

# *The Distribution and Abundance of Invertebrates in the Grande Ronde River, Oregon, U. S. A.*

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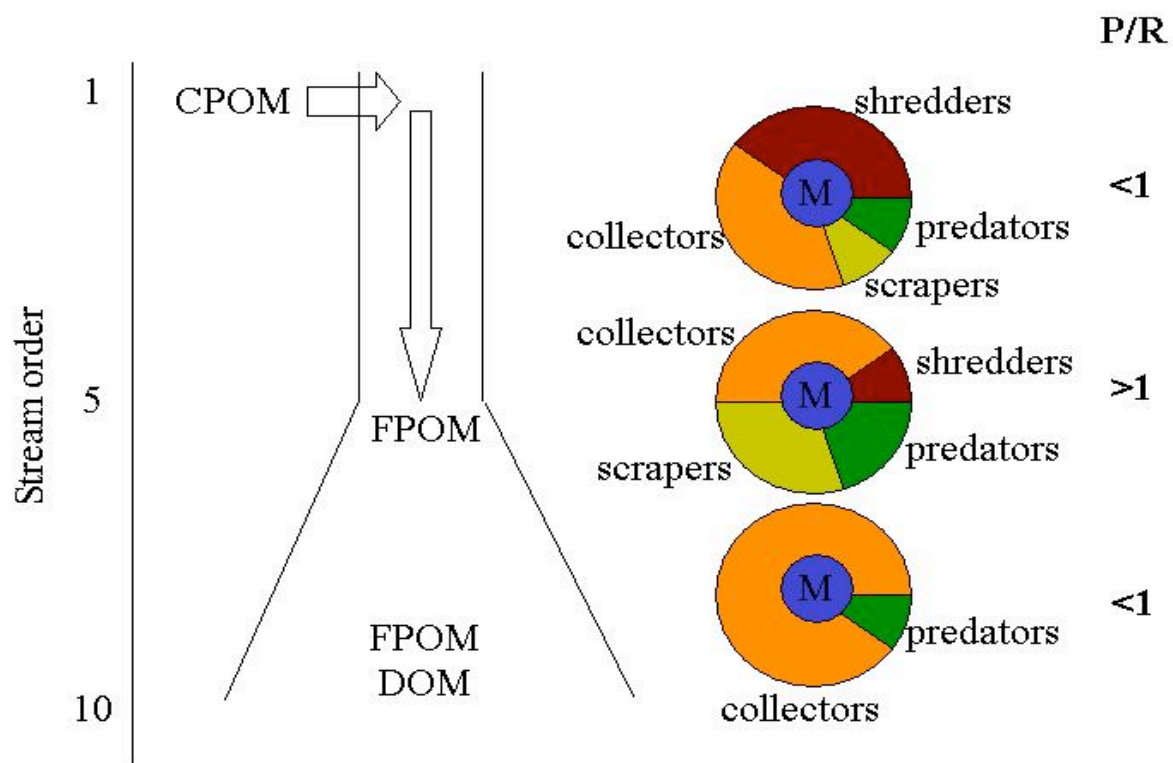
## **ABSTRACT**

The River Continuum Concept (RCC; Vannote et al. 1980) predicts that the composition of invertebrate communities will change gradually in the longitudinal direction with the concomitant, smooth gradation of physical stream features. However, alternative hypotheses incongruous to the RCC have explained the distribution of invertebrates with different factors (e.g., geomorphic stochasticity, tributaries, flow regime, floodplains). The Grande Ronde River in northeastern Oregon and southeastern Washington provides a perfect example for evaluating these different views. In this paper I discuss in depth the RCC and its opposing hypotheses, followed by a summary detailing the important ecological attributes of the invertebrates found in northeastern Oregon. I then present the major abiotic and biotic factors controlling the distribution and abundance of aquatic invertebrates, and provide the expected invertebrate communities to be found in different reaches of the Grande Ronde River. I conclude by reconsidering the RCC in light of the distribution and abundance of the Grande Ronde River's invertebrates.

## **INTRODUCTION**

Understanding the distribution and abundance of invertebrates in streams has long been a goal of aquatic ecologists, for the immature stages of aquatic insects are a vital link between primary producers and fish. However, due to the extreme spatial and temporal complexity of lotic (i.e., running-water) systems, a concept accurately and satisfactorily describing the ecology of invertebrates has been elusive. One attempt at explaining the distribution of functional feeding groups of aquatic invertebrates is the widely known River Continuum Concept (RCC; Vannote et al. 1980). It is rooted on the idea that lotic systems display a longitudinal, smooth gradation of physical and biotic variables (e.g., discharge, stream width, canopy cover, etc), and that such a continuum results in a predictable change in the composition of the proportions of invertebrate functional feeding groups. Specifically, the RCC states that allochthonous material

(i.e., material produced outside the stream), in the form of coarse particulate organic matter (CPOM, such as leaf litter), is the dominant source of carbon in the headwaters, and thus the major proportion of the aquatic insect community will be made up of those most adapted to exploiting that resource: shredders (Fig. 1). In the middle reaches, due to the lower ratio of channel area covered by riparian vegetation and the concomitant increase in sunlit water, autochthonous (i.e., organic material produced within the stream) carbon inputs will become significant (e.g., periphyton=attached algae), and thus grazers (i.e., scrapers) will become the dominant type of insect primary consumer (Fig. 1). Finally, in the lower reaches, where depths and turbidity are great (and hence primary production is low), the major carbon source will be that which has been processed by the communities upstream (i.e., fine particulate organic matter, FPOM, and dissolved organic material, DOM), and thus the major functional feeding group will be collectors (Fig. 1).



**Figure 1.** Graphical representation of the RCC, where P/R is the ratio of photosynthesis to respiration. (<http://www.esf.edu/efb/schulz/Limnology/RCC.jpg>)

Despite the pervasiveness and general acceptance of the RCC, many objections have been raised. Montgomery (1999), for instance, took issue with the fact that the RCC ignored the impacts of variable, local geomorphic effects (e.g., mass movements) on habitat, with the corollary influence on the invertebrate community. As an alternative, Montgomery (1999) proposed the Process Domains Concept (PDC), which essentially states that habitats are primarily formed by local, physical disturbances, which are in turn determined by larger scale processes *ad infinitum*. Thus, a process domain is a region characterized by a unique set of geomorphic controls. For example, a wet drainage on a low relief landscape with a substantial fine sediment load would be expected to meander, with the consequent creation of the riffle-pool sequence. In this case, the climate would be determining the amount of water available, the topography and geology would route that water and determine the shape and cross-section of the channel, and the lateral erosion on the outside of the meander bend would give rise to a process domain, the pool. Implied in this is that, due to the stochasticity of these nested, geomorphic processes, a smooth gradation in physical and biotic factors will not be observed, contrary to the RCC.

Benda et al. (2004a, 2004b) also addressed the evident spatial and temporal heterogeneity of rivers with their Network Dynamics Hypothesis (NDH). Central to their idea is that certain tributary confluences contribute substantially to the structure and function of main stems, and in that process give rise to physically and chemically diverse geomorphic patches. For instance, a large tributary will deposit its sediment at its junction with the main stem, creating a fan. That fan will often cause a decrease in the gradient of the main stem upstream (with an attending decrease in deposited grain size), while simultaneously increasing the gradient downstream, which is characterized by a resultant coarser substrate. Thus, the tributary's fan creates a range of grain sizes within a relatively small area. Many aquatic insects (e.g., Chironomidae; Armitage et al. 1995) are known to segregate according to grain size; hence, the diversity of substrate sizes around a tributary fan should consequently have a greater diversity of invertebrate species relative to an equal-size area with a narrower range of grain sizes.

As a result, the NDH is consistent with the PDC in that it recognizes distinct geomorphic patches which, even if spaced widely apart, will have a greater similarity to each other than to adjacent yet different types of geomorphic patches (Thorp et al. 2006). This, combined with the

discontinuous distribution of tributary confluences, implies that invertebrate communities will also be spatially discontinuous and will not conform to the predictions of the RCC.

Another criticism of the RCC is that it ignores lateral inputs, i.e., the role of floodplains in lotic systems. In response, Junk (1989) proposed the Flood Pulse Concept (FPC), which describes the relationships between floodplains and river channels. The main tenet of the FPC is that the major force determining the ecology of a floodplain-river complex is the flood pulse. The frequency, magnitude, and duration of the recurring connection and disconnection between a channel and its adjacent floodplain is the physical template to which the biota are adapted. Floodplains, which are often rich in nutrients through a variety of mechanisms (e.g., nitrogen fixation by cyanobacteria, accelerated decomposition, high rates of primary productivity), provide a bountiful, if transient, feast for consumers of all types and sizes. Additionally, due to their shallow depths and hence warm waters (and the aforementioned high food concentration), floodplains promote rapid growth rates and are thus ideal nursery grounds for fish and other organisms. When the water level recedes and the floodplain is returned to terrestrial biota, the channel provides a refuge or link to more favorable habitats (e.g., cooler upstream reaches). Thus, river-floodplain complexes are characterized by the superimposition of life history strategies upon the flood pulse, and are relatively independent of the longitudinal processes that govern non-floodplain river stretches.

Poff et al. (1997) addressed the temporal dimension with their Natural Flow Regime (NFR) concept. They argued that five characteristics of discharge significantly structure lotic communities: magnitude (the size of discharge), duration (how long a given discharge lasts), frequency (how often a given discharge occurs), predictability (the seasonal timing of a given discharge), and flashiness (the rate of change of discharge size). For instance, flood-stage discharges often deliver substantial amounts of large woody debris (LWD), which provide cover and food for a myriad of organisms until it decomposes. The frequency and duration of those large discharges determine how often and how much of that lost LWD will be replaced. Some species are specifically adapted to the predictability of a given discharge; for example, the eggs of some invertebrates undergo diapause in ephemeral streams during the summer when there is *no* discharge (Brittain 1990). A high flashiness can often lead to large longitudinal shifts of invertebrates due to drift, and can concomitantly lead to high mortality of less mobile species due to stranding (Corrarino and Brusven 1983).

All of these seemingly opposing hypotheses provide a conceptual framework with which predictions about the distribution and abundance of invertebrates can be proposed and tested. The Grande Ronde River in the northwestern U. S. A., due to the paucity of work performed on its invertebrate communities, provides the perfect opportunity to evaluate the concepts summarized above.

## **AQUATIC INVERTEBRATES OF THE GRANDE RONDE RIVER**

Despite the lack of information regarding the constituents of the invertebrate community of the Grande Ronde, surveys from adjacent watersheds and anecdotal accounts (e.g., from fly fishermen) provide a rough idea of the invertebrates that are present in the system. Following is a summary of the most common clades, with charts listing the salient features of the more diverse aquatic orders.

### *Ephemeroptera: the mayflies*

Ephemeropterans are hemimetabolous (i.e., exhibit incomplete metamorphosis with three life stages: egg, immature juvenile or naiad, and sexually mature adult) insects that pass the egg and naiad stages in the water. Usually stimulated by the cue of a specific water temperature, most ephemeropterans emerge (i.e., metamorphose from the juvenile to adult stage) in the spring or summer (Takemon 1990). Mayflies commonly transform from naiads to adults at the water's surface, leaving them vulnerable to a variety of predators (e.g., fish). Unique among all insect orders, ephemeropterans have two terrestrial adult forms: the sexually immature subimago and the sexually mature imago (Brittain 1990). Most species are univoltine (i.e., have one generation per year), and the subimago/imago stage rarely lasts more than 24 hours (Brittain 1990).

Mayfly naiads are characterized by gills running the length of the abdomen and either two or three tails (McCafferty 1981). Subimagos and imagos are easily recognized by the upright posture of their wings when at rest, since they cannot fold them over their backs (McCafferty 1981). Naiads can be classified by morphology into four ecologically important groups: swimmers, clingers, crawlers, and burrowers (Merritt and Cummins 1978, Schollmeyer 1997). Each group's morphology predisposes them for exploiting a specific habitat: swimmers are defined by their elongate, fusiform bodies, which decrease frictional drag and allow for rapid locomotion in slower waters; clingers and crawlers have stout, thick limbs and dorsoventrally

flattened bodies that allow them to cling to rocks in fast currents; and burrowers have long gill filaments which allow them to maximize their oxygen uptake and survive in burrows within the silty sediments of lentic (i.e., slow or still) waters (Fig. 2). While mayflies have members



**Figure 2.** Adaptive morphologies of mayfly naiads; note abdominal gill filaments on all three species. a) Swimmer (Baetidae; <http://www.troutnut.com/hatch/90/Mayfly-Baetidae-Blue-Winged-Olives/4>). b) Crawler (Ephemerellidae; <http://www.digital-museum.hiroshima-u.ac.jp/~insect/Insects-Notes/Insects/Ephemeroptera/Ephemerellidae/Drunella%20cr yptomera.htm>). c) Burrower (<http://www.uwsp.edu/water/biomonitoring/index3.htm>).

in each functional feeding group, most species graze on periphyton and therefore the order is often dominant in reaches lacking significant shade (Cummins and Klug 1979, Carlson et al. 1990). The families known to commonly occur in Oregon's lotic waters are listed in Table 1 (Merritt and Cummins 1978, Corrarino and Brusven 1983, Porter and Meehan 1987, Tait et al. 1994, Li and Wright 1995).

Family	Functional Feeding Group(s)	Common Habitats	Emergence Times	Ecological Group
Baetidae	grazers	lentic, lotic	all year	swimmers
Ephemerellidae	grazers	coarse-grained, lotic waters	spring, summer	crawlers
Heptageniidae	grazers	fast, gravelly streams	summer	clingers
Leptophlebiidae	grazers, shredders	Low velocity stream regions	spring, summer	crawlers
Siphonuridae	Grazers, predators	Low velocity stream regions	spring, summer	swimmers

**Table 1.** Major mayfly families of the Grande Ronde and their important ecological attributes.

*Plecoptera: the stoneflies*

Plecopterans are easily distinguished from mayflies by their naiads, which lack gills down the entire abdomen and possess only two cerci, or tails (McCafferty 1981). Due to their primitive gill structure, plecopterans are confined to well-oxygenated waters (Fig. 3a; Cutter 1991). Egg-hatching success is greatest in cool water temperatures (e.g., 10-15 °C), and suffers tremendously in water over 20°C (Brittain 1990). These morphological and physiological constraints, coupled with their generally flattened, elongate bodies and well-developed, clawed legs, restrict stoneflies to cool streams with moderate-to-fast currents (Fig. 3b; Merritt and Cummins 1978, McCafferty 1981).

a)



b)



**Figure 3. Stoneflies.** a) Chloroperlid stonefly naiad; note lack of abdominal gill filaments (<http://ceratium.ietc.wvu.edu/IWS/Images/Biota/Animalia/Arthropoda/Insecta/Plecoptera/Chloroperlidae>). b) Perlid stonefly naiad exhibiting a morphology adapted for rocky riffles (<http://www.hlug.de/medien/wasser/gewaesserguete/ref/permar.htm>).

Like mayflies, stoneflies are hemimetabolous, passing the egg and naiad stages in water; however, they have only one terrestrial adult stage (Milne and Milne 1998). While a few families have species that metamorphose to adults in winter, most emerge in spring and summer. Adults capable of feeding on various plant materials (e.g., pollen, plant buds) are common throughout the order; those that do generally have longer adult lifespans than those that do not (McCafferty 1981, Brittain 1990). Many species' eggs and naiads undergo diapause through the summer, allowing them to persist in highly stressful conditions (e.g., ephemeral streams; Brittain 1990). A few families are primarily predaceous, but most are detritivorous and are thus

important in the decomposition and assimilation of organic matter. Common families of Oregon's streams and some of their important features listed in Table 2 (Kerst and Anderson 1974, Merritt and Cummins 1978, Porter and Meehan 1987, Cutter 1991, Tait et al. 1994, Li and Wright 1995, Schollmeyer 1997, DeLong and Brusven 1998, Wooster and DeBano 2006).

Family	Functional Feeding Group(s)	Emergence Season(s)
Pteronarcidae	shredders, grazers	spring
Peltoperlidae	shredders, grazers	spring
Nemouridae	shredders, collectors	throughout the year
Capniidae	shredders	winter
Perlidae	predators	spring, summer
Perlodidae	predators, a few grazers	summer
Chloroperlidae	collectors, grazers, predators	summer
Taeniopterygidae	shredders, collectors, grazers	winter, spring

**Table 2.** Major stonefly families of the Grande Ronde River and their notable ecological features.

#### *Hemiptera: the true bugs*

Hemipterans are aeropneustic (i.e., air-breathing), hemimetabolous insects that often pass all three life stages in water. The naiads and adults look very similar, with both possessing the order's characteristic beak and anteriorly thickened, posteriorly membranous fore wings (McCafferty 1981). Most species acquire oxygen via a bubble of air obtained from the atmosphere (i.e., a plastron). The familiar water boatmen (Corixidae) and backswimmers (Notonectidae) have oar-like fore limbs, making them efficient, powerful swimmers (McCafferty 1981).

Most aquatic species in the order are univoltine and have females that oviposit in spring (McCafferty 1981). With the exception of the corixids, all families are predators that feed primarily on washed-in terrestrial and aquatic insects (Merritt and Cummins 1978). Due to their skilled swimming ability, need for atmospheric oxygen, and food preferences, they are most frequently found in shallow, lentic habitats (Merritt and Cummins 1978).

#### *Coleoptera: the beetles*

Coleoptera is the largest order of insects in the world. The adults are defined by their hardened fore wings, or elytra (McCafferty 1981). All members are holometabolous (i.e., go



through four life stages: egg, larva, pupa, and adult), and the order contains species that spend one, many, or all life stages in the water (Merritt and Cummins 1979). They also have representatives in each functional feeding group: the elongate, slow-water larvae of Dytiscidae are voracious predators, Elmidae contains both scrapers and shredders, and many water-scavenging beetles (Hydrophilidae) are collectors (Merritt and Cummins 1978).

Elmidae, the riffle beetles, are characteristic of fast, well-oxygenated streams and hence are useful indicators of water quality (McCafferty 1981). The long tarsal hooks of the adults, and the clawed legs and opercular hooks of the worm-like larvae, enable both life stages to effectively cling to the substrate in fast currents (Merritt and Cummins 1978, McCafferty 1981). They are undoubtedly important in Oregon streams as they are widespread, locally abundant, and occasionally dominate invertebrate fauna biomass (Tait et al. 1994, Li and Wright 1995).

#### *Megaloptera: the dobsonflies and alderflies*

Megaloptera is a holometabolous order characterized by having only the larval stage passed in water; the egg, pupal, and adult stages are all terrestrial (Merritt and Cummins 1978). Most species emerge in early summer, and the adults usually survive for only a few days (Merritt and Cummins 1978). After fertilization, the females deposit their eggs on structures above a stream or lake (e.g., rocks, bridge abutments); the larvae drop into the water at night after hatching (Merritt and Cummins 1978).

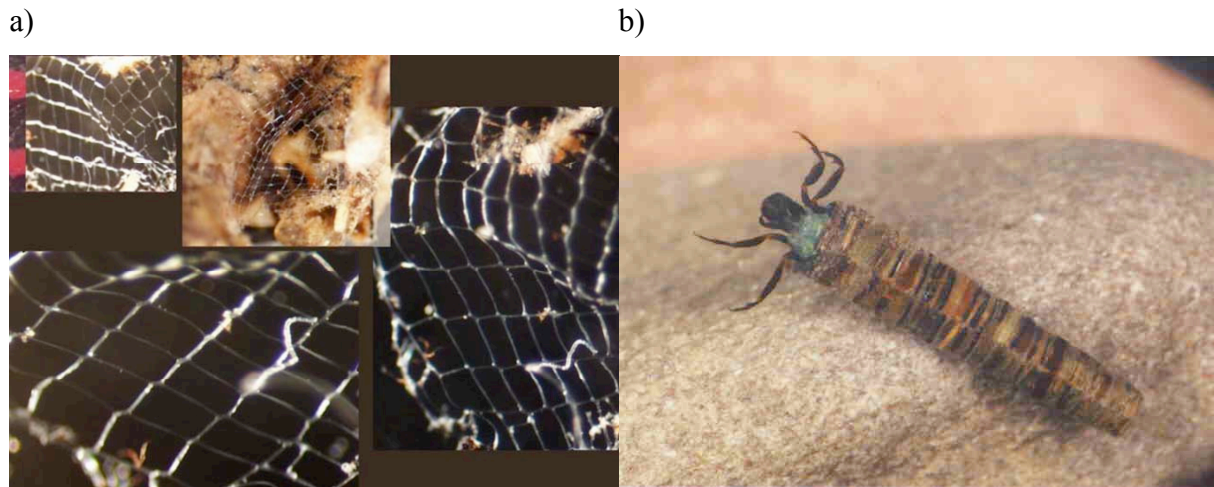
Members of the family Corydalidae (dobsonflies and fishflies) are most commonly found in flowing, well-oxygenated streams, whereas Sialidae (the alderflies) is more general in its distribution, inhabiting both lentic and lotic waters (McCafferty 1981). Larvae from both families possess well-developed thoracic legs, which, combined with their elongate, somewhat dorsoventrally compressed body profiles, facilitates their efficient movement among cobbles in moderate currents (Merritt and Cummins 1979, McCafferty 1981). All species in the order also have abdominal filaments which increase the surface area for oxygen diffusion; some corydalids (e.g., *Corydalus*) also have gill tufts, further enhancing their ability to extract oxygen (Merritt and Cummins 1979, McCafferty 1981). They are voracious predators, feeding frequently upon such invertebrates as hydropsychid and black fly larvae (McCafferty 1981).

*Trichoptera: the caddisflies*

Trichopterans are diverse, holometabolous insects that generally pass all three immature stages aquatically (McCafferty 1981). Larvae have caterpillar-like bodies, often with gill filaments running down the length of the abdomen (e.g., Limnephilidae), and two hooked, anal prolegs at the posterior tip of the body (Merritt and Cummins 1978). Adults superficially resemble moths (not surprising, as the two clades are sister groups), but can be easily recognized by the fine hairs covering the wings (Merritt and Cummins 1978).

Caddisflies exhibit two main modes emergence: the pupae crawl out onto an exposed surface (e.g., *Dicosmoecus*), or emerge at the water's surface (e.g., *Brachycentrus*; Merritt and Cummins 1978, Schollmeyer 1997). Most adults live less than a month, and, reflecting the diversity of the order, the females oviposit in a variety of ways: dipping their abdomens on the water's surface, diving or swimming to the bottom and attaching their eggs to the substrate, or laying eggs on riparian vegetation overhanging the water (LaFontaine 1981, Schollmeyer 1997).

The ability of caddis larvae to make and spin silk is of paramount importance to the biology of the order. This remarkable capacity determines not only the feeding style exhibited by a species, but also its vulnerability to predators and its benthic position within a stream. One major way (of three) that silk is used is in the construction of cases (Fig. 4b). These cases can be made out of a number of different materials (e.g., sand, stone, twigs, leaf chunks) that are chosen for specific ecological functions. For instance, glossosomatid caddisflies make dome-shaped stone cases, which provide both a ballast and a hydrodynamic shape that allows them to inhabit cool, rapid riffles (LaFontaine 1981). The limnephilid *Dicosmoecus* larva avoids fish predation by having an impenetrable stone tube case (Johansson 1991). Tube cases of Limnephiloidea act as ventilation chambers, thus allowing these caddisflies to exploit warm, lentic waters (LaFontaine 1981).



**Figure 4.** a) Nets made by various species of Hydropsychoidea (<http://www.xerces.org/CD-ROM%20for%20web/id/Trichoptera/index.htm>). b) Brachycentrid displaying a case made of plant material (<http://www.hlug.de/medien/wasser/gewaesserguete/ref/bramon.htm>).

The second major use of silk is in the construction of nets, which is a defining feature of the Hydropsychoidea (Fig. 4a). Members of this superfamily use nets for straining the current of drifting morsels, with a mesh size and structure woven to capture a specific type of food in a certain water velocity (Anderson 1976, LaFontaine 1982, Allan 1995). However, due to this behavior (and their lack of abdominal gill filaments), hydropsychoidids are restricted to well-oxygenated, lotic habitats where their nets can be continually replenished with food (LaFontaine 1981). Additionally, hydropsychoidid densities can be limited by a lack of suitable net-spinning sites, further limiting their distribution (Lancaster et al. 1988).

The free-living family Rhyacophilidae displays the third significant function of silk: rappelling lines. These caddisflies, which lack distinct gill structures, are voracious predators inhabiting riffles in mountain streams (Anderson 1976, LaFontaine 1981). As they search cracks and crevices of the substrate for prey, they maintain and adjust their position in the current by using a silk thread attached to upstream rocks (LaFontaine 1981).

Table 3 lists families found in Oregon's running waters and their pertinent ecological characteristics (Anderson 1976, Merritt and Cummins 1978, LaFontaine 1981, McCafferty 1982, Porter and Meehan 1987, Tait et al. 1994, Li and Wright 1995, Delong and Brusven 1998, Tall et al. 2006).

Family	Functional Feeding Group	Silk Function	Main Habitat
Rhyacophilidae	predators, a few grazers	rappelling thread	cool riffles
Hydropsychidae	collectors	nets, retreats	cool riffles
Philopotamidae	collectors, grazers	nets	riffles
Psychomiidae	collectors	retreats	riffles
Glossosomatidae	grazers	stone cases	cool riffles
Hydroptilidae	grazers, collectors	purse-type case	cool riffles
Limnephilidae	shredders, collectors, grazers, and predators	tube cases	all habitat types
Brachycentridae	shredders, collectors, grazers	tube cases	cool headwaters
Lepidostomatidae	shredders	tube cases	cool headwaters
Phryganeidae	shredders, predators	tube cases	slower stream reaches

**Table 3.** Caddisfly families of the Grande Ronde River and their ecological attributes.

#### *Diptera: the true flies*

Diptera contains some of the most ecologically and medically important insect families in the world. While all species in the order are holometabolous, three major aquatic families found in Oregon are different enough for each to warrant its own separate discussion.

#### Tipulidae: the crane flies

Tipulids are important species with aquatic larvae (e.g., *Tipula*) that are characterized by their retracted heads, lack of thoracic limbs, and possession of star-shaped spiracular discs at the tips of their abdomens (McCafferty 1982). These spiracular discs allow the worm-like larvae to breathe atmospheric oxygen (McCafferty 1982). Most species pupate in moist shoreline areas, from where they emerge in spring (Merritt and Cummins 1978, McCafferty 1982). The adults, distinguished by their large, mosquito-like shape and extremely long legs, generally oviposit during the late afternoon and evening hours (Cutter 1991).

*Tipula* and *Hexatoma* are both found in Oregon and inhabit lentic and lotic waters (Li and Wright 1995, DeLong and Brusven 1998). In streams, both genera are most prevalent among benthic detritus, where they either shred decaying organic matter or prey on other invertebrates (Merritt and Cummins 1978). Conversely, another Oregon genus, *Antocha*, frequents solid

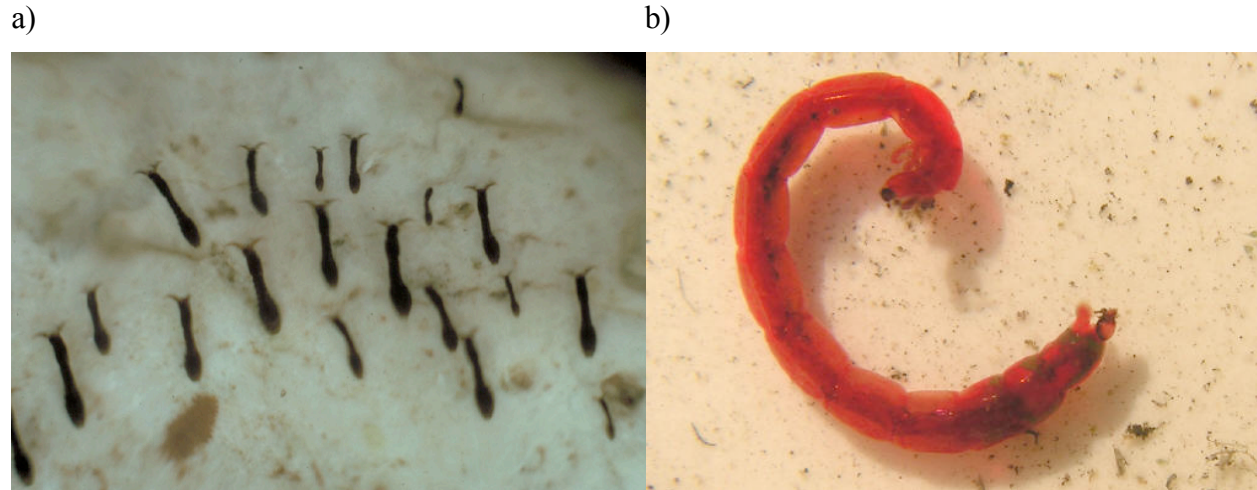
substrates exposed to fast-flowing water, where it collects drifting organic material (Merritt and Cummins 1978).

#### Simuliidae: the black flies

Simuliid larvae are easily identified by their swollen abdomens, which are attached via posterior hooklets to silken mats woven onto stones (McCafferty 1981, Allan 1995). Larvae are invariably found on rock surfaces in very thin, laminar water, from which they sieve food with fan-like mouth brushes (Fig. 5a; McCafferty 1981, Corrarino and Brusven 1983). Due to this very specific habitat requirement, changes in discharge often cause the larvae to detach from their rocks en masse and drift in the current (Corrarino and Brusven 1983). Black flies pupate in cocoons attached to hard surfaces, from which adults emerge by pulling themselves out of their shucks and rising to the water surface in bubbles of air (Merritt and Cummins 1978). Females of many species oviposit on the water surface after the acquisition of a blood meal and mating (Merritt and Cummins 1978).

#### Chironomidae: the midges

Chironomidae is the most diverse, widespread, and abundant aquatic insect family in North America. The small, wormy aquatic larvae are defined by the presence of two pairs of prolegs (i.e., fleshy appendages): one set is placed just posterior to the head, the other at the tip of the abdomen. Cued by photoperiod and/or temperature, aquatic pupae emerge into mosquito-like adults at the water's surface (Armitage et al. 1995). In most perennial, ice-free waters, different species of midges emerge throughout the day and in all seasons. Most species have adults that lack a proboscis and thus do not feed, live only a few days, and have females that commonly oviposit on the water's surface at dusk (Armitage et al. 1995).



**Figure 5.** Diptera. a) Simuliid larvae; note enlarged abdomen and mouth brushes used for collecting organic material (<http://insects.tamu.edu/extension/youth/bug/bug139.html>). b) Chironomid larva containing hemoglobin (<http://lechpietrzak.inter.net.pl/stawy/bezkregi/muchowki.htm>).

Regardless of the theory that best explains the infiltration of this family into virtually all aquatic nooks and crannies (e.g., genetic plasticity, lineage age, short generation times), the fact remains that chironomids are everywhere (Armitage et al. 1995). Larvae are particularly diverse and abundant in fine-grained sediments, where they construct burrows of various shapes and feed by collecting or grazing algae and detritus (Merritt and Cummins 1978, Armitage et al. 1995). Due to hypoxic (i.e., low oxygen) conditions of such areas, chironomids have evolved adaptations (such as high affinity hemoglobin in *Chironomus attenuatus*) that maximize their uptake of oxygen (Fig. 5b; McCafferty 1981, Armitage et al. 1995). Hence, midges are capable of surviving in polluted or highly eutrophic waters. From this fact, coupled with the relative intolerance of stoneflies, mayflies, and caddisflies to disturbed waters, a ratio of ephemeropteran, plecopteran, and trichopteran abundances versus chironomid abundance can be calculated. This ratio, commonly known as the EPT:chironomid, serves as an index of water quality: streams with high EPT:chironomid ratios are often pristine, while those with low ratios are frequently degraded (Allan 1995, Li and Wright 1995).

#### *Astacidae: the crayfishes*

Crayfishes are familiar, fully aquatic benthic crustaceans found in both lakes and streams. They are easily identified by their lobster-like morphology, which consists of five pairs of legs

(the most anterior of which are modified into pincers), two body segments (the cephalothorax and abdomen), and a hard exoskeleton composed of chitin and calcium carbonate (Bronmark and Hansson 1998). They are secretive animals that frequently hide in burrows and under rocks and only become active during low-light periods (Goldman and Rundquist 1976, McCafferty 1981). While they are omnivorous and thus eat a variety of materials (e.g., periphyton, other crustaceans, their own species), they most commonly feed on detritus (Mason 1974, Mason 1976, Bronmark and Hansson 1998). Additionally, they are the primary prey of many fish, especially smallmouth bass *Micropterus dolomieu* (Goldman and Rundquist 1976, Bronmark and Hansson 1998).

The dominant species in northeastern Oregon, *Pacifastacus leniusculus* (Porter and Meehan 1987, DeLong and Brusven 1998), mates in the autumn as water temperatures fall (Mason 1974). Eggs are attached to the underside of the female's abdomen, where they remain until hatching in the following spring (Mason 1974). Juveniles subsequently stay attached to the mother for approximately two weeks; after their second molt, they become free-living (Bronmark and Hansson 1998). Time to sexual maturity is generally three years, an unusually long time period for an aquatic invertebrate (Mason 1976).

#### *Amphipoda: the scuds*

Scuds are shrimp-like creatures that reach a length of about 20 mm and possess 7 pairs of legs (McCafferty 1981). They are common in lentic and lotic waters that have mean summer temperatures greater than 10°C (Bousfield 1953). Scuds are found in shallow habitats, where they frequent benthic regions rich in periphyton and detritus (McCafferty 1981). As a result, areas with high structural complexity (e.g., thick macrophyte beds) may host tremendous numbers of these animals (Gray et al. 1983, Bronmark and Hansson 1998). Like crayfishes, scuds are omnivorous, though periphyton and detritus are their main foods (Bronmark and Hansson 1998).

Mating begins in spring for *Hyaella azteca*, the main scud of northeastern Oregon (Porter and Meehan 1987, DeLong and Brusven 1998), when eggs are fertilized by a male and deposited into the female's brooding pouch (Gibbons and Mackie 1991). Juveniles remain within the pouch for a few days and are then released, reaching sexual maturity within about a

month (de March 1977, Gibbons and Mackie 1991). Reproduction often continues unabated until fall, at which time adults and subadults will overwinter (Gibbons and Mackie 1991).

### *Gastropoda: the snails*

The distinctive shells, the single muscular foot, and the lazy movements of snails make them well known to casual observers. They are found in both lakes and streams, and are most common in shallow areas where they feed on detritus and periphyton (McCafferty 1981, Bronmark and Hansson 1998). Snails exhibit two modes of obtaining oxygen: going to the water surface and breathing air into a rudimentary lung (the method of pulmonate snails), or by passing water over a gill (the method of prosobranch snails; Bronmark and Hansson 1998). They can be either hermaphroditic or dioecious (i.e., have two distinct sexes) and have lifecycles of one or more years (Bronmark and Hansson 1998).

## **DISTRIBUTION AND ABUNDANCE OF AQUATIC INVERTEBRATES IN THE GRANDE RONDE RIVER**

### **Factors affecting distribution and abundance**

Aquatic invertebrates are adapted for specific abiotic and biotic factors; thus, their distributions and abundances are dependent upon both the location and density of those factors. It is expected that the location where the most factors are in the preferred range for a given invertebrate will host the highest density of that species. Therefore, in order for us to understand where in the Grande Ronde a taxon (e.g., Hydropsychidae, Corydalidae, etc) will be, it is necessary to review the factors that most influence an invertebrate's ecology.

While the number of factors that could affect a lotic invertebrate is seemingly endless, five are disproportionately and universally important: current velocity, substrate type and size, temperature, oxygen, and riparian vegetation.

Rivers are defined by the fact that their water is running. As a result, some (e.g., Statzner and Hilgner 1986) have argued that hydraulics is the most important factor in determining the makeup of a river's invertebrate community. Regardless the truth of that statement, current velocity undoubtedly affects three vital aspects of an invertebrate's life: food acquisition, dislodgement, and dissolved oxygen concentration. As previously mentioned, black fly larvae



are always found in a thin sheet of high-velocity water, where their fan-like mouth brushes sieve virtually all of the water of its suspended organic material (McCafferty 1981, Corrarino and Brusven 1983). Additionally, hydropsychid caddisflies build their nets with a structure suited for a certain water velocity. Baetid mayflies are streamlined to reduce the drag they face when swimming in riffles, while the dorsoventrally flattened body of heptageniids allows them to avoid fast currents by slipping under rocks (Allan 1995). Increasing current velocity results in more turbulence and hence higher rates of oxygen diffusion, and thus allows cold stenothermic taxa (e.g., plecopterans) to survive in unusually warm water.

Substrate type, size, and stability are important for protection, food, and its effects on current velocity. Many taxa are adapted for living within or on top of a substrate of a certain grain size: *Hexagenia* mayflies burrow into silts, the flattened water pennies (Psephenidae) are most common on the undersides of boulders, and stoneflies, as their name suggests, are often found clinging to cobbles (McCafferty 1981, Allan 1995). A stable substrate provides an immediate retreat and one likely to persist in times of peak discharge, thus affording greater security than more labile zones to cover-seeking invertebrates. For instance, plecopteran densities were highest in immobile gravel and cobble substrates of an Ozark stream (Philips and Kilambi 1994). Substrates that are composed of a significant amount of organic material (e.g., leaf litter, woody debris) offer a diversity of food resources and shelters; as a result, the density of invertebrate individuals in such areas is often very high (Allan 1995). Some species (e.g., *Agapetus* caddisflies) are adapted for exploiting eddies created by cobble-sized substrates that provide food and a refuge from the current, and are thus restricted to such areas (Wellnitz et al. 2001).

Temperature is the cue most responsible for orchestrating the lifecycle of invertebrates. Both the actual temperature (measured in degree-days) and its rate of change are important in determining the time period from oviposition to hatching (Ward and Stanford 1982). Given unlimited food supplies, juveniles grow faster in warmer water since metabolic rates (and hence food assimilation and tissue building) are directly proportional to temperature (Ward and Stanford 1982). While photoperiod plays a role in cueing emergence, it is nearly always coupled with and overshadowed by temperature (Allan 1995). Temperature regime, combined with degree-days, often determines the number of generations a given insect displays per year, with the number of generations increasing with decreasing latitude or elevation (Ward and Stanford

1982, Allan 1995). Because oxygen solubility decreases with increasing water temperature, temperature can often limit the longitudinal distribution of stenothermic invertebrates through this mechanism (Allan 1995).

Oxygen is necessary for all animals, and its concentration is intricately tied to the previous three factors. Increasing substrate size and current velocity increases turbulence, which leads to higher rates of oxygen diffusion (Allan 1995, Mount 1995). As mentioned above, when water temperature increases, dissolved oxygen concentration decreases. Additionally, high densities of periphyton can cause large diel swings in oxygen concentration, with hypoxic conditions occurring at night due to periphyton taking up oxygen for respiration but not replenishing it via photosynthesis. As a result, certain oxygen-sensitive, benthic species (e.g., crawler mayflies) may expose themselves to predation by moving to the tops of stones where the current velocity (and thus oxygen concentration) is highest (Wiley and Kohler 1980).

Riparian vegetation is vital for the health of lotic communities, and its effects are both indirect and direct. Indirectly, abundant riparian vegetation stabilizes stream banks and thus acts as a sediment sink, leading to increased grain sizes (Allan 1995, Mount 1995); consequently, these streams also tend to be deeper. Shading provided by riparian vegetation often results in a decrease in water temperatures and periphyton density (Oregon Department of Environmental Quality 2000, Ebersole et al. 2003). Directly, the leaves and branches of riparian vegetation serves as a food resource created outside the stream (i.e., allochthonous). This input and how it is processed is a major factor controlling the longitudinal distribution of aquatic invertebrates according to the RCC (Vannote et al. 1980). Thus, riparian vegetation's effects on the aquatic community are widespread and significant.

### **The expected distribution and abundance of invertebrates in the Grande Ronde River**

So now that we know the attributes of invertebrates in the Grande Ronde and factors controlling their distribution, what will be the most common taxa in the different river reaches? The headwaters of the Grande Ronde (river-mile 175) are characterized by cold, moderately flowing water, coarse-grained substrates, and a significant, though not complete, canopy (Fig. 6a; Oregon Department of Environmental Quality 2000, Fissekis, A., Hersh-Burdick, R., Stewart, J., White, J, this volume). As a result, the incomplete canopy should supply a significant amount of CPOM in the form of leaf litter while still allowing enough sunlight

through to the water to support a sizeable periphyton population. Hence, the invertebrate community is expected to be dominated by robust populations of shredders (e.g., Nemouridae, Leptophlebiidae, Tipulidae) and grazers (e.g., Baetidae, Elmidae, Glossosomatidae). Additionally, oxygen-sensitive collectors (e.g., Hydropsychidae) and predators (e.g., Rhyacophilidae) should make up significant portions of their respective functional feeding groups. This community composition would be reflected by a high EPT:chironomid ratio.

a)

b)



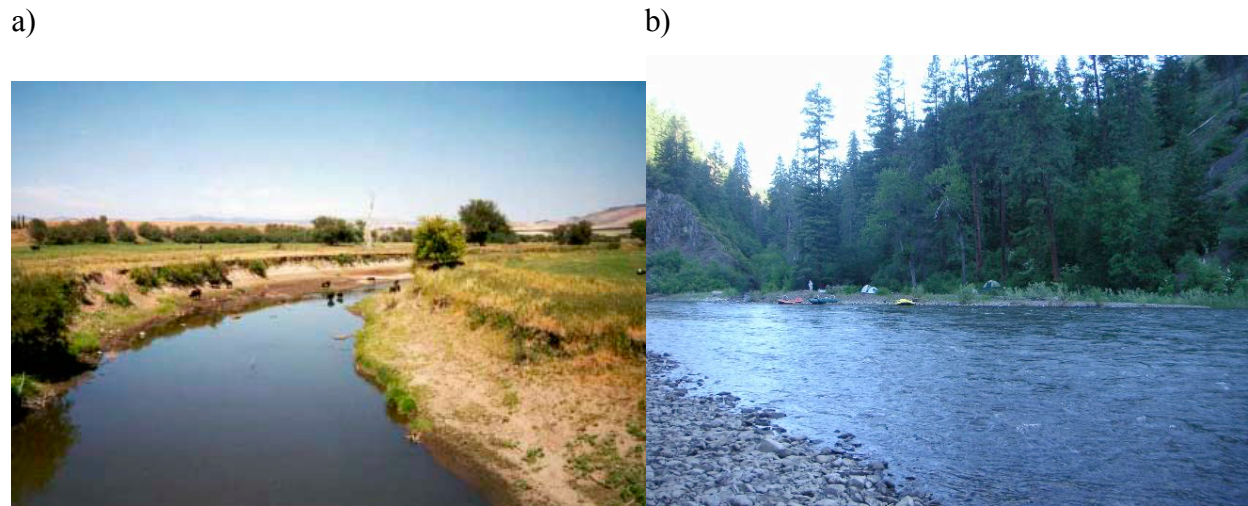
**Figure 6.** a) Well-shaded, coarse-grained headwaters of the Grande Ronde River (<http://arcweb.sos.state.or.us/county/images/scenic/ohrp/scenicunion14.htm>). b) Grande Ronde River at Vey Meadows displaying finer sediment and no riparian vegetation (Oregon Department of Environmental Quality 2000).

Further downstream in Vey Meadows (river-mile 167) the physical characteristics of the river change substantially. The gradient lessens, substrate becomes finer, riparian vegetation is nearly absent, and temperature reaches a local peak (Fig. 6b; Oregon Department of Environmental Quality 2000, Fissekis, A., Hersh-Burdick, R., Stewart, J., White, J, this volume). While these features are no doubt the result of meadow topography, they are likely magnified by copious grazing that occurs in the area (Lawson, A., this volume). Hence, this region should be characterized by dense periphyton mats and increased FPOM from upstream CPOM processing. These carbon sources, coupled with the high temperatures and finer substrates, create an ideal habitat for chironomids. Concomitantly, the lowered water quality, lack of leaf litter, and decreased current velocities (due to the lower gradient) would likely result in a situation found

by Tait et al. (1994) in tributaries of the nearby John Day River: fewer plecopterans and hydropsychids. Thus, the EPT:chironomid ratio should decrease significantly.

The stretch between Vey Meadows and the Grande Ronde Valley (river-miles 156-131) can be somewhat thought of as a recovery zone, where riparian vegetation once again encroaches upon the banks and the channel slope increases (Oregon Department of Environmental Quality 2000). However, water provided by the numerous tributaries in this stretch have widened the river substantially; thus, less of a canopy shades the river than in the headwaters. Consequently, these physical characteristics result in a reach that is warm, flowing moderately, and has coarse-grained sediment (Fissekis, A., Hersh-Burdick, R., Stewart, J., White, J, this volume). Concurrent with these conditions should be dense periphyton growths and significant FPOM. Thus, this reach would likely be dominated by hydropsychid collectors and grazing mayflies and caddisflies (e.g., Hydroptilidae, Baetidae, Heptageniidae). Additionally, the higher water velocities and coarser substrate increase oxygen concentrations, which, when considered with this reach's other characteristics, provide favorable habitat for predaceous stoneflies. Hence, this reach's EPT:chironomid ratio should be intermediate between that of the headwater's and Vey Meadows' ratios.

The stretch of river that flows through the Grande Ronde Valley bears little resemblance to any of the other reaches, for it is by far the most anthropogenically altered (Lawson, A., this volume). Channelization, grazing, irrigation diversions, urban development, and the naturally low gradient of the valley creates a river that completely lacks riparian vegetation, is extremely warm, occasionally suffers hypoxic events due to thick growths of aquatic vegetation, and has very fine sediment and low current velocities (Fig. 7a; Oregon Department of Environmental Quality 2000, Fissekis, A., Hersh-Burdick, R., Stewart, J., White, J, this volume). As a result, it is prime habitat for warm-water loving hemipteran and coleopteran predators (e.g., notonectids, dytiscids) and tolerant chironomids (Tall 2003). Conversely, Minshall et al. (1992) found a paucity of both grazers and collectors in a similarly degraded segment of the Salmon River; hence, few mayflies, caddisflies, and stoneflies are likely to be found in this region. Thus, this river reach will have the lowest EPT:chironomid ratio found in the Grande Ronde River.



**Figure 7.** a) Grande Ronde River in the Grande Ronde Valley, exhibiting a lack of riparian vegetation and eroded banks (Oregon Department of Environmental Quality 2000). b) Grande Ronde River around river-mile 80; note coarse-grained material in lower-left foreground (<http://www.whitewatercampsites.com/Grande%20Ronde/index.php>).

As the river leaves the valley (~river-mile 95) and enters an erosion-resistant canyon formed by flood basalts emplaced during the Miocene, it increases its gradient and velocity significantly for a second and final time (Reidel 1998, Oregon Department of Environmental Quality 2000, C. Jeffres pers. comm. 2007). Consistent with the greater slope is the increase in grain size (Fig. 7b). Shading is minimal due to both the river's width and lack of canopy; thus, periphyton and FPOM are the major carbon sources, and water temperature remains high. However, two tributaries, Lookingglass Creek (river-mile 85) and the Wenaha River (river-mile 46), locally cool the temperature of the Grande Ronde at their respective confluences (Hersh-Burdick, R., this volume). Hence, this reach should contain a high population of collectors (hydrpsychids, chironomids) and grazers (mayflies, amphipods); additionally, predatory stoneflies should be present throughout the reach but especially abundant at the mouths of the two tributaries. The EPT:chironomid ratio should reflect these parameters by being higher (with local peaks at the mouths of the Wenaha River and Lookingglas Creek) than in the Grande Ronde Valley.

The final stretch of the Grande Ronde (river-mile 46 to river-mile 0) flows through arid grasslands with few trees and thus lacks a canopy of any kind. As a result, temperatures,

periphyton biomass, and FPOM should be very high. Point and mid-channel bars are present, while the high-velocity main channel remains dominated by coarser sediments. These physical characteristics are favorable for grazers (e.g., Baetidae, Heptageniidae, gastropods) and collecting caddisflies (e.g., Hydropsychidae); they are especially conducive to collector-feeding chironomids. Additionally, the high velocities should keep oxygen concentrations high enough to maintain some grazing and predaceous stoneflies. Thus, the EPT:chironomid ratio should be in between those values obtained from the reaches in the Grande Ronde Valley and within river-miles 95-46.

## CONCLUSIONS

So, does the sketch of invertebrate distribution in the Grande Ronde River above show a pattern predicted by Vannote et al.'s RCC (1980)? On the surface, no. The most glaring and obvious departures from the RCC's smooth gradient are the discontinuities caused by tributaries (e.g., the Wenaha River's cooling of water temperature) and changes in geomorphology (e.g., decreased gradients and grain sizes in Vey Meadows and the Grande Ronde Valley). In fact, these discontinuities and their effects on invertebrate communities are predictions of Montgomery's PDC (1999) and Benda et al.'s NDH (2004*a*, 2004*b*). Additionally, the nonexistence of stoneflies in the Grande Ronde Valley followed by their reappearance downstream intimates that tributaries may be a source of water quality-sensitive invertebrates for the main stem; this further heightens the importance of tributaries in structuring main stem communities. Also, high magnitude flows can cause large-scale displacements of invertebrates, and thus may be a force replenishing impoverished downstream reaches (Corrarino and Brusven 1983, Allan 1995). Thus, the NFR concept may, coupled with the NDH, adequately explain the presence of stoneflies downstream of the Grande Ronde Valley.

These discontinuities may seem to be incongruous with the RCC and therefore refute its claims. However, subtracting out Vey Meadows, the Grande Ronde Valley, and the two cooling tributaries would leave a river with a very smooth change in the proportions of the functional feeding groups, supporting the predictions of the RCC. Thus, the river conceptualized by the RCC can be thought of as a longitudinal base upon which complexity, in the form of lateral (e.g., tributaries and floodplains), temporal (e.g., flow regime), and geomorphic features, are

superimposed. Hence, the Grande Ronde River does not reject the RCC, but merely shows it to be incomplete.

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