

LONGITUDINAL CHANGES IN STREAM BENTHIC
MACROINVERTEBRATE COMMUNITY TROPHIC STRUCTURE
ALONG TWO CENTRAL TEXAS HEADWATER RIVER CONTINUA

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INTRODUCTION

The River Continuum Concept (RCC) of Vannote et al. (1980) describes predictable abiotic and biotic changes in stream communities as a function of increasing stream size. According to the RCC, terrestrial inputs, heterotrophy, and a macroinvertebrate fauna of detritus-feeding shredders and collector-gatherers will dominate small headwater streams (orders 1-3). Mid-sized rivers (orders 4-6) mark a shift to autotrophy, decreased canopy cover effects, and importance of macroinvertebrate particle-feeding collectors and surface film feeding scrapers. Large rivers (orders 7-12) show a return to heterotrophy, and an invertebrate fauna composed mainly of collectors. Predators maintain a relatively constant percentage of the invertebrate fauna along the continuum.

Although many stream ecologists agree on the usefulness of the RCC (Minshall et al. 1983, Bott et al. 1985, Minshall et al. 1985, Welcomme et al. 1989), its applicability to large rivers and individual streams across a wide geographic spectrum is still unclear. For example, studies by Winterbourn et al. (1981) and Lake et al. (1986) questioned the global applicability and narrow geographic focus of the RCC, and others the degree large rivers receiving

floodplain inputs conform to the RCC (Sedell et al. 1989, Welcomme et al. 1989, Johnson et al. 1995). Large rivers appear to conform to the RCC only when they remain within their banks and do not receive organic loading from the surrounding environment (Naiman et al. 1987). Sudden changes in benthic community structure also occur and suggest a punctuated gradient (Magdych 1984, Perry and Schaeffer 1987, Owen 1996). A large-scale evaluation of the RCC found that, although predictions are not always met, the inherent value of the RCC is as a sliding framework (Minshall et al. 1985) with predictions shifted upstream, downstream, or reset when the continuum is interrupted by modifiers such as dams (Ward and Stanford 1983) and tributaries (Bruns et al. 1984).

The RCC was developed from studies in north temperate stream ecosystems located in Oregon, Idaho, Michigan and Pennsylvania where headwater streams are small and heavily canopied, and it assumes that, under such conditions, coarse particulate organic matter (CPOM) is the primary energy source. In contrast, many central Texas headwater stream systems have a different ecological template than their north temperate counterparts. Significant differences exist in climate, topography, geology and groundwater influence. The dominant limestone karst geology of the region gives rise to numerous open-canopied, high-volume, alkaline springs with high water clarity and a drainage basin morphology that promotes high amounts of storm runoff. Frequency of large-magnitude floods in central Texas is near the highest in the world (Caran and Baker 1986). Frequent floods have the effect of removing CPOM and

associated retention structures from an ecosystem as well as dislodging macroinvertebrates. Poor detrital retention (Short 1984) combined with a poorly developed canopy cover provide contrasting environmental forcing functions than those in the RCC-based template for headwater streams. Consequently, a biota reflecting these differing factors should be observed, specifically a reduction in the abundance of fauna dependent on allochthonous-derived carbon sources and an increase in fauna using autotrophic carbon sources (Owen 1996, Levine 1999).

Disturbance in streams of the Edwards Plateau comes from a variety of natural and anthropogenic sources. Resh et al. (1988) defined disturbance in stream ecosystems as “any relatively discrete event in time that is characterized by a frequency, intensity, and severity outside a predictable range, and that disrupts ecosystem, community, or population structure and changes resources or the physical environment.” Types of disturbance in lotic ecosystems include scouring, drought, channelization and pollution (Yount and Niemi 1990, Mumma et al. 1996). More recently, recreation has been identified as a disturbance impacting benthic plant and animal communities (Mumma et al. 1996, Breslin 1997, Wright and Li 1998).

In this study, I evaluated the changes in stream benthic communities along two river continua, one of which had a large (order 4) tributary. To do so, I measured the effects of: 1) increasing stream order, 2) a large tributary and 3) the applicability of a sliding scale (Minshall et al. 1985) on benthic

macroinvertebrate functional feeding group composition. I also evaluated certain disturbances on these ecosystems by examining: 1) the effects of a 500-year (USDA 1998) flood event on macroinvertebrate community composition and 2) effects of recreation (wading, tubing, and channel alteration) on macroinvertebrate communities.

STUDY AREA

The Edwards Plateau (Figure 1) is a 93,340-kilometer² region in central Texas designated as the Balconian biotic province (Blair 1950). Elevations range from 167 to 734 meters above mean sea level (msl), with high gradient drainages common (Riskind and Diamond 1986). The area is characterized by limestone karst topography (Bowles and Arsuffi 1993), frequent severe spates (Slade 1986) and thousands of springs (Brune 1981). Dominant streamside vegetation (Riskind and Diamond 1986) consists of bald cypress (*Taxodium disticum*) and sycamore (*Platanus occidentalis*). The upland land use is primarily livestock grazing (Palmer 1986) and some evidence indicates this practice, along with lowering water tables, has significantly altered the flora of this area (Brune 1981). Upland vegetation (Blair 1950) is commonly a mixed scrub forest of ashe juniper (*Juniperus ashei*), Texas oak (*Quercus texana*) and live oak (*Quercus virginiana*). Most of the plant and animal species in the Balconian biotic province are derived from the bordering Austroriparian, Tamaulipan, Chihuahaun and

Kansan biotic provinces (Blair 1950). Geology of the region is dominated by underlying limestone rock primarily of Cretaceous origin (Longley 1986). Soil types are highly variable, with deep soils occurring in valleys and thin, gravelly soils occurring on slopes (Riskin and Diamond 1986).

Three major river systems originate in the Edwards Plateau: the Nueces, San Antonio and Guadalupe rivers (Figure 1). These river systems all receive contributions to their base flow from the Trinity Aquifer in the Edwards Plateau and from the Edwards Aquifer along the Balcones fault zone. Spring-fed streams are of major importance to this semi-arid region that receives average precipitation of $86 \text{ cm}\cdot\text{yr}^{-1}$ in the eastern portion and $35 \text{ cm}\cdot\text{yr}^{-1}$ in the western portion (Riskin and Diamond 1986). Over 90 described endemic species exist in the Edwards Plateau region, including several in the San Marcos River (Bowles and Arsuffi 1993). High population growth in the area extending from San Antonio to Austin has caused many Edwards Plateau springs to cease to flow and reductions in the flow of other springs (Brune 1981, Bowles and Arsuffi 1993). Future population growth and increased water demand could cause the extinction of the unique biota of these ecosystems.

STUDY SYSTEM

Guadalupe River

The Guadalupe River has its origins in western Kerr County, Texas at an elevation of 610 meters above msl and is characteristic of many first-order streams of the Edwards Plateau, possessing a wide (>10 meters) channel flowing over limestone bedrock with little to no canopy cover. Base flow is from springs of the Trinity Aquifer and turbidity is extremely low at sites near the headwaters, with a slight murkiness developing downstream (Young et al. 1973).

Four locations in the upper Guadalupe River watershed upstream of Canyon Reservoir were sampled (Figure 2). Site G1 (30°3.55'N, 99°29.57'W) is located within Kerr Wildlife Management Area, 300 meters downstream of the head springs of the Guadalupe River. Water flowing from numerous spring openings forms a wide (20 meters) channel with little riparian vegetation and no canopy cover. There were no discreet riffles in the headwaters; therefore I used stratified random sampling of the two main habitats to characterize the macroinvertebrate community present. G1A refers to a narrow (1 meter) strip of madicolous habitat spanning the 20-meter wide stream channel where water flows in a thin sheet over a small limestone cascade. The water is shallow enough to allow terrestrial weeds to grow in patches where detritus has accumulated. G1B is 10 meters downstream of G1A, where the stream channel

becomes a narrow, deep, sluggish run. Several springs adjacent to this site provide additional flow volume and localized stenothermic (20 °C) habitat to this area. Numerous aggregations of gravel, cobble and debris are interspersed over a largely exposed limestone bedrock substrate throughout G1B. These patchy accumulations were the focus of my sampling efforts at this site.

Site G2 (30°3.60'N, 99°23.74'W) is 6 kilometers downstream of site G1 where the Guadalupe River is a second order stream after merging with a small tributary known as Bear Creek. Sampling was downstream of the FM 1340 bridge near Camp Waldemar. The riffle is 5 meters long, 6 meters wide and flows beneath a dense canopy of bald cypress trees.

Site G3 (30°4.44'N, 99°21.34'W) is 15 kilometers downstream of site G2, near the FM 1340 bridge located 0.5 kilometers west of Hunt, TX. The riffle is 8 meters long, 4 meters wide, and flows beneath a dense canopy of bald cypress and sycamore trees.

Site G4 (30°4.03'N, 99°13.34'W) is 16 kilometers downstream of G3 and flows through Riverview Campground in Ingram, TX. The riffle is 5 meters long, 9 meters wide and little canopy cover is present. The riffle is part of the north branch of the river formed by a small island separating it from a wider and sluggish main channel. From G1 to G4, the river length studied is 37 kilometers.

San Marcos River

The San Marcos River (Figure 3) originates from multiple springs at an elevation of 175 meters above sea level (Ogden et al. 1986). Source springs with an average combined discharge of 4.5 m³/s emerge within an 18-hectare impoundment known as Spring Lake. Spring Lake and adjacent lands are located on property known as Aquarena Center owned by Southwest Texas State University. Water in the San Marcos River is very clear (<2 NTU) and supports a dense growth of attached algae and rooted macrophytes (Hannan and Doris 1970). Temperature of the San Marcos River is about 22 °C until it joins with the Blanco River 7.5 kilometers downstream of Spring Lake.

Site S1 (29°52.82'N, 97°56.02'W) is a riffle 20 meters downstream of the Rio Vista Dam and upstream from the Cheatham St. Bridge in the City of San Marcos. The riffle is 19 meters long and 18 meters wide. Canopy cover of bald cypress trees is about 20% and the substrate consists mainly of large cobble interspersed with small patches of *Hydrilla verticillata*. The site is a popular access point for tubers during summer, with moderate recreational use during spring and fall.

Site S2 (29°52.18'N, 97°55.62'W) is a riffle 16 meters long and 7 meters wide with a 60% canopy cover of sycamore and bald cypress. It is 20 meters downstream of River Road in Thompson's Island Park in San Marcos. Recreational activities are minimal at this site.

Site S3 (29°51.69'N, 97°55.39'W) is located 10 meters upstream from the San Marcos Wastewater Treatment Plant outfall. At this site, the river channel is 18 meters wide, with a 15 meter wide run section adjacent to a 3 meter wide riffle section. Sampling was confined to a 9 meter length of the riffle section. Canopy cover is dense over the stream channel and recreation is minimal.

Blanco River

The Blanco River arises from springs of the Trinity Aquifer in northeastern Kendall County and flows 112 kilometers to its confluence with the San Marcos River (Chandler 1976). The stream flows over limestone bedrock with little canopy cover for much of its length. Even during normal rainfall years, long segments of the river may have no flow as the stream loses water to alluvial deposits and through aquifer recharge features. Some flow lost as recharge by lower reaches of the Blanco River re-emerges as flow in San Marcos Springs (Brune 1981). The Blanco River is technically a fourth-order stream in my study reach, however the considerable upstream loss of flow decreases the applicability of the stream ordering system to this stream segment.

Site B1 (29°53.63'N, 97°53.95'W) is located 100 meters downstream of the Uhland Road Bridge and 5 km prior to where the Blanco and San Marcos rivers merge. Canopy cover is dense, and riffle dimensions vary dramatically with discharge. Recreational impacts at this site are few. The riffle was 6 meters

wide, 9 meters long on the 6 March 1999 and 1 June 1999 sampling dates. By 16 August 1999, riffle width had narrowed to 1 meter with drastically reduced surface flow. The riffle was dry on the 15 November 1999 sampling date.

Site B2 (29°52.27'N, 97°54.93'W) is located 40 meters downstream of the Old Martindale Road Bridge. The west bank is steeply cut, providing some shading of the river channel; otherwise riparian canopy cover is minimal. Recreational impacts are few and rocks in the stream channel were always densely covered with filamentous algae. The riffle was 16 meters long and 11 meters wide on the first two sampling dates (6 March 1999 and 1 June 1999). On 16 August 1999, the riffle had narrowed to 4 meters in width, and was dry by the 15 November 1999 sampling date.

Confluence of the San Marcos and Blanco Rivers

Upstream of their confluence, the San Marcos and Blanco rivers are characteristic of streams of the Edwards Plateau, possessing high water clarity, little canopy cover and limestone substrate. After confluence, the river retains the San Marcos River name, is characterized by shaded runs separated by infrequent riffles, and flows 100 kilometers to its confluence with the Guadalupe River. Beyond its confluence with the Blanco River, the San Marcos River also becomes more turbid as it flows onto the eroding soils of the Blackland Prairie bioregion (Blair 1950, Groeger et al. 1997).

Site C1 (29°51.42'N, 97°53.78'W) is 2 km below the confluence of the San Marcos and Blanco rivers, downstream of the Old Bastrop Highway Bridge. A dense canopy of cypress trees shades the north side of the river, but canopy cover is minimal for the south side. The riffle is 25 meters long and 19 meters wide, with a small raised portion of emergent grasses in the center. This site is popular for swimming, tubing and fishing during the summer. Presumably, recreational users altered the riffle morphology prior to the 1 June 1999 sampling date by rearranging rocks to create a deeper channel through the center of the river.

Site C2 (29°44.68'N, 97°46.52'W) is located near the town of Fentress, Texas, in a private park known as Leisure Camp. According to the camp's owner, the 21-meter long, 12-meter wide riffle was displaced 50 meters downstream by the October 1998 floodwaters. Canopy cover is minimal, despite a tall cut bank on the west side of the channel. Recreational use at the site is high during the spring and summer, consisting mainly of large numbers of picnickers wading and playing in the riffle.

MATERIALS AND METHODS

Four (n=4) replicates at each sample location were collected four times during 1999, corresponding to winter, spring, summer and fall. Samples were collected from riffles using a Hess sampler with a 364 um mesh size at all sites except G1 (G1 possessed no true riffle). To prevent sampling bias, Hess sample

locations were determined by random selection of riffle length and width coordinates. Beginning with the most downstream selection, the length and width was stepped off and the Hess sampler was embedded at this spot to a depth of 10 cm. If the sampler could not be used due to the presence of deep water, root mats, or large boulders, the closest suitable spot was used. Once the sampler was seated into the substrate, large rocks were systematically inspected and the surface cleaned of macroinvertebrates. Smaller substrates within the sampler were then disturbed for two minutes to dislodge remaining macroinvertebrates. The net was shaken to concentrate invertebrates in the collection bucket and the sample emptied into a container containing 80% ethanol. Invertebrates and debris clinging to the inside of the bucket were rinsed into the collection container. An Orion model 840 meter was used to measure temperature and dissolved oxygen.

The samples were taken to the Aquatic Station Stream Ecology Lab on the campus of Southwest Texas State University where sample containers were refrigerated until identification. Macroinvertebrates were identified to the lowest possible taxonomic level using the keys of Merritt and Cummins (1996), Pennak (1989), Wiggins (1996), Davis (1996) and Peters (1977). Each taxon identified was subsequently assigned to a functional feeding group (FFG) according to designations in Merritt and Cummings (1996). The following community structure metrics were calculated: relative FFG abundance, taxa richness, percent dominant taxa, density and standard deviation.

To sample the madicolous habitat at site G1A on the Guadalupe River, I blocked the flow of water and using a template, drew a 12-centimeter diameter circle by gouging the soft limestone with forceps. The template was removed, and the porous circle of rock was chiseled out using a carpenter's wood chisel and hammer. Chunks of rock with their associated invertebrate fauna were removed and placed into a sampling container. The empty circle was visually inspected for remaining invertebrates, which were removed with forceps. Because flow was blocked, macroinvertebrates were not able to drift downstream.

Site G1B had slow-moving, deeper (40-centimeter) water with patchy aggregations of rocks and debris on an exposed bedrock substrate. Random Hess sample coordinates in this habitat were stepped off and the nearest aggregation of rocks was sampled.

Sites B1 and B2 were not sampled on 15 November 1999 due to inadequate flows that dried the riffle surface. At this time, the Blanco River consisted of a series of standing pools connected by subsurface flows.

RESULTS

Physical parameters

The monthly 1997-1999 Guadalupe River hydrograph (Figure 4) shows relatively constant base flow derived from groundwater sources and increases in flow of 1-2 orders of magnitude during storm events, with a quick return to base flow conditions once rain ceases. The San Marcos River hydrograph shows little fluctuation in flow, except for a 500-year flood event on October 17-18, 1998 (USDA 1998). This storm caused an increase in flow from $6.1 \text{ m}^3 \cdot \text{sec}^{-1}$ to $175.3 \text{ m}^3 \cdot \text{sec}^{-1}$ within one day. A steady decline in flow followed the October 1998 flood event. Average discharge was $5.1 \text{ m}^3 \cdot \text{sec}^{-1}$ during the study period, which was above the historical average of $4.5 \text{ m}^3 \cdot \text{sec}^{-1}$. The Blanco River hydrograph shows the highly variable nature of this watercourse. The river can be dry for extended periods during drought and flow fluctuations of 3 orders of magnitude are not uncommon. During the year of my study, the Blanco River had a high flow of $17.9 \text{ m}^3 \cdot \text{sec}^{-1}$ in January and was dry from 11 September to 9 December.

Water temperature on the Guadalupe River during the study ranged from $15.9 \text{ }^\circ\text{C}$ during winter to $30.0 \text{ }^\circ\text{C}$ during summer (Table 1). Each season, the highest water temperature observed on the Guadalupe River was at site G4, the farthest downstream sample site. Water temperature of the San Marcos River prior to its confluence with the Blanco River ranged from 22.0 to $23.4 \text{ }^\circ\text{C}$, with no

observable seasonality. Temperatures on the Blanco River varied from 20 °C in winter to 31.5 °C in the summer. The post-confluence sites on the San Marcos River remained at or near pre-confluence temperatures except during the spring and summer, when temperatures reached a high of 30.5 °C. Thermal influence of the Blanco River on post-confluence sites was not evident during winter and fall because Blanco River temperature was similar to the San Marcos River. During the spring and summer, the Blanco River thermal influence was minimal due to lack of flow.

Macroinvertebrate Analysis

This study identified (Table 2) five functional feeding groups comprised of 73 taxa of Hexapoda, as well as representatives (# of taxa in parenthesis) of Gastropoda (9), Pelecypoda (2), Crustacea (1), Hirudinea (1), Oligochaeta (1), Hydracarina (1), Ostracoda (1), Nematoda (1), Copepoda (1), Cladocera (1) and Platyhelminthes (1). Density, standard deviation, dominant taxa and dominant taxa relative abundance for the Guadalupe River are presented in Table 3, and for the San Marcos, Blanco and post-confluence locations in Table 4.

With the exception of the macicolous habitat on the Guadalupe River (G1A), taxonomic richness varied little among sample sites (Figure 5) on the Guadalupe, San Marcos and Blanco rivers. There were no clear longitudinal changes in functional feeding group composition for Guadalupe River sites, with

collectors dominating at all sites (Figure 6). Collector-filterers and scrapers dominated site G1A, whereas 10 meters downstream, G1B was dominated by collector-gatherers and shredders, mainly comprised of the amphipod *Hyaella azteca*.

The San Marcos, Blanco and post-confluence sites did not differ greatly with respect to their functional feeding group compositions (Figure 6). Collector-gatherers dominated at all sites; scrapers were abundant in the San Marcos River headwaters (S1, S2), and were less abundant in the Blanco River and post-confluence sites. Benthic macroinvertebrate abundance did not vary seasonally (Tables 3 & 4), with the exception of site C2 on the San Marcos River (Figure 7). This site received heavy recreational use during spring and summer. The lack of seasonality with respect to benthic macroinvertebrate functional feeding group composition allowed me to combine data from all seasons during the study.

A longitudinal analysis of dominant collector-filterer taxa in the Guadalupe River showed black fly larvae (Diptera: Simuliidae) at densities above $2000 \cdot m^{-2}$ at site G1A, largely absent from site G1B only 10 meters downstream, but overall decreasing in abundance downstream (Figure 8). Other taxa, such as *Chimarra* (Trichoptera: Philopotamidae) and *Traverella presidiana* (Ephemeroptera: Leptophlebiidae), were more variable in distribution and abundance downstream. Dominant collector-filterer taxa of the San Marcos and Blanco rivers, comprised mainly of *Chimarra*, *Traverella presidiana* and Simuliidae, were present in low

numbers in the San Marcos River headwaters (S1, S2, S3), but were more abundant in the Blanco River and post-confluence sites (Figure 8).

Chironomids (Diptera: Chironomidae) were the dominant collector-gatherer or were present in substantial numbers at every sample location on the Guadalupe, San Marcos and Blanco rivers (Figure 9). The mayflies *Leptohyphes* (Ephemeroptera: Tricorythidae) and *Thraulodes gonzalesi* (Ephemeroptera: Leptophlebiidae) dominated or co-dominated the downstream sites on the Guadalupe River, headwater sites on the San Marcos River and sites on the Blanco River.

The damselfly larva *Argia* (Odonata: Coenagrionidae) occurred at every sample location on the Guadalupe, San Marcos and Blanco rivers (Figure 10). It was the dominant predator in riffles on the Guadalupe River, except site G1B where water mites (Hydracarina) occurred in excess of $1100 \bullet m^{-2}$. *Corydalus* (Megaloptera: Corydalidae) larvae were present in small numbers in all rivers. In the San Marcos River, the abundant predator taxa *Argia* and *Corydalus* co-dominated with the dragonfly larva *Brechmorhoga* (Odonata: Libellulidae) and two genera of Hemiptera in the family Naucoridae: *Ambrysus* and *Criphocricos*. *Argia* was 2-3 times as abundant in the Blanco River than in the San Marcos River and post-confluence sites.

Scraper abundance was greatest at the Guadalupe and San Marcos river headwaters (Figure 11). Site G1A was exceptional in the seasonal nature of its functional feeding group composition. *Baetodes* (Ephemeroptera: Baetidae) was

the dominant scraper in the madicolous habitat of site G1A and during autumn it replaced the collector-filterer Simuliidae as the dominant taxa (Table 4).

Baetodes was gradually replaced by the caddisfly *Hydroptila* (Trichoptera: Hydroptilidae) in riffles downstream (Figure 11). *Hydroptila* was also the dominant scraper at locations on the Blanco River and at post-confluence sites with the San Marcos River. Scrapers in the San Marcos River headwaters (S1, S2, S3) were not as abundant and were dominated by *Protoptila* (Trichoptera: Glossosomatidae) or *Petrophila* (Lepidoptera: Pyralidae) larvae.

A depauperate shredder fauna in terms of number of taxa, density and dominance was observed in all study systems (Figure 12). The amphipod *Hyaella azteca* and the riffle beetle *Microcyloepus pusillus* (Coleoptera: Elmidae) were the only shredders present in notable numbers in the Guadalupe, San Marcos and Blanco rivers. *Hyaella azteca* was normally found associated with filamentous algae.

DISCUSSION

Longitudinal Zonation of Functional Feeding Groups

The longitudinal changes in benthic macroinvertebrate functional feeding groups I observed in the Guadalupe and San Marcos rivers differed from the trophic structure model explained by the original RCC (Vannote et al. 1980). Further, macroinvertebrate trophic structure differed between the Guadalupe and

San Marcos river headwaters despite occurring in the same bioregion and having similar taxonomic compositions. The Guadalupe River headwaters exhibit an atypical RCC gradient in that collector-filterers or scrapers dominated at site G1A just below the river's head springs. This contrasts the RCC prediction that detritus-feeding shredders should dominate in this type of habitat. Further, where the Guadalupe River is a mid-sized river (G4), riffles do not have a well-developed scraper community and the proportion of collectors remains high, which contrasts the RCC prediction that benthic communities in mid-sized streams should be co-dominated by scrapers and collectors.

Differing from the Guadalupe River headwaters, the area downstream of the head springs of the San Marcos River has a well-developed macrophyte community, with a 29:1 ratio of plant surface area to streambed (Hannan and Dorris 1970). The high amount of surface area gives rise to an abundance of biofilms and autochthonous FPOM from the sloughing of dead cells from plant and substrate surfaces (Petts and Callow 1996). Collectors feeding on FPOM in this part of the stream therefore depend mainly on autochthonous FPOM. Under the north temperate RCC model, the productivity of collectors in headwater streams is dependent on allochthonous FPOM derived from the instream decomposition of CPOM and erosion from terrestrial sources. High turbidity in the post-confluence portion of the San Marcos River restricts the development of macrophytes, and this section of the river is less productive than headwater reaches (Groeger et al. 1997). The decreasing primary productivity in

downstream reaches suggests collectors in lower reaches are dependent upon FPOM transported from upstream sources.

The homogeneous taxonomic richness along both continua also did not conform to the prediction that greater diversity should be found in mid-order reaches (Vannote et al. 1980). The authors of the RCC equated a high biotic diversity with higher habitat variability as indicated by the variable temperature regime usually found in mid-sized streams. Conversely, low biotic diversity was equated with decreased habitat variability exemplified by invariable temperature regimes in the smallest and largest streams. Using similar logic, the thermally constant San Marcos River headwaters should be markedly less diverse than the thermally variable lower reaches. This was not the case, with all sample sites except the madicolous habitat of site G1A exhibiting a nearly uniform taxonomic diversity. G1A had a markedly lower taxonomic diversity, the likely result of the low substrate heterogeneity exhibited by madicolous habitats. My results compare with those of Naiman et al. (1987), who found no correlation with stream order and invertebrate diversity, despite significant thermal and food resource gradients along a river continuum.

Another consideration in this study was the effect of a major tributary, the Blanco River, on longitudinal benthic macroinvertebrate changes in the San Marcos River. During this study, flow on the Blanco River was variable, decreasing from $17.9 \text{ m}^3 \cdot \text{sec}^{-1}$ to 0. At the beginning of the study, flow volume of the Blanco River was slightly higher than that of the San Marcos River.

Consequently, one would expect a marked adjustment in benthic macroinvertebrate trophic structure as the Blanco River ceased to flow and its influence on post-confluence macroinvertebrate communities gradually lessened over the course of the study. However, below the confluence with the Blanco River, macroinvertebrate community characteristics of the San Marcos River did not change with this temporal fluctuation in flow. Instead, regardless of the flow of the Blanco River, the proportion of collectors in the San Marcos River increases at post-confluence sites and community development continues to move toward that predicted for a large river. The progressive downstream increase in collectors below the Blanco River confluence contrasts with a modification of the RCC put forth by Bruns et al. (1984) that large tributaries should set stream community development backward. Instead, the lower San Marcos River conforms to the RCC's tenet of gradual changes in community composition, with collectors gradually replacing scrapers downstream of the confluence with the Blanco River.

Although a gradual shift in functional feeding group composition is indicative of the RCC's hypothesis of gradual integration of community characteristics, certain faunal assemblages in my study streams departed markedly from the RCC's predictions. When compared to north temperate headwater streams, the Guadalupe and San Marcos river headwaters possessed a depauperate shredder fauna. Lack of detrital loading and retention partly explains the paucity of shredders in the study streams. Streams in central Texas

lack large woody debris-retaining structures found in north temperate streams. Although large woody debris makes up only a small portion of the benthic area of almost every stream, such structure is necessary to retain the CPOM used by shredders (Jones 1997). The Blanco and Guadalupe rivers also regularly experience high-magnitude spates that lack any discernable seasonal pattern. These events serve to pulse CPOM downstream, making CPOM unreliable for the development of an obligate (sensu Cummings and Klug 1979) shredder fauna. The size of CPOM also effects its ability to be retained within an ecosystem, with a positive relationship existing between CPOM size and retention time within an ecosystem (Benfield 1997). Thus, an additional factor contributing to the lack of CPOM in my study streams was the presence of bald cypress as the dominant headwater canopy tree. The small size of the (<1.9 cm, Vines 1984) leaves of this deciduous conifer allow for quick removal by the stream's current before they can be used as a food resource.

Actual shredder abundance may also be less than estimated by this study. The classification of *H. azteca* as a shredder may be inappropriate for my study system because they are thought to be facultative shredders (Short 1984, Pennak 1989). In my study streams, *H. azteca* is normally found in association with mats of filamentous algae, indicating they behave as grazers. Furthermore, when collected their translucent bodies were usually green in color, indicating a diet of living plant material. The classification of *Microcyloepus pusillus* as a

shredder may also have been inappropriate because, although they are detritivores, their small size probably limits their food sources to FPOM.

The lack of shredder diversity in my study streams also is conspicuous. Largely absent were shredders from following orders and families: Plecoptera: Pteronarcidae, Peltoperlidae, Nemouridae and Trichoptera: Limnephilidae, Lepidostomatidae, Sericostomatidae (Abbott et al. 1997, Anderson and Sedell 1979, Szczytko and Stewart 1977, Edwards 1973). Plecoptera are cold stenotherms and are therefore intolerant of summer water temperatures in central Texas, which can climb above 30 °C (Huntsman et al. 1999). Most Plecoptera families in Texas are restricted to the heavily-forested big thicket region of east Texas and it is thought that the few Plecoptera taxa that exist in central Texas are relic populations from the last ice age and are mainly predaceous (Abbott et al. 1997).

The relative proportion of scrapers was highest in the headwaters of both river continua. This was expected because of the obvious autotrophic conditions present in both rivers' headwaters. However, there is evidence that the 500-yr flood event of October of 1998 lowered scraper abundance in the San Marcos River headwaters. A prior study on the San Marcos River headwaters showed that scrapers were >50 percent of relative functional feeding group abundance, and that the combined abundance of two gastropods, *Elimia comalensis* and *Melanoides tuberculatus*, were always above 400 • m⁻² (Owen 1996). A marked reduction in abundance of these two gastropods has occurred, as their combined

density dropped to $<40 \bullet m^{-2}$. Gastropod life cycles typically last for 9 to 15 months (Pennak 1989), and prosobranch snails such as *E. comalensis* and *M. tuberculatus* are known to have longer life cycles than insects (Thorp and Covich 1991). On the San Marcos River, the current assemblage of insect scrapers such as *Protophila*, *Hydrophila* and *Petrophila* have short multivoltine life cycles and flight dispersal that can facilitate their recovery from scouring floods. (Merritt and Cummings 1996, Wiggins 1996, Tiemann 1992).

To account for atypical streams receiving high-volume point source flows from springs (such as San Marcos Springs and the Guadalupe River headwaters), the authors of the RCC proposed a sliding scale framework (Minshall et al. 1985). In this model, high volume spring-fed headwater streams would skip the RCC's predictions of heterotrophy for small streams (orders 1-3) and instead would proceed directly to the prediction of autotrophy for mid-sized rivers (orders 4-6). Likewise, mid-sized rivers should shift to large river (orders 7-12) continuum predictions of a dependence upon downstream transport and an invertebrate fauna dominated collectors. Within this adjusted model, the San Marcos and Guadalupe river continua generally support these predictions in that scrapers co-dominate in the headwaters and collectors fully dominate order 4 reaches. However, in contrast to the sliding scale predictions, I observed a smaller proportion of scrapers than predicted for a mid-size river possessing high water clarity and open canopy cover. In addition, certain elements of trophic structure for large rivers, such as the absence of bivalve mollusks, differ than that

predicted by the RCC. In the absence of mollusks, downstream reaches of both rivers are co-dominated by midge larvae and various collector-gatherer mayflies.

Seasonality

The macrolithic habitat on the Guadalupe River (G1A) had a macroinvertebrate community dominated by the collector-filterer Simuliidae during winter, spring and summer. During autumn, the scraping mayfly *Baetodes* replaced Simuliidae as the dominant taxa. No other seasonal patterns of FFG composition were evident at any of the other sample locations. The lack of seasonality of my study streams differs from north temperate streams that have macroinvertebrate communities that are synchronized to emerge during certain times of the year in response to predictable thermal and resource cycles (Wallace and Anderson 1996). The benthic macroinvertebrates in mid-latitude streams are also adapted to high flows in the spring associated with snowmelt and a predictable pulse of CPOM in autumn associated with the loss of leaves from deciduous trees. Seasonality was probably suppressed in my study streams due to: 1) stenothermic groundwater, 2) flow patterns with no seasonality 3) lack of retention of CPOM within the headwaters, 4) year-round availability of autochthonous-produced biofilms and FPOM and 5) the presence of Trichoptera and Ephemeroptera taxa with multivoltine life cycles and year-round emergence patterns (Bayer 1975, Tiemann 1992). In these respects, my study streams were similar to other streams in central Texas (Owen 1996, Levine

1999) and streams with unforested headwaters (Winterbourn et al. 1981, Lake et al. 1986, Arnold and Skinner 1998). Such headwater streams have benthic communities comprised mainly of collectors and scrapers in their headwaters, and are therefore not strongly linked to terrestrial CPOM as a primary food resource.

Disturbance in the San Marcos River

A *pulse* disturbance is a punctuated event in which a system briefly deviates from a steady state and a *press* disturbance is a sustained adjustment of an ecological system from an existing steady state to a new state (Bender et al. 1984). A pulse disturbance may describe the dramatic shift in functional feeding group composition that occurred on the San Marcos River headwater sites (S1, S2, S3) between Owen's (1996) study in 1992-1993 and this study. Under this scenario, the October 1998 flood would have caused the transition from a scraper-dominated system to one dominated by collector-gatherers, and the community has yet to recover. It is also possible that under a press disturbance scenario, inputs of allochthonous-produced FPOM from erosion-producing land use practices in the watershed have caused a sustained shift in community structure away from scrapers and toward collectors using the increased allochthonous FPOM as a food resource. Long-term studies of land use practices in the watershed and benthic communities in the San Marcos River would be necessary to make this determination.

Recreational disturbance at the farthest downstream sampling location on the San Marcos River (C2) occurred by trampling, as concentrated groups (>10 people) spend long periods of time wading, standing and sitting on lawn chairs in the riffle. During spring and summer, this gave the riffle the appearance of scouring, with a conspicuous lack of attached algae when compared the winter sampling date. My data regarding macroinvertebrate density supports the contention that heavy recreational activity dramatically decreased the abundance of benthic macroinvertebrates in this riffle. Abundance of macroinvertebrates appears to rebound in the autumn, indicating that recreational disturbance at the site was a pulse disturbance (Wright and Li). Other sampling locations probably experienced less concentrated trampling as anglers and tubers walked through study riffles. However, my data does not show that this sort of sporadic low-intensity human activity causes decline in benthic macroinvertebrate abundance.

Conclusions

To rebut criticisms by Lake et al. (1986) and Winterbourn et al. (1981), the authors of the RCC clarified that the RCC was not purely a deterministic model, but instead was more of a holistic approach to viewing streams as discrete ecosystems tied to the surrounding terrestrial environment (Minshall et al. 1985). My study generally supports the latter interpretation because headwater streams reflected their surrounding environment and there was a gradual downstream

integration of community structure changes. With the exception of one sample site, temporal shifts in community trophic structure were not pronounced due to the non-seasonal nature of these subtropical streams. Other than depressed scraper and shredder communities, both river continua generally fit the sliding scale framework proposed by Minshall et al. (1985). The effects of a large tributary on the San Marcos River were not pronounced and did not fit the RCC corollary put forth by Bruns et al. (1984).

The last sentence of the much-cited River Continuum Concept paper (Vannote et al. 1980) states that, "Collection of extensive data sets... are needed to further test and refine these ideas." The streams I studied differed from streams in other parts of the continent, and differed from each other. This study shows that our knowledge of stream continua of the Edwards Plateau region is still largely unknown. However, the existence of these spring-fed streams is jeopardized by population growth, pollution and building over aquifer recharge features. Studies such as this one should be important first steps to allow for the incorporation of subtropical streams, such as those found in central Texas, into models explaining the longitudinal structure and function of streams.

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Table 1. Water temperature by season for the Guadalupe River (G), San Marcos River (S), Blanco River (B) and post-confluence (C) sample sites.

Site	Season	Temp °C	Site	Season	Temp °C
G1	Winter	19.1	S1	Winter	22.6
	Spring	27.4		Spring	22.4
	Summer	25.0		Summer	22.6
	Autumn	18.3		Autumn	23.4
G2	Winter	15.9	S2	Winter	22.8
	Spring	27.6		Spring	22.5
	Summer	28.7		Summer	22.8
	Autumn	18.7		Autumn	22.2
G3	Winter	16.1	S3	Winter	23.2
	Spring	26.5		Spring	22.9
	Summer	28.2		Summer	23.2
	Autumn	19.0		Autumn	22.0
G4	Winter	22.8	B1	Winter	20.0
	Spring	28.7		Spring	n/a
	Summer	30.0		Summer	31.5
	Autumn	20.2		Autumn	No Flow
			B2	Winter	20.9
				Spring	29.2
				Summer	30.7
				Autumn	No Flow
			C1	Winter	20.8
				Spring	25.5
				Summer	26.2
				Autumn	21.5
			C2	Winter	19.9
				Spring	29.1
				Summer	30.5
				Autumn	18.8

Table 2. Macroinvertebrate composition, distribution (G=Guadalupe, S=San Marcos, B=Blanco) and functional feeding group (FFG) designation (CG=collector-gatherers, CF=collector-filterers, SH=shredders, SC=scrapers, P=predators) in study rivers.

Taxa	FFG	G	S	B	Taxa	FFG	G	S	B
Ephemeroptera					Hemiptera				
<i>Baetis</i>	CG	X	X	X	<i>Ambrysus</i>	P	X	X	X
<i>Baetodes</i>	SC	X	X	X	<i>Criphocricos hungerfordi</i>	P	X	X	X
<i>Camelobaetidius</i>	CG	X	X	X	<i>Limnocoris lutzi</i>	P		X	
<i>Leptohyphes</i>	CG	X	X	X	<i>Merobates</i>	P		X	X
<i>Tricorythodes</i>	CG	X	X	X	<i>Microvelia</i>	P		X	
<i>Traverella presidiana</i>	CF	X	X	X	<i>Ragovelia</i>	P	X		X
<i>Thraulodes gonzalesi</i>	CG	X	X	X	Coleoptera				
<i>Choroterpes</i>	CG	X		X	<i>Psephenus texanus</i>	SC	X	X	X
<i>Isonychia</i>	CF	X	X	X	<i>Berosus</i>	P	X	X	X
<i>Stenonema ares</i>	SC	X			Staphlinidae	P	X	X	X
<i>Stenonema femoratum</i>	SC	X			<i>Lutrochus</i>	CG	X	X	X
<i>Caenis</i>	CG	X	X	X	<i>Heterelmis</i>	CG	X	X	X
<i>Hexagenia limbata venusta</i>	CG	X	X		<i>Microcyloepus pusillus</i>	SH	X	X	X
Trichoptera					<i>Phanocerus clavicornis</i>	SC	X	X	X
<i>Polycentropus</i>	P	X	X	X	<i>Macrelmis texana</i>	CG	X	X	X
<i>Polyplectropus</i>	P	X	X	X	<i>Hexacycloepus ferrugineus</i>	CG	X	X	X
<i>Atopsyche erigia</i>	P	X	X	X	<i>Stenelmis</i>	SC	X	X	X
<i>Chimarra</i>	CF	X	X	X	<i>Neaelmis caesa</i>	CG	X	X	X
<i>Hydropsyche</i>	CF	X	X	X	Diptera				
<i>Smicridea fasciatella</i>	CF	X	X	X	Chironomidae	CG	X	X	X
<i>Cheumatopsyche</i>	CF	X	X	X	Tipulidae	SH	X	X	X
<i>Potamyia flava</i>	CF			X	Culicidae	CF		X	
<i>Protophila</i>	SC	X	X	X	Simuliidae	CF	X	X	X
<i>Hydroptila</i>	SC	X	X	X	<i>Leucotabanus</i>	P		X	
<i>Ochrotrichia</i>	CG	X	X	X	<i>Bezzia</i>	P	X	X	X
<i>Leucotrichia</i>	SC	X	X	X	<i>Hemerodromia</i>	P	X	X	X
<i>Metrichia</i>	CG	X	X	X	<i>Euparyphus</i>	CG	X	X	
<i>Mayatrachia</i>	SC		X	X	<i>Atherix</i>	P	X	X	
<i>Neotrichia</i>	SC	X	X	X	Gastropoda				
<i>Helicopsyche</i>	SC	X	X		<i>Elimia comalensis</i>	SC	X	X	
<i>Triaenodes</i>	SH		X		<i>Cincinnatiatia comalensis</i>	SC		X	
<i>Nectopsyche</i>	SH	X	X		<i>Pyrogophorus cornutus</i>	SC		X	
<i>Oecetis</i>	P	X	X	X	<i>Thiara tuberculatus</i>	SC		X	
<i>Marilia flexuosa</i>	SH	X			<i>Thiara granifera</i>	SC	X	X	
Odonata					<i>Mansa comuanetis</i>	SH		X	
<i>Erpetogomphus</i>	P	X	X	X	<i>Biomphalana</i>	SC	X	X	
<i>Progomphus</i>	P	X	X	X	<i>Helisoma</i>	SC		X	
<i>Brechmorhoga</i>	P	X	X	X	<i>Physella</i>	SC		X	X
<i>Hetaerina</i>	P	X	X	X	<i>Melanoides tuberculatus</i>	SC		X	
<i>Argia</i>	P	X	X	X	<i>Hebetancylus excentricus</i>	SC		X	
Orthoptera					Pelocypoda				
Tetrigidae	SH		X		<i>Corbicula fulminea</i>	CF	X	X	X
<i>Ellipes</i>	SH		X	X	Sphaeriidae	CF	X	X	X
Plecoptera					Crustacea				
<i>Perlesta</i>	P	X		X	<i>Hyalella azteca</i>	SH	X	X	X
<i>Neoperla</i>	P	X	X	X					
Megaloptera					Hirudinea	P	X	X	X
<i>Corydalus</i>	P	X	X	X	Oligochaeta	CG	X	X	X
Neuroptera					Hydracarina	P	X	X	X
<i>Climacia</i>	P	X			Ostracoda	CF	X	X	X
Lepidoptera					Nematoda	CG	X	X	X
<i>Paraponyx</i>	SH		X		Copepoda	CF	X	X	X
<i>Petrophila</i>	SC	X	X	X	Cladocera	CF		X	X
Collembola					Platyhelminthes				
Entomobridae	CG	X			<i>Dugesia</i>	CG	X	X	X

Table 3. Mean (n=4) density per meter square, standard deviation, dominant taxa and relative abundance by season for the Guadalupe River (G) sample sites.

Site	Season	Mean density per meter ²	Standard Deviation	Dominant Taxa	Relative Abundance
G1A	Winter	2938	2331.3	Simuliidae	96.3%
	Spring	5407	3011.1	Simuliidae	58.0%
	Summer	3388	2200.3	Simuliidae	61.7%
	Autumn	1958	458.6	<i>Baetodes</i>	30.7%
G1B	Winter	5828	3912.6	<i>Tricorythodes</i>	43.2%
	Spring	16681	17872.8	<i>Hyallolela azteca</i>	30.7%
	Summer	666	409.0	<i>Tricorythodes</i>	36.4%
	Autumn	4116	1795.4	<i>Hyallolela azteca</i>	26.6%
G2	Winter	9690	4611.5	Simuliidae	44.0%
	Spring	10338	4918.8	<i>Hydroptila</i>	15.8%
	Summer	7433	1854.3	<i>Chimarra</i>	15.5%
	Autumn	6311	2367.2	Chironomidae	16.7%
G3	Winter	19318	10717.7	Chironomidae	20.5%
	Spring	7421	3392.7	<i>Leptohyphes</i>	20.5%
	Summer	8854	2546.2	<i>Thraulodes gonzalesi</i>	21.0%
	Autumn	5659	2267.2	<i>Hydroptila</i>	18.3%
G4	Winter	6179	2698.9	<i>Thraulodes gonzalesi</i>	29.4%
	Spring	6316	3373.6	<i>Traverella presidiana</i>	51.0%
	Summer	10727	5787.3	<i>Traverella presidiana</i>	28.7%
	Autumn	9163	1720.4	Simuliidae	16.8%

Table 4. Mean (n=4) density per meter square, standard deviation, dominant taxa and relative abundance by season for the San Marcos (S), Blanco (B) and post-confluence (C) sample sites.

Site	Season	Mean density per meter ²	Standard Deviation	Dominant Taxa	Relative Abundance
S1	Winter	1871	1200.0	<i>Protoptila</i>	28.4%
	Spring	2087	460.0	Chironomidae	15.0%
	Summer	1695	766.0	Chironomidae	19.0%
	Autumn	3765	894.0	Chironomidae	30.7%
S2	Winter	2563	806.6	<i>Protoptila</i>	32.6%
	Spring	3057	1563.8	<i>Leptohyphes</i>	34.1%
	Summer	2572	483.7	Chironomidae	16.9%
	Autumn	2710	2018	Chironomidae	19.4%
S3	Winter	1103	587.6	<i>Microcylloepus</i>	13.0%
	Spring	1597	590.3	<i>Leptohyphes</i>	24.2%
	Summer	2512	794.1	<i>Microcylloepus</i>	17.3%
	Autumn	3024	1605.6	Chironomidae	20.2%
B1	Winter	9614	6388.8	Chironomidae	36.9%
	Spring	5732	2693.4	<i>Hydroptila</i>	15.9%
	Summer	7918	5736.6	<i>Chimarra</i>	18.2%
	Autumn	*** No Samples Taken due to Lack of Flow ***			
B2	Winter	19438	3832.6	Chironomidae	34.3%
	Spring	4463	1434.9	<i>Hydroptila</i>	25.8%
	Summer	13010	5611.3	<i>Leptohyphes</i>	22.6%
	Autumn	*** No Samples Taken due to Lack of Flow ***			
C1	Winter	5150	2318	Chironomidae	37.9%
	Spring	4913	2002.5	<i>Hydroptila</i>	24.2%
	Summer	5016	197.0	Chironomidae	38.9%
	Autumn	5098	2563.9	Chironomidae	36.4%
C2	Winter	14621	6459.3	Chironomidae	38.6%
	Spring	4913	2002.5	<i>Hydroptila</i>	24.2%
	Summer	2914	794.5	Chironomidae	51.7%
	Autumn	10435	2079.0	Chironomidae	25.7%

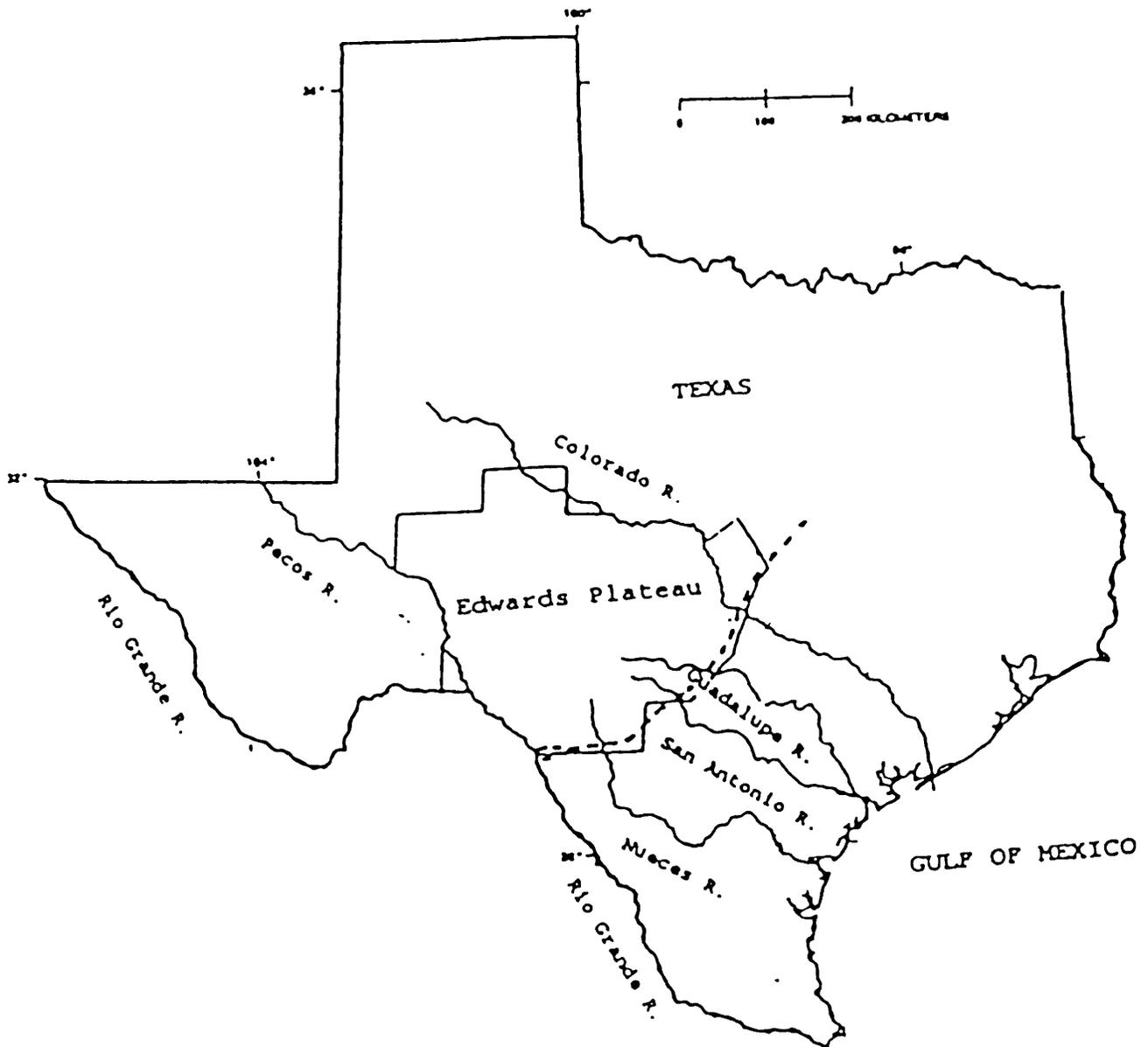


Figure 1. Location of the Edwards Plateau, Balcones fault zone and major river basins in central Texas.

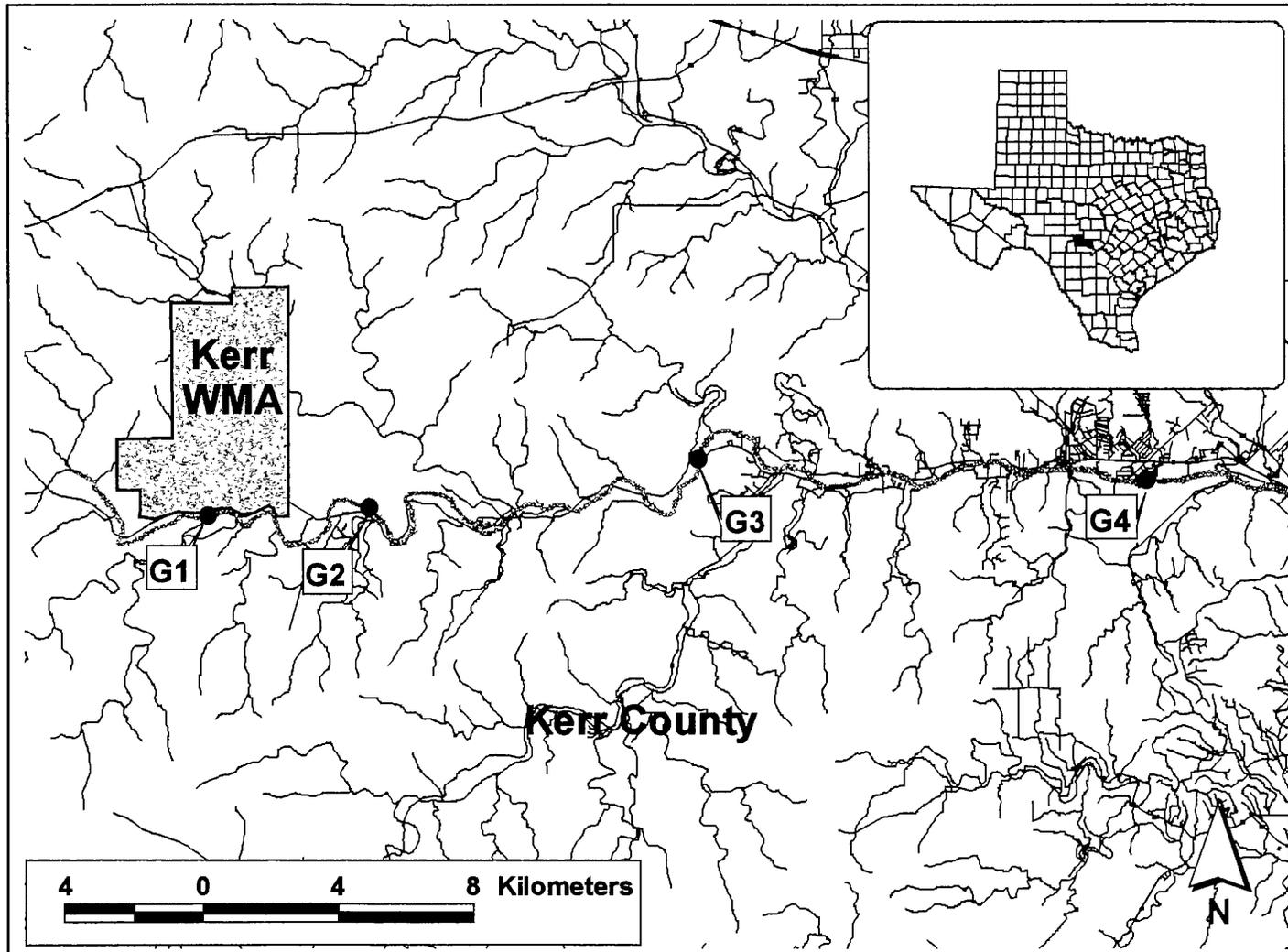


Figure 2. Map of sampling sites (G1, G2, G3, G4) on the upper Guadalupe River in Kerr county, Texas. WMA= Wildlife Management Area.

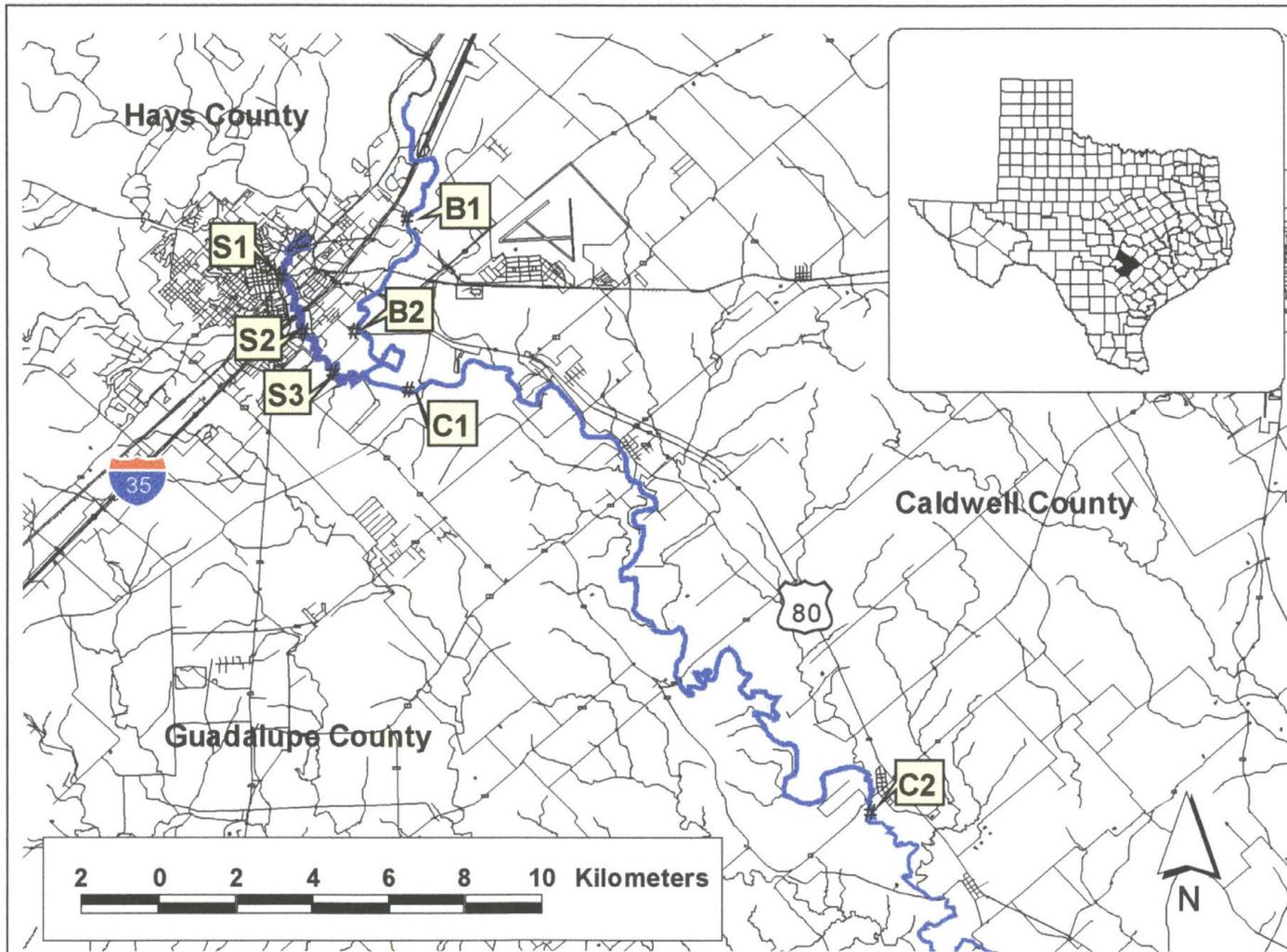


Figure 3. Map of sampling sites on the upper San Marcos River (S1, S2, S3), Blanco River (B1, B2), and post-confluence sites (C1, C2) in Hays and Caldwell counties, Texas.

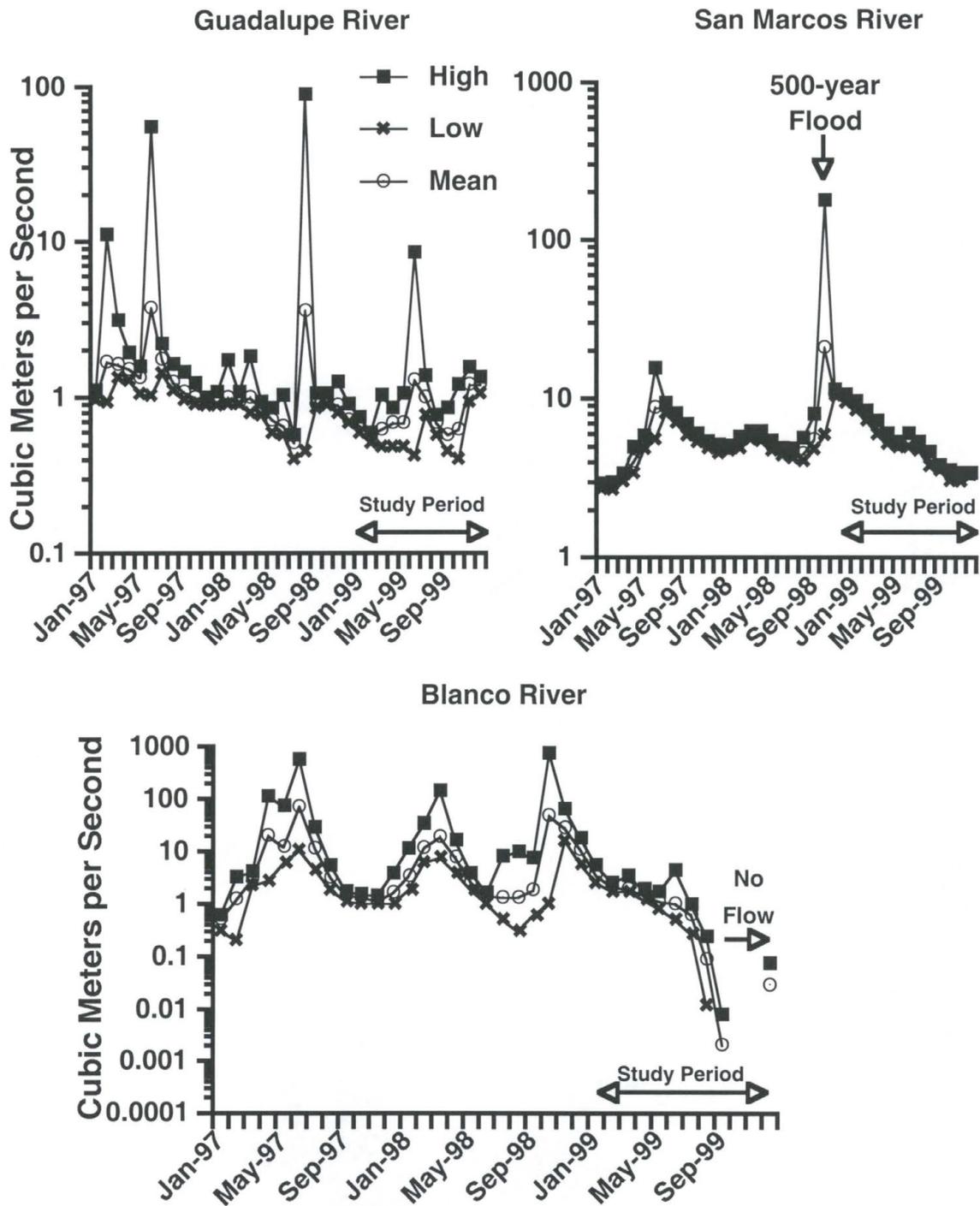


Figure 4. High, low and mean monthly discharge for study streams from January 1997 through December 1999. Stream gauge locations are as follows: Guadalupe River in Hunt, TX, San Marcos River in San Marcos, TX, Blanco River in Kyle, TX.

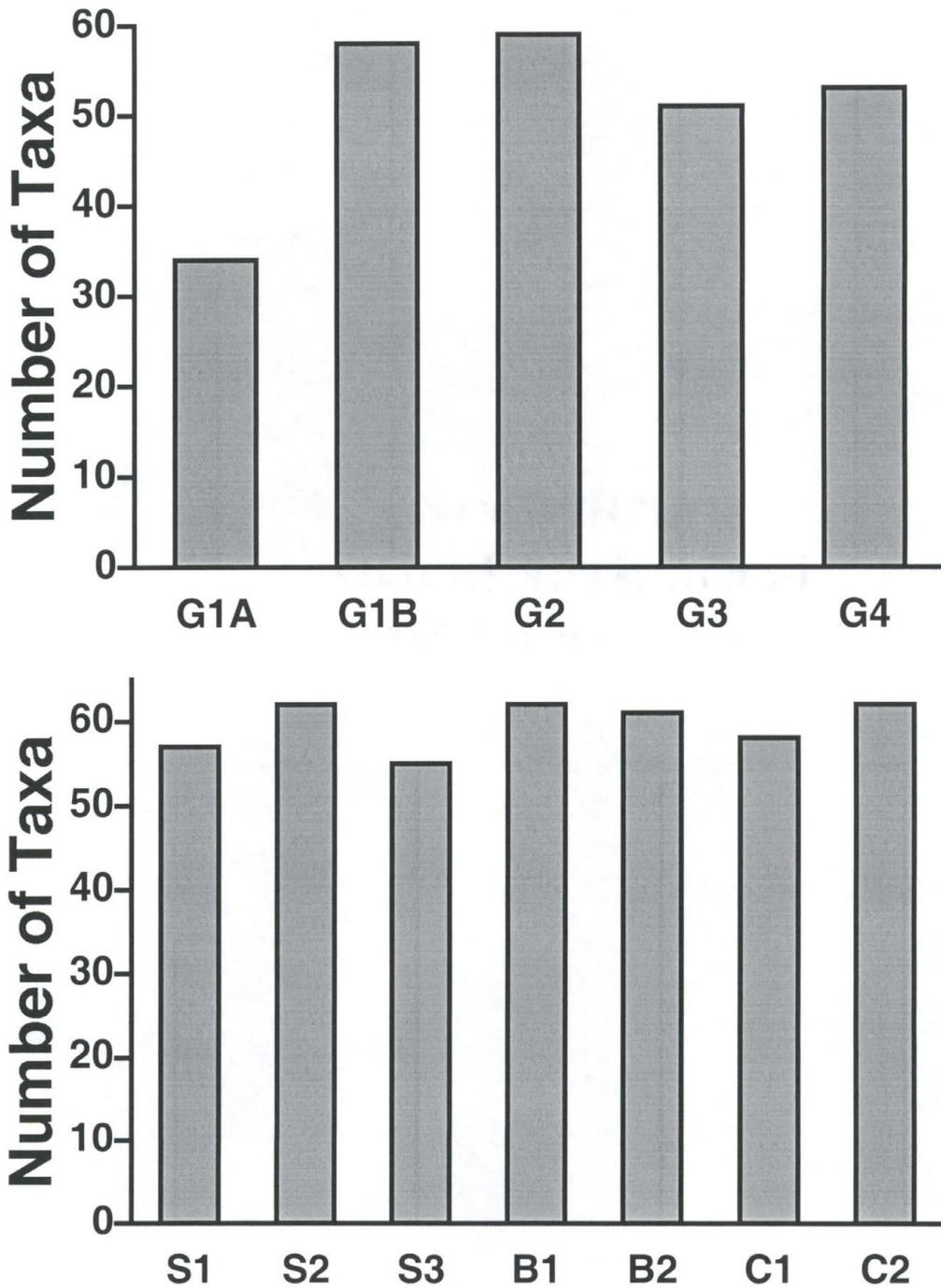


Figure 5. Taxonomic richness of the Guadalupe River (G), San Marcos River (S), Blanco River (B) and post-confluence (C) sample sites. Each bar reflects all samples and dates combined (N=16).

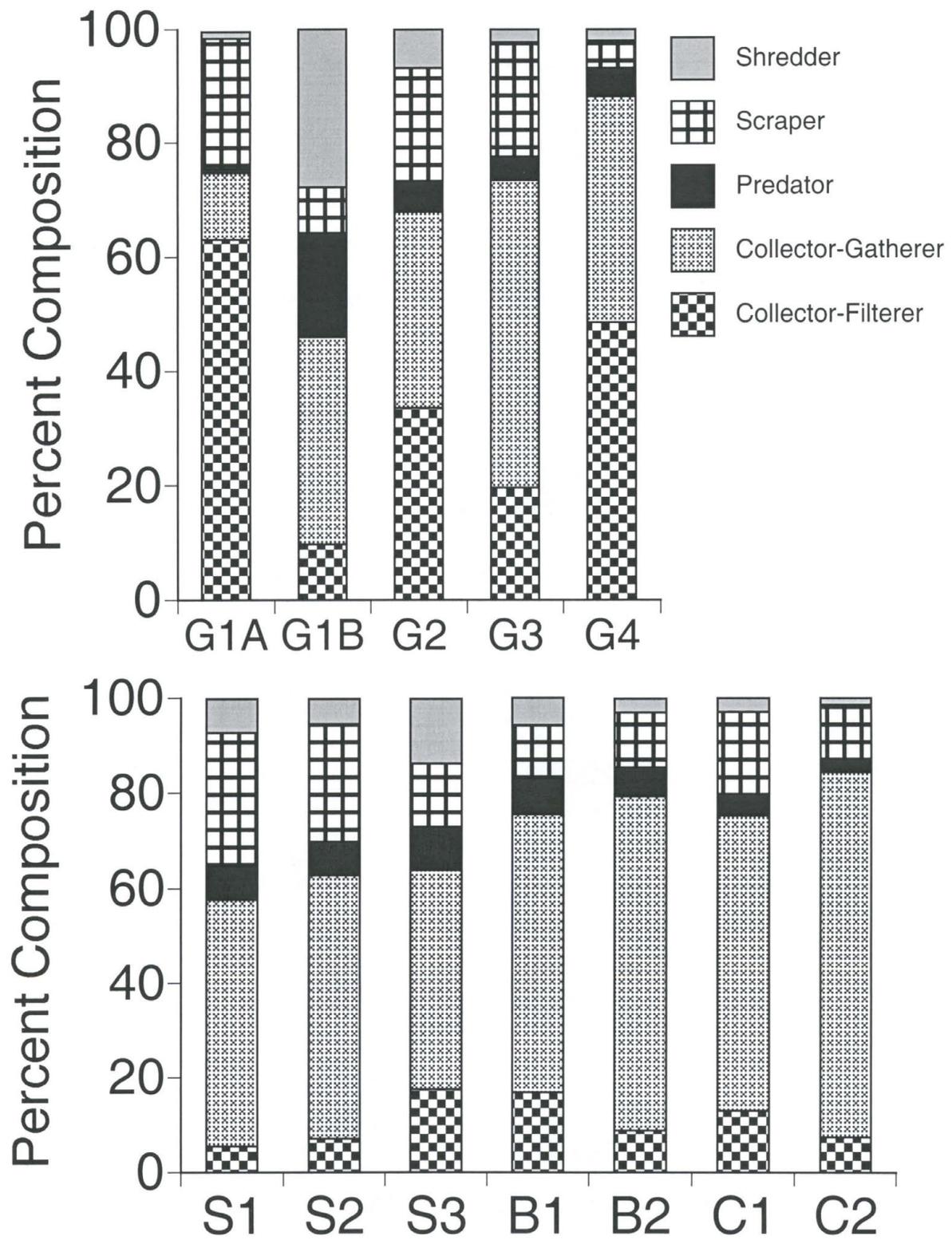


Figure 6. Relative abundance of functional feeding groups for the Guadalupe River (G), San Marcos (S), Blanco (B) and post-confluence sample sites. Each bar reflects all samples and dates combined (N=16).

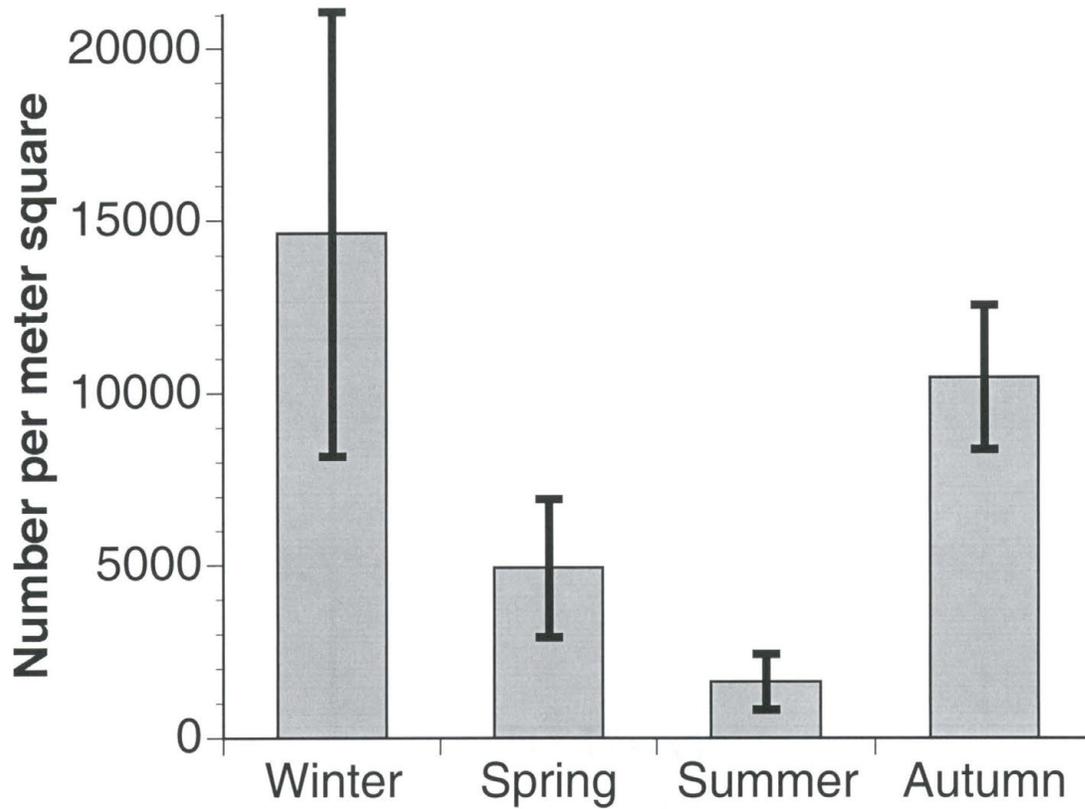


Figure 7. Mean benthic macroinvertebrate density per meter square by season for the farthest downstream sample site (C2) of the San Marcos River, after its confluence with the Blanco River. Each bar reflects 4 (n=4) replicate Hess samples per season. Error bars indicate ± 1 standard deviation.

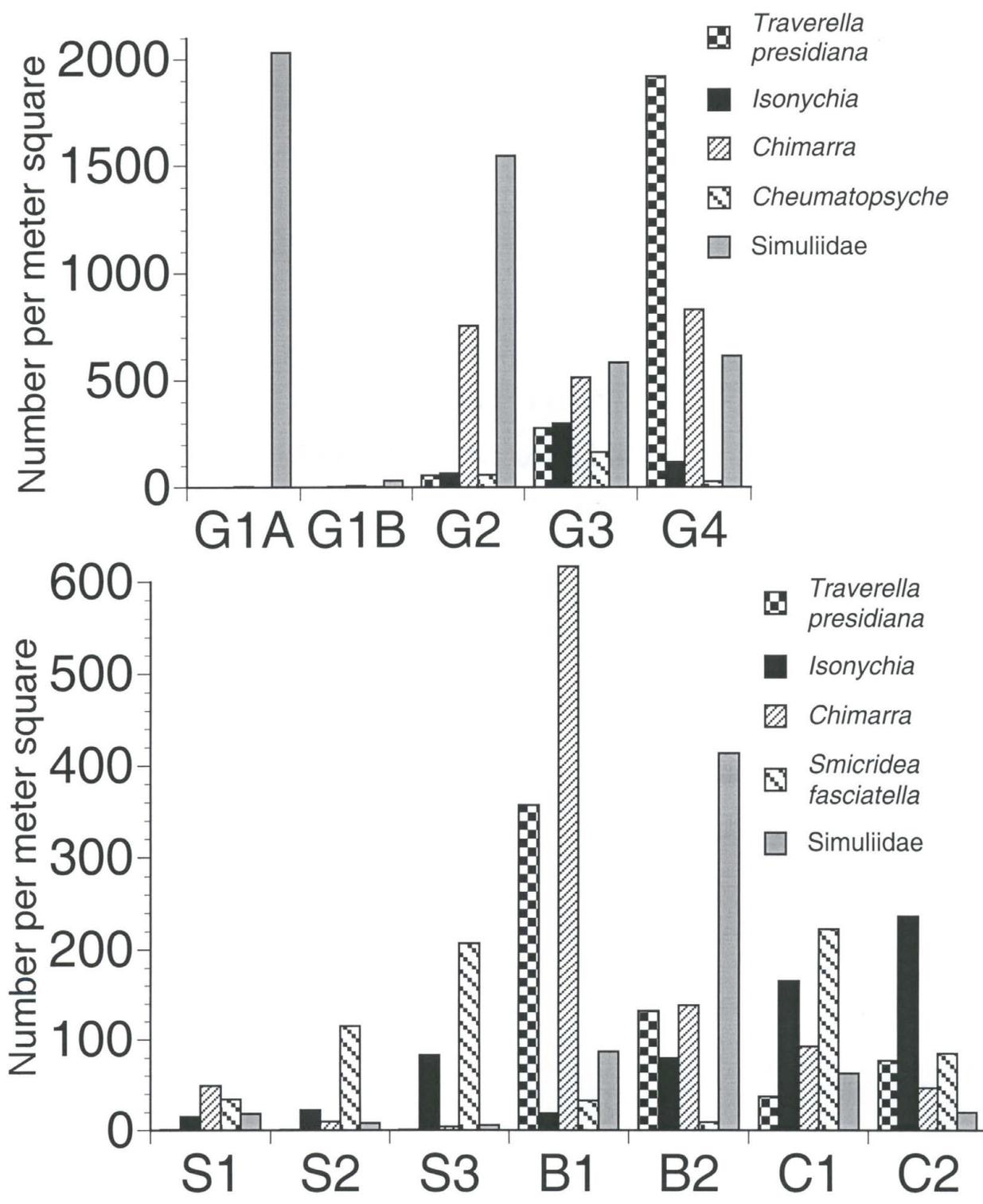


Figure 8. Longitudinal distribution of dominant collector-filterer taxa in mean number per meter square for the Guadalupe River (G), San Marcos River (S), Blanco River (B) and post-confluence (C) sample sites. Each bar reflects all samples and dates combined (N=16).

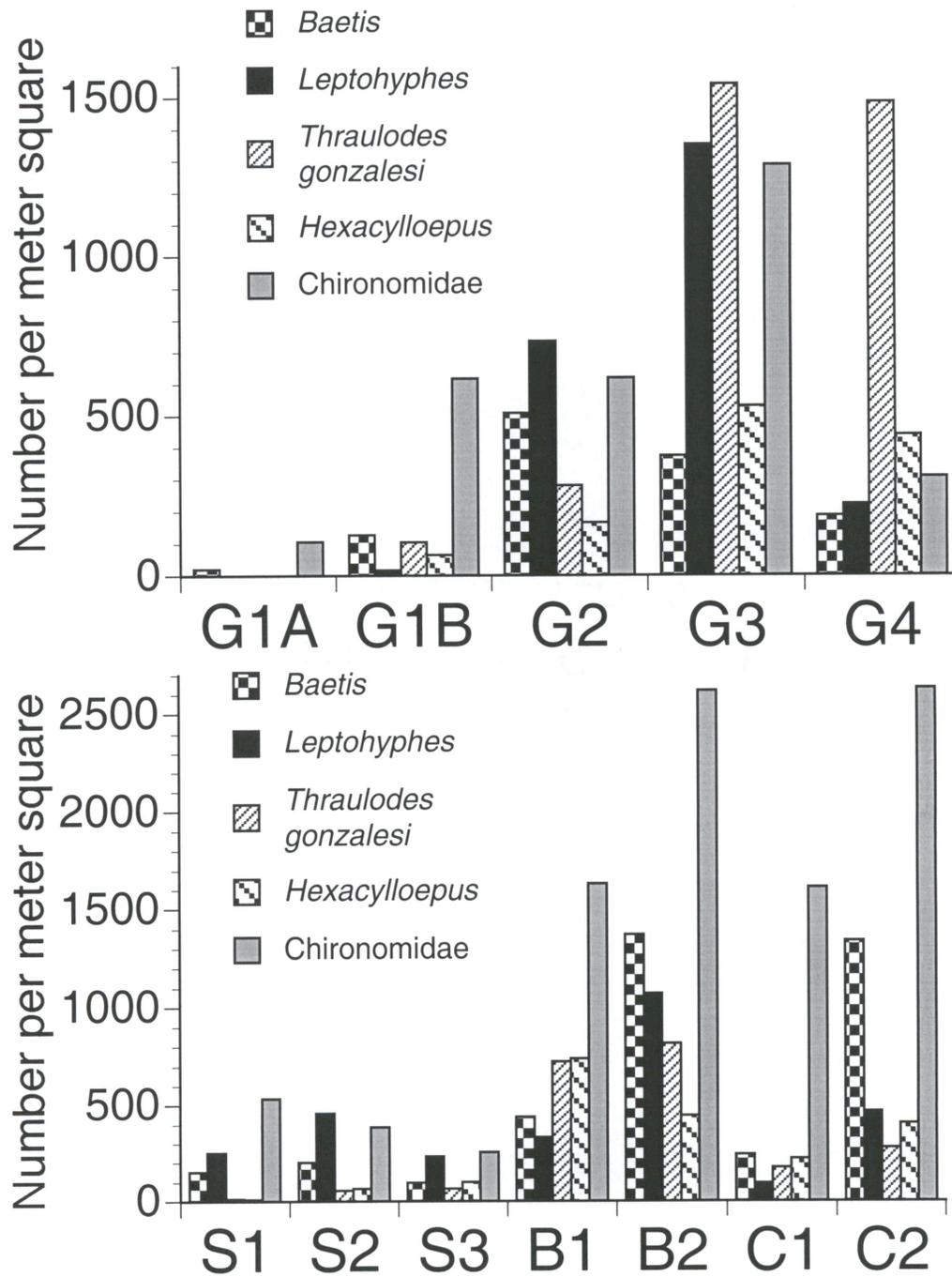


Figure 9. Longitudinal distribution of dominant collector-gatherer taxa in mean number per meter square for the Guadalupe River (G), San Marcos River (S), Blanco River (B) and post-confluence (C) sample sites. Each bar reflects all samples and dates combined (N=16).

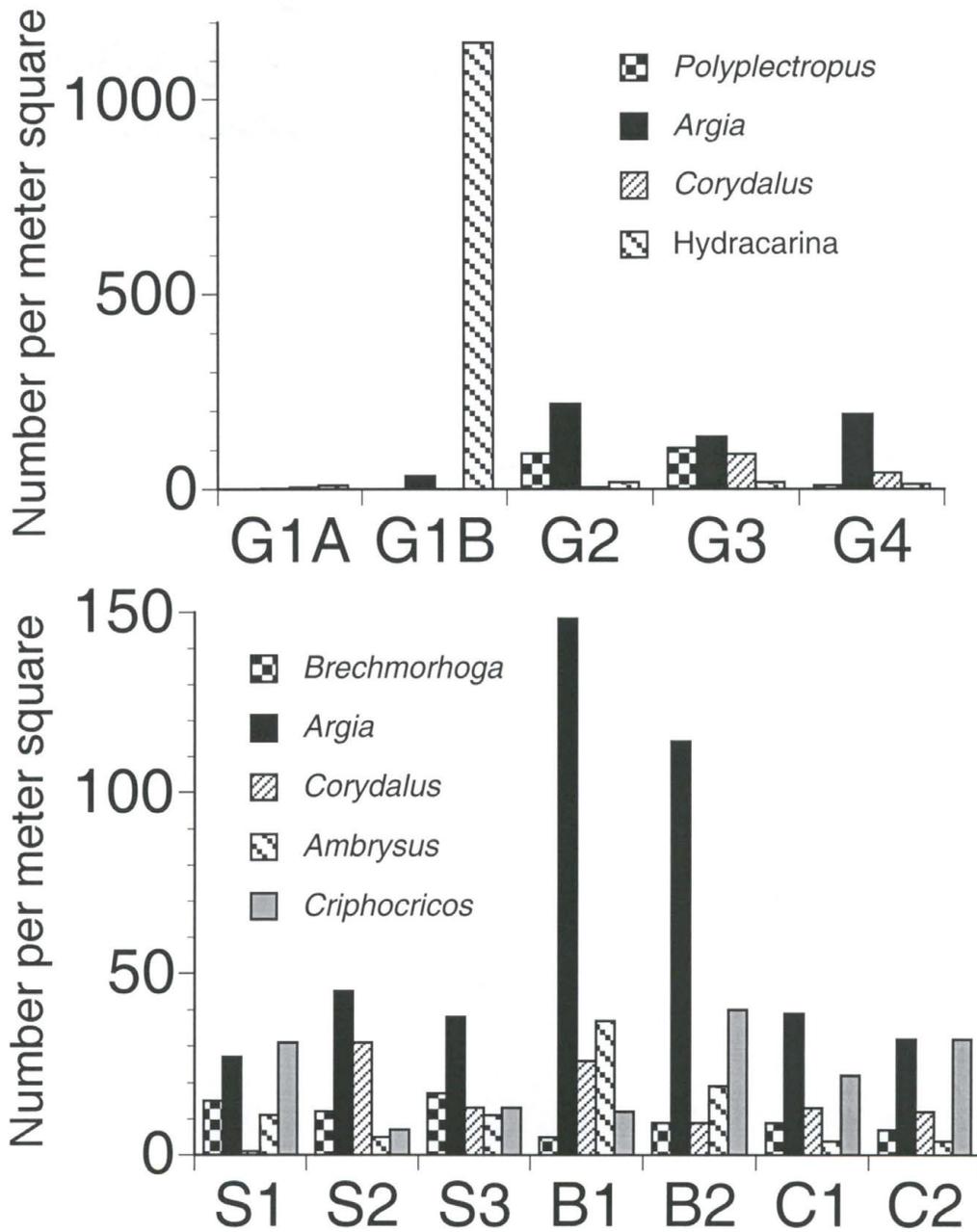


Figure 10. Longitudinal distribution of dominant predator taxa in mean number per meter square for the Guadalupe River (G), San Marcos River (S), Blanco River (B) and post-confluence (C) sample sites. Each bar reflects all samples and dates combined (N=16).

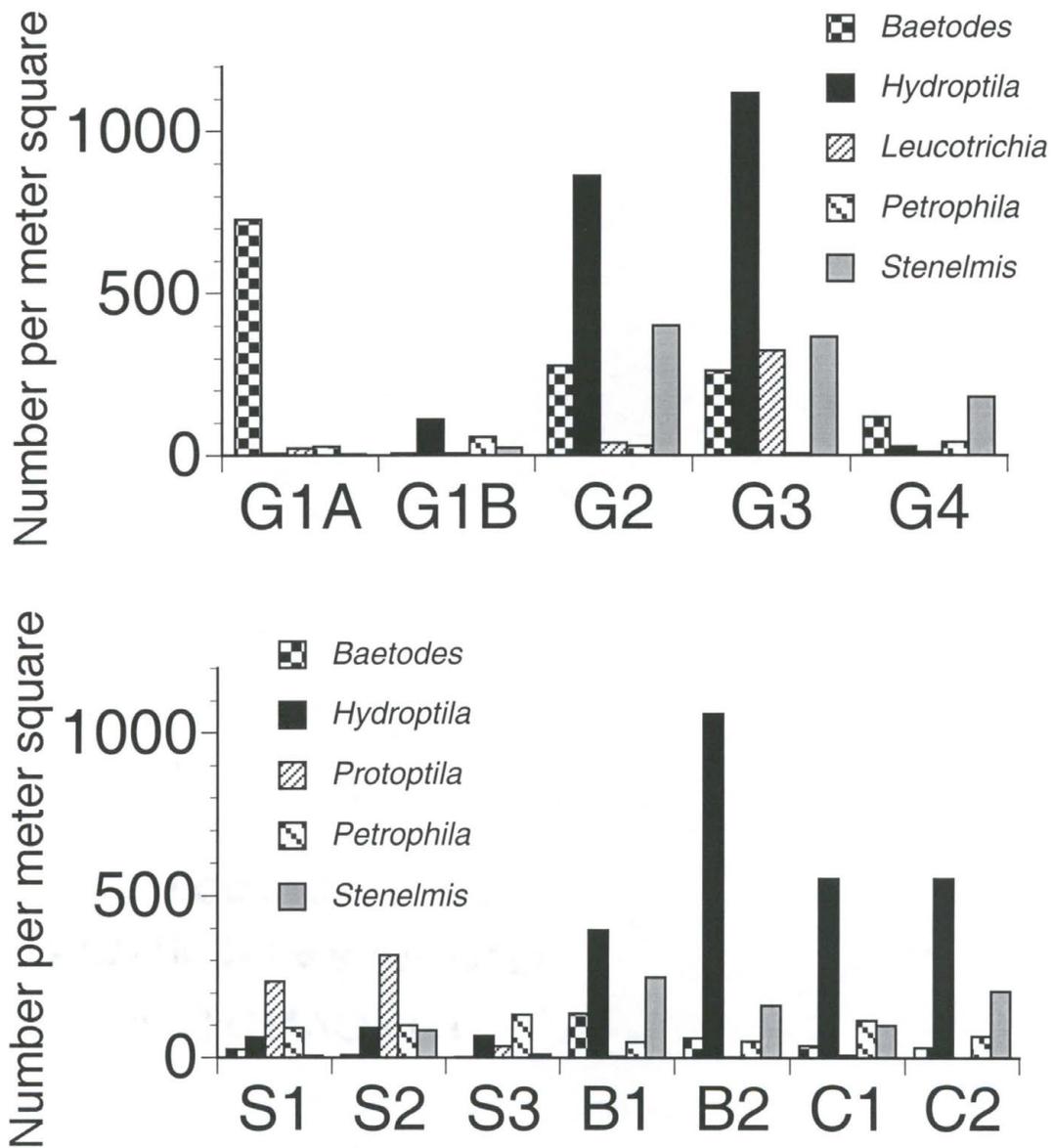


Figure 11. Longitudinal distribution of dominant scraper taxa in mean number per meter square for the Guadalupe River (G), San Marcos River (S), Blanco River (B) and post-confluence (C) sample sites. Each bar reflects all samples and dates combined (N=16).

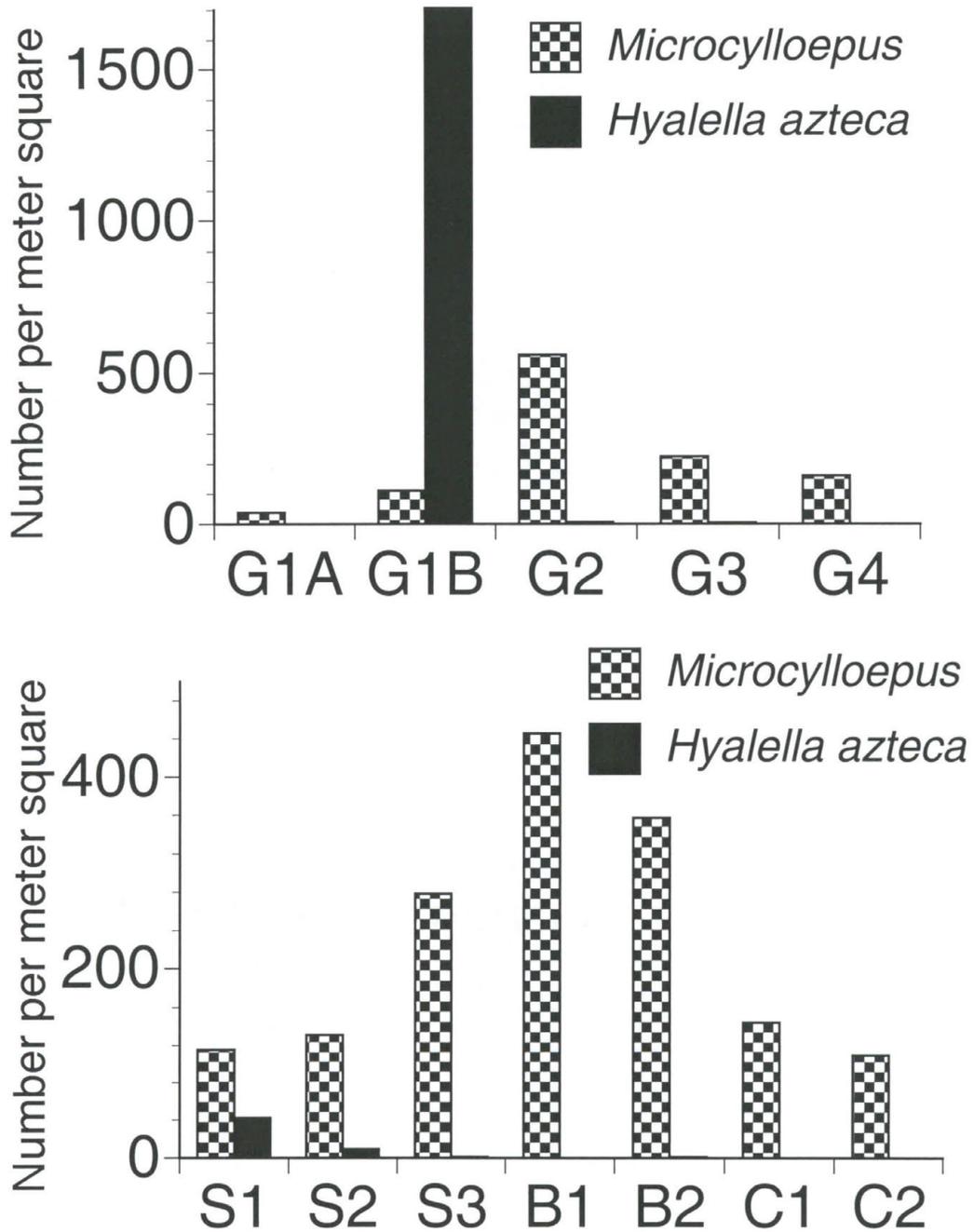


Figure 12. Longitudinal distribution of dominant shredder taxa in mean number per meter square for the Guadalupe River (G), San Marcos River (S), Blanco River (B) and post-confluence (C) sample sites. Each bar reflects all samples and dates combined (N=16).