STONEFLY (*PLECOPTERA*) FEEDING MODES: VARIATION ALONG A CALIFORNIA RIVER CONTINUUM[1]

Richard L. Bottorff and Allen W. Knight[2]

Abstract: The distribution of Plecoptera along a California river was used to test several predictions of the River Continuum Concept about how functional feeding groups should change along a stream's length. Stoneflies were collected from stream orders 1-6 (123 km) of the Cosumnes River continuum in the central Sierra Nevada. The 69 stonefly species collected were separated into three functional feeding groups – 26 shredders (detritivores), 39 predators (engulfers), and 4 scrapers. Stonefly shredders and predators reached maximum species richness at middle stream orders (3-5). The relative abundance of shredders was highest in the headwaters, then declined with increasing stream order. Predator relative abundance exhibited an inverse trend to shredders. Few scrapers were present, but these were most abundant at middle stream orders; they were almost entirely absent from the headwaters. These trends in diversity and relative abundance of functional feeding groups agree with predictions of the River Continuum Concept and emphasize the importance of riparian vegetation in the structure and function of Sierra Nevada streams. The type of terrestrial plant community through which the stream was flowing did not appear to affect the diversity or relative abundance of shredders.

The River Continuum Concept (RCC) was proposed to explain the structural and functional changes which occur in stream communities, especially to streams flowing naturally through undisturbed forested watersheds (Vannote and others 1980). Inputs of organic detritus to the stream and detrital processing by functional feeding groups (FFG's) of aquatic invertebrates are central themes of this concept. The RCC predicts that shredder organisms, which consume large particles of organic detritus (>1 mm) that has accumulated on the stream substrate, should be relatively abundant near the headwaters of a stream, then decrease downstream as the stream widens and the relative importance of coarse detrital inputs from terrestrial vegetation and upstream habitats decline. The rationale is that the smaller streams in the upper reaches of a river continuum (stream orders 1-3) are greatly influenced by riparian vegetation, the overhanging plant canopy supplying large amounts of organic detritus, but shading and limiting instream primary producers. As the stream widens downstream and detrital inputs from streamside plants become less important, more sunlight can reach the substrate and enhance instream primary production. Scraper organisms, which graze algae and fine particles from the substrate, are predicted to be relatively abundant in the middle reaches of streams (orders 4-6) (Vannote and others 1980). Maximum biotic diversity is predicted to occur in middle stream orders where environmental variation is greatest.

The RCC has been an important catalyst for recent stream research throughout the world (Minshall and others 1985, Statzner and Higler 1985), and the validity of its tenets and predictions are currently being tested. However, the predictions of the RCC and the importance of riparian vegetation to the macroinvertebrate community have not been studied in Sierra Nevada streams, despite the potential value for watershed and forestry management practices.

Stoneflies are ideal organisms for testing some of the RCC predictions about how FFG's change along a river continuum. First, stoneflies are common components of the aquatic benthos of most streams worldwide, often with many species and individuals present at any particular location. Since they extend in distribution from headwaters to far downstream, long distance changes in faunal composition, FFG's, and diversity can be studied. By concentrating on a single aquatic insect order, a relatively complete taxonomic list can be obtained at the species level, eliminating the uncertainties of incomplete identifications. In keeping with the idealized, undisturbed stream of the RCC, stonefly nymphs are almost exclusively restricted to unpolluted running waters. In contrast with some aquatic insect groups, stonefly nymphs belong predominantly to only two of the six main FFG's (Merritt and Cummins 1984) – shredders (detritivores) and predators (engulfers). This basic feeding dichotomy is reflected in the morphological differences of their mouthparts, and also in the two taxonomic groups of the suborder Arctoperlaria (Zwick 1973), the Euholognatha (mainly shredders) and the Systellognatha (mainly predators). A few stoneflies are classed as scrapers (the Brachypteriginae), but very few are classed as collectors (Merritt and Cummins 1984). Stoneflies are also good study organisms because most of the food resources needed during their life cycle are obtained as nymphs in the stream habitat, many adults being short-lived and not feeding (the Systellognatha).

Because of the advantages of stoneflies, we used

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[2] Graduate Student and Professor, Department of Land, Air, and Water Resources, University of California, Davis, California 95616

them to test several predictions of the RCC in an undisturbed California stream. The main objectives of the study reported here were to determine (1) if the relative abundance of stonefly shredders declines with increasing stream order (1-6), (2) if the relative abundance of stonefly scrapers increases with stream order to a maximum in middle stream orders (4-6), and (3) if the maximum diversity of FFG's occurs in the middle reaches. The RCC predicts little change in predator relative abundance along the continuum; however, because stoneflies are largely either shredders or predators, these two FFG's will demonstrate inverse trends. A final objective of the study was to observe if the diversity and relative abundance of the stonefly FFG's were influenced by the type of terrestrial plant community being traversed by the stream.

Study Stream

Plecoptera feeding modes were studied along one river continuum, the Cosumnes River and its North Fork, located in the central Sierra Nevada east of the city of Sacramento, California. The study stream flows westward 163 km from its headwater springs at 2249 m elevation to nearly sea level in the plains-like Central Valley, where it joins the Mokelumne River and enters the Sacramento-San Joaquin Delta estuary. Large physical gradients exist between the headwaters and lower reaches of the Cosumnes River, especially in mean discharge (0.007 - 13.8 m^3/sec), channel slope (12.9 - 0.06 percent), substrate (-8 to +3 phi scale), summer water temperature (4 - 28°C), and stream order (1-6). It is an unpolluted softwater stream (specific conductivity = 20-115 Mmho/cm), with dissolved inorganic solids increasing only slightly between the headwaters and lower reaches.

The Cosumnes River drains a largely undisturbed, forested watershed and traverses four major terrestrial plant communities as it descends the large elevation gradient of the Sierra Nevada (Griffin and Critchfield 1976) – red fir forest (> 2000 m elevation), mixed conifer forest (730-2000 m elevation), foothill woodland and chaparral (40-730 m elevation), and valley grassland (< 40 m elevation). Forests above 730 m elevation are primarily coniferous (*Abies, Libocedrus, Pinus,* and *Pseudotsuga*); forests below 730 m elevation are primarily broad leaf forms (*Aesculus, Arctostaphylos, Ceanothus,* and *Quercus*). In addition to these four terrestrial plant zones, the stream is bordered along its entire length by a narrow band of true riparian plants (*Alnus* 2 species, *Populus* 2 species, *Salix* many species, and other trees, shrubs, and herbs). The entire Cosumnes River drainage basin lies below tree line.

In contrast to most large rivers on the western slope of the Sierra Nevada, the Cosumnes River has no mainstream reservoirs; therefore, water temperature and discharge change naturally with the seasons. Because of the largely undisturbed watershed and lack of mainstream reservoirs, the Cosumnes River possesses the pristine conditions that formerly existed in many of the larger streams of the western Sierra Nevada and should be close to the typical stream defined in the RCC.

Methods

The distribution of stoneflies was determined for a 123 km reach of the Cosumnes River, extending from the headwaters (2249 m elevation) to the lower reaches (27 m elevation). Stonefly nymphs and adults were collected from nine sites in this study segment, which included stream orders 1-6 and four main terrestrial plant communities. Stoneflies were abundant at all nine sites of this study, including sites near sea level, but they were absent from the extreme lower reaches of the continuum (> 123 km, stream orders 7) in the Sacramento-San Joaquin Delta (California Department of Water Resources 1981).

Plecoptera nymphs were collected monthly (1980-1982) from both riffles and pools at each of the nine sites using a kick screen (0.9 mm mesh size). Most identifications were made to genus or species level; a few nymphs could be identified only to family level (some Capniidae, Leuctridae, and Chloroperlidae). The inability to identify all nymphs to species was not thought to greatly affect this study because identification to genus or family was often sufficient to determine the proper FFG. During this study, a total of 26,000 Plecoptera nymphs were collected and identified from the nine sites. Stoneflies were placed into FFG's based primarily on Merritt and Cummins (1984), plus the examination of gut contents for some stonefly nymphs when their feeding status was uncertain.

Plecoptera adults were collected in all seasons (1980-1986) using three methods: general search, timed sweep-net, and slit traps. General search along the streamside included examination of those substrates likely to contain adults, but difficult to adequately sample with a sweep net. In winter at high elevations, stoneflies were hand collected from snowbanks along the stream. Stream segments buried under snow were dug open, then adults collected as they emerged. Timed sweep-net collections (10 - 120 min) were made at all sites (biweekly 1981-1983, irregularly thereafter) to collect adults on streamside vegetation. Adults were also collected in slit traps (1981-1982) designed primarily to capture newly emerged Plecoptera (Kuusela and Pulkkinen 1978). These traps were placed on the stream bank just above water level immediately adjacent to the stream and operated continuously, day and night. Using these three methods, a total of 12,000 adults were collected from the nine sites, identified to species, and separated into their FFG's. In addition, stonefly exuviae were collected from rocks and vegetation along the stream banks and were identified to species for three families (Perlidae, Perlodidae, and Pteronarcyidae).

Since any collection of adult stoneflies along a river continuum represents a mixture of species derived directly from the river, plus those dispersing in from nearby smaller tributaries, an effort was made in this study to distinguish between these two faunas. To separate these two faunas, we (1) collected both nymphs and adults along the continuum, (2) associated many nymphs with adults, and (3) collected less intensively the nymphs and adults from side tributaries. The separation of adventitious species from the true river continuum fauna was important because our study was limited to FFG changes along a single continuum.

Stream order was used to define the position along the continuum. Stream order locates a stream segment within the drainage network (Strahler 1957) and is determined by the number and size of upstream tributaries. Headwater streams lacking inflowing tributaries are first order; higher order streams result from the confluence of two lower order streams (second order from the confluence of two first order streams; third order from the confluence of two second order streams, etc.) In this study of the Cosumnes River continuum, stream order was determined using U. S. Geological Survey topographic maps (1:24,000 scale), and all intermittent streams were included within the drainage network.

Results

A diverse stonefly fauna occurred in the Cosumnes River continuum. After excluding adventitious species, a total of 69 species, 36 genera, and all 9 North American families of stoneflies were collected in this study. Of these 69 species, 26 were shredders, 39 were predators, and 4 were scrapers (Brachypterinae: *Taenionema*). Four Chloroperlidae genera (*Alloperla, Bisancora, Kathroperla,* and *Paraperla*) may fit at least partially into the collector FFG; however, because few species were involved and little was known of their feeding mechanisms, the collector FFG was not considered further in this study.

The proportions of stonefly shredders, predators, and scrapers collected from the Cosumnes River continuum (fig. 1) were generally similar to the stonefly faunas of North America and California (Stark and others 1986), although the Cosumnes River fauna had slightly fewer shredders and slightly more predators than the other two areas. These slight differences were sampling artifacts caused by comparing the stonefly faunas of two large areas with a linear sample of one river continuum. Because we restricted our study to a single river continuum, stoneflies occurring in low order, low elevation streams in the Cosumnes River basin were excluded from the study, and these low order streams should contain higher proportions of shredders.

Species richness of stonefly shredders and predators was highest in middle stream orders (3-5) of the Cosumnes River continuum, with shredders reaching a maximum of 20 species at stream order 3 and predators reaching a maximum of 23 species at stream order 4 (fig. 2A). Near the headwaters and in the lower reaches of the stream, fewer species of both FFG's were present. At stream order 7, species richness was zero. These diversity trends in shredders and predators agree with the RCC prediction of maximum biotic diversity at middle stream orders. Stonefly scrapers were much less abundant than shredders and predators, but increased from none to three species along the continuum.

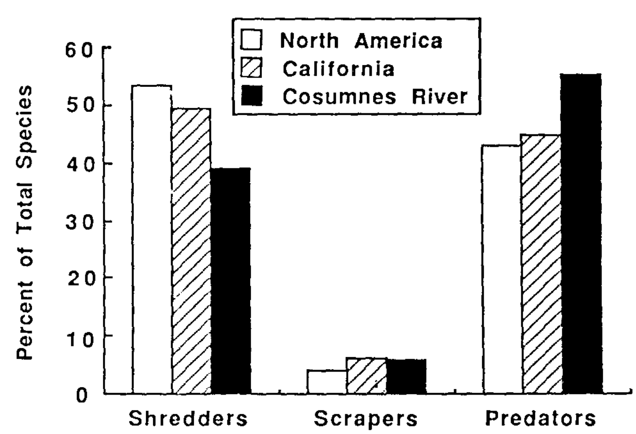

Figure 1 — Proportion (percent) of three functional feeding groups composing the stonefly faunas of North America, California, and the Cosumnes River continuum.

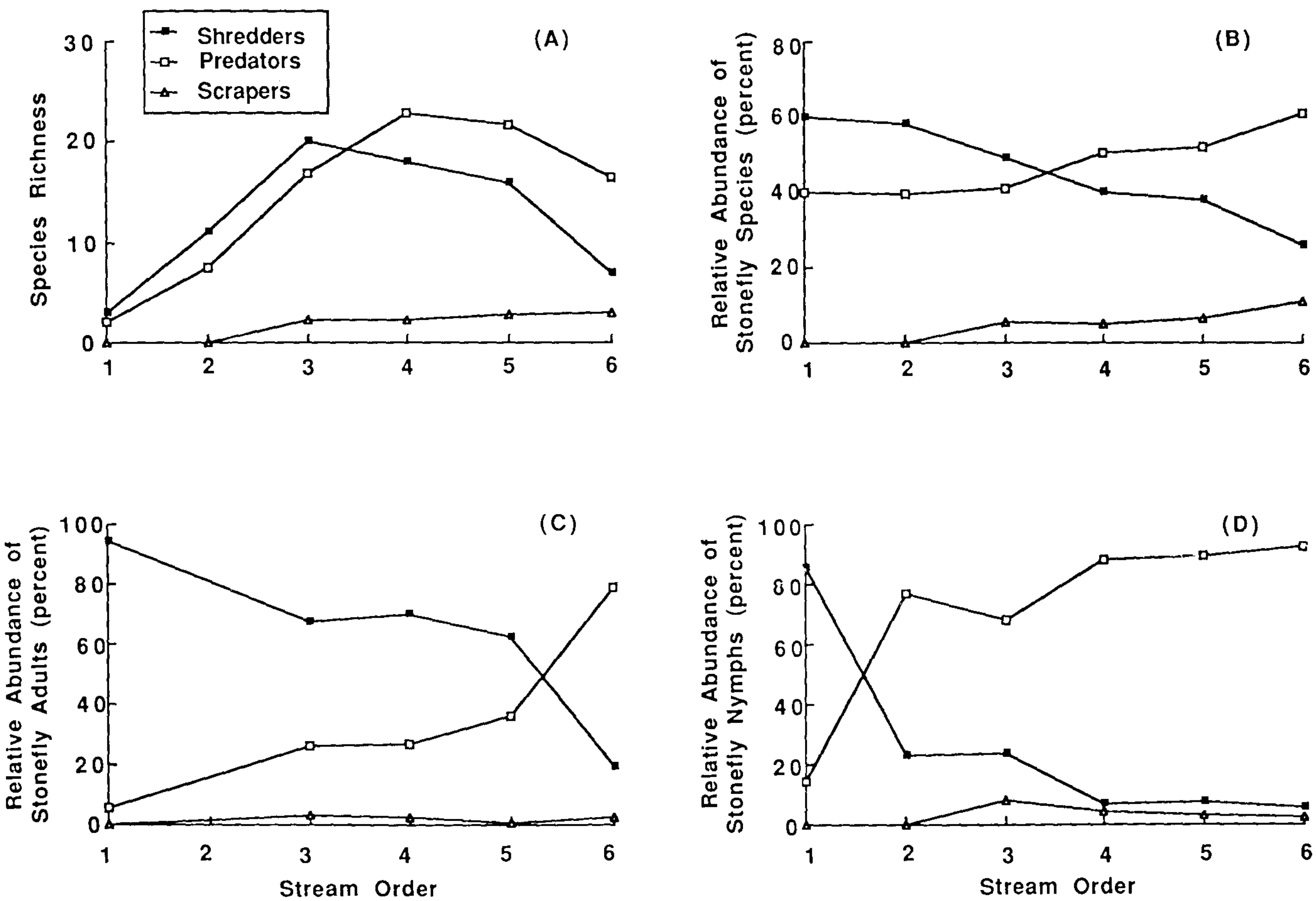

Figure 2 – Variation in species richness and relative abundance of stonefly functional feeding groups (FFG's) in stream orders 1-6 of the Cosumnes River continuum, California: (A) species richness of FFG's, (B) relative abundance (percent) of FFG's determined from the total stonefly species collected (adult + nymph data), (C) relative abundance (percent) of FFG's determined from the total number of stonefly adults collected, (D) relative abundance (percent) of FFG's determined from the total number of stonefly nymphs collected.

The relative abundance of stonefly FFG's along the Cosumnes River continuum was examined in three ways: (1) using the number of stonefly species collected (fig. 2B), (2) using the number of adult specimens collected (fig. 2C), and (3) using the number of nymph specimens collected (fig. 2D). All three data sets gave similar results (fig. 2B- D); shredder relative abundance decreased as stream order increased from 1 to 6, while predator and scraper relative abundance increased. Although the decrease in shredder relative abundance with increasing stream order occurred at slightly different rates in each data set, shredders were always most abundant (> 60 percent) near the headwaters and much less abundant in the lower reaches. Because of the basic FFG dichotomy in stoneflies, predator relative abundance exhibited an inverse trend to that of shredders. Scraper relative abundance was low (< 15 percent) at all stream orders and in all data sets, but did increase slightly in middle orders (3-6). Scrapers were especially sparse or absent from the Cosumnes River headwater region (orders 1-2).

The species richness and relative abundance of stonefly FFG's did not appear to be greatly affected by the type of terrestrial plant community through which the stream flowed (fig. 3A-B). Changes in species richness and relative abundance occurred gradually between sites, rather than exhibiting discontinuities at vegetation zone boundaries. The maximum number of shredder and predator species occurred within the mixed conifer forest zone (fig. 3A).

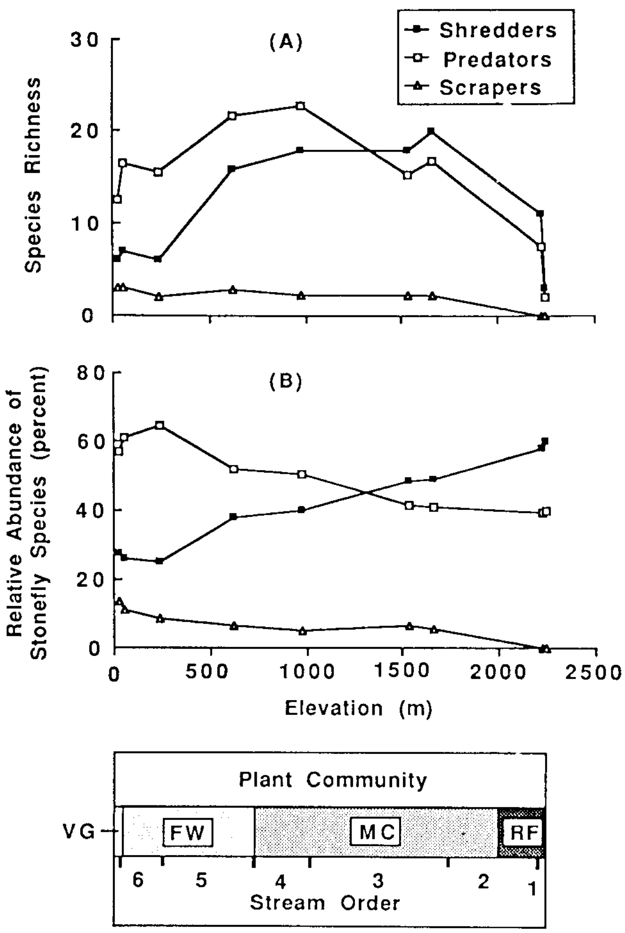

Figure 3 – Variation in species richness and relative abundance of stonefly functional feeding groups (FFG's) by elevation and terrestrial plant community along the Cosumnes River continuum, California: (A) species richness of FFG's, (B) relative abundance (percent) of FFG's determined from the total stonefly species collected (adult + nymph data). Plant community names: VG = valley grassland; FW = foothill woodland and chaparral; MC = mixed conifer forest; and RF = red fir forest. Stream orders are given to show their relation to elevation and the terrestrial plant communities.

Discussion

Since the RCC was first proposed (Vannote and others 1980), its worldwide applicability to all streams has been debated (Winterbourn and others 1981; Barmuta and Lake 1982; Minshall and others 1983, 1985; Statzner and Higler 1985), and certain modifications and exceptions have been noted, especially for streams in deserts and at high elevations where riparian vegetation is sparse (Busch and Fisher 1981). The concept was originally formulated for, and appears most applicable to, streams flowing through undisturbed, forested watersheds. Since the Cosumnes River has an undisturbed, forested watershed, the predictions of the RCC would be expected to apply. The results of this study agree with the RCC predictions that (1) shredders should be most abundant near the headwaters and decrease in relative abundance downstream, and (2) scrapers should be most abundant at middle stream orders. These changes in stonefly FFG's along the Cosumnes River continuum, plus observations of the watershed and stream canopy vegetation, strongly suggest that streamside vegetation (main terrestrial plant communities + true riparian plants) had an important organizing role on the stream biota, both as a source of organic detritus and as a controller of sunlight entry into the stream. It is likely that other streams traversing the heavily forested watersheds on the western slope of the Sierra Nevada are similarly influenced by riparian vegetation and demonstrate similar FFG changes with the Cosumnes River. Possible exceptions are those Sierra Nevada rivers extending above tree line where inputs of organic detritus may be sparse. Additional tests of the other RCC predictions should be made on Sierra Nevada streams using the entire macroinvertebrate community or various subsets.

Few other studies have examined stonefly feeding groups along a stream continuum. In contrast to our results, Knight and Gaufin (1966) found the proportion of predatory stonefly species increased with elevation in a Colorado drainage, while the proportion of vegetarian stonefly species decreased. These trends may be caused if the high elevation (> 10,000 feet) Colorado stream was above tree line and lacked sufficient inputs of organic detritus from riparian vegetation. Brink (1949) also found carnivorous stoneflies reached high dominance values on a mountain ridge in northern Sweden; however, these waters contained few plants and had little organic detritus. He found that phytophagous stonefly species were dominant in springs, trickles, and small eutrophic forest streams, all of which contained large amounts of organic detritus. These studies suggest that stonefly feeding modes vary directly with the food resources available in the stream habitat.

Stonefly scrapers were especially sparse or absent from the headwaters of the Cosumnes River continuum. We believe this is caused by the combination of heavy shading by riparian vegetation and by deep snow accumulations which bury the stream for many months in winter- spring. However, this possibility should be tested with other aquatic insect groups which naturally include more species of scrapers.

Although the RCC predicts maximum biotic diversity at middle stream orders, it was somewhat surprising to find this was also true for the different stonefly FFG's in the Cosumnes River continuum (fig. 2A). Originally, we expected shredder diversity to be highest near the headwaters where their food source of coarse organic detritus should have been most abundant. However, shredder diversity was maximum at stream order 3 and remained high at stream orders 4-5, suggesting that some factor other than detrital quantity controls diversity. Possibly, a favorable diversity of substrate or detritus promotes shredder diversity in middle stream orders. Maximum shredder diversity did occur slightly closer to the headwaters (order 3) than did maximum predator diversity (order 4-5).

Many studies have shown the importance of streamside vegetation to stream ecosystems, and it is well known that the type of terrestrial vegetation greatly affects the amount and timing of detrital input to streams, the decay rate of organic detritus, and the food preferences of shredders (see references in Hynes 1975, Minshall and others 1985). Some research suggests that the type of terrestrial vegetation through which the stream flows influences the composition of the benthic stream community (Ross 1963, Donald and Anderson 1977, Wiggins and Mackay 1978, Culp and Davies 1982, Molles 1982). Although the Cosumnes River continuum passed though four main terrestrial plant communities, no major discontinuities in species richness or relative abundance of stonefly shredders or predators were evident near vegetation zone boundaries. Species richness was maximum within the mixed conifer forest zone for both FFG's, but the gradual change in diversity across zone boundaries suggests vegetation type had little influence. Also, the decrease in shredder relative abundance with increasing stream order occurred uniformly across vegetation boundaries, suggesting that shredders were responding to the decreasing quantity of coarse organic detritus, rather than to the type of terrestrial vegetation.

The lack of FFG discontinuities at terrestrial vegetation zone boundaries may be explained by (1) the relative contribution of organic detritus coming from the main terrestrial plant communities versus that from the narrow border of true riparian vegetation, and/or (2) the downstream transport and mixing of organic detritus by the stream. Sierra Nevada streams are typically bordered by a few true riparian plant species which are adapted to the moist soil conditions near the stream. These riparian species often parallel the stream over much of its length, and extend their distribution through several terrestrial plant zones. Leaves shed from these true riparian species are known to quickly become preferred food items for shredders (Hynes 1975). If a major portion of the organic detritus originates from the true riparian species, then discontinuities in shredder relative abundance and diversity would not be expected to occur at the main terrestrial vegetation boundaries. The relative importance of the main terrestrial plant communities and the true riparian vegetation as detrital sources should be investigated further in Sierra Nevada streams.

Although stoneflies fit into two main feeding groups, shredders and predators (Merritt and Cummins 1984), much more research on food habits is needed for many genera and species. To accurately place a stonefly within one or more FFG's, it is not sufficient to just examine gut contents; in addition, observations of mouthpart morphology and feeding behavior are needed. Determination of FFG is complicated by food habit variations with stonefly age, size, and environment (Hynes 1976). Despite these uncertainties, few stoneflies seem to have evolved scraper and collector feeding modes, possibly as Wiggins and Mackay (1978) have speculated, because other aquatic insect orders (Ephemeroptera, Trichoptera, and Diptera) have completely exploited these feeding methods. Filter feeding is noticeably absent in Plecoptera nymphs, but is common in these other aquatic insect orders.

An interesting outcome of this study was that data from a small subset of the entire stream macroinvertebrate community could be used to test and support several predictions of the RCC, which was proposed to explain longitudinal changes in stream ecosystems and the entire macroinvertebrate community. Wiggins and Mackay (1978) used Trichoptera to test RCC predictions of FFG's and to compare differences between streams in eastern and western North America. The use of other taxonomic subsets to test the RCC could offer additional important insights into stream processes.

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