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Distribution and abundance of zoobenthos in channel springbrook and hyporheic habitats of an alluvial floodplain

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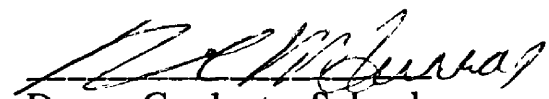
DISTRIBUTION AND ABUNDANCE OF ZOOBENTHOS IN CHANNEL, SPRINGBROOK, AND HYPORHEIC HABITATS OF AN ALLUVIAL FLOODPLAIN
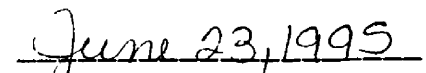
by

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ABSTRACT

Current river ecosystem theory (Stanford and Ward 1993) states that hyporheic habitats of gravel aquifers are landscape level phenomena that are predictable and repeated along the river continuum of glaciated, gravel-bed rivers. The occurence of bedrock configurations at the upstream end of the valley force river water deep into the sand and gravel alluvium resulting in interstitial flow which forms the hyporheic habitat. Ground water from the unconfined aquifer upwells into surface channels such as the main river channel and floodplain springbrooks (groundwater upwellings into surface channels). Floodplain springbrooks are of two types: floodchannels (springbrooks that erupt on the floodplain) and paleochannels (springbrooks that erupt on the floodplain terrace). Both springbrook types discharge into the main river channel downstream.

The purpose of this study was to assess the physical and biological interaction between these lotic habitats in the Nyack Floodplain, MT. Distinct biotic assemblages were expected in the river, springbrook, and interstitial habitats. Further, springbrook zoobenthos was predicted to more closely resemble interstitial biota (hyporheos) than surface taxa and have the greatest biodiversity due to the convergence of surface and ground water facies. The emergence of amphibitic stoneflies (species that spend all but the adult life stage in the interstices) was expected to occur primarily along springbrook shorelines.

Physical data indicated that annual temperature fluctuations were greatest in the river, more moderate in the springbrooks and relatively constant in the hyporheic environment. Dissolved oxygen concentrations were greatest in the river channel but maintained concentrations of >50% in both springbrook and hyporheic environments. Finally, specific conductance was highest in the interstices, intermediate in the springbrooks and lowest in the river channel.

Distinct biotic communities were documented in the river, springbrook, and hyporheic environments. River zoobenthos was composed of typical surface taxa. Springbrook zoobenthos more akin to river zoobenthos than hyporheos but samples were less diverse and abundant than that collected in the river. Hyporheos were rare or absent in river and springbrook samples Hyporheic organisms consisting of amphibites as well as obligate groundwater species (stygobites)were collected from wells in the floodplain and floodplain terraces up to 1.0 km from the river. Riverine species were incidental in all hyporheic samples. Springbrook environments did not prove to be highly biodiverse but instead highly bioproductive. Finally, adult plecopterans emerged mainly from the river shoreline and were rare or absent along the springbrooks. Temperature amplitudes in the river appeared to cue emergence activity. Thus, amphibites actively migrated toward the main channel rather than the springbrooks to complete life histories.

Results of this study support the theory of Stanford and Ward (1993) that hyporheic ecosystems of gravel aquifers are landscape level phenomena that may be regularly repeated along a river continuum given the proper hydrological and geological conditions.

Keywords: Amphibite, connectivity, floodchannel, hyporheic, interstitial, paleochannel, river basin, springbrook, stygobite, zoobenthos.

INTRODUCTION

Complex lotic habitats occur on the surface and subsurface of floodplains of large alluvial rivers. Lattice-like substrata are infiltrated by downwelling river water resulting in high volume flow through the interstitial area termed the hyporheic zone (Stanford 1975). The extent of the hyporheic zone is determined by the depth penetration of river water (Triska 1990), river discharge and head pressures (Stanford and Ward 1993) as well as changes in river stage, seasonal fluctuation in the water table and percentage of fines (Freeze and Cherry 1979). Ground water from an unconfined aquifer can upwell into surface environments of the main channel and floodplain springbrooks (Stanford and Ward 1993). Springbrooks are surface channels that have a ground water origin of flow and may connect with the main channel at the downstream end. These channels may occur as flood-channels on the active floodplain and as paleochannels on floodplain terraces (Stanford and Ward 1993).

Traditionally, physical processes occurring along the longitudinal dimension of rivers (Vannote et al. 1980) and lateral interactions within the riparian zone (Chauvet and Decamps 1989, Gregory et al. 1991) have been emphasized in lotic research. Consideration of the hyporheic dimension of rivers (Ward 1989) and the role ground water flux plays in rivers expands both the scale and complexity of river ecosystems (Stanford and Ward 1993). Thus, a more holistic conceptualization of lotic ecosystems is derived since interactions are considered at the landscape level (Amoros et al. 1988, Stanford and Ward 1992, Stanford and Ward 1993).

Further, biotic heterogeneity of lotic ecosystems is enhanced by the exchange of aquatic invertebrates (zoobenthos) between surface and groundwater environments. Several studies have documented interactions between surface and ground water assemblages over relatively small (cm^3) spatial scales (Coleman and Hynes 1970, Danielopol 1976, Poole and Stewart 1976, Godbout and Hynes 1982, Pennak and Ward 1986, Kowarc 1992). Riverine species were most commonly collected in shallow bed sediments. However, hyporheic crustaceans and obligate ground water species were also present in some studies (Godbout and Hynes 1982, Kowarc 1992).

Research performed over somewhat larger spatial scales (m^3) in alluvial floodplains in France yielded more diverse collections. Riverine (benthos), interstitial (hyporheos), and obligate ground water (stygobites) taxa were all found in samples from the hyporheic zone (Obdrlik and Lozano 1992, Maridet et al. 1992, Creuze et al. 1992, Olivier and Marmonier 1992, Marmonier et al. 1992). Distribution and composition of zoobenthos was related to river discharge (Creuze et al. 1992), areas of upwelling and downwelling (Olivier and Marmonier 1992), and hydrologic connectivity between surface and ground water habitats (Marmonier et al. 1992). Thus, the hyporheic zone was theorized to function as a biophysical filter (ecotone) between ground and surface water systems (Vervier 1992). As such, the interstices serve as an area where zoobenthos comingle with ground water fauna, depending on the rate of interstitial flow (Vervier 1992, Stanford and Ward 1993).

European researchers also investigated the biota of floodplain springbrooks and found them to be sites of increased biodiversity

and zoobenthic dispersion (Chafiq et al. 1992). Springbrooks were also found to increase floodplain connectivity by linking ground water and surface water biotopes (Chafiq et al. 1992, Gibert et al 1990) thereby serving as an ecotone between surface and ground water systems (Plenet et al. 1992).

While connectivity between lotic systems was documented in these studies, landscape level evaluations of connectivity could not be made. Extensive regulation of the Rhine and Rhône rivers has significantly reduced hydraulic interactions between the channel and adjacent floodplains

Research conducted in the more pristine alluvial floodplains of the Tobacco and Flathead rivers of Montana facilitated the study of landscape level interactions. The size of the hyporheic zone was found to be much more extensive (km^3) than that reported in Europe (Stanford and Gaufin 1974, Stanford and Ward 1988). Additionally, physical connectivity between the hyporheic zone and the main channel was demonstrated. Water level fluctuations in wells located up to 2 km from the main channel corresponded to changes in river flow volume (Stanford and Ward 1988). Dissolved oxygen concentrations in the wells also indicated interaction was occurring between interstitial and surface water in the main channel. Dissolved oxygen concentrations remained at >50% throughout the hyporheic zone due to high volume interstitial flow derived primarily from the Flathead River (Stanford and Ward 1988). Specific conductance generally increased with distance from the main channel as a function of increasing ground water residence times. Interstitial temperatures fluctuated on a seasonal basis but the observed

thermal regime was more moderate than that of the river (Stanford and Ward 1988).

Stanford and Ward (1988) found biotic exchanges to occur on a much larger scale in the Flathead River and to be much more speciose (>70 metazoan taxa) than those reported in Europe. Zoobenthos were collected from approximately 10 m depth and up to 2 km distant from the main channel. The discovery of specialized organisms with epigean affinities (amphibites) of which the dominant forms were large-bodied stoneflies (> 2cm in length) was unprecedented. Amphibitic stoneflies were found to spend all but the adult life stage deep in the floodplain gravel aquifer and emerge into the channel only to complete life histories. Emergence appeared to be cued by attainment of precise temperature thresholds in the river (Stanford and Ward 1982, Stanford and Ward 1988). Species included two chloroperlid (Kathroperla perdita and Paraperla fontalis) and four capniid (Isocapnia grandis, I. crinata, I. missouri, I. vedderensis) stoneflies. Nymphs of these taxa had only rarely been collected in the river zoobenthos of previous studies (Stanford and Gaufin 1974, Stanford and Ward 1988). Similarly, obligate ground water fauna, including many species new to science, were also present in near surface ground waters (Stanford and Ward 1988, Reid et al. 1988).

The distribution of these organisms was associated with gradients in temperature, specific conductance, and dissolved oxygen concentration. Stygobites were more prevalent in waters with higher specific conductance and lower temperatures. Amphibites were more common in lower conductance, warmer waters. Zoobenthos

were not associated with distinct dissolved oxygen concentrations since levels were relatively high throughout the hyporheic zone (Stanford and Ward 1988).

In order to demonstrate that these findings were not isolated to the alluvial floodplain of the Kalispell Valley, research was initiated on an upstream reach of the Flathead River in the Nyack Floodplain, Montana. Given the observation that channel, hyporheic, and springbrook habitats probably existed in this system, the primary objective of this study was to examine the distribution, composition, and abundance of zoobenthic assemblages within these habitats. Springbrook zoobenthos was hypothesized to be more analogous to hyporheos due to the ground water source of springbrook flow. Furthermore, biodiversity was expected to be greater in springbrooks than in the river due to the convergence of surface and ground water facies. Abiotic factors, such as dissolved oxygen concentration, specific conductance, flow and temperature dynamics, were also predicted to affect insect distribution.

Adult hyporheic plecopterans were originally expected to emerge from the springbrook environments. The effect of temperature upon the phenologies of springbrook zoobenthos, specifically plecopterans, had never been investigated in the Flathead River. While the presence of hyporheic organisms in springbrook channels was anticipated, it was unknown if springbrooks would be available to amphibites as emergence sites due to the comparatively cooler thermal regime. Interstitial flow from the river into the springbrook upwellings was thought to depress average water temperatures. Therefore, comparisons of

plecopteran emergence patterns were also made between river and springbrook habitats.

Finally, community composition and distribution of hyporheos in the Nyack floodplain was expected to be similar to the findings of Stanford and Ward in the Kalispell Valley (1988).

STUDY SITE

Selection of the Nyack Floodplain study site was based upon hydrologic and biotic similarity of the Nyack and Kalispell Valley floodplains. However, the Nyack floodplain is relatively pristine compared to the alluvial system in the Kalispell Valley, which is modified by extensive agriculture and urbanization.

The Nyack study area is located at latitude $113^{o}10$', longitude $114^{o}45$' on the Middle Fork of the Flathead River 15 km upstream from West Glacier, MT. Discharge from the 5th order river averaged 1070 m^3 sec $^{-1}$ in 1991 and 465 m^3 sec $^{-1}$ in 1992. The average annual discharge for both years was 768 m^3 sec $^{-1}$ (Stanford et al unpubl.). The river hydrograph characteristically peaks during spring snow melt in May and June, reaching baseflow by mid-August.

The floodplain is composed of large cobbles, gravels, and fine grained sands reworked by fluvial processes. Terraces (Fig. 1) are composed primarily of overbank deposits (silts and clays) left by extreme floods. Based on well drilling logs, substrata of the Nyack Valley is uniformly composed of cobble alluvium overlying either

Tertiary clays or Precambrian bedrock of the Belt Series which compose the mountains of Glacier National Park.

The Nyack Valley, including terraces that border the active channel, covers an area approximately 1.5 km wide between the valley walls (Fig. 1). Natural bedrock-knickpoints define the up and downstream limits of the valley. Geohydrologic investigations and water mass balance measures for the entire valley (Stanford et al. unpublished) demonstrate that approximately 30% of the river volume downwells into the floodplain alluvium downstream from the bedrock knickpoint located on the northeastern end of the floodplain. Massive upwelling into the main channel and springbrooks occurs at various points beginning near the confluence of Nyack Creek and concludes just upstream of the bedrock knickpoint located on the southeastern end of the valley. Much of the upwelling water derived from the alluvial aquifer occurs in springbrooks. These channels flow across the floodplain and floodplain terraces (Fig. 1). Seasonal variations in the water table clearly demonstrate that interstitial springbrook flow rates are directly controlled by river flow. The alluvial aquifer of the Nyack Valley is apparently dominated from valley wall to valley wall by interstitial flow derived mainly from the river (as opposed to water from side flows and hillside sources).

Four distinct lotic habitats were identified in the valley: 1) river channel, 2) flood-channel springbrooks (those erupting from channels on the floodplain), 3) terrace springbrooks (those erupting from paleochannels on the terraces), and 4) hyporheic habitat which we characterized by interstitial flow of river water from valley wall to valley wall.

METHODS

Sites were established across the floodplain from which taxa composition and abundance of zoobenthos in the channel and springbrooks could be compared and contrasted with hyporheos. Zoobenthos in the river were collected from a riffle site in the main channel approximately 1.0 km upstream of the mouth of Nyack Creek in a downwelling area of the floodplain (Fig. 1). Zoobenthos were collected monthly from the river (November 1990 through April 1992). Collections were not made during the spring runoff period (May through June 1991). Macroinvertebrates were dislodged by hand and foot action from a 0.5 m^2 area for one minute into a Nitex kicknet (240 um pore size) held downstream (after Hauer and Stanford 1981). Samples were then elutriated into a bucket and preserved in 10% formalin.

Hyporheos were collected from unscreened wells and sandpoints at various locations in the floodplain and on the terraces (Fig. 1). Four wells were drilled on the northwestern end of the floodplain approximately 10 m deep, using a hollow auger drilling rig. Two wells were drilled on the terrace 0.3 km (TW1) and 0.8 km (TW2) from the main channel of the river. Two more wells (FW1 and FW2) were drilled on the floodplain within flood-channels approximately 0.13 km from the river (Fig. 1). These wells (TW1, TW2, FW1 and FW2) were the primary sites for hyporheos sampling. Four additional wells were drilled in October 1991 to augment hyporheos collection efforts. Two wells were drilled on the floodplain terrace (TW3, TW4), approximately 0.5 km from Beaver

Creek. Two others (FW3, FW4) were located on the floodplain at the downstream end of the valley (Fig. 1).

Hyporheos from the four primary sampling wells were sampled bimonthly from November 1991 through April 1992, except during spring runoff (May through June 1991) when flood waters prevented access. Wells were pumped for 10 minutes using a gasoline powered diaphragm pump. The pump hose was raised and lowered throughout the pumping event in order to collect organisms over the entire depth of the well. Hyporheos were collected in a Nitex net (137 um pore size), elutriated into a hand-held net (40 um pore size), and then preserved in 10% formalin.

Hyporheos samples were also collected from floodplain sites (Fig. 1) using a sandpoint (perforated steel shaft 0.08 m x 1.5 m). The process involved first digging a pit to the depth of the water table. The sandpoint was then driven into the substrata as far as possible using a sledgehammer. Water from the hyporheic zone was sampled using the gas-powered diaphragm pump. Hyporheos were collected in the same manner as described above for well samples.

We sampled three of the floodplain springbrooks routinely; one terrace springbrook (Tom's Springbrook, TS1) was sampled incidentally (Fig. 1). Nyack Springbrook was located in a flood-channel and flowed 0.2 km toward the river from the upwell area. Water volume in the springbrook rose and fell concomitant with changes in river flow. Flow in this stream began just prior to spring runoff in March 1991 and dissipated gradually until the channel became dry in August 1991. Georgia's Springbrook (FS2) was located in a flood-channel that flowed 0.4 km toward Nyack Creek. The

upwelling area fluctuated 100 m longitudinally on a seasonal basis as a function of river flow. Beaver Springbrook (FS3) was also in a flood-channel and flowed 1.2 km to the river. During the spring runoff period in 1992, the river flooded this springbrook. Flow in Tom's Creek (FT1) upwelled into a paleochannel on the terrace approximately 0.5 km from the river channel (Fig. 1). Streamflow dynamics in this stream were similar to those observed in Beaver Creek, however this channel was not flooded by overland flow. Sampling periods for each of the springbrooks varied over the course of the study. FS1 was sampled from November 1990 through September 1991. Samples were not collected in this springbrook after September 1991 because it became dewatered as the river dropped to a very low baseflow. FS2 was sampled from April 1991 through April 1992 and FS3 was sampled from November 1991 through April 1992. Samples were not collected in any of the streams during spring runoff (May through June 1991). Zoobenthos were collected in a manner modified from that used in the river. However, samples were collected on a bimonthly basis in the springbrooks due to the comparatively small size of these sites. Macroinvertebrates were dislodged by hand for 60 seconds from a 0.25 m^2 area into a Surber sampler. Samples were then elutriated into a bucket and preserved in 10% formalin (after Hauer and Stanford 1981).

Physical measurements were taken during each sampling event. Dissolved oxygen and specific conductance field meters (YSI) as well as a Fisher digital thermistor were used at all sampling locations. Depth to water measures were taken in the wells prior to

each pumping event using a chalked tape. Continuous recording Omnidata Data loggers were mounted on three of the floodplain wells, as well as near each knickpoint (Fig. 1). Data loggers recorded temperature and water elevations hourly. These measurements were used to document water mass balance described elsewhere (Stanford et al. unpublished).

Zoobenthos and hyporheos were sorted in the lab. First, all large marcroinvertebrates were removed. Subsamples equaling no less than 1/15 of the total sample volume were examined at 6x and 12x power on a dissecting microscope. Identification of macroinvertebrates was made to the lowest taxonomic level possible using keys in Jensen 1966, Gaufin et al. 1972, Morihara and McCafferty 1979, Merrit and Cummins 1984, Stewart and Stark 1988. Chironomids and some crustaceans were grouped to the family level, owing to taxonimic uncertainties. Voucher specimens were prepared for river, hyporheic, and springbrook zoobenthos and placed in a permanent collection at the Flathead Lake Biological Station.

In order to document emergence patterns of the hyporheic stoneflies, shoreline pitfall traps were employed for collection of teneral adults and emerging nymphs. Plastic pails (0.95 L volume) were embedded in the shoreline and concealed by large flat rocks and wood debris. Five traps were placed in the shoreline of the river and at FS1 and FS2. The pails were half filled with 10% formalin or 70% ethanol during freezing weather. A thin film of glycerin was applied to the surface of the preservative. The oil film encumbered teneral adults and emerging nymphs which fell into the pitfall traps

while seeking shelter. The stoneflies would then sink into the preservative (after Stanford 1975). Collections were performed weekly during emergence periods of hyporheic species. Additionally, searches at the water-shore interface at each station were made to collect emerging and last instar nymphs, fresh exuviae, and teneral adults. Sweep-netting of bankside vegetation was also performed to collect stoneflies that avoided the pitfall traps.

Finally, community composition in the lotic habitats of the Nyack Floodplain was related to variation in the environment using canonical correlation analysis (CCA), a multivariate direct gradient analysis technique. This method was selected because of its ability to relate multiple species directly to multiple environmental factors (ter Braak 1986). In order to perform the analysis, two separate FORTRAN-based databases were created. The species database summarized the number of individuals per species or taxon collected per sample number. The physical database summarized all quantitative and nominal variables associated with each sample number. Quantitative variables included dissolved oxygen concentration, specific conductance, temperature and date. Nominal variables were habitat types (river, springbrooks, hyporheic). Multiple iterations by CCA related the two databases by sample number. Thus, patterns of variation in the species abundance data that were best explained by one or more environmental variables were detected. Continuous axes of variation were extracted from the species abundance data to produce four ordination axes (e.g. explanatory variables). The number of ordination axes corresponded to the number of quantitative environmental variables in the

physical database. Variation in species data was thus constrained or given an environmental basis since ordination axes were formed by linear combinations of the quantitative environmental variables (ter Braak 1986).

Thirty samples were deleted from the analysis due to suspected field or lab processing errors. A remaining 145 samples were then analyzed. Results were then transferred to CANODRAW, a FORTRAN-based graphics program, to develop ordination diagrams. A biplot of species and environmental variables was produced (Fig. 19). To enhance clarity, only 15 of the 163 total species were selected for graphical display. The fifteen species were composed of six species unique to the river, five species unique to the springbrooks, and five species unique to the hyporheic environment.

RESULTS

Physical Characteristics

Examination of physical measurements revealed that temperature fluctuations were greatest in the river. Thermal amplitudes were more moderate in the springbrooks due to the ground water origin of flow. The greatest annual constancy in temperatures was measured in the hyporheic zone (Table 1). Similarly, dissolved oxygen concentrations were greatest in the river channel but maintained concentrations of >50% in both the springbrook and hyporheic environments. Finally, the highest specific conductance values were measured in the hyporheic zone, particularly those wells located furthest from the main channel. Values were intermediate in the springbrooks and lowest in the river.

River Zoobenthos

Zoobenthos from the river channel consisted of 79 taxa (Fig. 2) with a total of 32,487 individuals collected in all samples. Midges (Chironomidae), mayflies (Rhithrogena undulata, Cinygmula spp, Ephemerella spp) and two closely related stoneflies (Taenionema pacificum, Doddsia occidentalis) were the most frequently occurring taxa (Fig. 2). Copepods, which are often found in the hyporheic zone (Pennak and Ward 1985, Reid et al. 1988, Creuze and Marmonier 1990, Boulton et al. 1992, Ward et al. unpubl.), were present in river samples in this study but were very rare (< 1.0 % of total).

Amphibitic stoneflies were never found in zoobenthos samples from the Nyack Floodplain.

Hyporheic Zoobenthos

Examination of hyporheos from the floodplain and terrace wells revealed an entirely different community composition from that found in the river. Hyporheos contained amphibites and stygobites (hyporheic crustaceans and archiannelids), as well as obligate surface species that were passively entrained in the interstices. A distinct distribution pattern was observed across the floodplain. In the primary study wells (TW1, TW2, FW1, FW2), stygobites accounted for 92% and 84% of total community composition in terrace wells TW1 and TW2, respectively (Fig. 3). Amphibites and typical riverine forms were found in each of these wells but in very small numbers. Conversely, amphibites accounted for 82% and 50% of the zoobenthos in FW1 and FW2, respectively (Fig. 3). Large numbers of stygobites and typically riverine forms (e.g. Rhithrogena robusta, Pteronarcella spp, Hydropsyche cockerelli) were present as well (Table 2, Fig. 3).

TW1 had the lowest abundance and diversity of invertebrates of the primary study wells. A total of 11 taxa and 294 organisms were collected over the study period (Fig. 4). Stygobites (Stygobromus spp, Archiannelida, Cyclopoida, Bathynella, Harpacticoida) comprised >90% of total community composition while amphibites (Isocapnia spp) contributed <5.0% to the total. Typically riverine taxa that appeared to have been swept into the interstices from the main channel of the river added >6% to the total community composition of TW1 (Fig 4). Riverine taxa collected in TW1 included

dipterans (Chironomidae), mayflies (Rhithrogena spp.) stoneflies (Sweltsa coloradensis), and nematodes (Fig. 4, Table 2).

A total of 14 taxa and 634 organisms were collected from TW2 (Fig. 5). Stygobites comprised >75% of the total community composition. Chironomidae, Hemiptera, and other species whose occurrence accounted for less than 2% of the total added another 15% (Fig. 5). Physical conditions were similar to those measured in TW1; therefore, the predominance of stygobites was expected. Unlike TW1, amphibitic stoneflies (Kathroperla perdita, Paraperla frontalis, were present but rare in TW2 samples. However, Isocapnia spp did account for 5% of the total abundance in TW2.

FW1 had a total of 28 taxa and 5,173 organisms - more than found in any of the other wells (Fig. 6). Approximately 80% of the total community composition was made up of large-bodied amphibitic stoneflies. Isocapnia spp dominated community composition by contributing >77% to the total (Fig. 6). Four species of Isocapnia were present in the well samples; however, larvae could not be differentiated at early life stages. Unlike the terrace wells, stygobites did not dominate community composition in floodplain well samples since they contributed less than 10% to the total percentage (Table 2, Fig. 6). However, raw abundance of stygobites was greater in this well (424 organisms) than the other three wells combined. Typically riverine taxa were incidental in samples from FW1 but combined to contribute >5% to the total community composition. Taxa included mayflies (Baetis bicaudatus, Ephemerella spp, Paraleptophlebia memorialis, Rithrogena spp), stoneflies

(<u>Claassenia sabulosa, Diura knowltoni, Zapada cinctipes</u>), beetles (<u>Narpus spp</u>) and dipterans (<u>Tipula spp, Antocha spp,</u> Chironomidae).

A total of 20 taxa and 738 organisms were sampled from FW2 over the study period (Fig. 7). The percentage of amphibites and stygobites in samples from this well was roughly equal: stygobites comprised >39% of the total community composition while amphibites contributed >49%. The remainder was made up of typically riverine species such as <u>Paraleptophlebia memorialis</u> and <u>Narpus spp</u> which may have been passively swept into the interstitial environment from the river.

Secondary wells were not sampled as often as primary wells owing to later installation of TW3, TW4, FW3, and FW4 in the study. Therefore, only general comparisons of hyporheos composition between the two sets of wells could be made. A distribution pattern unlike that observed in the primary wells was noted in TW3, TW4, FW3, and FW4. The percentage of stygobites in the floodplain wells (>85%) was greater than that observed in the terrace wells (>54%) (Fig 8). The distribution of amphibites also differed in the secondary wells. Amphibites were collected in only one floodplain well and one terrace well. Unlike the primary wells, the percentage of amphibites was greater in the terrace well (36%) than in the floodplain well (9%). The percentage of riverine taxa was greatest in TW4 comprising >50% of the community composition. Benthos were present in smaller percentages in the floodplain wells contributing 10% and 5% to the total in FW3 and FW4, respectively.

TW3 had the lowest abundance and diversity of all study wells. A total of 6 taxa and 44 organisms were collected over the study

period (Fig. 9). Hyporheic crustaceans and amphibitic stoneflies were almost equally represented and dominated samples collected over the study period (Fig. 9). Benthic taxa included Peltoperla brevis and Collembola which contributed only 9.2% to the total.

TW4 had a total of 8 taxa and 189 organisms in samples collected over the study period. Total community composition was roughly divided between stygobites (46%) and benthic species (52%) (Fig. 10). Benthic taxa included Chironomidae, Collembola, and Hydropsyche cockerelli. Amphibitic stoneflies (Isocapnia spp) were present in samples and contributed 2.8% to the total community composition.

FW3 had a total of 6 taxa and 211 organisms in hyporheos samples (Fig. 11). Styobionts dominated sample collections contributing >90% to the total. Amphibites were not present in any samples collected from this well. Benthic taxa (Collembola and Taeniopterygidae) were present in samples contributing 10% to the total. However, presence of benthic forms was more incidental than the percentage indicates since only 22 benthic organisms were collected.

A total of 9 taxa and 269 organisms were collected from FW4. Stygobites also dominated samples in this well contributing 86% to the total community composition (Fig. 12). Amphibitic stoneflies, Kathroperla perdita and Isocapnia spp, added 9% to the total (Fig. 12). Benthic taxa included Collembola and Ephemerella spp which added only 5% to the total.

Hyporheos were also collected from sandpoints. Thirty-eight taxa were collected from 14 sandpoint locations in August and

October 1991 (Fig. 13). Chironomidae, Capniidae, and other species totaling less than 2% of the total composition made up 26%, 20%, and 18% of the total community composition, respectively (Fig. 13). Early instars of typically riverine species accounted for 11 taxa. Amphibitic stoneflies, Kathroperla perdita, Paraperla frontalis, and Isocapnia spp, were present in samples (30 organisms), but accounted for less than 2% of the total. Stygobites were present in far greater abundance (491 organisms) and accounted for approximately 28% of the total abundance (Fig. 13). More stygobites were collected in two sandpoints sampling events than from all terrace well samples combined.

Springbrook Zoobenthos

Comparisons of springbrook community composition and abundance were made by evaluating zoobenthos from each of the three sites. Data from each site were also compared to results from the river and wells. The latter comparisons were made in order to examine the biotic connectivity between river, springbrook, and hyporheic habitats.

Nyack Springbrook (FS1) had a total of 61 taxa and 7,185 organisms with stoneflies (families Taeniopterygidae, Capniidae,) and dipterans (Chironimidae) accounting for >76% of the total community composition (Fig. 15). Contrary to our hypothesis, larval amphibitic stoneflies were never collected in FS1. This was somewhat surprising since hundreds of amphibitic stoneflies were pumped from FW2 which was situated within the upwelling zone of this springbrook. Stygobites were present in samples from FS1 but

accounted for less than 1% of the total community composition (Fig. 15). Community composition of zoobenthos collected from FS1 differed from that of the river. Dipterans comprised a much larger percentage of the total community composition in FS1 than the river (47% vs. 18%). Only six Ephemerellidae mayflies were collected in the springbrook compared to 10 for the river. Raw abundance of Taeniopterygidae stoneflies was roughly equal in both the river and FS1 despite the fewer sampling events for FS1.

A total of 45 taxa and 6,434 organisms were present in Georgia's Springbrook (FS2) (Fig. 14). As in FS1, chironomids comprised almost half of the total community composition (Fig. 14), and amphibitic forms were absent from collections. However, stygobites were present throughout the study and accounted for >5% of the total community composition. Community composition of FS2 differed somewhat from that of the river in terms of the prevalence of dipterans and hyporheic crustaceans, and the absence of the trichopteran family Hydropsychidae. Other caddisfly families, Limnephillidae, Rhyacophillidae, and Brachycentridae, were common in springbrook collections but rare in river zoobenthos (Fig. 14, Table 2). Likewise, nemourid stoneflies, Podmosta spp, and Malenka californica, were more common in FS2 benthos than in river samples (Fig. 14).

Beaver Springbrook (FS3) had a total of 63 taxa and 5,963 organisms (Fig. 16). Chironomids comprised >38% of the total species composition. Roughly 21% of the community was composed of taxa whose individual contribution was less than 2% (Fig. 16). As in the other springbrooks, amphibites were not present. Stygobites were

found in every sample but accounted for less than 2% of the total composition. Except for the predominance of chironomids, overall community composition and abundance of FS3 zoobenthos resembled that of the river. Similar mayfly, stonefly, and caddisfly taxa were found in both systems.

Tom's Springbrook (TS1) had a total of 39 taxa and 3,355 organisms (Fig. 17). Chironomidae dominated samples and contributed 39% to the total community composition. Consistent with other Springbrook sampling, amphibites were absent from zoobenthos. Stygobites were present in all samples but contributed less than 2% to the total composition (Fig. 17). Taxa whose individual contribution equaled less than 2% contributed 16.6% to the total. The number of dominant Plecoptera taxa in TS1 (5) was greater than in the other springbrooks and the river. Chloroperlidae (Sweltsa coloradensis, Kogotus modestus, Cultus aestivalis, and Zapada cinctipes), contributed >2% to the total (Fig 17). Additionally, Kogotus modestus was exclusive to TS1 and never collected in any other springbrook or river zoobenthos.

Stonefly Emergence

Emergence of Plecopteran adults was monitored at river and springbrook locations to determine if both habitats would be available to hyporheic stoneflies as emergence sites. Along the river, four hyporheic Isocapnia species (Isocapnia missouri, I. crinata, I. grandis, and I. vedderensis) were collected in abundance as they emerged in 1991. The following year, collections of all species were generally depressed and females were either absent or poorly

represented (Fig. 18). Of the four hyporheic stonefly species, Isocapnia missouri was collected in the greatest numbers from the shoreline pitfall traps. Males (long wing and short wing) and females appeared together in collections made in April through May 1991 with the largest numbers being collected in late April 1991. Males outnumbered females in both years and females were absent from collections in 1992 (Fig. 18). Isocapnia crinata males were collected throughout the collection period in 1991 and 1992. Unlike the other hyporheic species, the greatest number of males were collected in 1992. Females were absent from collections in both years. Isocapnia grandis males (long and short wing) appeared in greatest numbers in early April 1991 but were collected in far fewer numbers in 1992. Males outnumbered females in 1991 and females were absent from collections in 1992. Isocapnia vedderensis were collected in the smallest number of any of the hyporheic Isocapnia species. Males and females were collected in roughly equal number in 1991. However, females were entirely absent in 1992 (Fig. 18). Other hyporheic amphibites such as Kathroperla perdita and Paraperla fontalis were present but incidental in emergence traps. Additional species collected in pitfall traps and shoreline sweeps were typical riverine taxa.

Very little emergence activity of adult plecopterans was observed along Nyack (FS1) and Georgia's (FS2) Springbrooks. Only one amphibite, Isocapnia crinata, was collected in pitfall traps at FS1. Amphibitic stoneflies were absent from collections at FS2. Early spring collections were not performed due to a rapid rise in river

water level which impeded access to the springbrook This contributed to the paucity of emergence data at this site.

Multivariate Analysis

The distribution and community composition of the distinct biotic assemblages found in the lotic habitats of the Nyack floodplain were related to abiotic factors using CCA. Arrows produced by the analysis indicate the direction of each of the four environmental gradients (e.g. ordination axes) (Fig. 18). The length of the arrow generally denotes the importance of the variable (ter Braak 1986). Therefore, the temperature and dissolved oxygen gradients were ascribed the greatest importance of the four abiotic factors by CCA (Fig. 18). Points produced by the analysis indicate the distribution of each species relative to each of the environmental gradients. Species were more influenced by an environmental variable if their point was located on the same side as the origin of the arrow for that variable (ter Braak 1986).

In the hyporheic zone, the distribution of obligate ground water fauna (Bathynella and Archiannelida) was most closely tied to changes in specific conductance. However, the distribution of hyporheic stoneflies (Isocapnia spp, Paraperla frontalis, and Kathroperla perdita) was closely associated with changes in date or seasonality (Fig. 19). Numbers of amphibites were comparatively lower throughout the rest of the sampling period. Distribution of river and springbrook zoobenthos was tied to gradients in temperature and dissolved oxygen (Fig. 19).

In the surface habitats, the distribution of four river (_Rhyacophila coloradensis_, _Isogenoides colubrinus_, _Triznaka_ spp, and _Amaletus cooki_) and four springbrook (_Dicosmecus gilvipes_, _Epeorus deceptivus_, _Malenka californica_, _Podmosta_ spp) species was found to be associated with changes in temperature. Distribution of the remaining species were more influenced by changes in the dissolved oxygen gradient. These results were not unexpected since changes in temperature and dissolved oxygen concentrations were more pronounced in the surface habitats.

Physical characteristics of floodplain lotic habitats were influenced by the interstitial flow of downwelling river water. Indeed, the physical connectivity between surface and hyporheic environments appeared to be primarily controlled by river discharge Large volumes of river water were found to downwell into the deep floodplain aquifer (Stanford et al. unpubl.) and subsequently upwell into the main channel, flood channels located proximal to the river, and paleochannels in the floodplain terrace. Consequently, water volumes in the springbrooks and in the wells were observed to fluctuate concomitant with seasonal changes in river flow. Similarly, Stanford and Ward (1988) found that hyporheic water levels tracked changes in river flow in the Kalispell Valley. Residence times of water in the interstitial environment resulted in higher specific conductance values in the hyporheic sites and the springbrooks as compared to the river (Table 1). High average dissolved oxygen

concentrations measured in the hyporheic zone further supported the idea that interstitial waters were moving at a high rate. Such interstitial flow rates have been found to be characteristic of alluvial aquifers (Stanford and Ward 1988, Stanford et al. unpublished).

Physical connection between lotic habitats allowed for interaction of distinct biotic communities across the floodplain. The zoobenthos community collected from the main channel at Nyack was distinguished by large numbers of mayfly species and the highest taxa diversity of all sampled habitats. Zoobenthos were found to be similar to collections made elsewhere in the 5th and 6th order segments of the Flathead River (Stanford 1975, Hauer and Stanford 1986, Stanford et al. unpubl.). We observed that riverine taxa were not restricted to the main channel. River zoobenthos were collected in the hyporheic zone, probably as a result of passive entrainment, as well as from the springbrook habitats. Interaction between the hyporheic zone and the river appeared to controlled by river discharge. Stygobites were rare and amphibitic stoneflies were absent from collections, yet were abundant in the floodplain aquifer. We theorized that water pressures may have prohibited upward migration of hyporheic fauna in the sampling area since river zoobenthos were collected in an area of general downwelling (Stanford et al. unpubl.). Hence, river discharge appeared to influence not only the physical but also biotic interactions between the main channel and hyporheic habitat consistent with the findings of Danielopol and Marmonier (1992) in European aquifers.

Interstitial biota were characterized by unique taxa including obligate ground water organisms (crustaceans and archiannelids) and

species with affinities for the surface environment. Community composition and distribution of hyporheos changed across the floodplain. The terrace environment was dominated by stygobites, while amphibites contributed the greatest percentage to community composition in the floodplain wells. Further, the greatest numbers of both stygobites, amphibites, and riverine species occurred in the central floodplain area. A similar distribution pattern was observed in the Kalispell Valley by Ward et al. (1994). Maximum numbers of stygobites were concentrated in near and central-floodplain areas. Likewise, Marmonier et al. (1992) made similar observations of hyporheos in European aquifers; however, large-bodied amphibites were absent from those collections. Their presence in the Nyack floodplain indicated that interstitial space in the active channel was sizable. The presence Elmidae in TW2, FW1, and FW2 samples further signified that interstitial space was relatively large since Maridet et al. (1992) found riffle beetles (Elmidae) to be indicators of non-silted areas. Other benthic taxa collected in the floodplain wells compared well to those sampled by Stanford and Ward (1988) in the Kalispell Valley. The comparatively greater number of passively entrained riverine taxa in FW1 and FW2 also supported the idea that the interstitial space in the central floodplain was greater than that observed in the terrace environment. Based on these observations, we inferred that FW1, FW2, and TW2, to a lesser degree, had intercepted a network of paleochannels (historic channel beds). Paleochannels have been found to create spatial discontinuities in the lattice-like substrata of gravel aquifers. Thus, such channels have high hydraulic conductivities and greater interstitial space (Ward et

al. 1992). Therefore, floodplain wells were presumed to intercept paleochannels to a greater degree than wells located in the terrace environment. As a result, wells that intercepted or were proximal to paleochannels would have produced greater numbers of amphibites, stygobites, and passively entrained river zoobenthos than wells located further from a network (see also Stanford and Ward 1993). Additional study of fluvial stratigraphy is needed to confirm the influence of paleochannels upon interstitial zoobenthos distribution.

Taxa representation and overall abundance in TW3, TW4, FW3, and FW4 was very low in comparison to the primary study wells. It is possible that the secondary study wells did not intercept or proximate a paleochannel network (Stanford and Ward 1993) as noted above. The large percentage of benthic forms in TW3 may have been due to interaction between this well and nearby Beaver Springbrook.

The presence of amphibites in sandpoint zoobenthos indicated that we were sampling the hyporheic zone, but sampling was not considered effective since total numbers were low. Pieziometric tests (Stanford et al. unpubl.) indicated that the sandpoints were located in an area of general downwelling. However, total number of stygobites collected from the three sandpoint sampling events was greater than numbers collected from all primary terrace wells combined. This was as expected since the sandpoints were located in the central floodplain area adjacent to the main channel.

Contrary to our original hypothesis, springbrook zoobenthos was found to be more analogous to river zoobenthos than to hyporheos. Indeed, similar taxa were found in both the river and

springbrook systems. However, overall taxa diversity was comparatively lower and dipterans (Chironomidae) dominated sample collections in all springbrooks. Stygobites were either absent or incidental in all springbrooks. This was surprising due to the ground water origin of flow in these systems. However, obligate ground water fauna have been found to be specially adapted to groundwaters and can actively migrate within the interstitial habitat (Danielopol 1989). The infrequent appearance of ground water taxa was thus attributed to their ability to maintain position within the environment to which they were specialized. The incidental appearance of ground water taxa in springbrook zoobenthos was thought to be flow dependent. In other studies, ground water taxa were present in floodchannel zoobenthos following periods of high flow volume within the interstices (Pennak and Ward 1986, Creuze and Marmonier 1990, Plenet and Vervier 1992, Chafiq et al. 1992). Amphibites were absent from all springbrooks. It is feasible that hyporheic stoneflies were not present in samples because only surface sediments were sampled. Similar to stygobites, larval stages of hyporheic stoneflies appear to be specially adapted to the hyporheic environment and may actively avoid surface systems until later in their life histories. Their comparatively large size (>2cm) may aid in avoiding surface environments which is consistent with their adaptation to the interstitial environment. Presence of hyporheos in surface systems was therefore thought to be due to passive entrainment.

Further, the springbrooks did not prove to be hot spots of biodiversity as originally conjectured. The total number of taxa were

significantly lower in the springbrooks than in the river. However, total number of individuals per taxa in the springbrooks was generally greater than the river, despite the fewer springbrook sampling events. Dissimilarity in the number of sampling events for the two systems prevented direct comparisons of raw abundance. Instead, springbrooks appeared to be hot spots of bioproduction based upon qualitative observations and synoptic work performed toward the end of this study (Ellis unpubl.). Nutrients derived from upwelling areas appeared to stimulate algae and epilithic bacterial growth within the channel.

In the Nyack system, the floodplain landscape was diversified by springbrook channels that erupted at several points and connected to the river (Fig. 1). The ecological complexity of floodplain ecosystems is enhanced by the physical heterogeneity of floodplain features (Amoros et al. 1987); therefore, springbrook channels increased the overall physical complexity of the Nyack Valley. Additionally, Chafiq et al. (1992) found that tributary channels crossing floodplains increased connectivity between lotic habitats. Springbrooks, are integral features in the Nyack Valley since they contribute to the physical diversity and system connectivity of the floodplain.

The collection of adult amphibitic stoneflies in the Nyack Floodplain also demonstrated the connectivity between the river, hyporheic, and springbrook habitats. Hyporheic plecopterans were collected almost exclusively from the river shoreline rather than from the springbrooks. The presence of amphibites in river shoreline collections was not unexpected. Past studies in the

Flathead River system collected pre-emergent amphibites in benthic samples (Stanford and Gaufin 1974) and adults in shoreline pitfall traps (Stanford 1974). However, larval forms were rare or absent in routine benthos sampling. Emergence of hyporheic stoneflies from the Flathead River was found to depend upon attainment of 10 °C water temperatures (Stanford and Gaufin 1974). Similarly, life history events such as egg hatching and diapause in other stonefly species had been linked to attainment of precise temperature thresholds (Ward and Stanford 1982). Emergence data in this study supported these findings since adult hyporheic stoneflies were collected from river shoreline as water temperatures rose in spring. The depressed numbers of stoneflies collected in 1992 was attributed to comparatively lower river flow volumes and cooler water temperatures. The rarity of females collected in 1991 and absence in 1992 collections suggested avoidance of the pitfall traps. Females may have actively moved toward different cover types than the males upon emergence. More study of behavioral patterns would be needed to confirm this explanation.

Hyporheic plecopterans were initially theorized to utilize the springbrooks as emergence sites due to the ground water origin of flow in these systems. However, emergence activity appeared to be more influenced by the cooler thermal regime than by the physical connectivity between the aquifer and springbrook systems. For instance, no adults were collected from either FS2 or FS3 throughout the course of the study. The moderating influence of ground water inputs to the springbrooks probably depressed thermal regimes and prevented attainment of the necessary thermal amplitudes to cue

emergence of hyporheic stoneflies. Since these cues were attained in the river, amphibites appeared to actively migrate toward the main channel. However, adult stoneflies were collected incidentally in pitfall traps along FS1. This floodchannel had the greatest thermal amplitude of the three regularly sampled. Thus, thermal cues may have been provided in this springbrook environment. Emergence times roughly corresponded to collection of amphibites from the river.

Relating community composition to physical factors via CCA revealed that species unique to the river, springbrook, and hyporheic habitats were influenced by environmental variables. The association between obligate ground water fauna and specific conductance was expected. Physical measurements documented the highest specific conductance values to occur in the hyporheic habitat, particularly in the terraces. Similarly, Stanford and Ward (1988) had found stygobites to be closely associated with high specific conductance isopleths. Distribution of amphibitic stoneflies was most closely tied to changes in date. The influence of seasonality on these organisms was probably due to the large numbers collected during peak emergence periods in June of 1990 and 1991. Most river and springbrook zoobenthos were associated with the temperature gradient; remaining taxa were influenced by changes in dissolved oxygen. The importance of temperature was expected. As noted above, temperature has been found to play an important role in the life history events of stoneflies (Stanford 1975, Stanford and Ward 1982). Results indicated that mayfly and caddisfly species are similarly influenced. Due to the lotic nature of the river and

springbrooks, the influence of dissolved oxygen was also expected for surface zoobenthos. It should be noted that the ecological needs of biotic assemblages, especially hyporheos, are difficult to determine due to specialized needs of the organisms (Olivier and Marmonier 1992). Therefore, other environmental variables not directly measured in this study could play equal or more important roles in explaining community composition and distribution. Abiotic factors noted by other researchers include throughflow of water in the interstices and sediment deposition (Bretschko 1992), inputs of organic matter (Danielopol 1989, Olivier and Marmonier 1992, Maridet et al. 1992), localized areas of upwelling and downwelling (Vallett et al. 1990, Stanley and Boulton 1993, Chafiq et al. 1992) and nitrogen dynamics (Grimm 1987).

In conclusion, physical data as well as species composition and distribution documented in this study compared well to work performed downstream in the Kalispell Valley (Stanford and Ward 1988). Lotic habitats were biotically and physically interactive across the floodplain. River discharge appeared to control interaction between lotic habitats and to influence the extent of the springbrook and hyporheic habitats. Results supported the theory that floodplains of large gravel bed rivers may be comprised of physically diverse floodplain features that augment connectivity at the landscape level. As noted by Stanford and Ward (1993), large-scale hyporheic zones are not exceptional along river corridors but instead are repeated with regularity providing the proper hydrological and geological conditions exist.

ACKNOWLEDGMENTS

LITERATURE CITATIONS

Amoros, C., and A.-L. Roux. 1988. Interactions between water bodies within the floodplain of large rivers: function and development of connectivity. Pages 125-130 *in* K. F. Schreiber (editor). Connectivity in landscape ecology. Proceedings of the 2nd International Seminar of the International Association for landscape ecology. Munsteiche Geographische Arbeiten 29.

Boulton, A. J., H. M. Valett, and S. G. Fisher. 1992.Spatial distribution and taxonomic composition of the hyporheos of several Sonoran desert streams. Archiv fur Hydrobiologie125:37-61.

Bretscko, G. 1992. Differentiation between epigeic and hypogeic fauna in gravel streams. Regulated Rivers Research and Management 7:17-22.

Chafiq, M., J. Gibert, P. Marmonier, M. J. Dole-Olivier and J. Juget, 1992. Spring ecotone and gradient study of interstitial fauna along two floodplain tributaries of the river Rhone, France. Regulated Rivers: Research and Management 7:103-115.

Chauvet, E. and H. Decamps. 1989. Lateral interactions in a fluvial landscape: the River Garonne, France. Journal of North American Benthological Society 8:9-17.

Coleman, M. J. and H. B. N. Hynes, 1970. The vertical distribution of invertebrate fauna in the bed of a stream. Limnology and Oceanography 15:31-40.

Creuze des Chatelliers, M., and P. Marmonier, 1990. Macrodistribution of Ostracoda and Cladocera in a by-passed channel: Exchange between superficial and interstitial layers. Stygologia 5:17-24.

Creuze des Chatelliers, M. 1991. Geomorphological processes and discontinuities in the macrodistribution of the interstitial fauna. A working hypothesis. Verh. International Verein. Limnology 24:1609-612.

Creuze des Chatelliers, M., P. Marmonier, M.-J. Dole Olivier and E. Castella, 1992. Structure of interstitial assemblages in a

regulated channel of the river Rhine (France).Regulated Rivers 7:23-30.

Danielopol, D.L. 1976. The distribution of fauna in the interstitial habitats of riverine sediments of the Danube and the Piesting (Austria). Internatinal Journal of Speleology 8:23-51.

Danielopol, D.L. 1989. Groundwater fauna associated with riverine aquifers. Journal of the North American Benthological Society 8:18-35.

Danielopol, D. L., and P. Marmonier, 1992. Aspects of research on groundwater along the Rhone, Rhine, and Danube. Regulated Rivers: Research and Management 7: 5-16.

Freeze, R. A., and J. A. Cherry. 1979. Groundwater. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Gaufin, A. R., W. E. Ricker, M. Menu, P. Melain, and R. Hays. 1972. The Plecoptera of Montana. Transactions of the American Entomological Society 105: 139-221.

Gibert, J., M., J. Dole-Olivier, P. Marmonier, and P. Vervier. 1990. Surface water-groundwater ecotones. in: Ecology and management of aquatic-terrestrial ecotones. R.J. Naiman and H. Decamps (editors.) Parthenon Publishing, London. Pages199-225.

Godbout, L., and H. B. N. Hynes 1982. The three dimensional distribution of the fauna in a single riffle in a stream in Ontario. Hydrobiologia 97:87-96.

Gregory, S. V., F.J . Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. Bioscience 41:540- 551.

Grimm, N. B. 1987. Nitrogen dynamics during succession in a desert stream. Ecology 68:1157-1170.

Hauer, F. R., and J. A. Stanford, 1981. Larval specialization and phenotypic variation in Arctopsyche grandis (trichoptera: Hydropsychidae) Ecology 12:645-653.

Hauer, F. R., and J. A. Stanford, 1986. Ecology and coexistence of two species of Brachycentrus (Trichoptera) in a Rocky Mountain river. Canadian Journal of Zoology 64:1469-1474.

Jensen, S. L., 1966. The Mayflies of Idaho. Master's Thesis, University of Utah.

Kowarc, A. V. 1992. Depth distribution of a harpacticoid copepod within the bed sediment of an alpine brook. Regulated Rivers: Research and Management 7:57-63.

Maridet, L., J-G. Wasson, and M. Philippe, 1992. Vertical distribution of fauna in the bed sediment of three running water sites: Influence of physical and trophic factors. Regulated Rivers: Research and Management 7:45-55.

Marmonier, P., M. J. Dole-Olivier, and M. Chatelliers, 1992. Spatial distribution of interstitial assemblages in the floodplain of the Rhone River Regulated Rivers:Research and Management 7:75-82.

Merritt, R. W., and K. W. Cummins 1984. An introduction to the Aquatic Insects of North America. (2nd edition). Kendall/Hunt Publishing, Iowa.

Morihara, D. K., and W. D. McCafferty, 1979. The Baetis larvae of North America (Ephemeroptera: Baetidae). Transactions of the American Entomological Society 105: 139-221.

Obrdlk, P., and L. C. G. Lozano, 1992. Spatio-temporal distribution of macrozoobenthos abundance in the Upper Rhine alluvial floodplain. Archiv fur Hydrobiologie 124:205-224.

Olivier, M. J. D., and P. Marmonier. 1992. Ecological requirements of stygofauna in an active channel of the Rhone river. Stygologia 7:65-75.

Pennak, R. W., and J. V. Ward, 1986. Interstitial faunal communities of the hyporheic and adjacent groundwater biotopes of a Colorado mountain stream. Archiv fur Hydrobiologie Supplement 74:356-396.

Plenet, S., J. Gibert, and P. Vervier. 1992. A floodplain spring: an ecotone between surface water and groundwater. Regulated Rivers: Research & Management 7:93-102.

Poole, W. C., and K. W. Stewart. 1976. The vertical distribution of macrobenthos within the substratum of the Brazos river, Texas. Hydrobiologia 50:151-160.

Reid, J., E. B. Reed, J. V. Ward, N. J. Voelz, and J. A. Stanford. 1991. *Diacyclops languidoides* (Lilljeborg, 1901) s.l. and *Acanthocyclops montana*, new species (Copepoda, Cyclopoida), from groundwater in Montana, U.S.A. Hydrobiologia. 218:133-149.

Stanford, J. A. 1975. Ecological studies of Plecoptera in the upper Flathead and Tobacco rivers, Montana. Doctoral dissertation, the University of Utah. 241 pps.

Stanford, J. A., and A. R. Gaufin. 1974. Hyporheic communities of two Montana rivers. Science 185:700-702.

Stanford, J. A., R. F. Hauer, and J. V. Ward. 1988. Serial discontinuity in a large river system. Verh. International Verein. Limnologie 23:114-118.

Stanford, J. A., and J. V. Ward. 1988. The hyporheic habitat of river ecosystems. Nature 335:64-66.

Stanford, J. A. and J. V. Ward. 1992. Management of aquatic resources in large catchments: recognizing interactions between ecosystem connectivity and environmental disturbance. Pages 91-124 *in* R. J. Naiman (editor). Watershed management. Springer - Verlag, New York.

Stanford, J. A., and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. Journal of North American Benthological Society 12:48-60.

Stanley, E. H., and A. J. Boulton. 1993. Hydrology and the distribution of hyporheos: perspectives from a mesic river and a desert stream. Journal of the North American Benthological Society 12:79-83.

Stewart, K. W., and Stark, B. P. 1988. Nymphs of North America Stonefly Genera (Plecoptera).

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 76:1167-1179.

Triska, F. J., J. H. Duff, and R. J. Avanzino. 1990. Influence of exchange flow between the channel and hyporheic zone on nitrate production in a small mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 47:2099-2111.

Valett, H. M., S. G. Fisher, and E. H. Stanley. 1990. Physical and chemical characteristics of the hyporheic zone of a Sonoran desert stream. Journal of the North American Benthological Society 9:201-215.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Vervier, P. 1992. A perspective on the permeability of the surface freshwater - groundwater ecotone. Journal of the North American Benthological Society 11:93-102.

Ward, J. V. and J. A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. Annual Review of Entomology 27:97-117.

Ward, J. V., 1989. The four dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8:2-8.

Ward, J. V., J. A. Stanford, and N. J. Voelz, 1994. Spatial distribution patterns of crustaceans in the floodplain aquifer of an alluvial river. Hydrobiologia: 274:1-7.

Table 1. Annual average and range in temperature (0C), degree days, dissolved oxygen (mg/l), and specific conductance (umhos/cm) measured in the river, springbrook and hyporheic habitats. Sandpoint data represents the average of 14 sampling sites. Dashed lines indicate no data.

	Annual ΔC	Annual Degree Days	DO (mg/l)	Conductance (umhos/cm)
River	19	2161	12.5 10.3 - 13.98	119 89 - 140
Springbrooks				
(Floodchannels) Nyack Springbrook	8.3		9.17 7.30 - 13.60	147 138 - 160
Georgia's Springbrook	5.63 2.3 - 7.5		8.44 6.71 - 10.20	140 125 - 150
Beaver Springbrook	8.0 - 13.0	2521	11.46 11.05 - 12.10	125 115 -135
(Paleochannels) Tom's Springbrook	6, 8		10.09	135
Floodplain Wells				
FW1	7.71 0.5 - 14.1	2758	11.17 9.0 - 13.45	128 102 - 182
FW2	5.55 0.3 - 14.1	2846	10.35 6.31 - 12.11	142 110 - 182
FW3	5.6 3.5 - 7.6		5.16 4.97 - 5.40	177 169 - 185
FW4	4.5 1.12 - 6.60		3.26 2.60 - 3.99	182 169 - 195
TW1	7.16 3.80 - 9.60		8.54 4.93 - 11.56	133 119 - 155
TW2	7.46 3.8 - 9.6		12.05 3.3 - 12.45	147 119 - 162
TW3	5.39 3.36 - 7.20		3.1 2.10 - 3.80	191.67 175 - 210
TW4	5.28 3.36 - 7.2		7.7 4.9 - 10.5	175 170 - 180
Sandpoints	10.31 6.4 - 15.3		6.91 1.4 - 11.7	144 130 - 190

Table 2. Taxa collected from river, springbrook and hyporheic environments.

Total number of organisms in the springbrook habitat represent all zoobenthos collected from Nyack Springbrook, Georgia's Springbrook, Beaver Springbrook, and Tom's Creek. Total number of organisms in the hyporheic habitat represent all zoobenthos collected from the four floodplain and four terrace well locations.

% - Percent contribution of each taxon to the total community composition of each habitat type.
* - Immature forms that could not be identified to a lower taxonomic level.
● - Lowest taxonomic level identified.
† - Taxa unique to a habitat type

RIVER	%	SPRINGBROOK	%	HYPORHEIC	%
Ephemeroptera		**Ephemeroptera**		**Ephemeroptera**	
Family: Baetidae *	1.70	Family: Baetidae *	2.25	Family: Baetidae	0.04
Baetis bicaudatus	2.20	Centroptilum sp	0.01	Baetis bicaudatus	0.02
Baetis intermedius	0.80	Baetis paracloedes	0.12		
Baetis tricaudatus	0.38	Baetis tricaudatus	0.08		
Centroptilum sp	1.30	Baetis intermedius	1.4		
		Baetis bicaudatus	3.2		
Family: Ephemerellidae *	5.60	Family: Ephemerellidae		Family: Ephemerellidae	
Ephemerella aurivilli	0.12	Ephemerella aurivilli	0.03	Ephemerella spp	0.01
Ephemerella coloradensis	0.04	Ephemerella coloradensis	0.07		
Ephemerella doddsi	0.50	Ephemerella doddsi	0.13		
Ephemerella elleni	0.24	Ephemerella elleni	0.02		
Ephemerella flavilinea	0.05	Ephemerella flavilinea	0.22		
Ephemerella grandis grandis	0.02	Ephemerella grandis grandis	0.05		
Ephemerella grandis ingens	0.06	Ephemerella grandis ingens	0.05		
Ephemerella inermis	1.30	Ephemerella inermis	0.65		
Ephemerella tibialis †	0.02	Ephemerella infrequens	2.22		
Ephemerellla infrequens	0.50				
Family: Heptageniidae *	2.20	Family: Heptageniidae		Family: Heptageniidae *	0.03
Epeorus deceptivus	0.25	Epeorus deceptivus	0.22	Rhithrogena robusta	0.02
Epeorus grandis	0.04	Epeorus longimanus	0.2		
Epeorus longimanus	0.34	Rhithrogena hageni	0.12		
Rhithrogena hageni	0.03	Rhithrogena robusta	0.02		
Rhithrogena robusta	0.52	Rhithrogena undulata	2.4		

Taxon	Value	Taxon	Value	Taxon	Value
Rhithrogena undulata	10.20	Stenonema sp	0.12		
Stenonema sp	0.05	Cinygmula spp •	4.2		
Cinymigula spp •	7.72				
Family: Leptophlebiidae		Family: Leptophlebiidae		Family: Leptophlebiidae	
Paraleptophlebia sp †	0.80	Leptophlebia sp †	0.03	Paraleptophlebia memorialis	0.1
Family: Siphlonuridae		Family: Siphlonuridae	0.13	Family: Siphlonuridae *	0.2
Amaletus cooki †	0.20	Amaletus velox	0.24	Amaletus spp	0.8
Amaletus velox	0.40				
Parameletus sp †	0.02				
Plecoptera		**Plecoptera**		**Plecoptera**	
Family: Capniidae •	2.50	Family: Capniidae *	10.22	Family: Capniidae *	0.22
Eucapnosis brevicauda †	0.02				
Family: Chloroperlidae *	3.20	Family: Chloroperlidae	0.14	Family: Chloroperlidae	
Alloperla severa	0.60	Alloperla severa	0.43	Isocapnia spp *†	64.2
Suwallia sp	0.94	Neaviperla sp †	0.04	Alloperla severa	0.02
Sweltsa coloradensis	0.90	Suwallia sp	1.42	Kathroperla perdita †	4.2
Triznaka sp †	0.02	Sweltsa coloradensis	0.47	Paraperla fontalis †	2
				Sweltsa coloradensis	0.1
Family: Leuctridae		Family: Leuctridae	0.01		
Perlomyia sp †	0.02				
Family: Nemouridae *	0.06	Family: Nemouridae *	0.22	Family: Nemouridae *	0.03
Prostoia besametsa	1.40	Malenka californica †	2.52	Zapada cinctipes	0.06
Zapada cinctipes	0.61	Podmosta sp †	0.12		
		Prostoia besametsa	0.22		
		Zapada cinctipes	1.42		
Family: Perlidae		Family: Perlidae *	0.02	Family: Perlidae	
Claasenia sabulosa	0.20	Claasenia sabulosa	0.02	Claasenia sabulosa	0.02
Doroneuria sp	0.01	Doroneuria sp	0.03		
Hesperoperla pacificum †	0.02				
Family: Perlodidae *	0.40	Family: Perlodidae	0.01	Family: Perlodidae *	0.03
Cultus aestivalis	0.10	Cultus aestivalis	0.52	Diura knowltoni	0.03
Diura knowltoni †	0.30	Isogenoides colubrinus	0.01		
Isogenoides colubrinus	0.20	Isoperla fulva	0.02		
Isoperla patricia	0.20	Isoperla sp	0.04		

Column 1

Family: Blephariceridae
Bibiocephala sp 0.08

Family: Tabanidae 0.01

Family: Tipulidae
Tipula sp 0.03
Hexatoma sp 0.06
Prionocera sp 0.08
Antocha sp 0.76

Coleoptera
Family: Elmidae
Narpus sp 0.02

Family: Haliplidae
Peltodytes sp 0.03

Harpacticoida * 0.02

Column 2

Family: Psychodidae
Pericoma sp 0.02

Family: Tipulidae
Hexatoma sp 0.03
Antocha sp 0.05
Tipula sp 0.22
Prionocera sp 0.33

Coleoptera
Family: Elmidae
Narpus sp 0.82

Family: Haliplidae
Peltodytes sp 0.05

Family: Dytiscidae
Bidessini sp 0.02

Collembola
Family: Entomobryidae
Corynothrix sp † 0.01
Sinella sp † 0.01

Cyclopoida * 0.14

Harpacticoida * 1.8

Calanoida * 0.11

Amphipoda
Stygobromus sp 0.01

Cladocera
Daphnia sp 0.01

Column 3

Family: Tipulidae * 0.02
Antocha spp 0.04
Tipula spp 0.01

Family: Amphizoidae
Amphizoa sp 0.03

Coleoptera
Family: Haliplidae
Peltodytes sp 0.07

Family: Elmidae
Elmidae spp 0.01
Narpus sp 0.1

Collembola * 0.3

Archiannelida *† 0.9

Cyclopoida * 7.5

Harpacticoida * 1.8

Calanoida * 0.01

Amphipoda
Stygobromus sp * 11.7

Hemiptera * 0.02

Bathynella *† 0.8

		Ostracoda *	0.03	Ostracoda *	0.3
		Isopoda *	0.03	Homoptera *†	0.02
Oligochaeta	0.02	Oligochaeta *	0.03	Oligochaeta *	1.7
		Tardigrada	0.01	Arachnida *	0.01
Turbellaria		Turbellaria *†		Nematoda *	0.04
Planaria spp	0.03	Planaria sp	2.62		
Acari *	0.20	Acari *	0.3	Acari	0.34
Total Taxa	79.00	Total taxa	89	Total Taxa	40
Total Number of Organisms	32487		22937		7552
	100.00		100.02		100

Figure 1

FW - Floodplain Well
TW - Terrace Well
FS1 - Nyack Springbrook
FS2 - Georgia's Springbrook
FS3 - Beaver Springbrook
TS1 - Tom's Springbrook
* River zoobenthos sampling site
Sandpoint sampling sites
Active Floodplain
Floodplain Terrace

500 m

Nyack Creek

Nyack Floodplain

Middle Fork
Flathead River

FS2

FW1
FW2
FS1

FS3

TW3

TW2

TS1

TW1

Direction of Flow

FW4
FW3

TW4
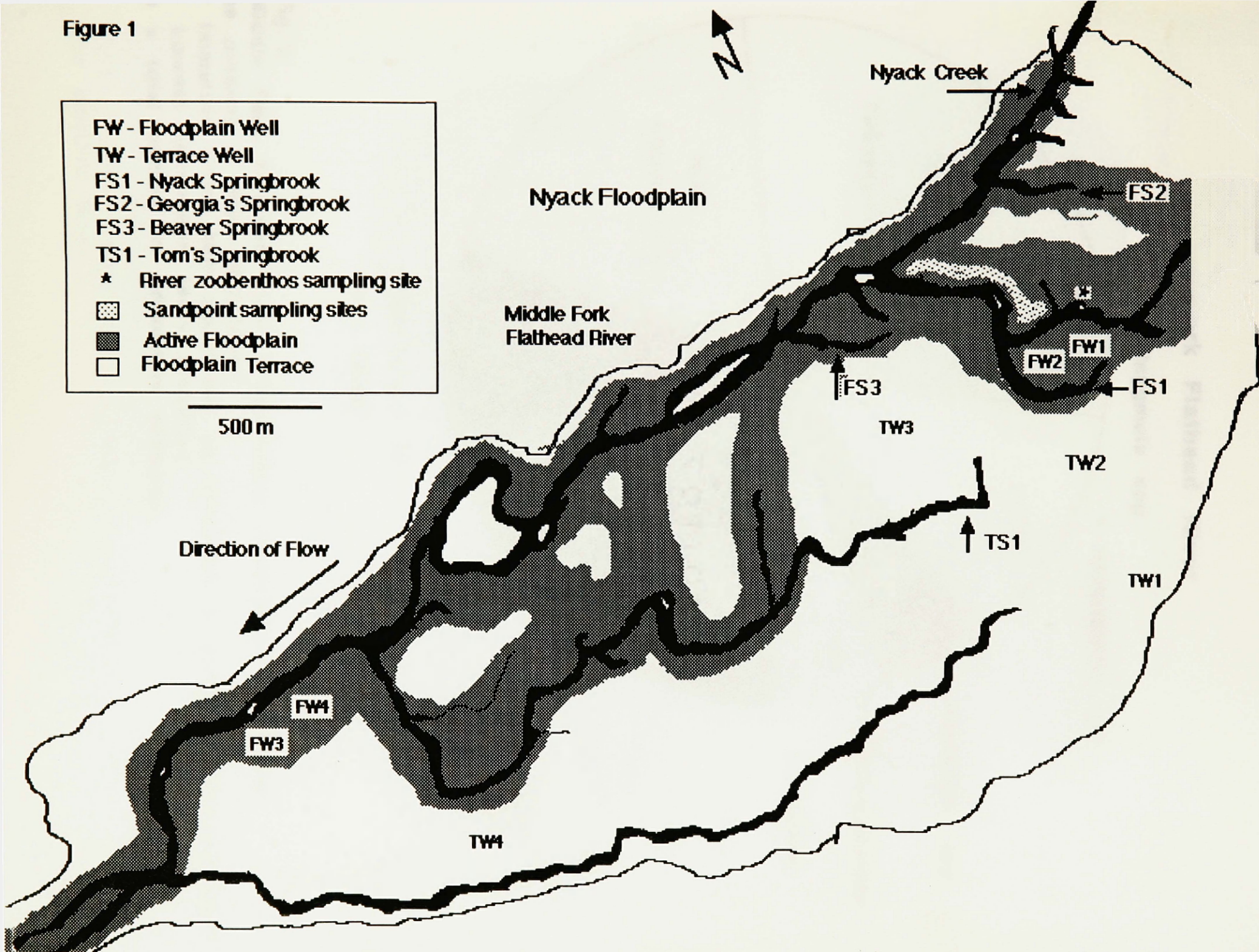
Middle Fork Flathead River
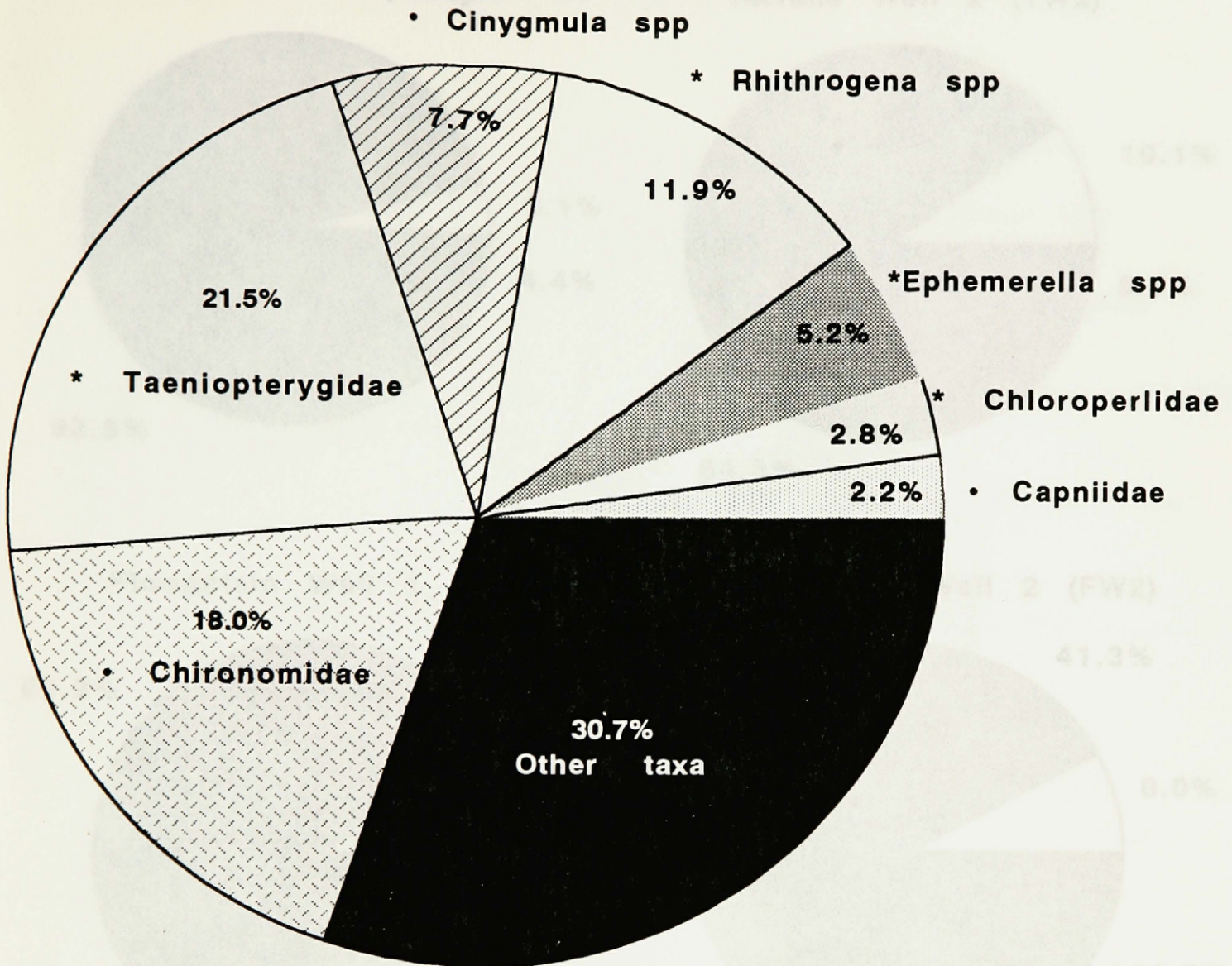
Total taxa = 79

n = 32,487

Fig. 2
Middle Fork Flathead River - Community composition expressed
as percent of total abundance.
* Immature forms that could not be identified to a lower taxonomic level.
• Lowest taxonomic level identified.
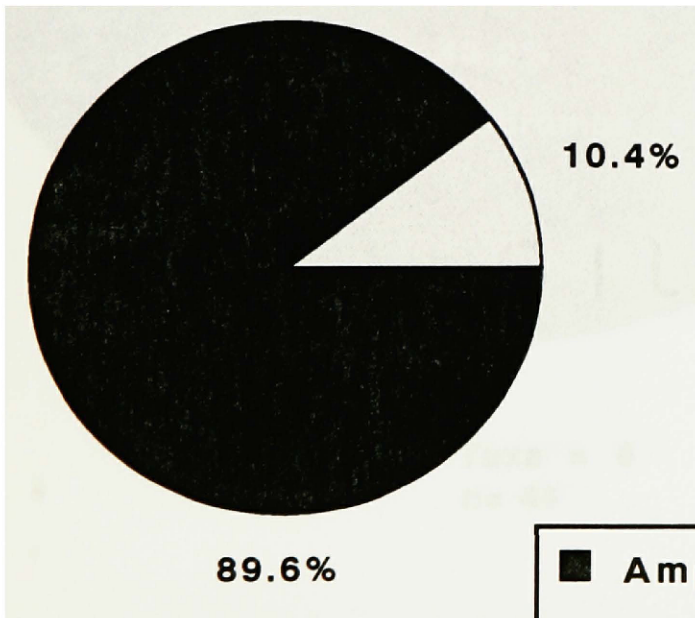n = total number of organisms collected.

Terrace Well 1 (TW1)
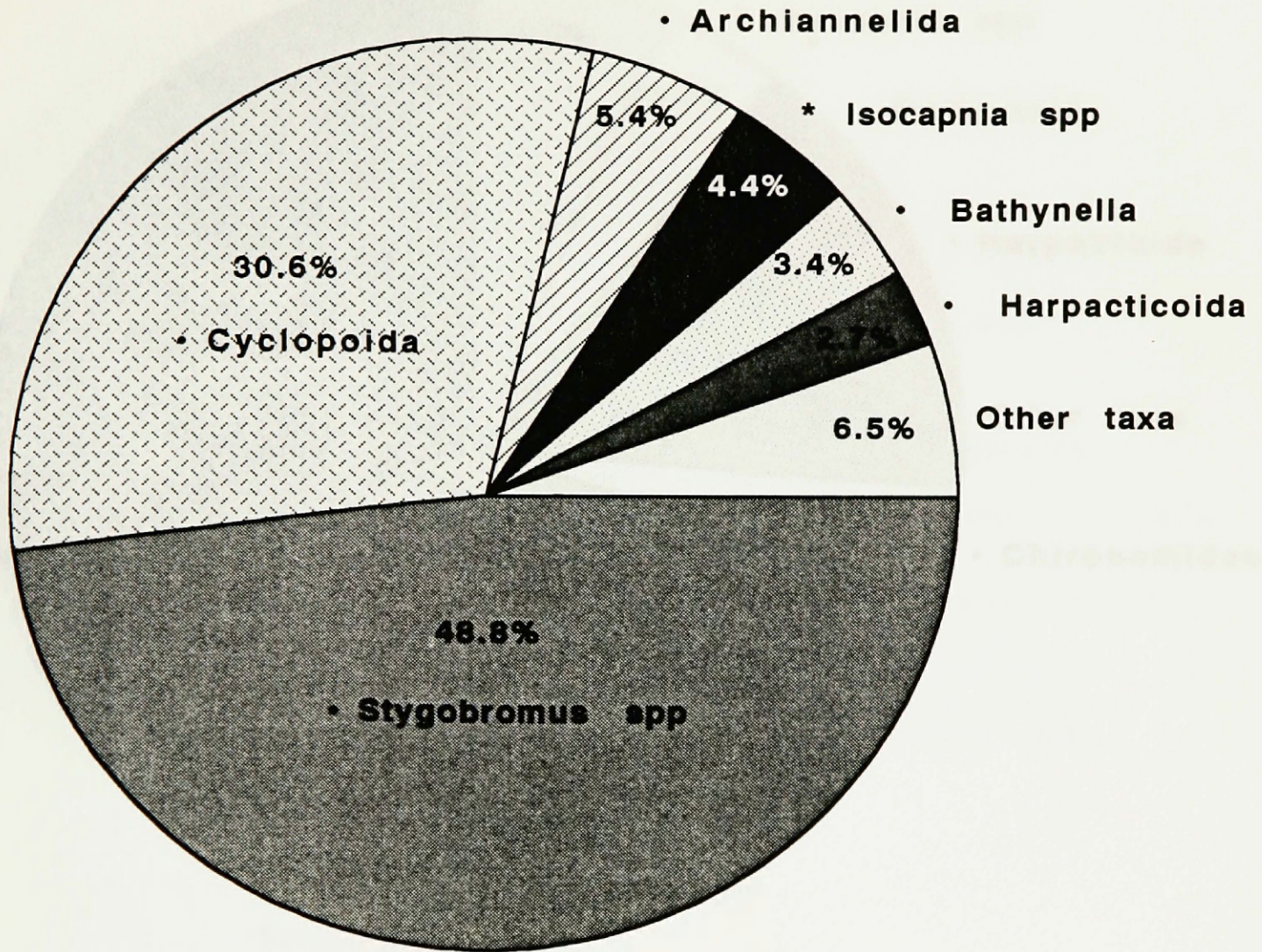
Fig. 4
Community composition of Terrace Well 1.
* Immature forms that could not be identified to a lower taxonomic level.
• Lowest taxonomic level identified.
n = total number of organisms collected.

Terrace Well 2 (TW2)

- Archiannelida

* Isocapnia spp

- Bathynella

- Harpactoida

Other taxa

- Chironomidae

3.6%

5.3%

4.7%

5.8%

4.0%

6.4%

37.4%
- Cyclopoida

32.8%
- Stygobromus spp
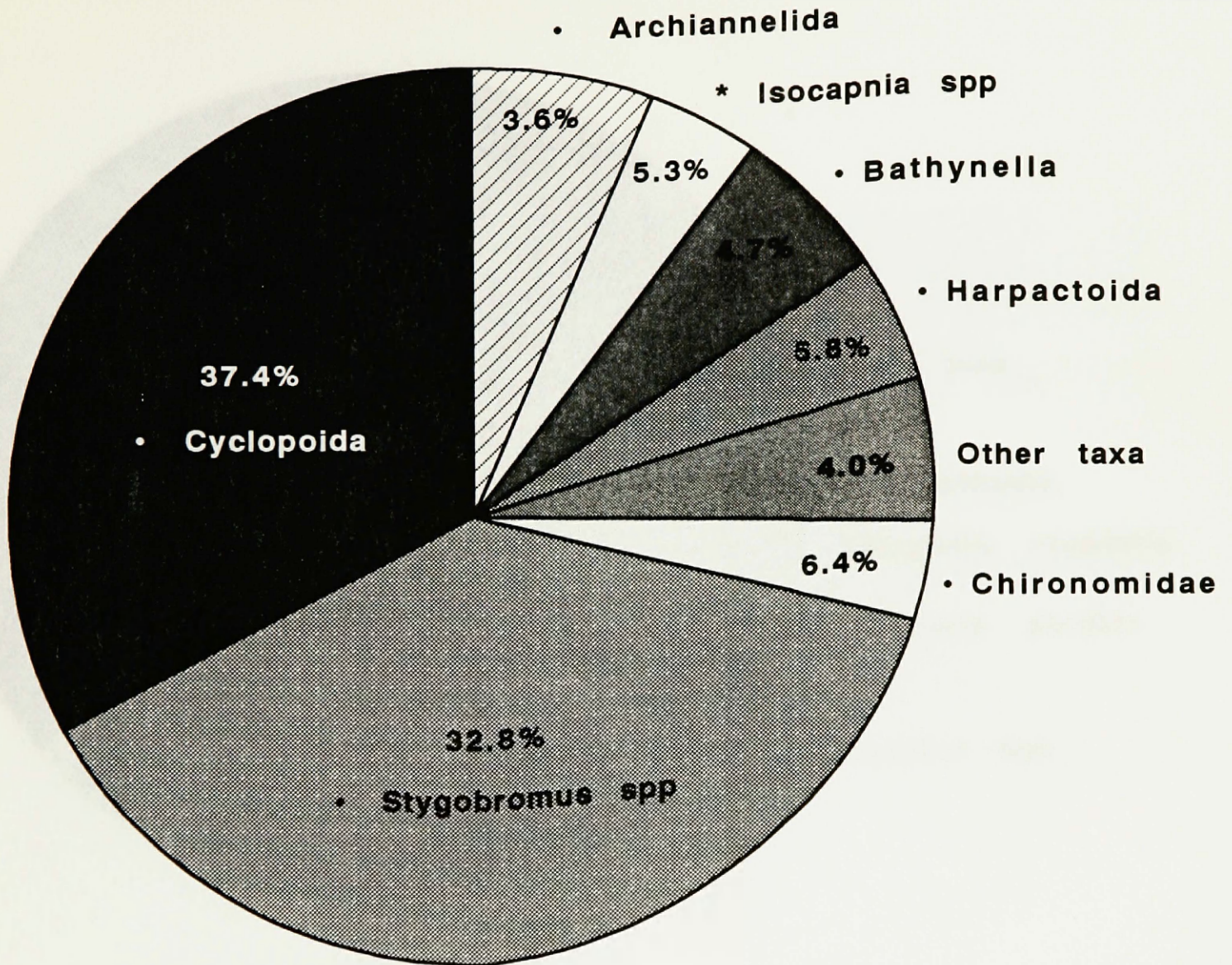
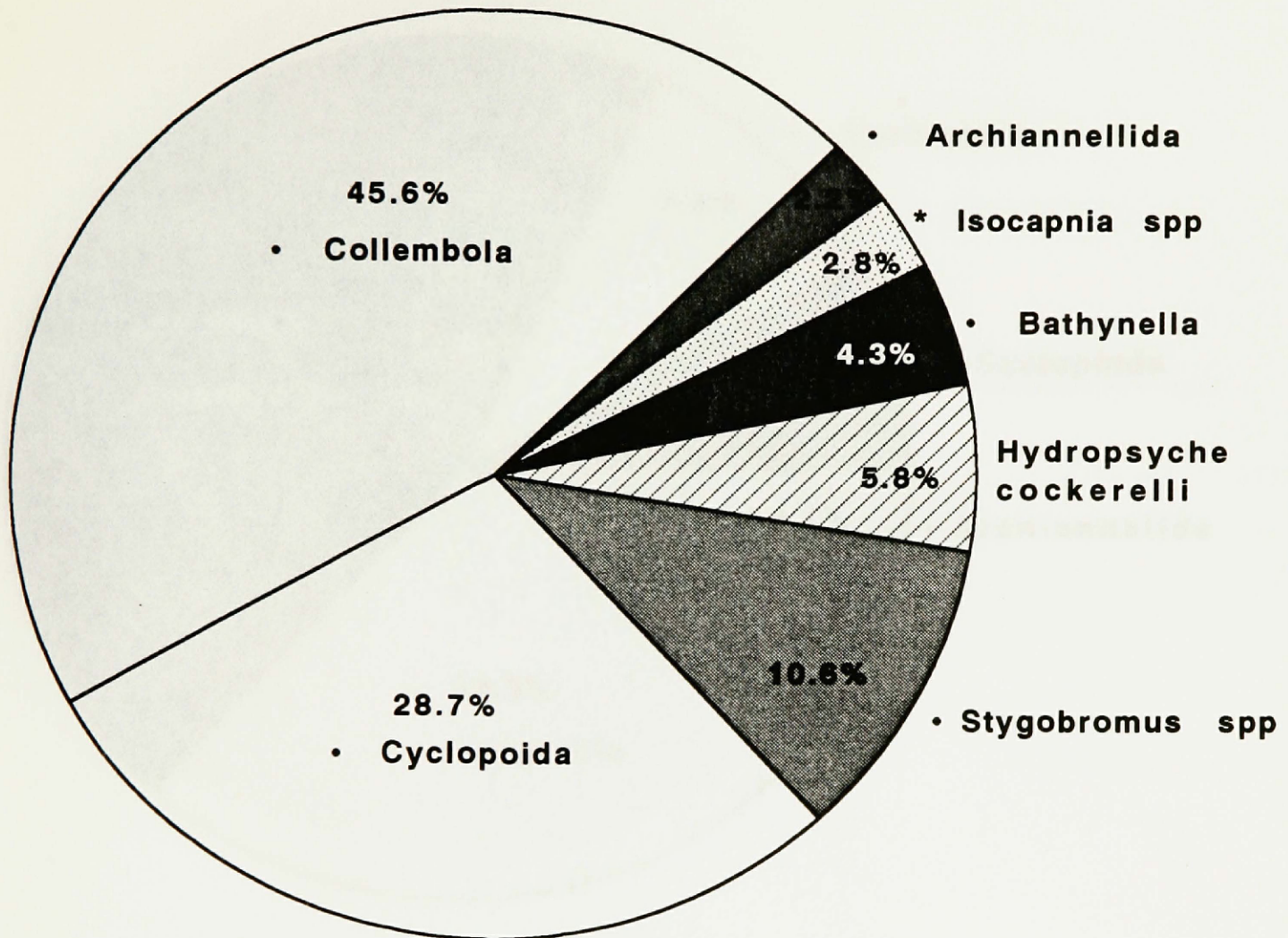Total taxa = 14

n = 634

Fig. 5
Community composition of Terrace Well 2.
* Immature forms that could not be identified to a lower taxonomic level.
- Lowest taxonomic level identified.
n = total number of organisms collected.

Floodplain Well 1 (FW1)
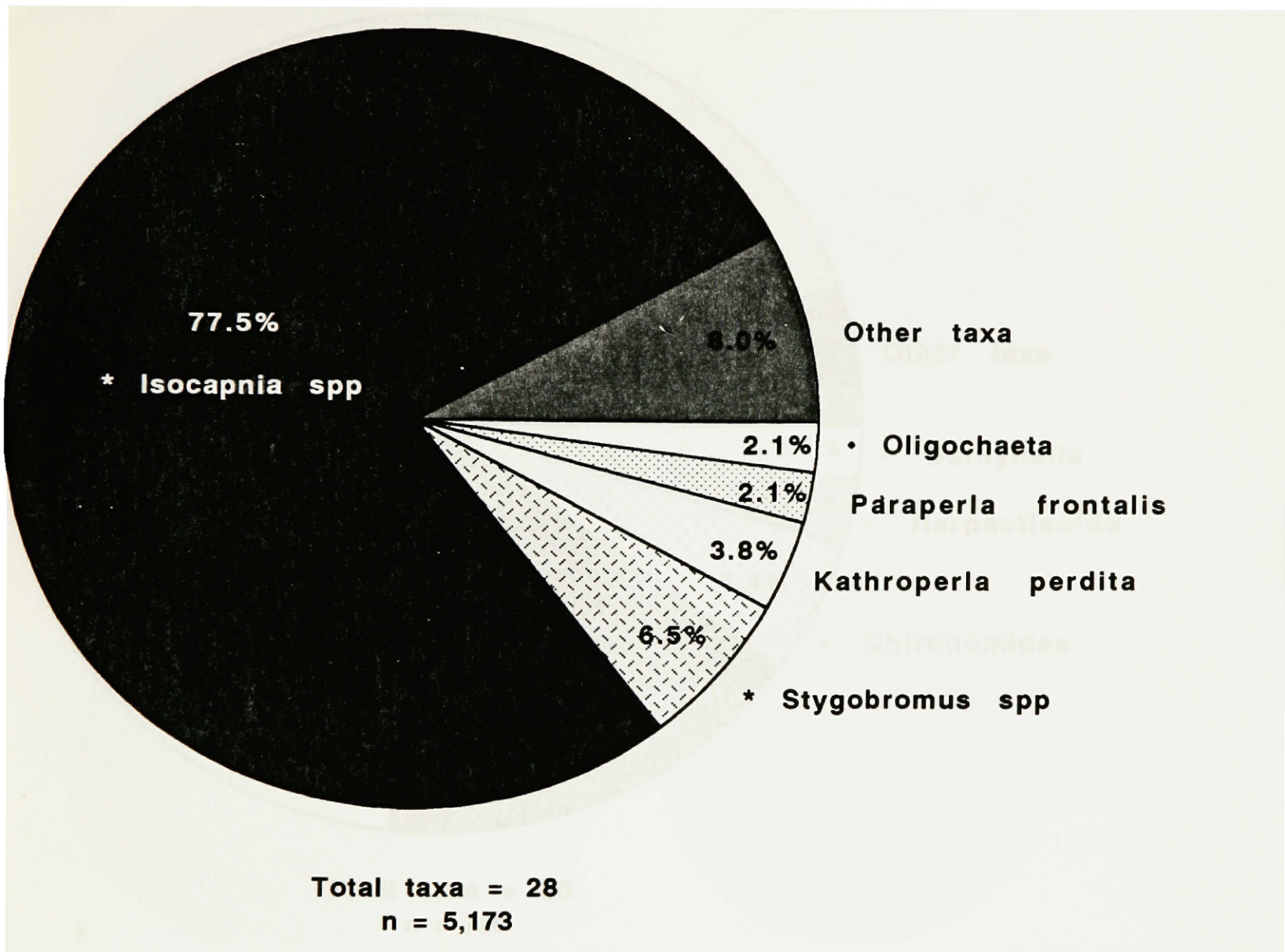
Fig. 6
Community composition of Floodplain Well 1.
* Immature forms that could not be identified to
a lower taxonomic level.
• Lowest taxonomic level identified.
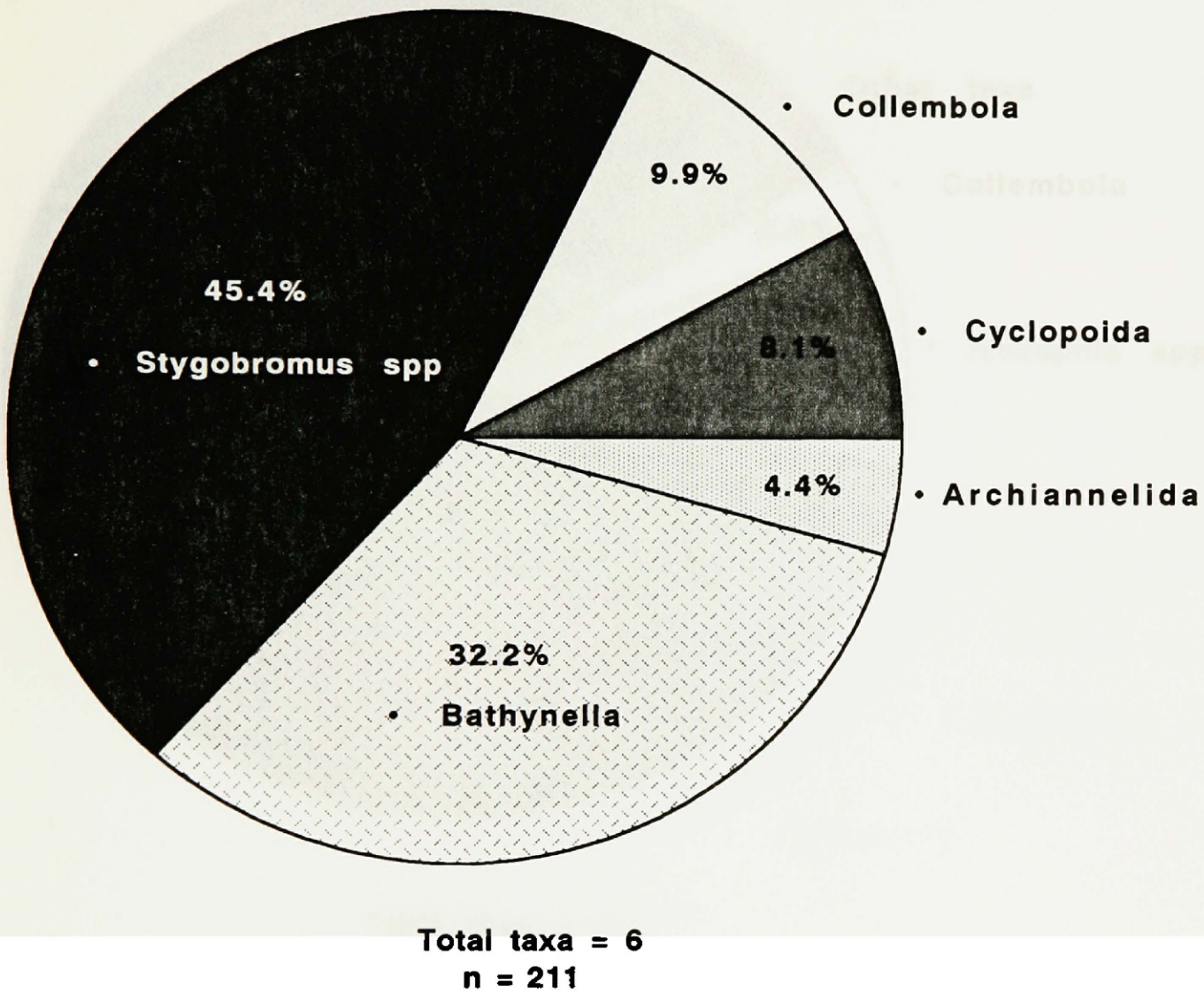n = total number of organisms collected.
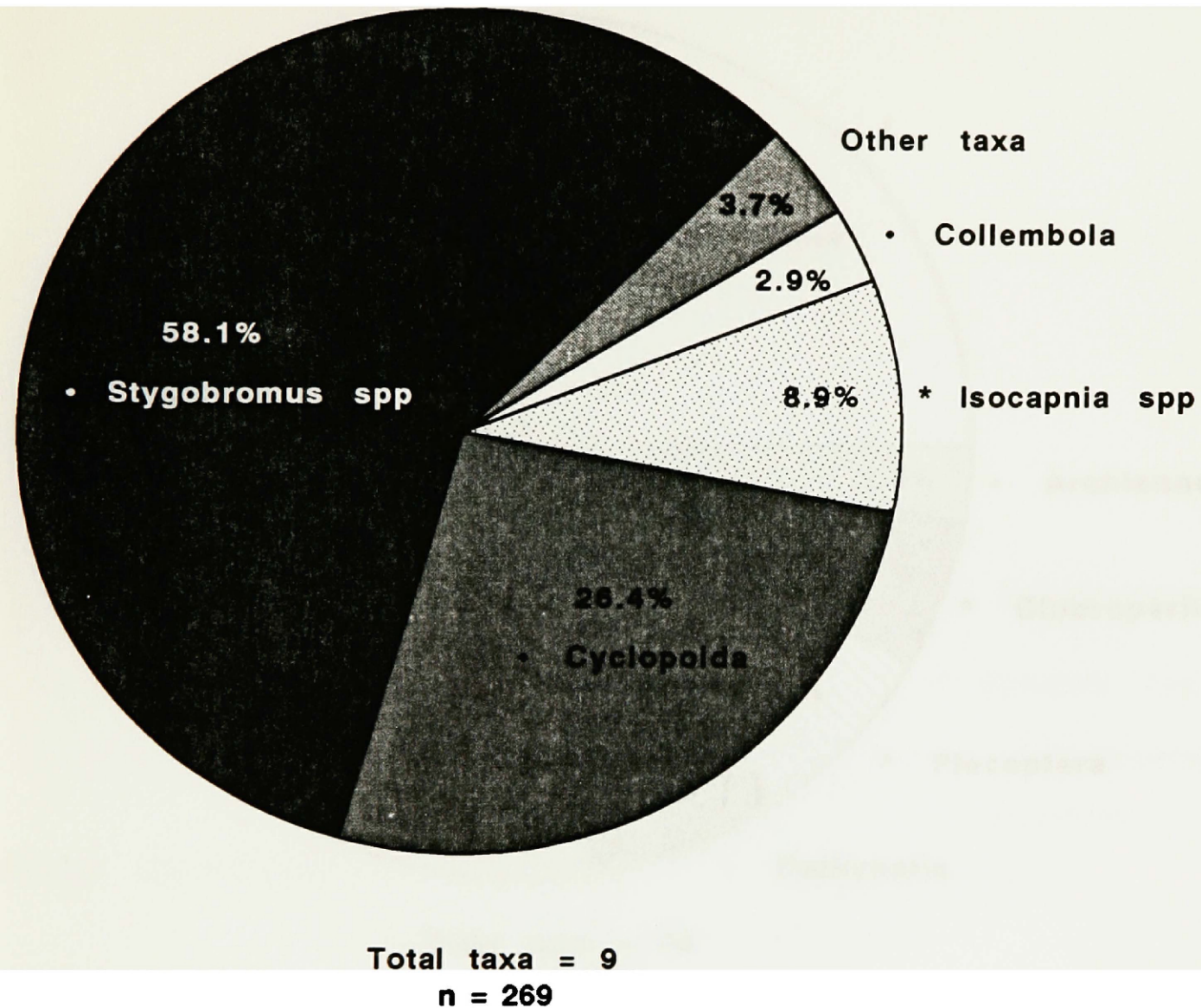
Floodplain Well 2 (FW2)
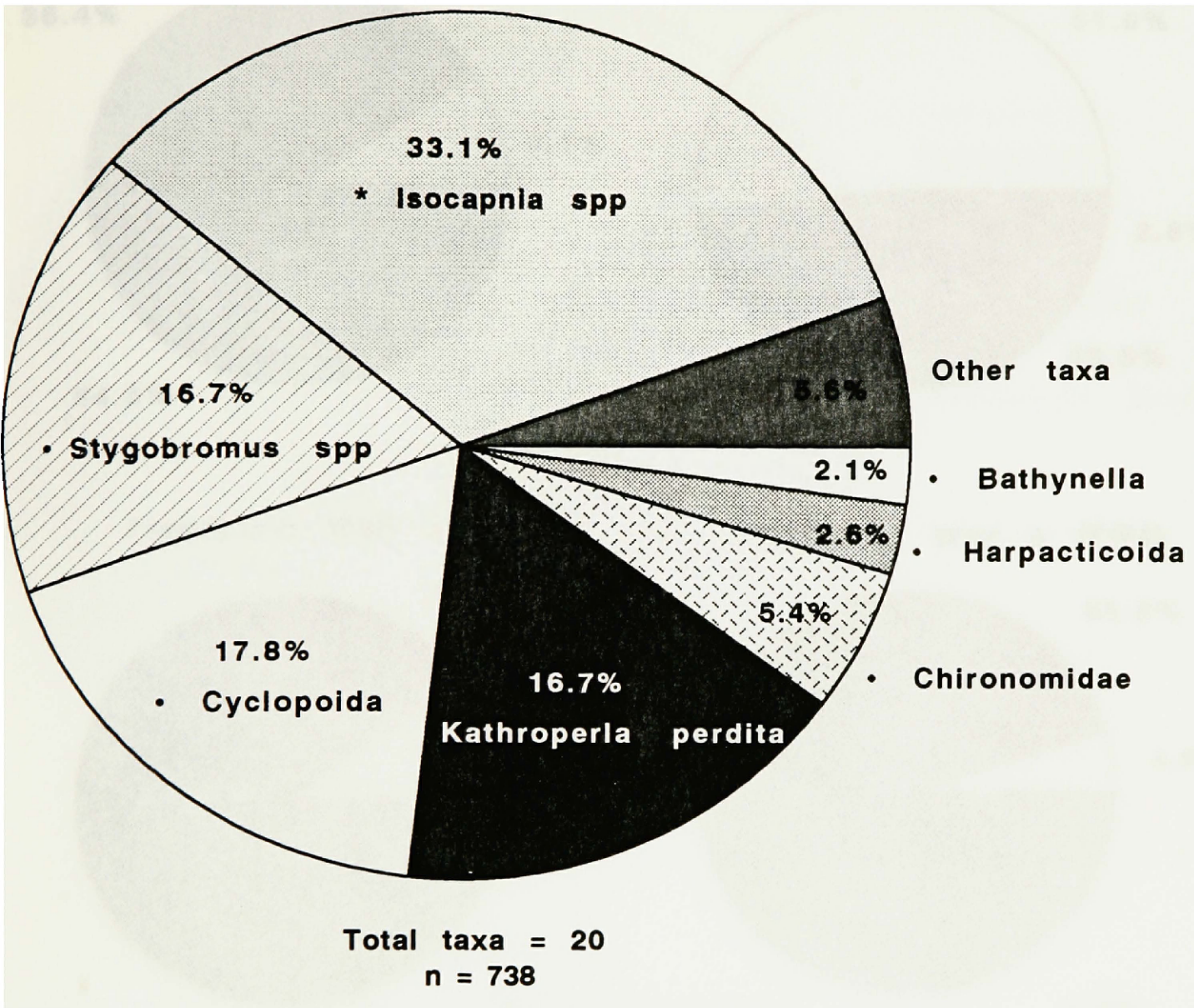
Fig. 7 Community composition of Floodplain Well 2.
  * Immature forms that could not be identified
  to a lower taxonomic level.
  • Lowest taxonomic level identified.
  n = total number of organisms collected.

Terrace Well 3 (TW3)

36.4%

9.1%

54.5%

Terrace Well 4 (TW4)

51.9%

2.6%

45.5%

Floodplain Well 3 (FW3)

10.4%

89.6%

Floodplain Well 4 (FW4)

85.6%

4.8%

9.3%

■ Amphibite

■ Stygobite

□ Benthos
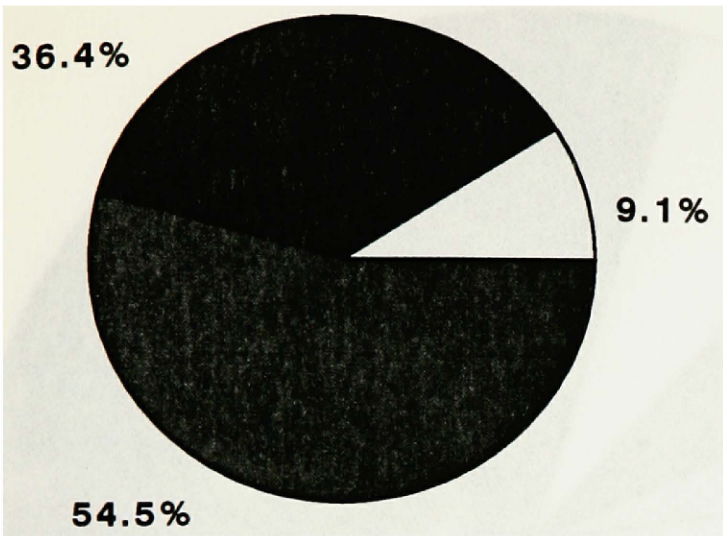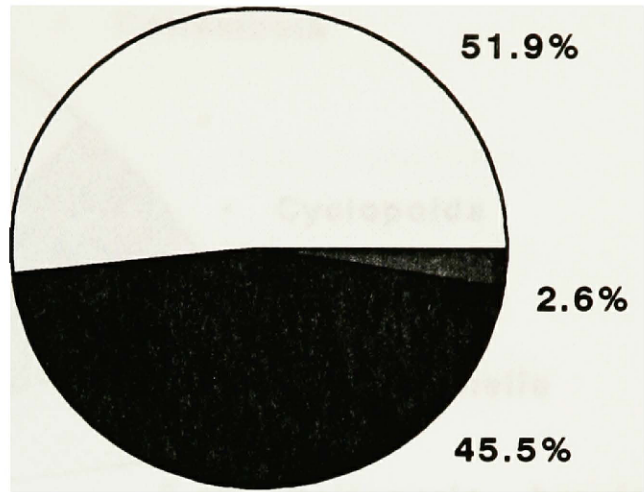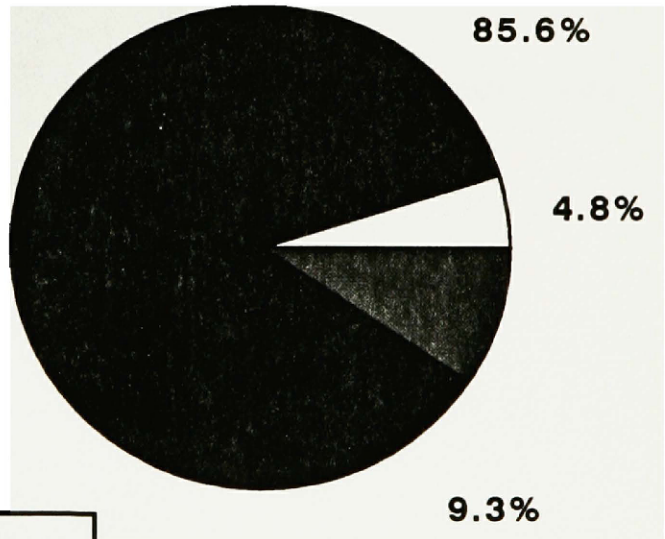
Fig. 8   Community composition of Terrace Wells 3 and 4 and FloodplainWells 3 and 4 expressed as percent amphibite, stygobite, and benthic taxa.

Terrace Well 3 (TW3)

- Collembola

6.8%

- Cyclopoida

6.8%

- Bathynella

4.5%

2.4% Peltoperla   brevis

36.4%
* Isocapnia spp

43.2%
- Stygobromus spp
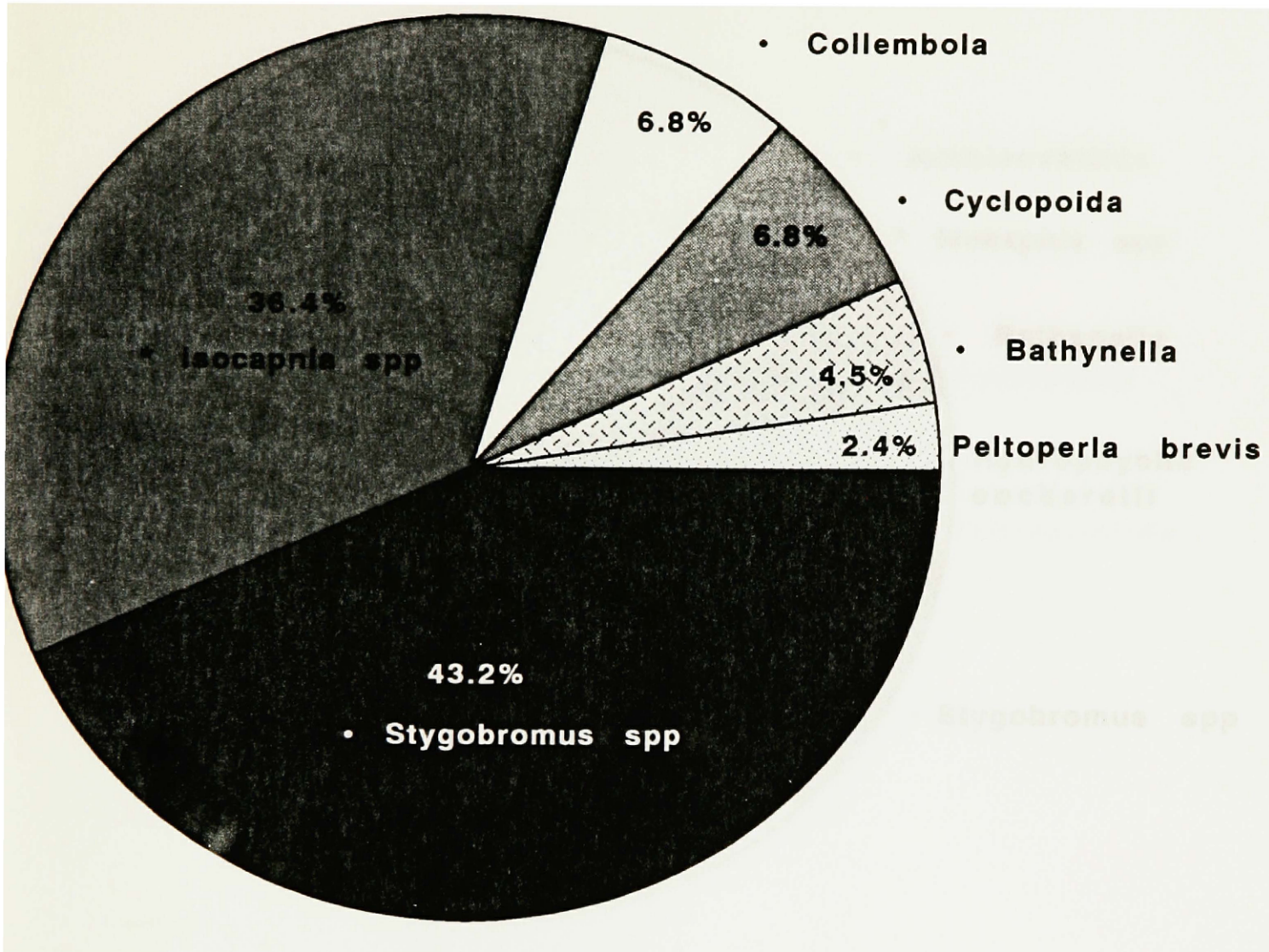
Total Taxa = 6
n= 44

Fig. 9
Community Composition of Terrace Well 3.
* Immature forms that could not be identified to
a lower taxonomic level.
• Lowest taxonomic level identified.
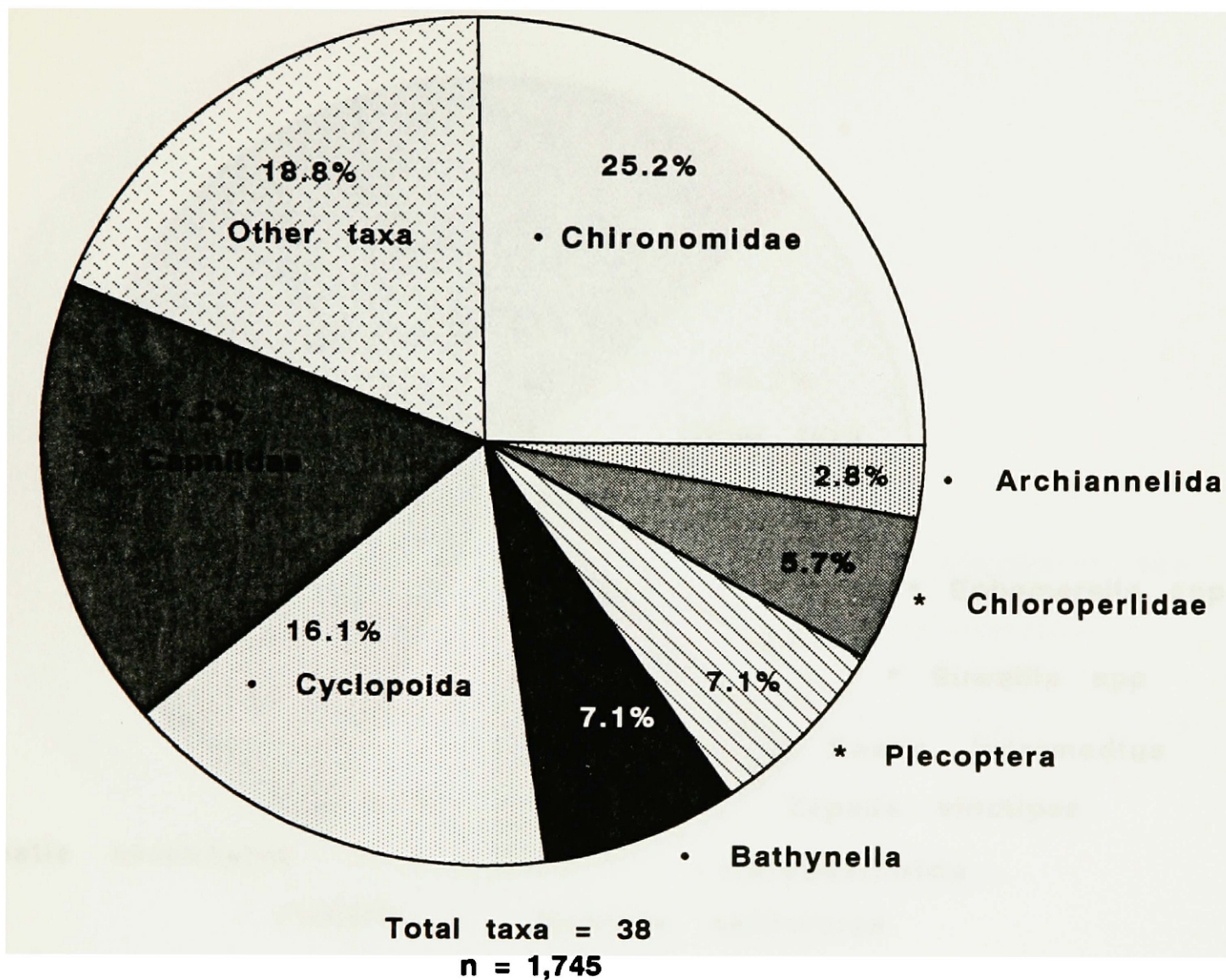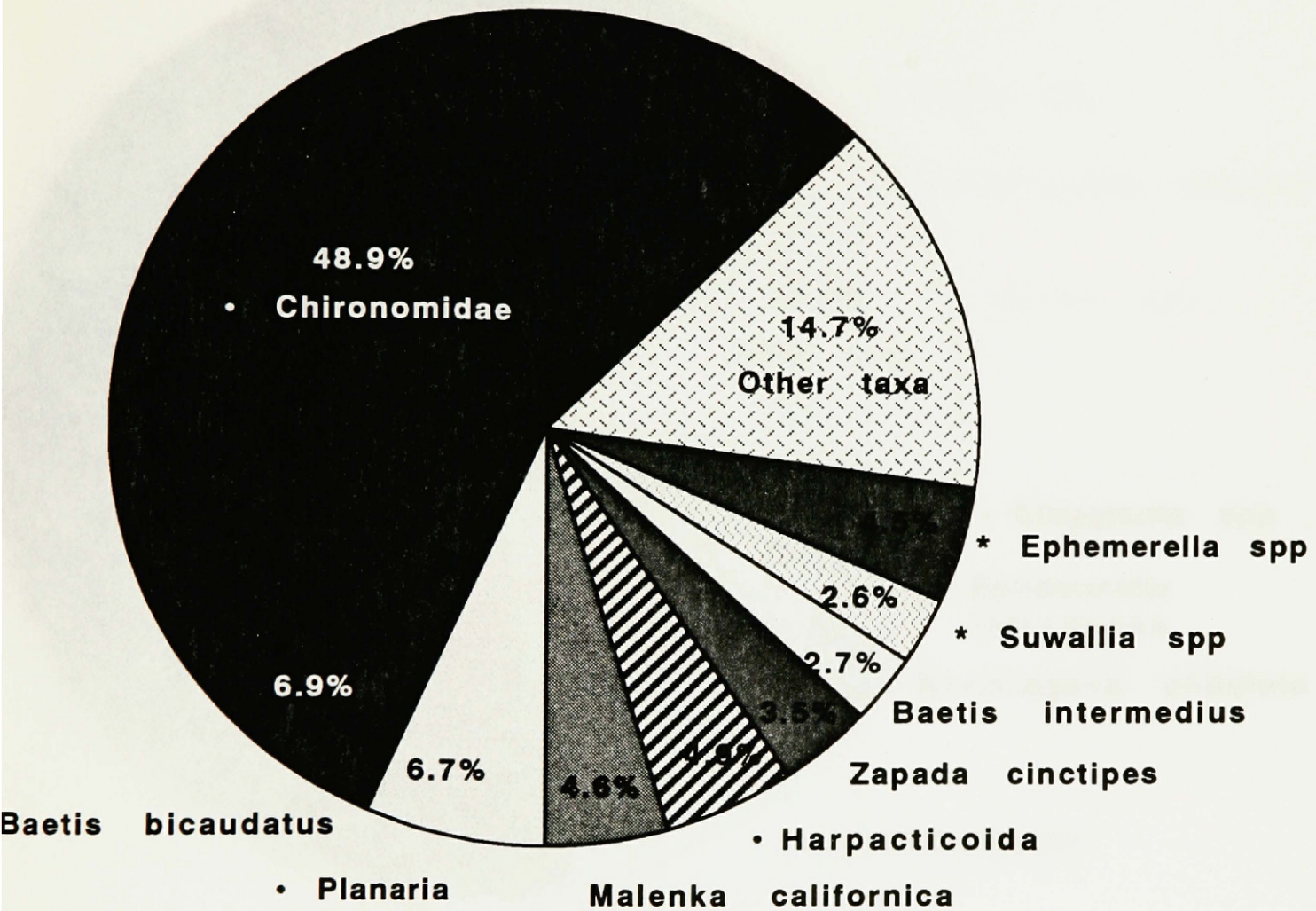**n = total number of organisms collected.**

Terrace Well 4 (TW4)

- **Archiannellida**
- * **Isocapnia spp**
- **Bathynella**

45.6%
- Collembola

2.8%

4.3%

5.8%

Hydropsyche
cockerelli

10.6%

28.7%
- Cyclopoida

- Stygobromus spp

Total taxa = 8
n = 189

Fig. 10
Community composition of Terrace Well 4.
** * Immature forms that could not be identified**
to a lower taxonomic level.
• Lowest taxonomic level identified.
n = total number of organisms collected.

Floodplain Well 3 (FW3)

Fig. 11
Community composition of Floodplain Well 3.
* Immature forms that could not be identified to
a lower taxonomic level.
• Lowest taxonomic level identified.
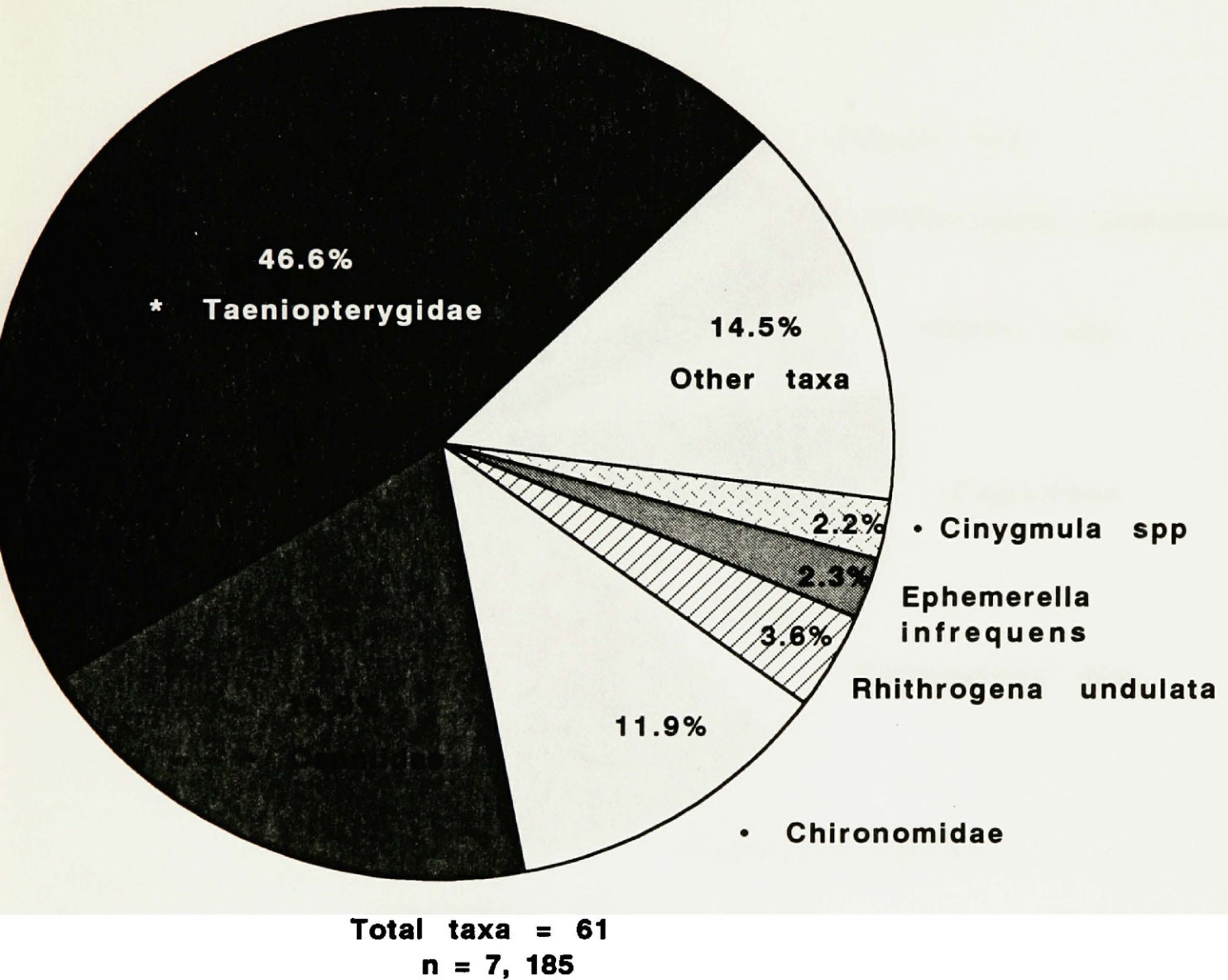n = total number of organisms collected.

Floodplain Well 4 (FW4)

Other taxa

3.7%

• **Collembola**

2.9%

8.9% * **Isocapnia spp**

58.1%

• **Stygobromus spp**

26.4%

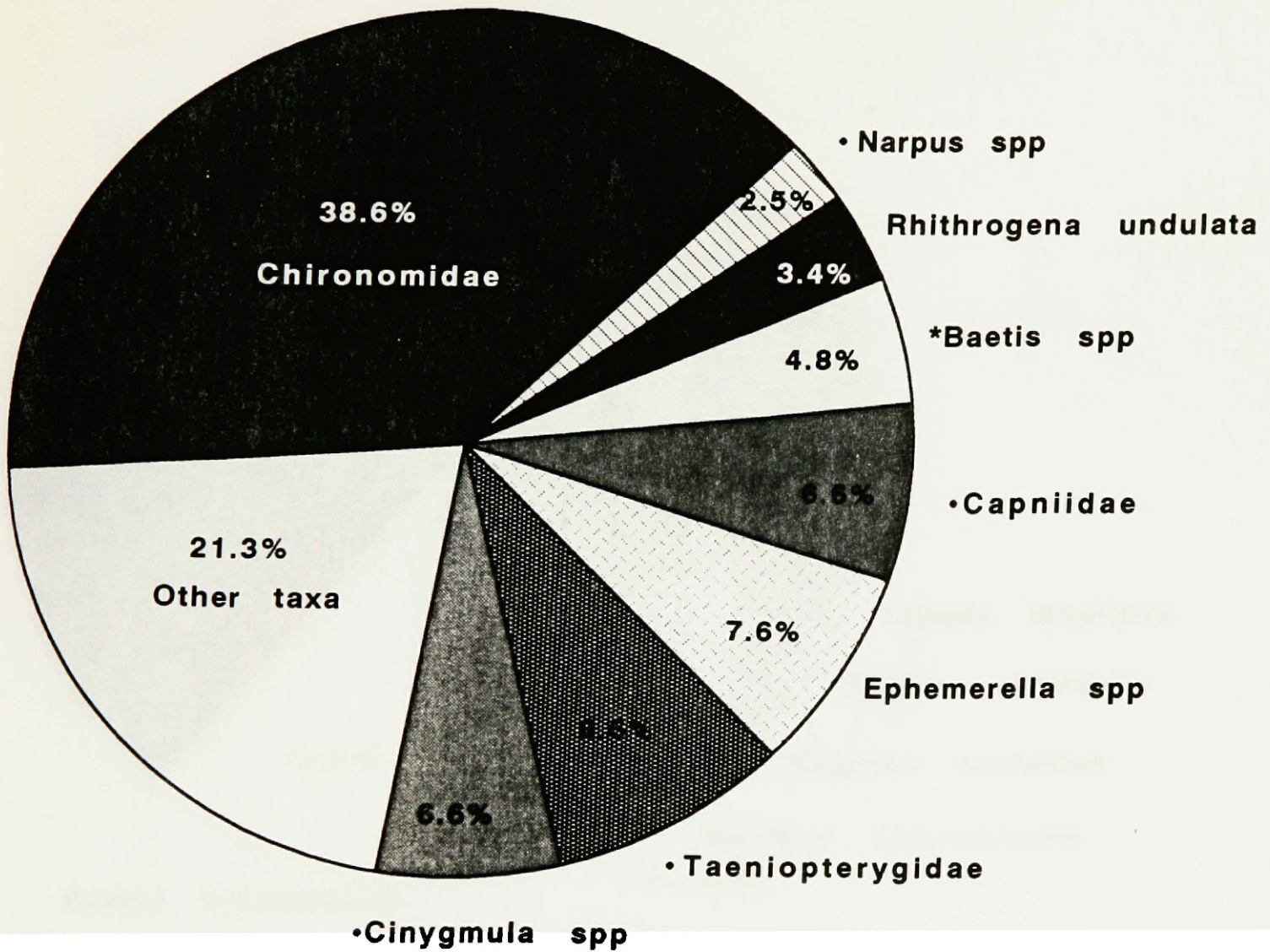• **Cyclopoida**

Total taxa = 9
n = 269

Fig. 12
Community composition of Floodplain Well 4.
* Immature forms that could not be identified to
a lower taxonomic level.
• Lowest taxonomic level identified.
n = total number of organisms collected.

Sandpoints

Fig. 13
Community composition of sandpoints expressed as percent of . total abundance.
* Immature forms that could not be identified to a lower taxonomic level.
• Lowest taxonomic level identified.
n = total number of organisms collected.

Georgia's Springbrook

48.9%
• Chironomidae

14.7%
Other taxa

* Ephemerella spp

2.6%
* Suwallia spp

2.7%
Baetis intermedius

3.5%
Zapada cinctipes

4.6%
• Harpacticoida

6.7%
• Planaria

6.9%

Baetis bicaudatus

Malenka californica

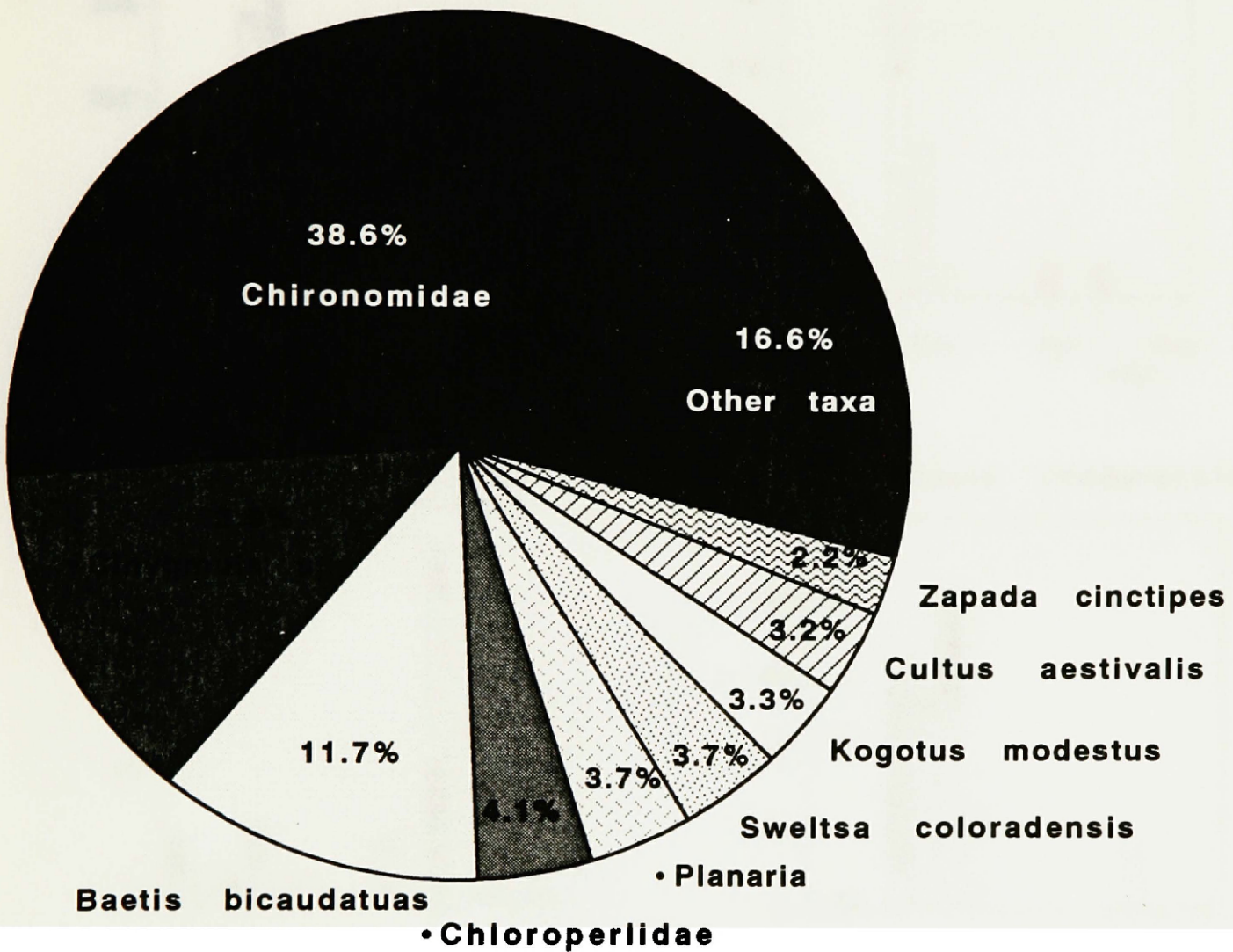Total taxa = 45
n = 6,434

Fig. 14
Community composition of Georgia's Springbrook.
* Immature forms that could not be identified to
a lower taxonomic level.
• Lowest taxonomic level identified.
n = total number of organisms collected.

Nyack Springbrook

46.6%
* Taeniopterygidae

14.5%
Other taxa

2.2% • Cinygmula spp

2.3% Ephemerella infrequens

3.6% Rhithrogena undulata

11.9%
• Chironomidae

Total taxa = 61
n = 7, 185

Fig. 15
Community composition of Nyack Springbrook.
* Immature forms that could not be identified to
a lower taxonomic level.
• Lowest taxonomic level identified.
n = total number of organisms collected.

Beaver Springbrook

Fig. 16
Community composition of Beaver Springbrook.
* Immature forms that could not be identified
to a lower taxonomic level.
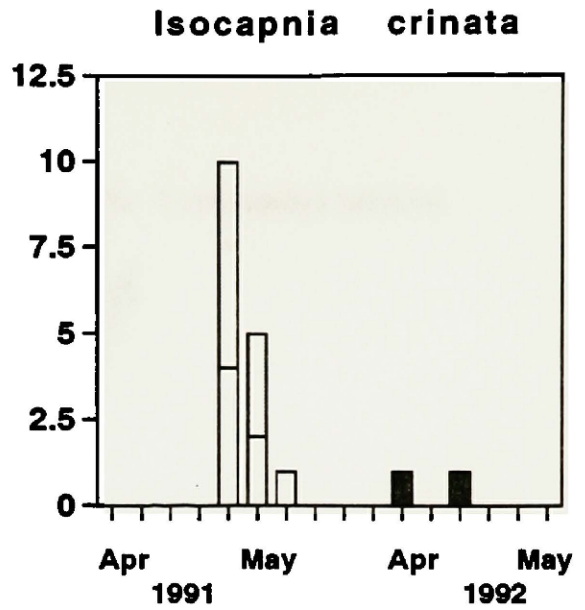•Lowest taxonomic level identified.
n = total number of organisms collected.

Tom's Springbrook

Fig. 17
Community composition of Tom's Springbrook.
*Immature forms that could not be identified
 to a lower taxonomic level.
•Lowest taxonomic level identified.
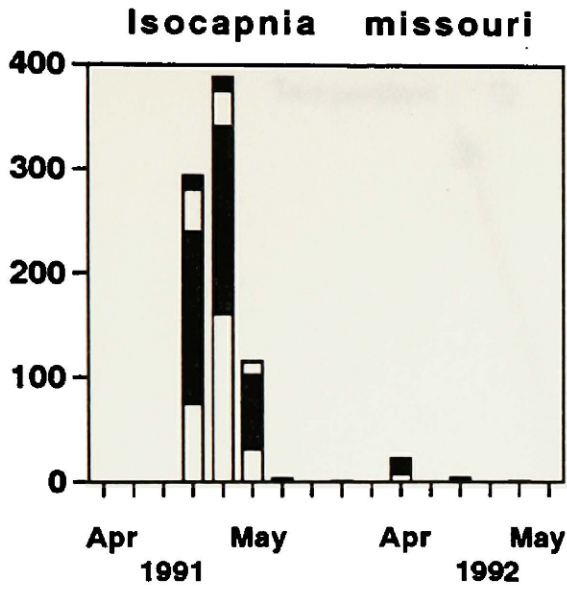n=total number of organisms collected.
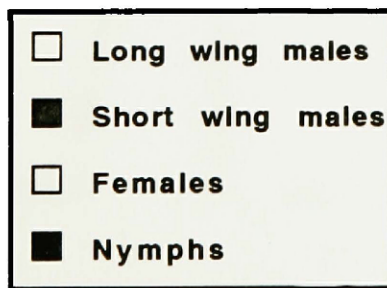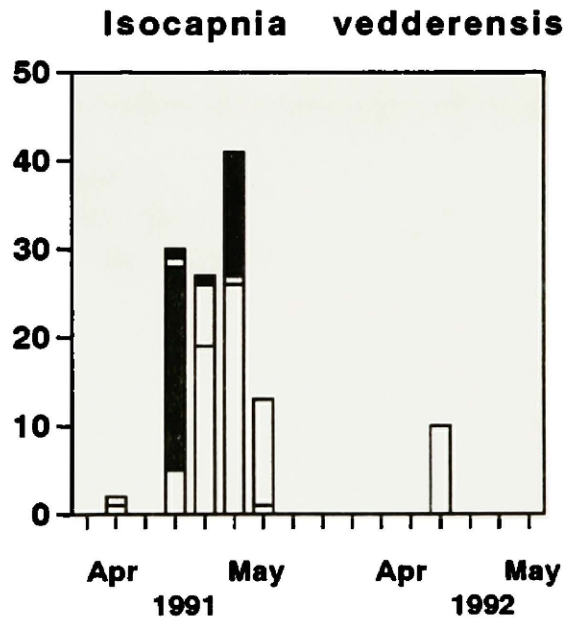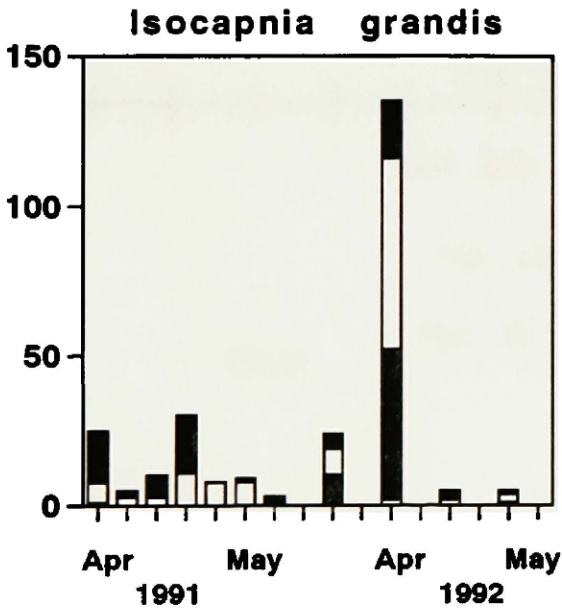
Fig. 18 Emergence of hyporheic plecopterans from the river effluent site April through May 1991 and 1992.
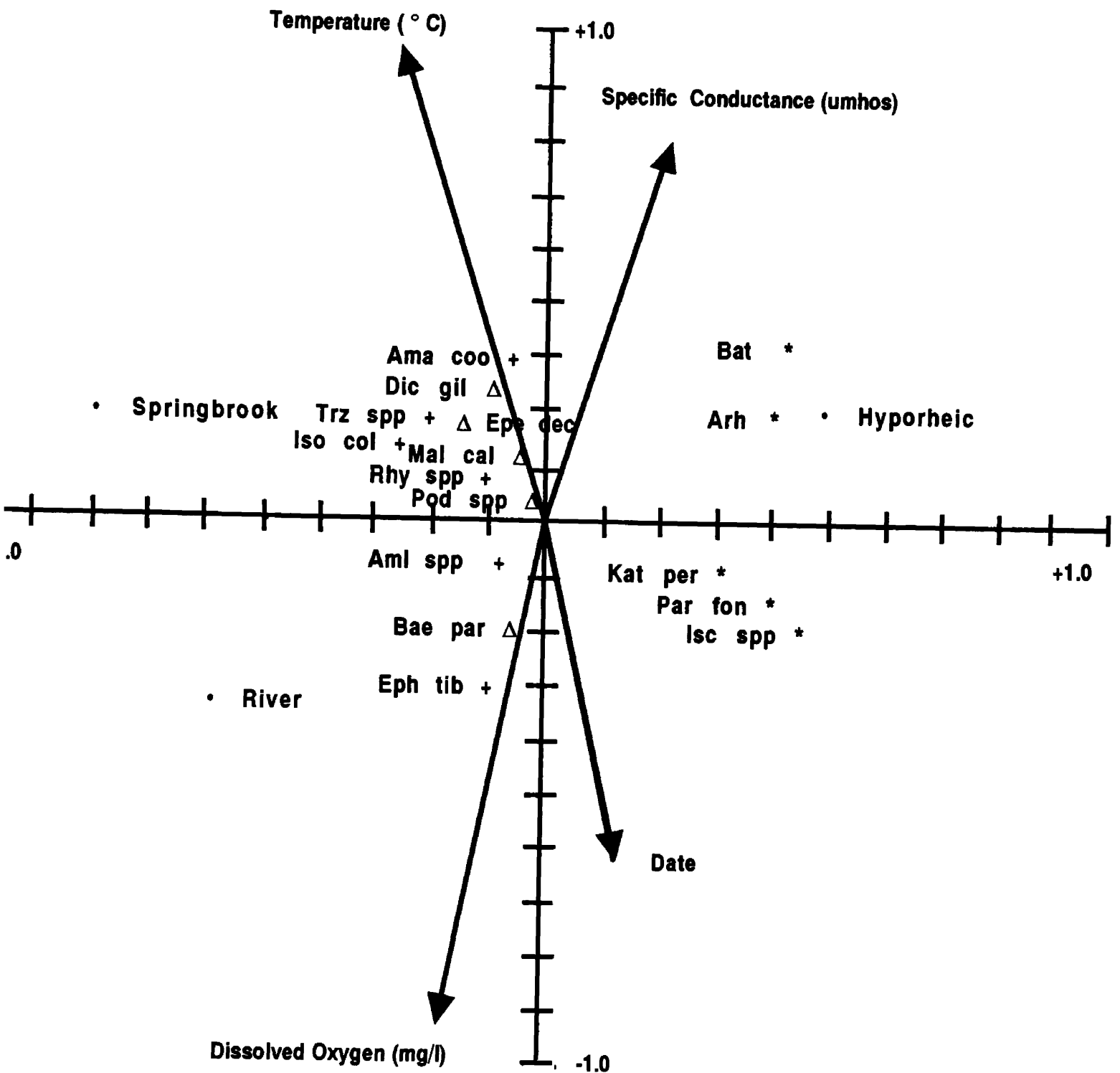
Fig. 19

Fig. 19 Canonical Correlation Analysis of representative taxa from river (+), springbrook (Δ) , and hyporheic (*) environments. Environmental gradients are indicated by arrows. First axis is horizontal. Second axis is vertical.