The importance of stream invertebrates to riverine ecosystem function
by Erika L. Gallo

INTRODUCTION

The Earth's running waters, from small springs, brooks and ephemeral streams to the great rivers like the Mississippi and Columbia comprise only about 0.0001% of the water on earth (Allan, 1996). Although small in comparison to the world's oceans, streams and rivers are essential in global biogeochemical processes, such as particulate transport and nutrient cycling; and are an indispensable component of the global hydrologic cycle. In addition, running waters provide numerous benefits for plants, wildlife and humans. Streams and rivers transport water and nutrients over long distances, provide habitat for numerous species of plants and animals, provide recreational use to people, and sustain the livelihood of many communities, such as the Native American and farming communities of the Klamath basin (Class Reader, 2003.)

There is a delicate balance between streams and their surrounding ecosystem. However, this balance has been altered by human disturbances such as agriculture, urban development, impoundment, channelization, mining, forest fire suppression, road construction and species introduction and subsequent invasion (Harding et al. 1998; Norris and Thoms, 1999; LaBonte et al. 2001; Class Reader, 2003), all of which have lead to severe stream degradation and loss of stream biodiversity (Vinson and Hawking, 1998). The streams within the Klamath basin have been affected by numerous human disturbances, which include road construction and subsequent increases in the stream sediment load, impoundment, which has resulted in decreased water flows and higher water temperatures, surface water diversions for mining, urban and agricultural use, and the transformation of numerous riparian wetlands to pasture grazing and farm land (Class Reader, 2003).

The downstream effects of watershed degradation are numerous, and scientists are only beginning to understand their long term impacts. Harding et al. (1998) found that sustained stream habitat degradation caused the fish species composition to shift from a forest stream type where fish are dependent on the stream substrate for foraging and breeding, to a species composition similar to that found on a stream adjacent to agricultural areas, where the fish are primarily bottom dwellers and filter feeders. Vinson and Hawkins (1998) found in their extensive literature review that the total number of taxa found in a particular stream decreased as the frequency of disturbances to their habitat increased.

Each physical and biological stream component plays a unique role in maintaining stream integrity. The importance of stream invertebrates becomes apparent when they are examined within the context of rivers as ecosystems that are composed of physical and biological gradients. The River Continuum Concept is a model that scientists utilize to discern the various components of running water ecosystems, and has improved our understanding of the interactions between biotic and abiotic ecosystem components. In this paper, I discuss the role of invertebrates in the River Continuum Concept (RCC) as defined by Functional Feeding Groups (FFG), and the use of stream invertebrates as biological indicators of stream health based on their taxonomic descriptions.

The River Continuum Concept:

In order to be able to explain and visually illustrate the complexities of a river, scientists have developed the River Continuum Concept (RCC) (Vannote et al, 1980). The River Continuum Concept is a model that tries to explain how the physical and biological characteristics of a river change in a downstream direction. The RCC largely focuses on the interaction of stream invertebrates with their habitat and food resources.

The foundation concept of the RCC states that rivers have physical gradients which are influenced by the surrounding environment; natural disturbance regime, local hydrology and upstream conditions, and they in turn impact and define the biological components of the stream (Vannote et al. 1980). Figure 1 is a visual representation of the RCC which indicates the various possible sources of headwater streams, and the biotic and abiotic changes within the river and associated riparian zone as the river increases in size and moves downstream (Craig, 2002).

In the following pages, I explain the functional feeding classification of invertebrates and their role in stream nutrient cycling and primary production as consumers of organic matter and prey.

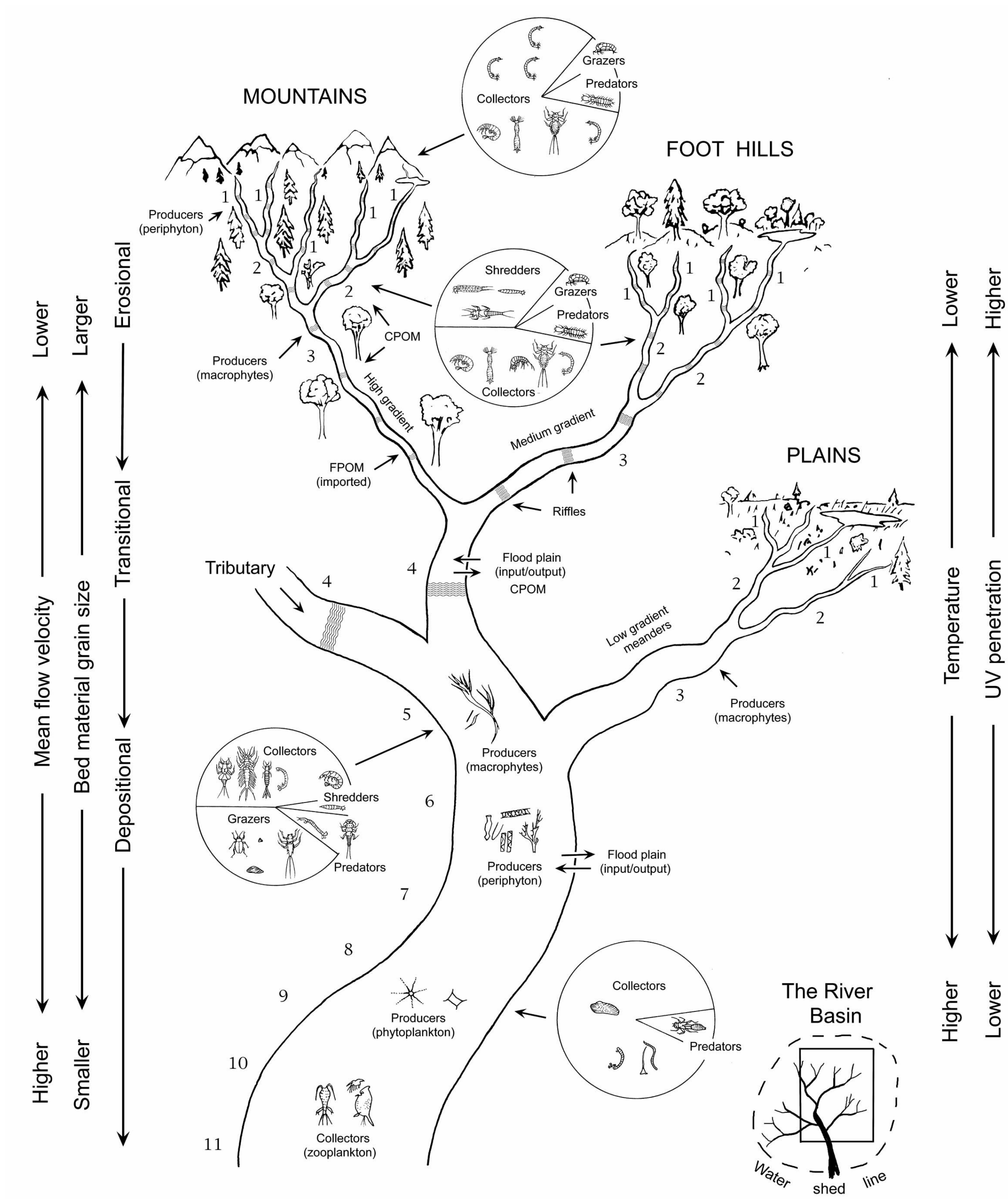

Figure 1. A visual representation of the River Continuum Concept (from Craig, 2002)

Feeding Classification of Invertebrates

Stream invertebrates are essential to stream nutrient cycling by consuming and transforming organic matter. There are 5 major functional feeding groups into which stream invertebrates can be classified: shredders, gathering-collectors, filtering collectors and scrapers (grazers). Most aquatic invertebrates are not obligate feeders, meaning that they are not restricted to one type of food or feeding strategy (Steen, 1971), and therefore do not exclusively fit into only one of the FFG categories (Merritt and Cummings, 1996). Numerous studies suggest that stream invertebrates demonstrate preferential feeding, which depends on the food resources available (Chaloner and Wipfli, 2002, Burrell and Ledger 2003). However, the classification of stream invertebrates into functional feeding groups is a useful tool that enhances our understanding of stream nutrient cycling and trophic interactions, which impact stream integrity and function. Following is a brief explanation of each functional feeding group:

Shredders

To many scientists, shredding invertebrates are the most important organisms along a river continuum because they set off the nutrient cycling processes within a stream (Graca, 2001). Shredding invertebrates are the dominant FFG in low order streams, where the main food source is coarse particulate organic matter (CPOM) (Vannote et al. 1980, Allan, 1996). Large sized organic matter such as animal carcasses, leaves, needles and woody debris are termed coarse particulate organic matter (CPOM) and are the primary inputs of nutrients into the rivers (Vannote et al., 1980; Allan, 1996b; Merritt and Cummings, 1996). The mouth parts of shredding invertebrates function much like scissors, which they use to cut and shred apart CPOM. Generally, shredding invertebrates consume CPOM particles greater than 1mm in size (Merritt and Cummings, 1996). Through chewing and fecal production, shredding invertebrates transform of CPOM to fine particulate organic matter (FPOM) (Merritt and Cummings, 1996;

Allan, 1996), and contribute to the incorporation of organic nutrients into the foodweb (Graca, 2001). The organic matter that shredding invertebrates consume can be nutritionally poor, therefore they will consume large quantities of CPOM, which will translate into high rates of organic matter breakdown into FPOM (Allan, 1996). Through this process, shredding invertebrates make the previously unavailable organic matter resources available to numerous stream organisms. Common shredding invertebrate taxa are found among amphipods, Ephemeroptera (mayflies), Plecoptera (stoneflies), Diptera (flies and midges) and Trichoptera (caddisflies) (Merritt and Cummings, 1996; Graca, 2001)

Gathering Collectors

Stream invertebrates labeled as gathering collectors consume FPOM and ultra-fine particulate organic matter (UFPOM) found on the stream substrate (Vannote et al. 1980; Graca, 2001). Collectors contribute to the further decomposition of FPOM by collecting and feeding on organic matter that settles out of the water column into the stream bed, which is generally smaller than 1mm in size (Merritt and Cummings, 1996). The mouth parts of gathering collectors function much like a broom, though which they can sweep and collect FPOM and UFPOM from the stream substrate. Gathering collectors depend on the organisms associated with FPOM, such as fungi and bacteria, in order to derive nutritional value from the food that they consume, and will preferentially feed on FPOM that has been colonized by biofilms (Vannote et al. 1980; Allan, 1996). Common collecting taxa include members of the Ephemeroptera (mayflies), Plecoptera (stoneflies), Diptera (flies and midges), nematodes, oligochaetes, crustaceans and gastropods (Allan, 1996).

Scrapers (Grazers)

Scrapers or grazing invertebrates are the primary consumers of benthic autotrophs. They feed on attached algal communities (periphyton) and biofilms (Vannote et al. 1980; Allan, 1996; Graca, 2001). Their mouthparts, which act much like chisels, are specially adapted to remove periphyton and biofilms of less than 1mm in size attached to rocks, woody debris and aquatic macrophytes (Merritt and Cummings, 1996). Scraping invertebrates are limited to stream reaches where production periphyton and biofilms occurs; therefore they will be most abundant in middle stream reaches (Vanotte et al., 1980). In their foodweb study, Marks, Power and Parker (2000) found that grazing invertebrates significantly impact stream primary production and periphyton species composition. In their experimental enclosures, algal primary production decreased from approximately 2.5 g/m^2 to 0.5 g/m^2 when grazing insects were present in their experimental enclosures. This decrease in algal production was due to changes in algal species composition, which respond to the presence or absence of grazing invertebrates. In the presence of grazers, highly productive filamentous algal species were replaced by less productive prostrate algal species. Less productive prostrate algae are more difficult to consume and are better adapted to withstand grazing. Common grazing taxa include members of Ephemeroptera (mayflies), gastropods, Lepidoptera, Coleoptera (Allan, 1996).

Filtering Collectors

Like their functional feeding group names states, filtering collectors consume organic matter suspended in the water column (Merritt and Cummings, 1996; Graca, 2001). Suspended organic matter includes phytoplankton, FPOM and UFPOM (Allan, 1996). Filtering collectors are dominant feeders in high order streams, where phytoplankton is abundant. Filtering feeders may be benthic or planktonic. Planktonic filter feeders include taxa such as rotifers, copepods, cladocerans and Diptera larva (Allan, 1996). Benthic filter feeders include many species of caddisflies, whom spin nets on the stream substrate to collect organic matter from the water column (Merritt and Cummings, 1996). Filtering mechanisms in this group of organisms can vary greatly. For example, cladocerans pump water through their abdomen, which contains a filtering apparatus that collects suspended particulate matter. Other organisms, such as Simuliidae dipterans (black fly larvae), possess large fans in their mouth, which they use to collect the suspended particulate matter from the water column (Merritt and Cummings, 1996).

Predators

Predators are organisms that derive their metabolic energy from living animal tissue (Merritt and Cummings, 1996; Graca, 2001). Predators feed in a variety of ways. Some predators consume their prey whole or in pieces, but some possess piercing mouth parts which function much like a straw, enabling the predator to extract nutrients from its prey without having to chew it or shred it (Allan, 1996, Merritt and Cummings, 1996). In addition, some predators are ambush predators, while others search for their prey (Allan, 1996). Invertebrate predators often compete for the same food resources as young fish. For example, damselfly larvae and fish may compete for chironomid (midge) larvae (Allan, 1996). Therefore the absence of one competing predator may enhance the growth and increase the population size of another competitor. Common predatory taxa include members of Diptera (flies and midges), Coleoptera (beetles), Trichoptera (caddisflies), Plecoptera (stoneflies), Megaloptera (dobsonflies) and Odonata (dragonflies and damselflies) (Merritt and Cummings, 1996b).

Nutrient inputs and primary production

Energy fluxes within the river and between the river and the riparian area change along a physical gradient as stream size increases (Vannote et al. 1980). Energy is contained within organic matter, which is material derived from living organisms (Steen, 1971), and may be in the form of leaf litter falling into the river; biofilms (colonies of algae, fungi and bacteria that form on river particles and stream substrate), dissolved organic matter (DOM) in the water column or as plants and animals that inhabit the river (Allan, 1996).

Generally, in low order streams or small river tributaries, the riparian or river bank vegetation is the primary source of organic matter for the river, and therefore stream processes are dependent on fluxes of energy into the stream (Vannote et al. 1980, Allan, 1996, Harding et al. 1998, Graca, 2001). Low order streams are considered heterotrophic systems that depend on influxes of organic matter produced outside the stream (allochthonous material) (Steen, 1971) in order to sustain biological activity (Vannote et al. 1980, Allan, 1996). For example, studies show that the carcasses of salmonid fishes in addition to providing habitat for numerous invertebrates, are important sources of stream nutrients that are quickly incorporated into the foodweb by shredders and collectors (Chaloner and Wipfli, 2002, Minakawa, Gara and Honea, 2002). In addition, low order streams tend to be heavily shaded and are characterized by low primary production, because the water column is generally depleted in dissolved inorganic nutrients (DIN) such as dissolved inorganic nitrogen and phosphorous, which are the nutrients necessary for algal tissue formation.

After entering the stream, CPOM is partially consumed and processed by shredders, which results in the breakdown of CPOM into smaller particles such as FPOM and DOM (Allan, 1996). Organic matter resources not utilized in the upstream reaches of a river will be transported downstream, where they can be utilized by collectors and filter feeders (Vannote et al. 1980). The importance of organic material breakdown becomes apparent in studies such as that by Dieterich, Anderson and Anderson (1997). They found that in ephemeral western Oregon streams, shredding taxa emerged before collecting taxa. They suggested that the emergence of shredder taxa enhanced the growth of collecting taxa by making food resources available in the form of FPOM and that combined they have a close and important role in the processing of allochthonous particulate material.

By being consumed, FPOM and DOM undergo further breakdown, which makes available the necessary nutrients for primary production (Vannote et al. 1980). Incorporation of organic matter into the foodweb increases downstream (Rosi-Marshall and Wallace, 2002), and is accompanied by a shift in the type of organic matter consumed (Vannote et al. 1980, Rosi-Marshall and Wallace, 2002). The middle reaches of a river will be characterized by a decrease in allochthonous material and an increase in the production of autochthonous organic matter such as aquatic macrophytes, periphyton and biofilms (Vannote et al. 1980, Allan, 1996).

Because the nature of the food resources changes, invertebrate communities associated with food resources available will also change. In the middle reaches, production of algal mats and periphyton will increase because the nutrients necessary for algal production will be available in the water column. Therefore, the invertebrate community will be dominated by grazers and gatherers (Vannote et al. 1980, Allan, 1996). In addition to providing high quality habitat, periphyton and algal mats provide protection from predators for large numbers of invertebrates (Rosi-Marshall and Wallace, 2002).

The largest reaches of a river are characterized by slow flows and channels that are wide and deep with silty substrates that are unsuitable for benthic macroinvertebrate production (Allan, 1996). Algal production is limited by water turbidity and depth (Vannote et al. 1980), and rather than benthic algal communities, planktonic algae will become the dominant primary producer. By the time they reach high order stream and rivers, organic matter resources have been highly broken down and are present as FPOM and UFPOM (Vannote et al. 1980). The invertebrate community is mostly composed of planktonic invertebrates, which live suspended in the water column. Planktonic and benthic invertebrates, if present, are mostly predators and filtering collectors (Vennote et al. 1980).

Stream Foodwebs

Several studies emphasize the importance of macroinvertebrates on nutrient cycling and highlight the importance of food resources at a river length level. For example, Rosi-Marshall and Wallace (2002) found that CPOM decreased from being 58% of the total food consumed in the low order streams, to only about 6% of the total food consumed in high order streams. In addition, they found that FPOM consumption increased from 18% in low order streams to 64% in high order streams and that consumption of animal material, as live prey or organic detritus, increased from 3% upstream to 27% downstream.

In addition, stream invertebrates are a major part of nutrient cycling because a large number of them will be prey to one type of animal or another, regardless of their functional feeding group (Allan, 1996). For example, Marks, Power and Parker (2000) experimented with 2 types of grazers in enclosures: mayflies and chironomid larvae. Stickleback fish preferentially feed on mayflies. They found that in the absence of stickleback, algal biomass decreased in the presence of either of these grazers. However, when the fish were introduced into the enclosures, algal biomass increased in the mayfly enclosure, but remained low in the chironomid enclosures. This is because sticklebacks ate the mayflies, and the decreased grazing allowed the algal biomass to build up. However, because chironomid larvae are not as easy to hunt by sticklebacks, the chironomid populations remained high and the grazing pressures on the algae did not change.

Anadromous fishes and stream invertebrates have important and reciprocal relationships. Young salmonid fishes feed on a variety of invertebrates. For example, juvenile Chinook salmon feed on mayflies, caddisflies and midges, as well as on zooplankton (Moyle, 2002), and can exhibit a variety of feeding habits.

Several studies demonstrate the importance of decaying salmonid fish carcasses to the invertebrate community. Minakawa, Gara and Honea (2002) found that a single salmon carcass can support 15 insect genera, mostly shredders and grazers. Because salmon carcasses are considered to be very high food quality (due to their protein levels in their tissue), they enhance the growth of individual insects and locally increase the total biomass and nutritional value of stream invertebrates (Chaloner and Wipfli, 2002; Minakawa, Gara and Honea, 2002). In addition, salmon carcasses had a positive indirect effect on predacious taxa, like stoneflies, through increasing the biomass of their prey, chironomid midges (Chaloner and Wipfli, 2002).

These studies suggest that the enhanced growth and increased nutritional value of invertebrates in the stream produces higher food quality for juvenile salmon. In addition, invertebrates enhance the decomposition process of salmon carcasses, which increases stream concentrations bioavailable nutrients for primary production (Schuldt and Hershey, 1995; Dahlgren, unpublished data). Schuldt and Hershey (1995) found that periphyton biomass and concentrations of total phosphorous and soluble reactive phosphorous were higher in streams reaches where salmon spawn and die that in upstream reaches lacking salmon.

The types of studies mentioned above demonstrate the importance of food sources, and shed light on the importance of macroinvertebrates in nutrient cycling and stream health. Figure 2 demonstrates 2 foodwebs along the Eel River, which visually demonstrates the importance of invertebrates in nutrient cycling as consumers, prey and predators (Power and Dietrich, 2002)

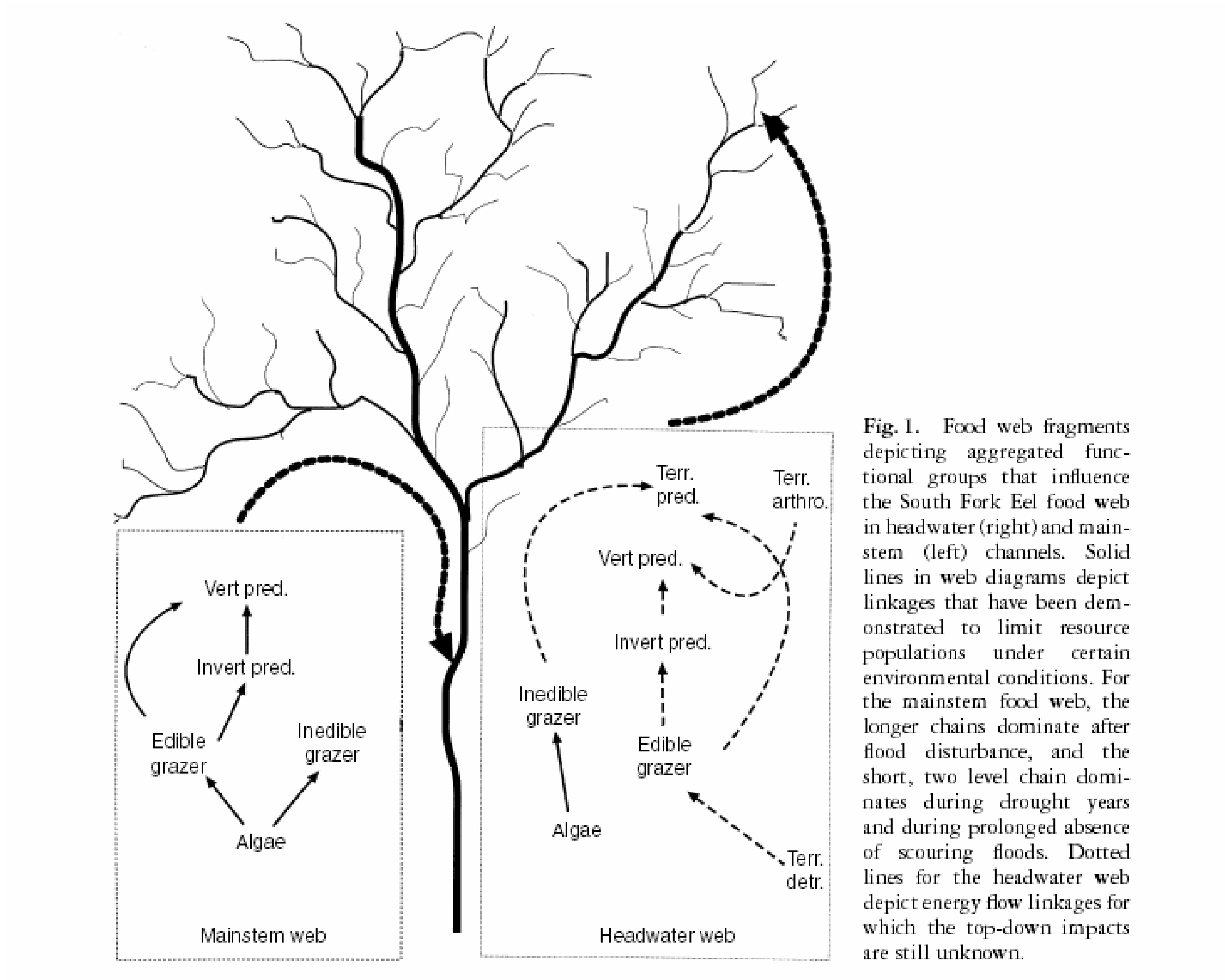

Figure 2. Foodwebs on the Eel River (Power and Dietrich,2002).

Geomorphology and spatial heterogeneity

As the RCC points out, scales are important in invertebrate distribution. While we may expect to find the same invertebrate communities within the same stream reach, we would expect invertebrate community composition differences to increase as the river length increases (Vannote et al. 1980).

The type of habitat present will strongly influence the stream biotic composition (Norris and Thoms, 1999). Common habitats for stream invertebrates include stream runs, riffles and pools, as well as suspended algal mats and submerged vegetation near the stream bank (Merritt and Cummings, 1996). Geomorphology and the processes that modify the stream's geomorphology control the types of habitats created within a stream, and that in turn has a direct impact on the types of invertebrates found at a specific location (Parsons, et al., 2003). Natural disturbances create habitat heterogeneity which is positively correlated to biotic diversity (Vinson and Hawkins, 1998). For example a stream that has a substrate that incorporates woody debris, various size ranges of cobbles and stones, mosses and aquatic plants will support more biodiversity than sites that are primary one type of substrate such as bedrock and sand (Vinson and Hawkin,1998).

River Health and Invertebrates as Biological Indicators

River health is difficult to assess (Norris and Thoms, 1999), particularly when the reference condition of a stream is unknown, and the stream has been subject to long term anthropogenic disturbances. For many politicians and scientists, river health is implicit in river integrity, as the objective of the Clean Water Act, section 101 (a) states:'to restore and maintain the chemical, physical and biological integrity of the Nation's waters'; where integrity, as defined by congress, means that 'the natural structure and function of ecosystems is maintained' (Karr, 1999).

Stream invertebrates are often used by scientists as indicators of stream health because they are very sensitive to changes in their environment. Aquatic invertebrates live in small scale habitats, therefore they are much more vulnerable to anthropogenic disturbances (LaBonte et al. 2001). Under conditions of no or minimal disturbance, the biota within a stream will be defined by the natural processes that their habitat is subjected to; however, under highly disturbed conditions such as those that arise form human disturbances, the biota within the stream will change (Karr, 1999), which will result in downstream ecosystem degradation.

Shredders and scrapers are consider to be more sensitive to environmental disturbances because they exhibit the highest level of feeding specialization, whereas filter feeders and gathering collectors are more tolerant to disturbances because they exhibit generalist feeding habits (Barbour et al. 1996). In addition, stream invertebrates are very sensitive to factors affecting water quality, such as thermal pollution, pesticides and anthropogenic organic compounds (Hilsenhoff, 1988).

Because stream invertebrates readily respond to stream disturbances, they are often used as an indictor of overall ecosystem health and integrity.

Conclusion

Stream invertebrates can tell us a lot about our environment. The role that they play in overall river function has far reaching consequences. Invertebrates not only enhance stream nutrient cycling through their feeding strategies, but also support communities of larger organisms such as salmon. The integrity of invertebrate communities heavily relies upon the structural integrity of the stream and the processes associated with the physical habitat. Habitat degradation negatively impacts stream invertebrate communities, which in turn results in decreased nutrient cycling and salmonid production.

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