrate populations. Stream ecosystem attributes are as varied as the questions that can be asked about them. These attributes include water quality parameters however they are defined; for example, organic and/or inorganic chemical pollution, sedimentation issues, invasive species, etc. The FFG method is better at defining general stream ecosystem attributes than specific pollution effects. However, changes in selected attributes can provide early warnings of impairment that include some types of pollution.

The primary example of a fundamental stream attribute for which the relative proportions of FFGs can serve as a surrogate is the balance between ecosystem autotrophy and heterotrophy. Autotrophy is largely regulated by light. When the stream is autotrophic, in-stream primary production is the basic energy source driving the ecosystem (Fig. 2). If the stream is heterotrophic it is dependent on the input and in-stream processing (respiration) of riparian plant litter (Fig. 2). Measured directly, the ratio of Autotrophy to heterotrophy is determined as gross primary production/total community respiration (P/R). When P/R=>I, the stream ecosystem is autotrophic. The FFG macroinvertebrate surrogate for directly measured P/R is: the ratio of scrapers+herbivore shredders to detrital shredders+total (both filtering and gathering) collectors (Merritt *et al*., 1996, 2002). The surrogate ratio has been shown to represent autotrophy when FFG P/R=>0.75 ecosystem (Cummins 2000, Cummins *et al*., 2005).

Fig. 5. Gathering collector midge larva (Diptera, Chironomidae, Chironomini) brushes FPOM into the mouth with the aid of a single proleg located behind the head. Some larvae of *Chironomus, Chironomini* species, like the one shown, are red because they contain hemoglobin, which increases their ability to survive in low dissolved oxygen conditions.

Other surrogate FFG ratios have been related to stream ecosystem attributes and others remain to be demonstrated (Cummins *et al*., 2002). Elaboration of the relationship of macroinvertebrate taxonomy and their functional adaptations for use in predicting the condition of Mexican stream/river ecosystems is a very fertile area for future study.

CONCLUSIONS

Stream macroinvertebrates are operationally defined as those retained by a field sampling device with a 250 µm mesh screen. Macroinvertebrate populations provide the ideal monitoring tool for the analysis of stream ecosystem condition. This is the appropriate time to officially merge the separate but related taxonomic and functional approaches that have been employed when using macroinvertebrates to characterize stream ecosystem condition. The imperfect state of the taxonomy of stream macroinvertebrates need not limit their use in evaluating stream ecosystem condition in any region worldwide. Since there are a limited number of basic habitat types in all streams (*e.g.*, riffles, pools, rooted vascular plant beds, large woody debris) there are a limited number of macroinvertebrate adaptations to them: morphological and behavioral adaptations for occupying one or more of the habitats and for feeding. As there is significant taxonomic overlap among the macroinvertebrates exhibiting these adaptations, functional group analysis can be conducted at a less detailed taxonomic level. Usually order or family and in some cases genus level is sufficient to place macroinvertebrates into functional (*i.e.*, adaptation) groups. Five functional feeding groups (FFG) have been widely used to link habitat use and feeding behavior. The relative abundance of the six FFGs (scrapers, detrital shredders, herbivore shredders, filtering collectors, gathering collec-

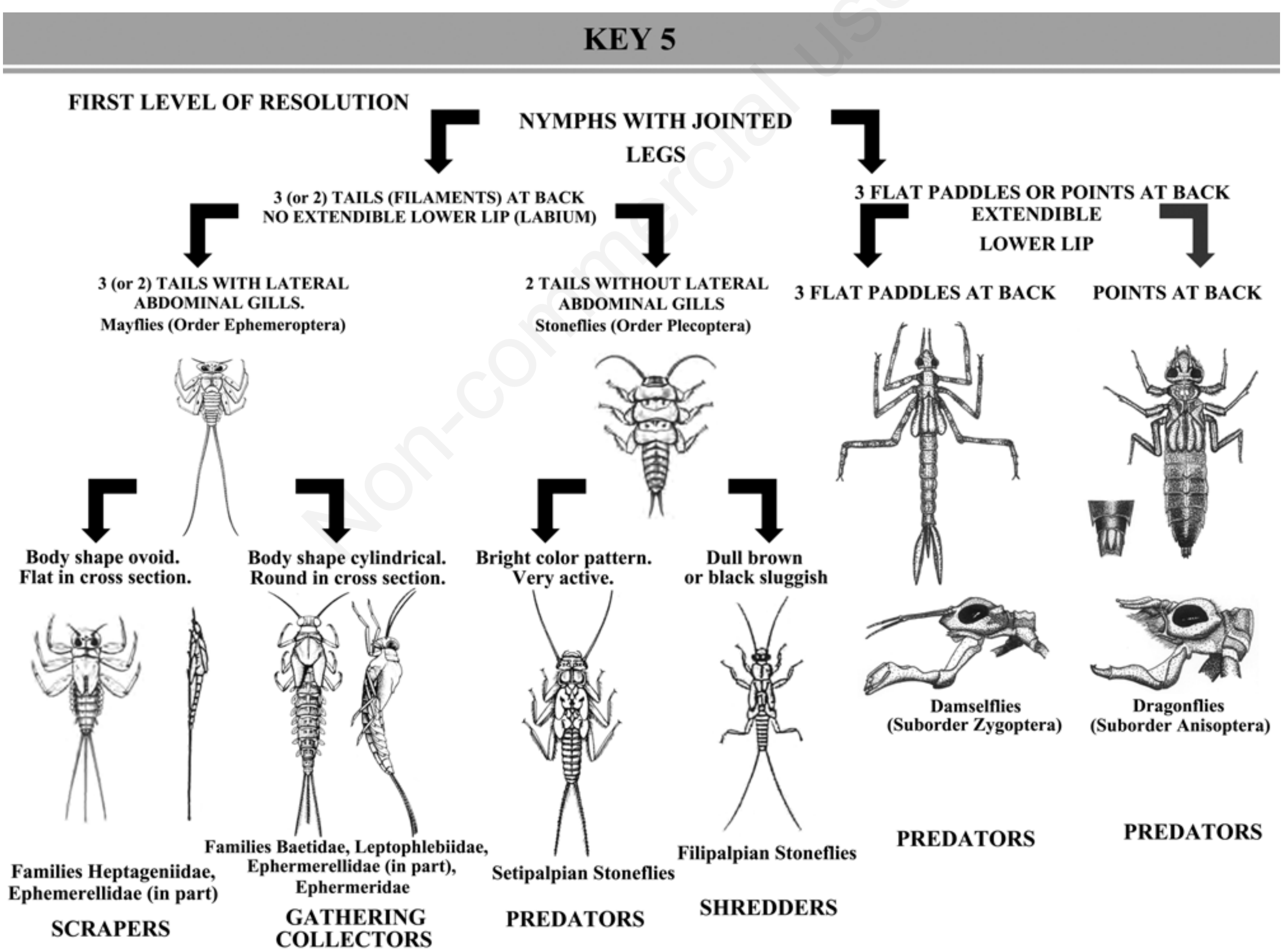

Fig. 6. An FFG key that allows mayflies, stoneflies, dragonflies and damsel flies to be sorted into FFGs. Oval, dorso-ventrally flattened mayfly nymphs are scrapers; with few exceptions, cylindrical tapered mayfly nymphs are gathering collectors. Brightly colored, active stonefly nymphs are predators, those uniformly dark colored, and sluggish are shredders. All the Odonata nymphs are predators; they have an extendible labium used to grasp their prey.

tors, and predators) can be used to characterize the status of the required habitats and food resources and, therefore, stream ecosystem condition.

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