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Stream Invertebrate Zoology

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Abstract

For over a century, there has been strong interest in freshwater streams and rivers. Since the inception of studies on running waters, invertebrates have been a central theme. Early descriptive work in Scandinavia and New Zealand was followed by work in Europe, England, and then North America and Australia. Presently, there is a very significant interest worldwide including Asia, Central and South America, and Africa in freshwater invertebrates. Throughout, insects have dominated the focus on invertebrates. Although the major marine invertebrate groups are present in freshwaters, there are essentially no marine insects. A clear picture of the habitat and food requirements of running water invertebrates shows that they serve as important indicators of water quality and fisheries. Major paradigms, such as the River Continuum and functional feeding groups, have provided frameworks for studies of running water (lotic) invertebrates. Once stream and river research achieved an international status by separation from lake domination of the limnology discipline, there has been an avalanche of running water invertebrate research.

Keywords: stream and river ecology, lotic invertebrates, functional feeding groups (FFG), River Continuum, FFG ecosystem surrogate ratios

1. Introduction

For over a century, there has been significant interest in stream and river (lotic) ecology. A major foundation fueling this interest has been the aquatic invertebrates. From the beginning, focus has been on certain marine-derived groups and on insects. Lotic macroinvertebrate communities are usually dominated by insects [1], but some marine taxa, such as annelids, mollusks, and crustaceans, are often abundant as well [2, 3]. There are essentially no marine insects, the argument being that by the time insects evolved, all the marine ecological niches were filled. Macroinvertebrates conventionally have been defined as those individuals greater than 1 mm in size. However, many present-day studies include all invertebrates retained on a 0.25 -mm mesh screen as macroinvertebrates (1). The far less studied and much smaller microinvertebrates include taxa also found in the marine ecosystem such as protozoans, rotifers, and annelids. But, some very small insect taxa (Diptera, *Chironomidae*) and the first instar of most aquatic insects are also in this arbitrarily small size category.

Examples of earlier investigations of running water invertebrates can be found in Shelford [4] and Shelford and Edy [5] (North America), Moon [6, 7] (Great Britain), Wessenberg-Lund [8] (Denmark), and Allen [9] (New Zealand). The North American references [4, 5] contain early descriptive work on the components of lotic invertebrate populations and their habitats. The British publication [6]

established the fundamental classification of flowing water habitats as either erosional (riffles) or depositional (pools). This basic view endures to the present time and is similar to the lake (lentic) designations of littoral or profundal [10]. The basic morphological and behavioral adaptations of lotic invertebrates, to either erosional or depositional habitats, are discussed below. The Scandinavian volume by Wessenberg-Lund contains a treasure trove of biological and ecological information on freshwater insects including habitat descriptions [8]. Someone could contribute significantly to the study of lotic invertebrates by translating this book from Danish German into English. The famous New Zealand publication by Allen [9] used unique illustrations of the fauna to represent relative densities of the stream macroinvertebrates. A wide-ranging geographical scope of lotic invertebrate study was, and is, an important component of the broad development of the field of stream and river ecology. The discussion on running water invertebrates that follows is greatly informed by recent advances in taxonomy, biology, and ecology [2, 3], especially of insects. Examples are the new (5th) edition of the aquatic insects of North America (Berg et al. [1]), DNA barcoding to validate taxonomic affinities [11, 12], stable isotope (carbon 13, nitrogen 15) analysis of food webs [13, 14], and functional feeding group (FFG) characterization of trophic relationships [15]. It is now possible to identify most genera of North American aquatic insects using morphological characters [1]. It should be noted that many of the North American families and genera occur on other continents.

2. Taxonomic invertebrate groups of lotic invertebrates

2.1 Macroinvertebrates

The typical macroinvertebrate groups and their characteristics in headwater streams are summarized in **Table 1**. The conterminous continent-wide US study of selected river basins, the River Continuum Project [16], developed a paradigm linking position along a river basin channel network that was described as stream order [17]. Energy sources for the component communities of macroinvertebrates were predicted along the continuum. Headwater streams (orders 1–3) receive their energy supply from streamside (riparian) terrestrial vegetation (plant litter) along the stream channel. This is termed an allochthonous energy source.

Wider mid-sized stream/river are less shaded by riparian trees, allowing much more light to reach the channel. This additional light input drives in-stream primary production by algae and aquatic vascular plants. This is termed an autochthonous energy source. The macroinvertebrate communities of the mid-sized stream/river ecosystems are populated with taxa that utilize the greatly increased beds of rooted aquatic vascular plants, especially herbivore shredders. Also, these order 4–6 running waters have fauna which contains headwater taxa derived from terrestrial ancestors (insects) together with taxa of marine ancestral origin (e.g. mollusks) (**Table 2**) [16].

The dominant energy source for larger rivers (orders 7–10 or greater) is input from the upstream channel network (orders 1–7) plus periodic return flow from the floodplain [16, 18–21]. These larger rivers are usually turbid, and, although adequate light reaches the surface of the water, penetration to the bottom is poor and primary production is restricted. The dominant food resource for the invertebrates is fine particulate organic matter (FPOM). FPOM consists of particles >1 mm in size, organic and mineral particles surface-colonized by bacteria, and algae and microinvertebrates in suspension. The primary mode of feeding for the

Taxa	Primary energy source; and habitat	Food resource category	Habit (mode of attachment, concealment, movement)	FGG
Oligochaeta (segmented worms)	Autochthonous FPOM produced by invertebrate feeding, mechanical breakage of CPOM, and from the stream bank, pools, backwaters, and margins	FPOM (organic particles, coated and colonized by bacteria, including invertebrate feces); deposited on or in the bottom sediments	Burrowers, mostly in fine sediments	GC
Gastropoda (snails)	Autochthonous attached nonfilamentous algae; in riffles	Periphyton: attached nonfilamentous algae and associated FPOM and microinvertebrates	Clingers, on coarse sediments in riffles	SC
Crustacea Amphipoda, <i>Gammarus</i> (scuds) [22], Isopoda, <i>Assellus</i> (sow bugs)	Allochthonous CPOM riparian plant litter; accumulations against obstructions, in backwaters, pools, and stream margins	Conditioned (colonized by microbes, especially aquatic hyphomycete fungi) CPOM plant litter	Burrowers, in plant litter accumulations	DSH
Ephemeroptera (mayflies) Heptageniidae, Ephemerellidae, <i>Drunella</i>	Autochthonous attached nonfilamentous algae; in riffles	Periphyton: attached nonfilamentous algae and associated FPOM and microinvertebrates	Clingers, on coarse sediments in riffles	SC
Baetidae, <i>Baetis</i> Leptophlebiidae, <i>Paraleptophlebia</i>	Autochthonous FPOM produced by invertebrate feeding, mechanical breakage of CPOM, and from the stream bank, pools, backwaters, and margins	FPOM (organic particles, coated and colonized by bacteria, including invertebrate feces); deposited on or in the bottom sediments	Swimmers, in pools, backwaters, and margins, occasionally moving through riffles	GC
Ephemeridae <i>Ephemera</i>	Autochthonous produced by invertebrate feeding, mechanical breakage of CPOM, and from the stream bank; gravel riffles	FPOM (organic particles), including invertebrate feces, coated and colonized by bacteria in the size range that can be pumped through burrows	Burrowers, in gravel riffles where they pump water through burrows	FC
Trichoptera (caddisflies) Limnephilidae ¹ , <i>Hydatophylax</i> , <i>Pycnopsyche</i>	Allochthonous riparian plant litter; accumulations against obstructions in the current and in backwaters or pools	Conditioned (colonized by microbes, especially aquatic hyphomycete fungi) CPOM plant litter	Burrowers, in plant litter accumulations	DSH ¹ (SC)
Hydropsychidae, Philopotamidae	CPOM, FPOM, and small invertebrates in the appropriate size that can be retained in filtering nets; retreats fastened to coarse substrate in riffles	FPOM (organic particles, including invertebrate feces, coated and colonized by bacteria and small invertebrates in the appropriate size that is caught by capture nets)	Clingers, on coarse sediments in riffles	FC
Hydroptilidae	Autochthonous filamentous algae	Individual filamentous algal cell contents	Climbers, in filamentous algal colonies	PC
Rhyacophilidae	Autochthonous in-stream invertebrate prey; riffles or plant litter accumulations	Invertebrate prey of appropriate size	Clingers on coarse sediments or sprawlers in plant litter accumulations	P

Taxa	Primary energy source; and habitat	Food resource category	Habit (mode of attachment, concealment, movement)	FGG
Coleoptera (beetles) Psephenidae (water pennies) Elmidae (adults)	Autochthonous attached nonfilamentous algae; in riffles	Periphyton: attached nonfilamentous algae and associated FPOM and microinvertebrates	Clingers, on coarse sediments in riffles	SC
Dytiscidae (larvae and adults) Gyrinidae (larvae and adults) Hydrophilidae (larvae)	Autochthonous macroinvertebrate prey in pools and backwaters	Invertebrate prey of appropriate size	Sprawlers (larvae), swimmers (adults)	P
Hydrophilidae (adults)	Autochthonous FPOM detritus settled in pools and backwaters	FPOM organic particles plus microbes	Swimmers, in pools and backwaters	GC
Diptera (true flies) Tipulidae, <i>Tipula</i> Orthocladiinae, <i>Brillia</i>	Allochthonous plant litter accumulations against obstructions, in backwaters, pools, and at stream margins	Conditioned (colonized by microbes, especially aquatic hyphomycete fungi) CPOM plant litter	Burrowers, in plant litter accumulations	DSH
Chironomidae (midges) Chironomini Orthocladiinae genera	Autochthonous FPOM deposited in sediments in pools, backwaters, and slow riffles	FPOM (organic particles, including invertebrate feces, coated and colonized by bacteria); deposited on or in the bottom sediments	Burrowers, in fine sediments	GC
Tanytarsini	Autochthonous FPOM in transport in habitats with moderate flow	FPOM (organic particles), including invertebrate feces, coated and colonized by bacteria of appropriate size to be captured	Clingers, on substrates in moderate current	FC
Simuliidae (blackflies)	Autochthonous clingers; coarse sediments, or wood in riffles	FPOM (organic particles), including invertebrate feces, coated and colonized by bacteria in the size range that can be captured by the filtering head fans; suspended in the passing water column	Clingers, on coarse sediments in riffles	FC
Chironomidae Tanypodinae Ceratopogonidae (biting midges, no-see-ums)	Autochthonous small invertebrate prey	Small prey (e.g. midges, blackflies)	Clingers, on coarse sediments in riffles or in plant litter accumulations	P

Allochthonous energy has source from outside the stream channel (riparian zone); autochthonous energy source within the stream; CPOM is coarse particulate organic matter >1 mm size [23]; FPOM is fine particulate organic matter <1 mm size [24]. Conditioned CPOM is riparian plant litter (e.g. leaves and needles); conditioning involves colonization by microbes, especially aquatic hyphomycete fungi [25]; FFG is functional feeding group: SC = scrapers, DSH = detrital shredders; HSH herbivore Shredders, GC = gathering collectors; FC = filtering collectors, PC = algal cell piercers, P = predators [1, 16, 19, 22, 26–28].
¹Many genera have organic cases in the first four instars and are DSH but have mineral cases in the 5th instar and are scrapers.

Table 1.
Typical North American macroinvertebrates of headwater streams (orders 1–3) [22, 27, 29].

Taxa	Primary energy source; habitat	Food resource category	Habit (mode of attachment, concealment, or movement)	FFG
Oligochaeta (segmented worms)	Autochthonous FPOM produced by invertebrate feeding, mechanical breakage of CPOM, and from the stream bank; gravel riffles	FPOM particle in the bottom sediments	Burrowers in the sediments	GC
Bivalvia (bivalve clams) <i>Sphaerium</i> , <i>Pisidium</i>	Autochthonous FPOM (transport from upstream and from river banks, invertebrate feces, and mechanical breakage of CPOM); bottom sediments	FPOM organic particles of appropriate size to be filtered through incurrent siphon of material in transport at water sediment interface	Burrowers (with incurrent siphon above sediment surface to allow for filtering of FPOM)	FC
Crustacea Decapoda (crayfish)	CPOM detritus; rooted aquatic plant beds, pools, backwaters, side channels, and river margins where CPOM detritus accumulates	Fragmenting and decomposing rooted vascular plant tissue (and some live vascular plant tissue)	Sprawlers (in accumulations of CPOM surface and rooted plant beds)	DSH HSH
Crustacea Amphipoda, <i>Hyalella</i>	Autochthonous rooted aquatic plant beds; stems of rooted plants	Periphyton (algae and associated detritus and microarthropods on rooted plant stems)	Climbers (on rooted aquatic vascular plant stems)	SC
Ephemeroptera Ephemeridae	Autochthonous FPOM produced by invertebrate feeding, mechanical breakage of CPOM from bank and riffles	FPOM in the size range that can be pumped through burrows	Burrowers in river bed gravel, sand, mud sediments with sufficient flow to provide FPOM to be pumped through burrow tube	FC
Ephemeroptera Baetidae	Autochthonous FPOM, settled in depositional areas, especially rooted vascular plant beds	FPOM (organic particles, coated and colonized by bacteria, including invertebrate feces)	Swimmers (among rooted aquatic plant beds and backwaters)	GC
Hemiptera Corixidae	Autochthonous rooted aquatic plant beds; stems of rooted plants	Periphyton algae on rooted plant stems	Climbers (on rooted aquatic vascular plant stems)	SC
Ephemeroptera Baetidae	Autochthonous FPOM, settled in depositional areas, especially rooted vascular plant beds	FPOM (organic particles, coated and colonized by bacteria, including invertebrate feces)	Swimmers (among rooted aquatic plant beds and backwaters)	GC
Trichoptera Hydropsychidae	Autochthonous cell contents of filamentous algae	Individual cell contents of filamentous algae		FC

Allochthonous is energy source from outside the stream channel (riparian zone); autochthonous is energy derived within the stream; CPOM is coarse particulate organic matter >1 mm size; FPOM is fine particulate organic matter <1 mm size; conditioned CPOM is riparian plant litter (e.g. leaves and needles); conditioning involves colonization by microbes, especially aquatic hyphomycete fungi; FFG is functional feeding group: SC = scrapers; GC = gathering collectors; FC = filtering collectors; DSH = detrital shredders, HSH = herbivore shredders; PC = algal cell piercers; P = predators [1, 3, 19, 22, 26, 28, 29].

Table 2.
Typical North American macroinvertebrates of mid-sized rivers (orders 4–6).

Taxa	Primary energy source; habitat	Food resource category	Habit (mode of attachment, concealment, or movement)	FFG
Oligochaeta (segmented worms)	Autochthonous FPOM transported from upriver tributaries and settled on or trapped in the bottom sediments	FPOM benthic organic particles colonized by microbes	Burrowers, in the sediments	GC
Bivalvia (large bivalve clams)	Autochthonous FPOM transport from upriver tributaries in the water column past the bottom sediments where the clams reside	FPOM consisting of organic particles colonized by microbes and phytoplankton and zooplankton in suspension	Burrowers, in sediments with siphon above the surface allowing capture and filtration of FPOM in transport	FC
Crustacea (zooplankton) Cladocera, Copepoda	Autochthonous phytoplankton, bacteria, rotifers, and protozoans produced in situ and micro- FPOM in the water column	FPOM consisting of phytoplankton, bacteria, rotifers, and protozoans and microorganic particles	Swimmers, in the water column (limited directed movement, easily carried by any current)	FC
Megaloptera (Dobsonflies) Corydalidae	Autochthonous invertebrate prey on large woody debris along river bank or against point bars	Prey consisting of micro- and macroinvertebrates cohabiting large woody debris (e.g. Diptera Chironomidae)	Clingers, on large woody debris	P
Trichoptera Hydropsychidae	Autochthonous FPOM in transport in the water column from upriver tributaries in the water column past the capture nets on large woody debris where the larval retreats are attached	FPOM consisting of organic particles colonized by microbes and phytoplankton and zooplankton in suspension	Clingers, on large woody debris	GC
Coleoptera (beetles) Dytiscidae, Gyrinidae (larvae and adults), Hydrophilidae (larvae)	Autochthonous macroinvertebrate prey in pools and backwaters	Invertebrate prey of appropriate size	Sprawlers (larvae), swimmers (adults), in backwaters	P
Hydrophilidae (adults)	Autochthonous FPOM detritus plus microbes in backwaters	FPOM detritus consisting of dead organic matter plus microbes	Swimmers, in backwaters	GC
Diptera Simuliidae (blackflies)	Autochthonous FPOM in transport in the water column from upriver tributaries past boulders and large cobbles in rapids and large woody debris surfaces	FPOM consisting of organic particles colonized by microbes in suspension	Clingers, in rapids and on large woody debris	FC
Chironomidae (midges) Chironomini	Autochthonous FPOM in from upriver tributaries and deposited in the	FPOM consisting of deposited organic particles colonized by microbes	Burrowers, in sediments and crevices in large woody debris	GC

Taxa	Primary energy source; habitat	Food resource category	Habit (mode of attachment, concealment, or movement)	FFG
	sediments and crevices on large woody debris			
Tanytarsini	Autochthonous FPOM in transport in the water column from upriver tributaries past large woody debris surfaces along river bank or against point bars	FPOM consisting of organic particles colonized by microbes in suspension	Clingers, on the surface of large woody debris	FC

Allochthonous is energy source 7–10i derived from upstream channel network (orders 1–6); FFG i = functional feeding group: SC = scrapers; GC = gathering collectors; FC = filtering collectors; DSH = detrital shredders, HSH = herbivore shredders; PC = algal cell piercers; P = predators [1, 16, 19, 20, 30, 31].

Table 3.
Typical North American macroinvertebrates of large rivers (orders 7–10).

microinvertebrates (zooplankton) and macroinvertebrates (e.g. clams) of the rivers is filtering (filtering collectors) (**Table 3**) [16].

Thus, the River Continuum model predicts that the small headwater streams will be dominated by invertebrate taxa that are dependent on an allochthonous energy [16]. The most common macroinvertebrates are Detrital Shredders utilizing coarse particulate organic matter (CPOM) plant litter: (DSH) scuds (Amphipoda), several stonefly (Plecoptera), and caddisfly (Trichoptera) families and crane flies *Tipula* (Diptera, *Tipulidae*) are the macroinvertebrates that feed on the plant litter inputs. Certain mayflies (Ephemeroptera) and midges (Diptera, *Chironomidae*) supported by FPOM generated by FFG DSH taxa. Macroinvertebrates of mid-sized rivers utilize autochthonous food resources, especially aquatic plants. Large river invertebrate food chains depend on autochthonous FPOM in suspension delivered from the upstream channel network and the floodplain.

2.2 Microinvertebrates (zooplankton)

The very small lotic microinvertebrate taxa are shared with marine environments, such as Protozoa, Rotifera, Nematoda, and micro-Crustacea (Cladocera and Copepoda) [32]. The unofficial definition of microinvertebrates is individuals smaller than 1 mm. Defined this way, early stages of macroinvertebrates need to be included. The difference is that “true” microinvertebrates do not grow beyond the 1 mm size-defined category. In the vast majority of studies in running waters (almost exclusively in rivers), the term microinvertebrates can be replaced by zooplankton. Zooplankton are small invertebrates that live suspended in the water column and have limited ability to control their location [2]. Studies of running water macroinvertebrates vastly exceed those of zooplankton. The River Continuum project [16] recognized zooplankton as a dominant group in rivers of orders 7–10 together with benthic macroinvertebrate such as oligochaetes, bivalve gastropods, and some micro-crustaceans [1]. Studies of river zooplankton have focused on their role in food chains of fish and organic matter cycling. Although most of the zooplankton inhabit the water column of the river where they filter feed on suspended FPOM [32] the benthic forms filter FPOM from the water column and on depositional FPOM [1, 2, 24].

3. Habitats of lotic invertebrates

3.1 Erosional habitats

Erosional habitats encompass coarse sediments (boulders, cobbles, and gravel) and large wood debris in fast-flowing water (riffles and runs). Because these habitats are well oxygenated, they normally support invertebrate populations that are the most sensitive to degradation of water quality. Microbes in the organic waste can reduce dissolved oxygen levels sufficient to stress-sensitive invertebrates [33, 34]. Erosional habitats are normal features of headwater streams and mid-sized rivers but occur less frequently in large rivers. In larger rivers, erosional habitat is found primarily in sections having a significant change in grade.

Macroinvertebrates adapted to erosional habitats (clingers) include Gastropoda (snails, e.g. Sulcospiridae, *Juga*), Ephemeroptera (mayflies, e.g. Heptageniidae), Trichoptera (stone case-bearing and net-spinning caddis), Plecoptera (stoneflies, predaceous Perlidae), and Coleoptera (Psephenidae, water pennies). The ecological tables in Berg et al. [1] identify erosional habitat adaptations by taxonomic group. Structures, such as suckers, hook, or claws of various sorts, silk that fastens down their retreats or provides anchors, and body shape and behavior that avoids the major force of the current are the main adaptations to erosional conditions [35].

3.2 Depositional habitats

Depositional habitats are drop zones where fine sediments settle out. Substrates of sand, silt, and clay are found in pools, backwaters, and along channel margins. FPOM, and in some cases. CPOM plant litter lotter [23], also accumulates in depositional habitats. These depositional habitats are dominated by sprawlers and burrowers that move across the soft substrate or are concealed beneath it [1]. Some of the Ephemeroptera sprawlers have modified first abdominal gills that cover the remaining gills to protect them from smothering by depositional silt (e.g. Caenidae, Tricorythidae) [1]. Burrowing depositional taxa include Oligochaeta, Ephemeroptera (Ephemeridae), Diptera (Chironomidae midges), and predator Odonata dragonflies (Gomphidae) [1].

3.3 Rooted aquatic vascular plants

Aquatic vascular plants occur in both erosional or depositional habitat but are more common in the depositional areas, especially in larger rivers. The macroinvertebrates associated with vascular plants feed on floating leaves such as Lepidoptera (moth larvae, e.g. Noctuidae) and Coleoptera (beetles, e.g. Chrysomelidae, *Galeracella*) and some Diptera, Chironomidae (midges). These are all herbivore shredders (HSH) that mine leaves or burrow into stems, or feed on roots, especially of *Nuphar*, where they penetrated foot tissue and extract oxygen (Coleoptera, Chrysomelidae, *Donacia*)) [1].

In the Lepidoptera ecology table [1], all genera are described as herbivore shredders (HSH) occurring in lentic (standing water) habitats. Two families (Cosmopterigidae, 180 sp., and Noctuidae, 12 sp.) are in a category “generally lentic” because they also occur in lotic systems. The emergent and floating-leaf plant beds are in backwaters, along margins and in areas of slow current of mid-sized and larger rivers. Some streams of orders 2 and 3 support floating-leaf plants in erosional habitats (e.g. *Valsineria*).

4. Functional feeding groups (FFG)

Investigation of lotic invertebrates has been taxonomy based since its inception [1]. In the 1980s, Robert Penna, a major authority on freshwater invertebrates of the day [2], argued that ecology of freshwater invertebrates must be based on *species*-level taxonomy (personal communication). This goal was, and still is a valid one, but then, and even now, rarely possible to achieve. There are very few groups of lotic invertebrates for which complete species inventories have been accomplished. For example, the most recent compilation of the taxa of aquatic insects of North America [1] allows identification of almost all known genera, but not species, collected in lotic samples. The emphasis is on immature nymphs and larvae. Coleoptera adults, which are aquatic, and adult females of some aquatic insects that enter the water in order to deposit eggs are also keyed [1].

In 1973 and 1974, Cummins [36, 37] argued that while efforts will continue toward expanding the taxonomy of freshwater invertebrates (especially insects), it should be possible to address ecological study of lotic macroinvertebrates by employing analyses of their morphological and behavioral adaptations. The proposal was to use five functional feeding group (FFG) adaptation categories and match them to the five basic food resource categories available in varying amounts in streams and rivers [15, 16, 26, 36, 38]. In this FFG analysis, scrapers are matched with periphyton (attached nonfilamentous algae and associated material), gathering collectors with FPOM deposited on or in the sediments and filtering collectors with FPOM transported in the water column, shredders with CPOM (conditioned plant litter or live vascular plants), and predators with their prey [15, 25, 26, 39, 40].

More recently, a refinement of two more FFG matching categories has been utilized [41]. The shredder category is divided into detrital shredders (DSH) matched with CPOM conditioned plant litter or wood [42] and herbivore shredders with live vascular aquatic plant tissue [41]. Piercers are matched with filamentous algae (**Tables 1–3**) [26, 38]. Taxa that share morphological (e.g. moth parts, body structure, color pattern) and/or behavioral (e.g. movement patterns, silk net-spinning, case construction) adaptations can be grouped in the same FFG. Through parallel or convergent evolution, they share features that result in the same modes of food acquisition. An example is the striking similarity between North American Heptageniidae and Brazilian Leptophlebiidae mayfly nymphs which are both scrapers [26, 38]. Also, as shown in [26], caddisfly genera in three different families (Glossosomatidae, *Glossosoma*; Helicopsychidae, *Helicopsyche*; and Uenoidae, *Neophylax*) and a beetle genus *Psephenus* scrape substrate surfaces in riffles.

A simple picture key can be used to sort macroinvertebrates collected in lotic field samples into FFG categories with an 80% or greater accuracy. This can be accomplished using structural and behavioral characters that can be readily observed in the field on live specimens with the unaided eye or a simple hand lens. For example, case-bearing Trichoptera can be separated based on the materials used in case construction: larvae with organic cases constructed of leaf or wood pieces are detrital shredders (DSH), and those with mineral cases made of sand or fine gravel are scrapers (SC). An example of a key used to separate Ephemeroptera nymphs (lateral abdominal gills) from Plecoptera nymphs (no lateral abdominal gills), separate mayfly scraper nymphs (clinger flat body shape) from mayfly Gathering Collector nymphs (swimmer cylindrical body shape). Dragonfly and damselfly nymphs can be separated from mayfly and stonefly nymphs by an extendible grasping labium (**Figure 1**) [15, 26, 40].

When separating live macroinvertebrates collected in a stream field sample into functional feeding groups, individuals in different taxa that share similar

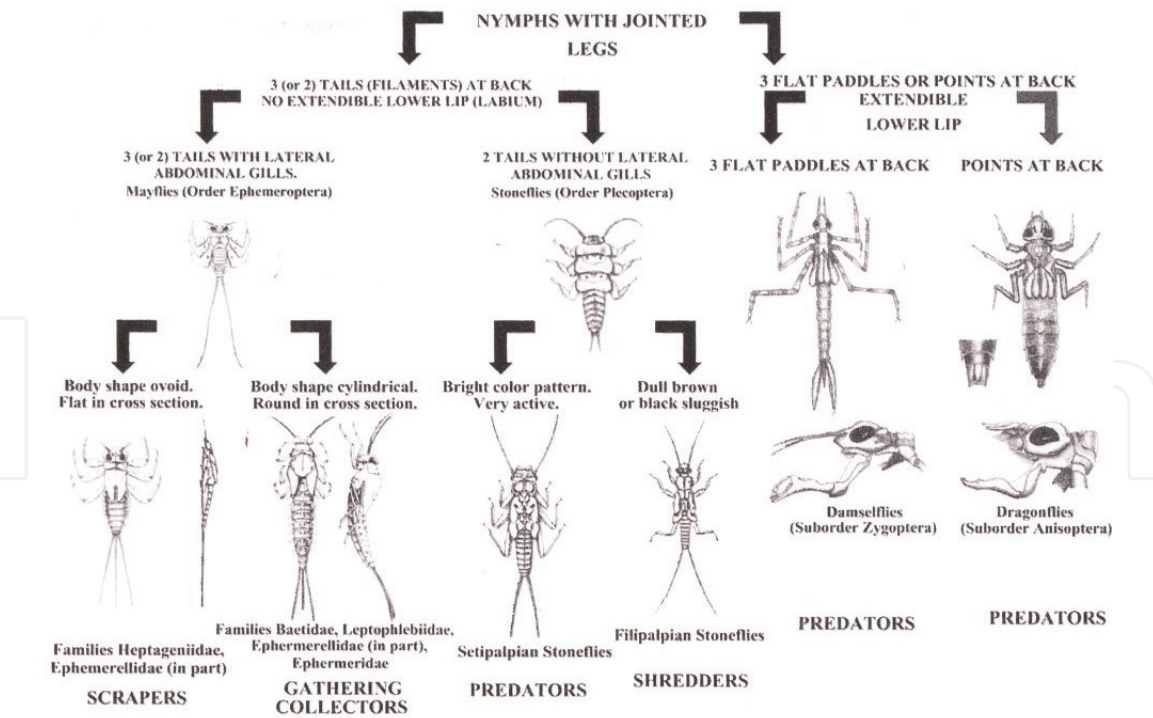


Figure 1. A simple picture key for separating nymphal stream insects into functional feeding groups (FFG). Mayflies and stoneflies are separated by the presence or absence of lateral abdominal gills. Mayflies are separated into scrapers or gathering collectors by body shape. Stoneflies are into detrital shredders or predators by color pattern and activity level. Dragonflies and damselflies are all predators and are separated from all the other nymphs by having extensible, grasping labia (lower lips). Modified from [38].

adaptations are enumerated together. All muffin tin with the wells is marked by FFGs (e.g. SC, GC, etc.). For example, all snails, dorsal-ventrally flattened mayfly nymphs, mineral case-bearing caddisfly larvae, and water-penny beetle larvae are sorted into the scraper (SC) category [40]. Because scrapers usually feed on surfaces in riffles, they are adapted to maintain their location; they are clingers on the substrate surface. Common North American scraper taxa found in running waters are Gastropoda snails that have a rasping radula; Ephemeroptera mayfly Heptageniidae and Ephemerellidae *Drunella* nymphs that are dorsal-ventrally flattened; Trichoptera caddisfly Limnephilidae, *Hydatophylax*, *Pycnopsyche*, Uenoidae, Glossosomatidae, and Helicopsychidae larvae; and flattened Coleoptera water-penny beetle Psephenidae larvae (Tables 1–4) [1, 40]. Similar taxonomic groupings for gathering and filtering collectors, detrital shredders, herbivore shredders, or predators are given in Table 4 and [40].

5. Macroinvertebrates used for evaluation of lotic ecosystem condition

The known North American aquatic insect species in genera for each order found in lotic habitats are listed in the ecological tables in Merritt et al. [43]. No lentic (standing water) genera are included in Table 4. The lotic genera are also assigned to FFGs in Table 4. Every FFG entry in Table 4 is divided into % obligate or facultative number of species. The obligate category is defined as having a maximized % conversion of ingestion to growth. Obligate taxa are predicted to be most affected by environmental changes that alter their food resource. By contrast, the facultative forms are predicted to have flexible food requirements and to be better adapted to adjust to changes in food supplies, but the conversion of ingestion

[illegible]

Taxa	Functional feeding group (FFG) categories														
	Scrapers			Gathering collectors			Filtering collectors			Shredders			Predators		
	Fac.	Obl.	Total	Fac.	Obl.	Total	Fac.	Obl.	Total	Fac.	Obl.	Total	Fac.	Obl.	Total
Lepidoptera															
Crambidae, Noctuide										0	100	100			
Coleoptera															
Larvae and Adults Dytiscidae, Gyrinidae Hydrophilidae Larvae													0	100	100
Hydrophilidae Adults				0	100	100									
Diptera															
Tipulidae, <i>Tipula</i> <i>Holorusia</i>										100	0	100			
Dicranota, Pedicia, <i>Hexatoma</i>													100	0	100
Chironomidae Chironomini				0	84.2	84.2	12.2	0	12.2						
Tanytarsini				26.3	11.3	37.6		0	73.7	73.7					
<p>For each taxon (column 1), the % species for each taxon is apportioned among the FFG categories representing that taxon. Fac. = facultative taxa, that is, these taxa are listed in the ecological tables in [43] as having several alternative FFG classifications. The Fac. values given in the table are the FFG that appears first (as the most likely) of the alternatives of the several presented. If the accompanying obligatory (Obl.) entry for that taxon is 0, this means there were no Fac. possibilities listed in [43]. Similarly, if there is an Obl. entry in the table and a 0 given for the accompanying Fac., this means that no Fac. alternatives were given in entries for that taxon in [43]. If there are % entries in both columns, there are values given for both categories in [43]. When selecting the % to be used to assign the proportion of each FFG to each taxon, the clearest approach would be to use only the Obl. designations throughout; the most conservative approach would be to use the total % values, that is, combining those taxa that are restricted to a given FFG with the most probable Fac. species per genus. The % values in this table will be subject to some changes when [1] is published.</p> <p>¹Early instars of larvae with organic cases are obligate Detrital Shredders (DSH).</p> <p>²Last (5th) instar of larvae with mineral cases are obligate Scrapers (SC).</p> <p>³Because of uncertain Chironomidae taxonomy, the FFG percent values are based on approximate species per genus numbers [43].</p>															

Table 4.
Percent species in genera of North American lotic macroinvertebrates [43].

to growth would be less efficient. Facultative taxa would be predicted to better survive environmental changes [15, 43]. When selecting the % to be used to assign the proportion of each FFG into each taxon, the least ambiguous approach would be to use only the obligate designations throughout; the most conservative approach would be to use the total % values, that is, combining those obligate taxa which are restricted to a given FFG with the most probable facultative species per genus. The % values in **Table 4** undoubtedly will be subject to some changes when [1] is published.

Using counts of numerical abundance of macroinvertebrates in field samples, ratios of the % numerical abundance of FFGs, like those in **Table 4**, can be used to calculate ratios of the FFGs. These ratios have been used as surrogates for stream and river ecosystem attributes [1, 26, 40, 41]. Because such ratios are dimensionless numbers, the resulting calculated ratios are essentially independent of sample size. For example, the FFG ratio from one riffle (coarse sediment) sample produces the same ratio as five samples, or one plant litter sample is the same as five.

A number of FFG ratios that serve as surrogates for running water ecosystem attributes are summarized in **Table 5**. Thresholds for evaluating the ratios are also proposed ([1], Table 6E). The ecosystem attributes can be measured directly, but this usually requires significant equipment, time, and direct tending by researchers. In addition, the actual measurements represent only a fraction of the temporal and spatial scales at which the processes occur. By contrast, the macroinvertebrates continuously monitor ecosystem conditions over their life stages in the water, at least weeks and usually annual or semiannual periods.

Arguably, the most all-encompassing and informative ratio is gross primary production (P) compared to community respiration. The P/R ratio also reflects the relative dominance of autotrophy (energy source within the stream or river relative to energy input from outside the aquatic ecosystem) (**Table 5**) [44–46]. The surrogate macroinvertebrate P/R ratio is all FFGs that depend on autochthonous primary production (algae and vascular plants) compared to all the FFGs that depend on FPOM and CPOM organic matter. That is, scrapers + herbivore shredders + algal cell piercers to detrital shredders + gathering collectors + filtering collectors (**Table 5**) [1, 10, 41, 47]. The P/R ratio that corresponds to a directly measured P/R, using closed, recirculating chambers that monitor dissolved oxygen, of $P/R > 1.0$ is a macroinvertebrate $P/R > 0.75$ (**Table 5**) [19, 44, 45]. The other surrogate ratios described compare detrital shredders available CPOM storage (Detrital Shredder index), relative abundance of filtering collectors to FPOM in transport (Filtering Collector Index), macroinvertebrates that require stable attachment or clinging sites compared to substrate stability, and predator abundance relative to prey available (Predator Index) (**Table 5**).

The ecological tables in [1, 43] also include US Environmental Protection Agency values for macroinvertebrate susceptibility/resistance that are indicators of pollution. As a general rule, the EPT Index will indicate the vulnerability of macroinvertebrates to stream and river water quality degradation. This index compares the abundance of Ephemeroptera (mayflies) + Plecoptera (stoneflies) + Trichoptera (caddisflies) to the rest of the macroinvertebrate fauna; the more dominant the EPT, the less polluted the stream or river is rated [33, 48].

Organic pollution reduces dissolved oxygen (DO) levels in freshwater due to the large oxygen demand by microbial respiration [33]. Significant reduction in DO is a major stressor for aerobic (DO requiring) invertebrates. This includes those with gills or some with cutaneous respiration: Mollusca, Crustacea, Ephemeroptera, Plecoptera, Odonata, Trichoptera, Megaloptera, some Lepidoptera, some Coleoptera larvae, and some Diptera. Oligochaeta and some Chironomidae have biochemical adaptations that allow them to tolerate low DO levels [1].

Lotic ecosystem attributes	FFG ratios	Symbols	Proposed thresholds	Descriptions
Autotrophic to heterotrophic Index (P/R, primary production/ community respiration)	Scrapers + herbivore shredders to detrital shredders + gathering collectors + filtering collectors	SC + HSH to DSH + GC + FC	P/R > 0.75	A P/R > 0.75 corresponds to P/R > 1 when primary production and community respiration are measured directly
Shredder Index (CPOM/FPOM) [27, 28]	Detrital shredders to gathering collectors + filtering collectors	DSH to GC + FC	CPOM/FPOM >0.5 (fall–winter); CPOM/FPOM >0.25 (spring–summer)	The CPOM/FPOM >0.5 during fall–winter when fast processed deciduous plant litter enters streams; > 0.25 in spring–summer when slower processed needles and wood remain in streams
Filtering collector Index (suspended FPOM to deposited FPOM)	Filtering collectors to gathering collectors	FC to GC	FC/GC > 0.5	FC > 0.5 favors filtering collectors capturing FPOM in transport; impaired lotic systems usually have values much higher than 9.5
Substrate stability Index (stable coarse substrates to unstable fine sediments)	Scrapers + filtering collectors + herbivore shredders to detrital shredders + gathering collectors	SC + FC + HSH to DSH + GC	Stable substrates/ unstable substrates >0.5	Stable substrates (bedrock, boulders and cobbles, large wood, and rooted plants) provide attachment and clinger sites greater than unstable fine sands and clay. Channel disturbance can reduce stable substrates or flush out fines
Predator Index (top-down to bottom-up control of macroinvertebrate communities)	Predators to scrapers + detrital shredders + herbivore shredders + filtering collectors + gathering collectors	P to SC + DSH + HSH FC + FC	Predators/all other FFGs present =0.10–0.15	The abundance of predators between 10% and 15% of the lotic macroinvertebrate community indicates sufficient prey (turnover to support predators)

Table 5.
Functional feeding group (FFG) ratios as surrogates for running water lotic ecosystem attributes and proposed thresholds.

However, there are stream and river macroinvertebrates that are adapted to breathe atmospheric oxygen (AO) by returning to the water surface to obtain air, such as some Diptera (the best known example being Culicidae mosquitoes). Others like some Coleoptera adults trap air in body surface hairs or under elytra that they carry under the surface and from which they extract DA. An index that would

predict poor ability of lotic macroinvertebrate taxa to survive under declining DO conditions would be taxa with gills as a proportion of those taxa with adaptations, structural, behavioral, and/or biochemical, that allows them to breath AO.

The most widely used method to obtain qualitative samples in streams and shallow rivers is the D-frame dip net. The net usually has a 1.0 or 0.5 mm mesh size. However, nets with a 0.25 mesh are recommended to retain midges (Chironomidae and Ceratopogonidae) and early stages or instars of macroinvertebrate taxa. The samples collected with the D-frame net can be considered semiquantitative when fixed time (e.g. 30 s) sampling is employed. This method has been used to compare stream/river reaches, stream/river habitats, seasons, etc. D-frame net sampling has also been used to collect composite samples, that is, an effort to collect widely from all habitats in a stream or river reach [41, 47]. In such complete reach survey samples, it is useful to keep the major habitat samples (riffles, pools, CPOM plant litter accumulations, large wood) separate and compute a composite value by calculating a total value by combining the data after the samples have been processed. This method is even more useful if a percent of the stream/river bottom in the sample reach is covered by each habitat type. This is particularly helpful if the derived FFG ratios described above are to be used as surrogates for lotic ecosystem attributes. If the same person is used to collect the D-frame samples, the results are more comparable; if that same person is also used to collect quantitative Surber net samples, the variances are similar. Ratios and proposed threshold values are presented in **Table 5**.

6. Quantitative sampling

The two most commonly used quantitative devices used for sampling stream macroinvertebrates are the Surber and Hess samplers [3, 49]. Both of these confine an area of stream bottom and rely on the stream current to transport material disturbed by the hand into attached collection nets. The Surber net has a metal frame that delineates the bottom area to be collected with an erect frame at the back that holds the collection net. The net is washed into a sorting tray (usually a white enamel pan) for partial or complete processing in the field, or the contents are rinsed directly into a bottle and preserved in 70% ETOH. The Hess sampler is a cylinder that defines the bottom area sampled. It has mesh side panels and a collection net to retain material disturbed from the bottom similar to the Surber net. With both collection devices, the sample collected is better handled if cobbles are removed individually and scrubbed into the net and discarded. As with qualitative sampling, the net mesh size is a significant issue. Both Surber and Hess samplers are available with 1 or 0.5 mm mesh. However, as stated previously, a 0.25 -mm mesh is better because it will retain early instars and smaller species are lost with the coarser mesh sizes. If the samples are to be sorted for FFGs, it is highly recommended that this be done with live specimens following collection.

7. Concluding remarks

In the past and present, and predictably in the future, abundance and composition of stream and river invertebrate communities have been, and will be, the primary measuring biological tool used to evaluate ecosystem condition and to predict environmental change and vulnerability. These animals, because they continuously monitor the stream and river environment throughout their aquatic life, can provide better insight than the spatially and temporally and limited physical


and chemical grab samples or even recording electrodes. Unlike algal cells and microbes, macroinvertebrates can be observed with the naked eye and a simple hand lens. They are far less migratory than fish that respond to an environmental stressor by leaving. Because running water macroinvertebrates are ubiquitous, easily collected, and observed and can be classified into meaningful categories that chronicle the condition of freshwater resources, they are the perfect vehicle for use by basically and easily trained local volunteers. This yields a potential army of environmental stewards who can enlist our very best freshwater monitors—the invertebrates. Both conventional morphological taxonomy and DNA barcoding will undoubtedly continue to lead to ever-better answers to what is it (classification), but this is only the initial step to answering the ultimate question—what does it do (function)? So, students, researchers, and armature naturalists, let us continue on this promising track.

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