

EFFECTS OF VARIABLE FLOWS ON INVERTEBRATE DRIFT IN COMAL
SPRINGS, TEXAS

THESIS

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INTRODUCTION

In the coming century, demands on water resources by an increasing population will affect rivers and streams through a variety of anthropogenic disturbances, including diminished flow (Stalnaker et al. 1995). Reduction in stream flows below levels necessary to maintain aquatic life and instream uses such as water quality, aquatic habitat, and freshwater inflow to bays and estuaries is detrimental to aquatic ecosystems. While natural fluctuations in flow occur, the exacerbation of these fluctuations due to anthropogenic influences can alter or eliminate springs and streams and their associated biota. This is of particular concern where rare aquatic ecosystems and endemic species are found.

Although endemic species and rare aquatic ecosystems are found across the state of Texas, the vast majority of the threatened and endangered aquatic ecosystems are associated with the Edwards Plateau (Bowles and Arsuffi 1993). Some 281 major and historical springs have been identified as existing in Texas at some time in the past (Brune 1981). Of the original 31 large springs in Texas only 17 remain and of the four largest springs only two remain, Comal and San Marcos springs (Brune 1981). The source of the majority of these springs, including Comal and San Marcos springs, is the Edwards Aquifer, one of the most prolific artesian systems in the world (USFWS 1996). However, the Edwards Aquifer remains the principal source and in some cases the sole source of water for a rapidly growing central Texas population and for large metropolitan areas such as San Antonio (EPA 2002).

Primary threats to ecosystems dependent upon the Edwards Aquifer include reduction and cessation of flow due to over-pumping, reduced water quality, non-point source pollution, habitat modifications, the presence of several non-native species, impacts due to recreational activities, and urbanization of the river corridor (USFWS 1996). Total withdrawals from the San Antonio portion of the Edwards Aquifer have been steadily increasing over the last several decades as a result of increasing population and subsequent increases in water use (TWDB 1992). Water quality and quantity issues in the Edwards Aquifer and associated terrestrial and aquatic ecosystems are a major concern with more than local and regional implications. When combined, Comal Springs and nearby San Marcos Springs provide about 32% of base flow to the lower Guadalupe River and 70% or more during droughts (GBRA 1988). These flows not only sustain fish and wildlife resources along the river, but also provide valuable freshwater inputs to the San Antonio Bay estuarine environments.

The largest spring system in the southwest United States, Comal Springs, is especially sensitive to severe reductions in flow because of the historically stable nature of flow and the presence of a diverse, spring-flow dependent aquatic community. Votteler (2000) reported a mean daily discharge for Comal Springs from December 1927 to June 1998 of 8.0 cubic meters per second (cms) (283 cubic feet per second (cfs)). This included a range of values from 0 cms in 1954 to over 17 cms (600 cfs) in 1998, with daily fluctuations often as high as 0.85 cms (30 cfs). The Comal River ecosystem, including the spring runs, the Comal River, and their impounded headwaters, has one of the greatest known

diversity of species of any aquatic ecosystem in the southwestern United States and provides habitat for several endangered species (USFWS 1996). Among the endangered species that depend on the relatively constant temperature and flow of the spring waters are surface-dwelling organisms, the fountain darter (*Etheostoma fonticola*) and the Comal Springs riffle beetle (*Heterelmis comalensis*), and subterranean organisms, Peck's cave amphipod (*Stygobromus pecki*) and the Comal Springs dryopid beetle (*Stygoparnus comalensis*).

The Comal Springs riffle beetle belongs to the Elmidae Family (Coleoptera) and is one of three endangered invertebrates found at Comal Springs. It is the only one of the three endangered invertebrates that is surface dwelling and like most other elmids species is generally restricted to shallow, fast-flowing, cool or cold streams with high water quality (Brown 1987). Like most other adult elmids, *H. comalensis* are commonly found in gravel substrate and shallow riffles, in contrast, larvae of *H. comalensis* are often collected with adults in gravel and not on submerged wood as is common with larvae of other *Heterelmis* species (Bosse et al. 1988). Riffle beetles, such as *H. comalensis*, commonly exhibit appropriate adaptations to their particular benthic habitats, such as variations in size and color, length of legs and tarsal claws, and the proportion of the body sclerotized (Brown 1987). However, elmids live primarily in flowing, uncontaminated waters (Brown 1987) and have been listed as indicators of water quality (Brown 1972).

Conservation of the quantity and quality of spring waters emanating from the Edwards Aquifer is fundamental to the preservation of spring ecosystems such

as that found at Comal Springs (USFWS 1996). Studies modeling springflows at Comal and San Marcos springs show that regulation of groundwater withdrawal is necessary to ensure continuous flow (TWDB 1992; McKinney and Watkins 1993). Regulating and managing groundwater use is a complicated task, considering the diversity of water users and the increasing need for water. Because biological communities reflect the overall ecological integrity of a system and integrate the effects of different stressors, the evaluation of such communities can provide a broad measure of their aggregate impact and thus aid in the management of water resources (Barbour et al. 1999).

Benthic macroinvertebrate communities are often comprised of species that constitute a broad range of trophic levels and tolerances, thus changes in the structure and function of the invertebrate community provide important information for interpreting the cumulative effects of natural and anthropogenic influences (Barbour et al. 1999). Benthic macroinvertebrates are reliable indicators of localized alterations in stream conditions (Gore 1977; Corrarino and Brusven 1983; Rosenberg and Resh 1992), because differential habitat requirements make it possible to assess water quality and water quantity issues in stream ecosystems.

There are many different techniques for sampling macroinvertebrates that can be used to assess the environmental conditions of aquatic ecosystems (Rosenberg and Resh 1996). Where sensitive or critical habitat for endangered species is involved, drift sampling may be preferred due to its relatively non-destructive nature. The downstream transport of stream-dwelling organisms in

the water column by current is known as drift (Waters 1962). Because drifting invertebrates are derived from the benthos and all benthic species often occur in the drift, sampling the composition of the drift can provide a useful index for assessing the composition of the benthic macroinvertebrate community (Waters 1961; Dimond 1967; Bishop and Hynes 1969).

Drift is one of the most important methods for the dispersal to and recolonization of downstream habitats by benthic macroinvertebrates (Smock 1996). Brittain and Eikeland (1988) note that drift is an important means of transport for organisms to move between suitable microhabitats and escape unfavorable physical, chemical, or biological situations. Estimates of the percentage of individuals that arrive by drift to colonize an area range from 41% to 82% of the total number of organisms arriving (Townsend and Hildrew 1976; Williams and Hynes 1976). These findings are comparable to those of other similar studies (Shaw and Minshall 1980; Williams 1980; Bird and Hynes 1981) and suggest that drift has a significant impact on the recolonization of denuded stream bottoms (Williams and Hynes 1976). Dimond (1967) found that drift became a significant process only after one to two years of recovery for bottom populations of a denuded stream and suggests drift is density related (Waters 1961; 1965a) in that high benthic densities cause organisms to actively or passively enter the drift in search of more suitable habitat.

Several mechanisms for drift include dislodgement during movement and feeding, escaping predation, and the search for suitable habitat (Allan 1995). Biotic and abiotic variables such as current velocity and discharge, water

chemistry, endogenous rhythms, species characteristics and benthic densities may also affect drift directly or indirectly (Brittain and Eikeland 1988). Effects of current velocity and discharge on invertebrate drift are variable. Several studies show an increase in drifting invertebrates with either increased (Bailey 1966; Anderson and Lemkuhl 1968; Ciborowski et al. 1977; Bird and Hynes 1981) or decreased (Minshall and Winger 1968; Gore 1977; Hemsworth and Brooker 1981) flows.

Decreased flows often lead to a reduction in suitable habitat, which can cause invertebrates to enter the water column to escape and recolonize downstream (Gore 1977), whereas increased flows often result in the dislodgement of organisms (Waters 1965b). Minshall and Winger (1968) manipulated stream discharge and found that most taxa had an increased drift rate in response to a reduction in stream flow. Brusven et al. (1974) and Corrarino and Brusven (1983) found that a reduction in stream discharge clearly caused an increase in insect drift. This suggests that periodic decrease in discharges at Comal Springs as a result of reduced aquifer levels may cause an increase in the number of drifting invertebrates within the spring runs.

Waters (1972) classified drift into three categories according to cause: constant drift, catastrophic drift, and behavioral drift, each of which has unique ecological implications. Constant drift, also referred to as background drift, consists of species that continually drift in low numbers and is thought to be the result of accidental dislodgement. Catastrophic drift is drift that results from disturbance of the bottom fauna by abiotic factors such as flood, drought, high

temperature, pollution, and insecticides, but is most commonly associated with flood conditions that result in the physical disturbance of the substrate by high discharge (Brittain and Eikeland 1988). Catastrophic drift is generally the most easily recognized and offers a useful index of disturbance to a system (Corrarino and Brusven 1983).

Behavioral drift is periodic and results from foraging and life history activities (Waters 1962; Reisen and Prins 1972). Behavioral drift is observed as a temporal variation of drift with season, from day to day and diel periodicity (Waters 1972). Diel periodicity refers to the reoccurring pattern of changes in the number of individuals drifting over a 24-hour period. Numerous studies in various parts of the world (Tanaka 1960; Waters 1962; Reisen and Prins 1972; Muller 1974; Elliot 1967; Newman and Funk 1984; Allan 1987) show that invertebrate drift occurs with a diel rhythmic pattern. Most species exhibit a pattern whereby they drift in larger numbers at night, with distinct peaks soon after sunset and just before sunrise (Waters 1962; 1965a; Elliot 1967; Muller 1974). However, as with most aspects of drift, much variation exists among individual species and stream systems. Changes in light intensity appear to be the proximate trigger for drift and its patterns (Waters 1972), although there are numerous hypotheses concerning ultimate mechanisms that induce drift (Waters 1965b; Kohler 1985; Allan 1995).

Determining the patterns and magnitude of benthic macroinvertebrate drift in response to variable flows may be a useful tool in defining the springflows required to sustain benthic habitats and communities within the spring runs at

Comal Springs. Because invertebrates are sensitive to habitat variation, they can be valuable indicators of both short and long-term environmental disturbances (Harris et al. 1995). Historically, fish have been used to determine instream flow requirements (Bovee 1975). However, recent efforts are now incorporating invertebrates as indicators because they are less mobile, less tolerant to flow changes, and are more easily sampled than fish (Bovee et al. 1978; Barbour et al. 1999). Using biological indicator species as an early warning of pollution or degradation in an ecosystem can aid in the management of critical resources, such as those found in Comal Springs (Barbour et al. 1999).

One group of invertebrates we were particularly interested in evaluating as indicator insects were members of the Elmidae family. As mentioned previously, Brown (1972) listed elmids as indicators of water quality. Because elmids commonly inhabit riffles and crawl about on the surface of rocks and other submerged objects while feeding, it is likely that changes in their abundance will occur in relation to changes in current velocity and water depth. Because one of the elmids found at Comal Springs is endangered (*H. comalensis*), the response of the elmid community to changes in flow regime has a direct application.

To determine the relationship between current velocity and drift patterns of riffle dwelling macroinvertebrates in the Comal Springs, one approach is to use indicator species that are sensitive to changes in flow regime. I used the following *a priori* criteria to select candidate invertebrates to be studied as indicator flow species for Comal Springs: 1) should be widely distributed within the riffle-spring runs, 2) occur in large enough numbers that significant changes

in their abundance due to changes in current velocity and/or water depth are detectable, 3) be present through much of the year, and 4) published literature describing life history characteristics and biological requirements of candidate insects are available.

This approach assumes changes in the distribution and abundance of indicator invertebrates occur in response to changes in the flow regime. Previous studies (Minshall and Winger 1968; Corrarino and Brusven 1983; Allan 1987) show that changes in the composition and abundance of macroinvertebrate communities are markedly affected by changes in substrate and flow conditions. This suggests that some insects in the benthic riffle-spring run community of Comal Springs are likely indicators of hydrologic change through changes in their abundance and behavior. Thus, the objectives of this study are to: 1) provide comprehensive baseline data on the invertebrate community of the spring runs based on drift analysis, 2) determine the drift rates, densities, and patterns of selected aquatic invertebrates, especially riffle beetles (Elmidae) and 3) determine if changes in depth, season, and current velocity affect the composition and abundance of selected indicator insects.

DESCRIPTION OF STUDY AREA

-- *Comal Springs*

The Comal Springs system consists of several spring openings that originate from the Edwards Aquifer along the Balcones Escarpment in Central Texas. The springs issue under artesian pressure from the Comal Springs fault through a distance of about 1300 meters (m) at the base of a high bluff, which sits at an elevation of 190 m (Brune 1981). The spring water has great clarity and a temperature that ranges from 23.1 ° to 23.9° Celsius (Brune, 1975). The water is generally of a calcium bicarbonate nature and is fresh, very hard, and alkaline (USGS 2002). The average annual flow of the Comal River from 1928-1989 was 8.0 cms (284 cfs) and is comprised mainly of springflow (USFWS 1996).

The spring waters were partially impounded in 1847 to form Landa Lake, which is about 8.5 hectares (21 acres) in size, at the headwaters of the Comal River (USFWS 1996). When the city of New Braunfels acquired the park in 1936 the three largest springs were channeled with masonry work and filled with gravel/cobble to form spring runs, now known as spring runs 1, 2, and 3 (Fig. 1). These spring runs empty into the western end of Landa Lake and contribute significantly to the flow of the Comal River. Brune (1981) classified springs 1 and 3 as large springs and spring 2 as a medium spring. The majority of the remaining springs issue from the bottom of Landa Lake through gravel deposited from Blieders Creek (Brune 1981). Several springs and seeps are also found along the banks of Landa Lake and within the three spring runs (USFWS 1996).

The average discharge of the Comal River over the sampling dates was 8.7 cms (306 cfs), as measured at USGS gage #08169000 in New Braunfels, Texas (Table 1).

-- *Spring Runs*

The spring runs form a riffle-run habitat with coarse gravel to cobble dominated substrate. Spring Run 1 (Figs. 2-4) is the longest of the three spring runs at about 310 m in length from the main spring openings to the confluence with Landa Lake. The width of Spring Run 1 at the sampling location was about 9.0 m and the average depth was 0.29 m (Table 1), although it varies greatly with fluctuating springflows. The sampling location was about 6.0 m downstream of Land Park Drive. In descending order of dominance from the spring opening, the dominant aquatic macrophytes above the sampling site in spring run 1 are *Eleocharis* sp., *Bacopa monieri*, and *Hygrophila polysperma*. Interspersed within and around these hydrophytes are *Ludwigia repens*, the moss *Ambystegium riparium* and an unidentified liverwort species. The portion of the spring run below the sampling site was dominated by *Hygrophila polysperma*, *Cabomba caroliniana*, and *Vallisneria americana*. Abundant riparian vegetation, including bald cypress (*Taxodium distichum*), Southern magnolia (*Magnolia grandiflora*), live oak (*Quercus virginiana*), boxelder (*Acer negundo*), pecan (*Carya illinoensis*), American elm (*Ulmus americana*), sycamore (*Platanus occidentalis*), Eastern cottonwood (*Populus deltoids*), and anaqua (*Ehretia anacua*) shade much of the spring run and is a major source of detritus.

Spring Run 2 (Fig. 5) is the shortest of the spring runs at almost 100 m in length. The width at the sampling location was about 3.0 m and the average depth was 0.25 m (± 0.07 SD). Spring Run 2 empties into Spring Run 1 after flowing through a kiddie pool that was built at its lower end. The sampling site was located upstream from a road bridge and the kiddie pool. Overhanging vegetation is similar to that found over Spring Run 1. There was no aquatic vegetation present in Spring Run 2. Flows proved inadequate in Spring Run 2 for effective drift sampling. During the first three sampling dates only a few invertebrates were collected and were actually outnumbered by the number of western mosquitofish, *Gambusia affinis* collected, thus Spring Run 2 was dropped from analysis.

Spring Run 3 (Figs. 6-8) has abundant riparian vegetation, including bald cypress, sycamore, anaqua, and numerous other trees and shrubs that provide canopy. However, Spring Run 3 is intermediate in length (about 140 m), as compared to the other spring runs, and runs along the base of an escarpment that also shades the riffle-run habitat. As a result of the increased shade, Spring Run 3 generally lacks aquatic macrophytes. The upper part of the spring run contained a single stand of *Potamogeton illinoensis*. The width of Spring Run 3 at the sampling site was about 4.0 m and the average depth was 0.44 m (Table 2), although it also varies greatly with fluctuating springflows.

METHODOLOGY

Drift nets were placed at each site in the spring runs at roughly three-month intervals and when flow was less than 150 cfs, which was designated as a period of low flow. The sampling dates were as follows: 28 August 2000, 14 September 2000, 21 November 2000, 20 March 2001, 23 May 2001, 12 September 2001, 5 November 2001, 19 February 2002, and 20 May 2002. Low flow sampling occurred on 14 September 2000 and all subsequent sampling dates were scheduled sampling dates.

Drift nets consisted of a 0.45 m by 0.30 m rectangular frame that connects to a 1 m long tapered net with 250 μ m mesh size. The tapered end of the net connects to a detachable 0.15 m long cylindrical buckets for ease of collecting samples. The nets were anchored into the substrate with stainless steel rods with the bottoms of the nets positioned 2-3 cm above the sediment to reduce the possibility of organisms crawling into the nets (Fig. 9).

The depth of the water column entering the net and the current velocity (Marsh McBirney Flo-Mate model 2000) at the mouth of the net was recorded at the beginning and end of the sampling period (24 hours). Both depth and current velocity measurements were taken at three locations across the mouth of the net and the average was recorded. The buckets connected to the downstream end of the net were removed at 3-hr intervals and the contents preserved in 90% ethanol and stored for processing in the laboratory. After sorting, invertebrates were identified to genus using Merritt and Cummins (1996) and Thorpe and Covich (1991) and species level identification was achieved with voucher

specimens (David Bowles, personal communication, 2001). The taxonomic divisions were then enumerated and stored in 70% ethanol.

The number of invertebrates collected was used to calculate drift rate, the number of organisms drifting past a point per 24-hr, and drift density, the number of organisms per 100 cubic meters of water (Smock 1996). Graphical analysis of seasonal and daily drift rates was performed to identify and characterize patterns in total drift and drift among taxonomic divisions were determined by season. Jaccard's coefficient of similarity (C_j) was calculated to measure similarity of species between spring runs. Multiple regression analysis was used to determine the contribution of current velocity, water depth, and calendar day, expressed as day number on the Julian calendar, to overall drift rates and densities in each spring run. Data was converted using the natural log transformation equation $\ln(x+1)$ to meet the assumptions of normality and linearity for regression analysis. Water temperature, pH, turbidity, and dissolved oxygen were not monitored because of the thermal and chemical stability of the spring system (USFWS 1996).

Correlation coefficients were calculated to evaluate the relationship between the drift rates and densities of individual taxa and the three independent variables (current velocity, water depth, and Julian day). Taxa displaying significant relationships, especially those displaying a significant relationship to changes in current velocity and/or water depth, were then evaluated for presence/absence on sampling dates. Those taxa present throughout much of the year that showed significant changes in their abundance due to changes in

factors related to discharge (current velocity and water depth) were evaluated for life history characteristics to aid in the identification of candidate indicator species.

RESULTS

-- Taxonomic composition

Thirty-eight families of aquatic insects representing 7 orders and several other taxa of aquatic and semi-aquatic invertebrates were identified across all sampling dates within both spring runs. The taxonomic composition and richness, absolute and relative abundance, and dominant taxa of macroinvertebrates varied both seasonally and between spring runs (Tables 3-6). Taxonomic richness, as numbers of insect genera or families, was generally greater in Spring Run 1 than in Spring Run 3. The similarity in taxa as measured by Jaccard's coefficient of similarity (C_j) was 0.62, on a scale of 0 (no similarity) to 1 (total similarity).

Spring Run 1 displayed the greatest diversity of invertebrates over the course of sampling with 55 taxa recorded, compared to 44 taxa for Spring Run 3. Coleoptera was the most abundant order in Spring Run 1 with 13 taxa, followed by the orders Diptera and Trichoptera, with 11 and 8 taxa respectively. Coleoptera also dominated Spring Run 3 with 10 taxa. Trichoptera were the second most numerous taxa in Spring Run 3 with 8 recorded, followed by Ephemeroptera with 5 taxa present. The order Diptera was represented by only 4 taxa in Spring Run 3.

The dominant taxa in order of abundance in Spring Run 1 were *Microcylloepus pusillus* (Elmidae), *Leucotrichia sarita* (Hydroptilidae), *Baetis* sp. (Baetidae), *Tricorythodes* sp. (Tricorythidae), and *Procambarus* (Cambaridae) (Fig. 10) and they accounted for 69% of the 11,514 invertebrates collected in

Spring Run 1. The mayfly *Baetis* dominated the drift in Spring Run 1 on 28 August 2000, 21 November 2000, 23 May 2001 and 19 February 2002, comprising 30%, 27%, 35%, and 51% of the drifting invertebrates respectively. Drift in Spring Run 1 on 14 September 2000 and 20 May 2002 was dominated by the crayfish *Procambarus*. The mayfly *Tricorythodes* was the dominant species collected in Spring Run 1 on 12 September 2001 and the riffle beetle *M. pusillus* was dominant on 5 November 2001.

Taxa in order of abundance in Spring Run 3 were *M. pusillus*, *L. sarita*, *Baetis*, *Psephenus texanus* (Psephenidae) and Chironomidae (Fig. 11). These five taxa accounted for 75% of the 9,805 invertebrates collected from Spring Run 3. The microcaddisfly *L. sarita* was dominant most of the sampling dates in Spring Run 3 and comprised 28% of all invertebrates collected. Drift sampled on 21 November 2000 and 12 September 2001 was dominated by *M. pusillus*, while Chironomidae dominated the drift on 28 August 2000 and 14 September 2000.

An abundance of detritus and other matter was also collected in the drift nets, including macrophytes, sticks, leaves, algae, and cigarette butts among other trash. Samples from Spring Run3 tended to contain more coarse particulate organic matter in the form of leaves, while those from Spring Run1 tended to contain more fine particulate organic matter and aquatic vegetation. The most common leaves collected in both spring runs were bald cypress, sycamore, and anaqua. In Spring Run1, the most common aquatic macrophytes collected were *H. polysperma*, *B. monieri*, *A. riparium*, and an unidentified liverwort species. Despite the presence of filamentous algae in Spring Run1 on

all sampling dates, little to no algae was captured in the drift nets. The only aquatic macrophyte floating into the drift nets from Spring Run 3 was *P. illinoensis* and it was the only plant observed in the spring run upstream of the nets during the sampling period.

Insect exuviae were also collected across all sampling dates, but were most abundant in the spring and fall months. The most common taxa exuviae were from the mayfly *Baetis*, the caddisfly *M. pusillus*, and the water penny *P. texanus*. Exuviae were categorized for each 3-hour sample by taxa as scarce (0-10), moderate (11-100), or abundant (>100). Exuviae of the mayflies *Baetodes* and *Tricorythodes* were scarcely collected, while *Baetis* and *M. pusillus* were abundant on several sampling dates.

-- Drift Rate

Drift rates varied by season, over the course of the day, among taxa, and between spring runs. Drift rate was higher in Spring Run 1 than in Spring Run 3 on six of the nine sampling dates (Fig. 12). The highest drift rate for Spring Run 1 was recorded during the late spring/early summer of 2001. High drift rates were also recorded in Spring Run 1 in September 2000, during the lowest observed flows, and in the late winter and summer of 2002. The highest drift rate observed for Spring Run 3 occurred during the low flows of September 2000. Spring Run 3 also displayed peaks in drift rate during late spring/early summer of 2001 and the late winter and summer of 2002. The largest disparity in drift rate between spring runs occurred during the fall of 2001 on 12 September and 5 November when drift rate in Spring Run 1 was almost twice that of Spring Run 3.

Drift rates in both spring runs were generally greater (2x) by night than by day (Fig. 13), however, diel patterns in drift differed between the spring runs. Nocturnal increases were more pronounced in Spring Run 1 than in Spring Run 3 and marked crepuscular peaks were apparent in Spring Run 1 and were absent in Spring Run 3. Crepuscular peaks in Spring Run 1 on 28 August 2000, 14 September 2000, 21 November 2001, 19 February 2002, and 20 May 2002 were associated with sunset, while the peak observed on 23 May 2001 was associated with sunrise. The crepuscular peaks in Spring Run 1 are largely due to the diel drift pattern of a few taxa (*Baetis*, *Tricorythodes*, and *Procambarus*)

Diel drift patterns among taxonomic divisions generally differed between the spring runs. In Spring Run 1, the mayfly *Baetis* showed peaks in drift associated with sunset or the sampling interval following sunset on all dates, while no such peaks were observed in Spring Run 3 (Fig. 14). A similar relationship was present for the mayfly *Tricorythodes*, as marked peaks in drift associated with sunset or the following sampling interval were apparent in Spring Run 1 and not in Spring Run 3 (Fig. 15). The crayfish *Procambarus* showed marked crepuscular peaks in Spring Run 1 on three sampling dates (28 August 2000, 14 September 2000, and 20 May 2002) and showed no distinct pattern in either spring run for all other sampling dates (Fig. 16). Other dominant taxa, including *P. texanus*, *L. sarita*, and Chironomidae, showed no peaks in drift in relation to changes in light intensity.

Psephenus texanus generally showed greater drift rates at night than by day in both spring runs and drift often peaked during the middle of the night (Fig.

17). In contrast, the caddisfly *L. sarita* generally showed no increases in drift rate during the night as compared to day and drift rate often (28 August 2000, 20 March 2001, 23 May 2001, 12 September 2001, 5 November 2001, and 20 May 2002) peaked during the day in Spring Run 3 (Fig. 18). Diel drift of Chironomidae generally showed no marked difference between day and night, although drift in Spring Run 1 peaked close to noon on three (28 August 2000, 20 March 2001, and 19 February 2002) of the nine sampling dates (Fig. 19). The only other taxa consistently collected in large enough numbers to provide meaningful analysis of daily drift patterns was the riffle beetle *M. pusillus*, and will be discussed in the following section with other Elmidae genera.

-- *Drift Density*

In contrast to drift rate, drift density was generally greater in Spring Run 3 than in Spring Run 1 (Fig. 20). This was true for all sampling dates with the exception of 28 August 2000 and 14 September 2000. The greatest drift density for both spring runs was recorded on 14 September 2000 during the period of lowest recorded flow. In contrast, the highest flows recorded for Spring Run 1 and 3 occurred on 21 November 2000 and produced the lowest drift densities of 8.6 and 13.4 ind/100 m³, respectively.

-- *Analysis of Factors Affecting Drift*

Multiple regression analysis of the drift rate and drift density in each spring run was performed with water depth, current velocity and Julian day as the independent variables (Table 7). All regressions were performed on the raw data and on natural log plus one transformed data. Data were transformed after

scatter plots of the raw data revealed several slightly curvilinear relationships. Transformed data produced stronger relationships for all statistical data. The R^2 multiple regression values obtained showed that 72% of the variability in drift rates observed in Spring Run 1 was accounted for by water depth, current velocity, and Julian day. However, only the relationship between drift rate and Julian day was significant ($p = 0.05$).

Analysis of drift density in Spring Run 1 showed that 90% of the variability observed was due to Julian day, water depth, and current velocity, with a significant ($p = 0.03$) negative relationship ($R = -0.71$) between drift density and current velocity. Drift density displayed a weak negative relationship to both water depth ($R = -0.46$) and Julian day ($R = -0.38$) and did not show significance at the $\alpha = 0.05$ level to either variable, but did show significance at the $\alpha = 0.10$ level to both water depth ($p = 0.09$) and Julian day ($p = 0.06$).

Multiple regression analysis failed to produce any significant correlation results for drift rate or drift density versus the three independent variables in Spring Run 3. Simple linear correlations were calculated to further investigate the relationship between the drift of individual taxa in each spring run and the three independent variables. The taxa with significant relationships are displayed in Tables 8 and 9. Of particular interest were the strong positive relationships between current velocity and the drift rate for several taxa in Spring Run 3, while the drift rate and density of several taxa in Spring Run 1 showed significant negative relationships to current velocity and water depth.

-- *Elmidae Genera in the Drift*

Elmidae drift rates were higher in Spring Run 3 than in Spring Run 1 on six of the nine sampling dates (Fig. 21) and the seasonal drift pattern differed between spring runs. Drift rates were similar in both spring runs from August 2000 through March 2001 and were markedly different for the remaining sampling dates. Larval and adult elmids were collected on all sampling dates (Figs. 22 and 23) and overall drift abundance of Elmidae larvae was significantly higher than adults in both spring runs (1 tailed t-test $p = 0.03$). Analysis of Elmidae drift rates and densities in relation to current velocity, water depth, and Julian day revealed no significant ($p > 0.05$) relationships at the family level of resolution.

Three Elmidae genera were collected at Comal Springs, *Microcyloopus pusillus*, *Phanocerus clavicornis*, and *Heterelmis comalensis*. Differences in seasonal and daily drift rate were noted among the Elmidae species as well as between larval and adult stages. Larvae and adults of *M. pusillus* were collected on all sampling dates, while larval and adult forms of *H. comalensis* and *P. clavicornis* were not present year round. *Microcyloopus pusillus* was collected on all sampling dates and constituted the majority (97%) of elmids collected in both spring runs (Fig. 24). Drift of *M. pusillus* was greater in Spring Run 3 than in Spring Run 1 on six of the nine sampling dates and was highest in Spring Run 1 in February 2002 and in Spring Run 3 in May 2001.

Heterelmis comalensis larvae were collected on all sampling dates except for May 2002 in Spring Run 1, and adults were collected much less frequently

and were absent from both spring runs in August 2000, September 2001, November 2001 and from Spring Run 1 in February 2002 (Fig. 25). Larval forms constituted 78% of the 119 *H. comalensis* collected from both spring runs and the majority (65%) were collected from Spring Run 3 (Figs. 26 and 27). Drift of *H. comalensis* was greater in Spring Run 3 than in Spring Run 1 on six of the nine sampling dates (Fig. 25) and larvae constituted the majority of *H. comalensis* collected in both spring runs (Fig. 26 and 27). Although diel drift patterns for *M. pusillus* varied between spring runs, a distinct peak in drift occurred during the sampling interval before or after sunrise in both spring runs on five of the nine sampling dates (Fig. 28). No distinct diel drift patterns were apparent for *H. comalensis* in either spring run. Graphical analysis of *P. clavicornis* (not shown) daily drift rates did not reveal any patterns. *Phanocerus clavicornis* were present on only five of the nine sampling dates and only thirty-three specimens were collected from both spring runs during the course of sampling.

Simple linear correlation analysis of drift rate and density for the individual Elmidae species in relation to current velocity, Julian day, and water depth revealed several relationships. Drift rate of *M. pusillus* showed a significant ($p=0.03$) negative relationship ($R=-0.73$) to water depth in Spring Run 1 (Table 8) and no significant ($p<0.05$) relationships were found for *M. pusillus* in Spring Run 3 (Table 9). Drift rate ($R=0.81$) and drift density ($R=0.81$) of *H. comalensis* in Spring Run 3 showed a significant ($p=0.008$) relationship to current velocity and drift density of *H. comalensis* in Spring Run 1 was significantly ($R=-0.78$, $p=0.01$) related to water depth.

DISCUSSION

--Taxonomic Richness

In this study, 61 taxa of invertebrates were collected from both spring runs and the diversity and abundance of aquatic insect taxa was much greater than that of other invertebrates (Tables 3-6). Invertebrates such as crustaceans and mollusks are commonly greater in abundance and diversity than insects in spring systems in northern regions of the United States, especially in limestone springs (Glazier and Gooch 1987, Glazier 1991, Webb et al. 1995). Levine (1999) studied the macroinvertebrate assemblages of seven Edwards Plateau springs and found aquatic insects taxonomically and numerically dominated all of the spring systems and similar findings have been reported from karst, spring-fed streams in Florida (Mattson et al. 1995). The differences among spring systems in terms of the diversity and abundance of insects versus other invertebrates may be explained by several factors. The first reason why the diversity and abundance of insects versus other invertebrates varies among spring systems is that differences in the physical and chemical characteristics among the springs influence the composition of the invertebrate fauna. Glazier and Gooch (1987) reported that amphipods commonly dominate limestone springs in Pennsylvania, however, they reported that these spring systems lacked hard water and coarse substrate. While Comal Springs is a limestone spring, the water is hard in nature and the substrate of the spring runs is dominated by coarse cobble/gravel. Thus, major geographic differences in the physical and chemical characteristics among

the limestone spring systems are likely to influence the composition of the invertebrate fauna.

Hynes (1970) grouped faunal components of springs into four categories: 1) groundwater forms (primarily noninsects), 2) species evolved from invertebrates that normally inhabit wet margins (hydrophilids), 3) insects that are restricted to spring-fed reaches and may have evolved from species that were previously widespread but found refuge in thermally constant springs as climates changed on a geologic timescale (caddisflies, stoneflies, some mayflies), and 4) invertebrates of the normal stream fauna that find conditions favorable in springs (amphipods, snails, some mayflies). Consequently, the second possible explanation for the observed differences in the invertebrate fauna is the historical dependability of the spring systems and the subsequent faunal source from which these systems were colonized. Because of the historical flow dependence of Comal Springs and the taxa collected, it appears that many of the insect species present either evolved from relict populations that found refuge in the springs or from those that found conditions favorable. Whereas, in contrast, the dominance of amphipods in Pennsylvania limestone springs suggests that the species present evolved from groundwater forms or were part of the normal stream fauna that found conditions favorable.

The taxonomic richness reported (61 taxa) from Comal Springs is similar to that reported by Levine (1999) from Gunstock Springs (65 taxa), but much lower than is commonly reported in streams and rivers (Allan 1995). Insect diversity is typically reported to be depressed in source areas of rheocrenes

(Sloan 1956, Odum 1957, Minckley 1963, Minshall 1968, Ward and Dufford 1979). The constant thermal and hydrologic regime associated with rheocrenes not only allows colonization by certain species unable to maintain populations in highly variable conditions, but also depresses colonization by pioneer species and species requiring variability in environmental conditions (i.e. flow and temperature) to complete their life cycles (Ward and Stanford 1982). According to the intermediate disturbance hypothesis, a moderate degree of disturbance allows pioneer species to coexist with superior competitors as the importance of biotic interactions is constrained by abiotic disturbances. Downstream increase in species diversity in rheocrenes as thermal homogeneity decreases supports the intermediate disturbance hypothesis (Minckley 1963, Minshall 1968, Allan 1975). While spatial heterogeneity is generally high in rheocrenes due to the establishment of algae, mosses, and a well-developed macrophyte community that promotes diversity (Ward 1992); the stability of rheocrenes still allows biotic interactions to suppress diversity.

The overall taxonomic richness of invertebrates collected in Spring Run 1 (55 taxa) was greater than that of Spring Run 3 (44 taxa). The difference in diversity between the spring runs is likely attributable to differences in habitat heterogeneity between spring runs. Studies have shown that differences in substrate type (Minshall 1984) and other physical and chemical attributes of streams (Ward 1992) greatly affect the diversity of invertebrates. Although the spring runs share the same substrate and other attributes (i.e. flow, temperature, water quality, etc...), Spring Run 1 has a well-developed macrophyte community,

which is absent in Spring Run 3 and may be the proximate cause for the difference in diversity of organisms collected. Habitat complexity and the number of available niches are likely to increase as the abundance and types of macrophytes increase because of the different morphological features, surface area, biofilm, sedimentation of fine-sediments, and food resources (Ward 1992). Thus, the presence of a well-developed macrophyte community and the associated increased habitat complexity in Spring Run 1 may explain the larger diversity and abundance of organisms in Spring Run 1 as compared to Spring Run 3.

Several lines of evidence suggest that the presence of macrophytes in Spring Run 1 contributed to the increased invertebrate diversity and differences in taxonomic composition relative to Spring Run 3; 1) the larger number of *Procambarus* collected; 2) the increased number of taxa commonly associated with fine-sediments; 3) the increased number of sprawlers and climbers (Merritt and Cummins 1996) associated with macrophytes; and 4) shifts in dominant taxa between the spring runs. Crayfish of the Cambaridae family are commonly found in greater abundance in areas that afford concealment (Hobbs 1991). The abundance and diversity of aquatic macrophytes and associated fine sediments in Spring Run 1 likely provides suitable refuge for *Procambarus* and accounts for their greater abundance in Spring Run 1 as compared to Spring Run 3.

The larger diversity of organisms within each insect order, especially Diptera, in Spring Run 1 as compared to Spring Run 3 may also be attributed to the presence of a well-developed macrophyte community and associated fine

sediments. The presence of macrophytes not only leads to the deposition of fine sediments, but their root systems stabilize those sediments. The resultant stability of fine sediments and the increased habitat complexity associated with the presence of macrophytes allows insects with different modes of existence to be successful because more niches are available.

Merritt and Cummins (1996) categorized aquatic insect habits or modes of existence into 8 categories (Skaters, Planktonic, Divers, Swimmers, Clingers, Sprawlers, Climbers, and Burrowers) based on general habits, locomotion, attachment, and concealment strategies (Table 12). Four of the dipterans [*Culicoides* sp. (Ceratopogonidae), *Pericoma* sp. (Psychodidae), *Myxosargus* sp. (Stratiomyidae), and Muscidae] present in Spring Run 1 and absent from Spring Run 3 are classified as burrowers that inhabit fine sediments. The remaining dipterans [(*Dasyhelea* sp. (Ceratopogonidae), *Caloparyhus* sp. (Stratiomyidae), and *Simulium* sp. (Simuliidae)] are classified as sprawlers, clingers, or climbers, all of which commonly inhabit the surface of macrophytes or fine sediments among other strategies. Similarly, several other insect taxa often associated with macrophytes were more abundant in Spring Run 1 than in Spring Run 3. These included the odonates *Perithemis* (3x) and *Argia* (12x), the mayflies *Baetis* (5x), *Baetodes* (2x), and *Tricorythodes* (8x), and the microcaddisfly *Ochrotrichia* (3x). All of these taxa are categorized as sprawlers, swimmers, or climbers with the exception of *Ochrotrichia*, which is classified as a clinger and was commonly collected in Spring Run 1 attached to the moss, *Ambystegium riparium*, or an unidentified liverwort species, neither of which were present in Spring Run 3. All

of these examples point to the differences in habitat complexity between the spring runs affecting the taxonomic richness and abundance of organisms. Similarly, differences in the dominant taxa can also be explained by differences in habitat complexity between the spring runs.

-- *Dominant Taxa*

The dominant taxa in Spring Run 1 included the mayflies *Baetis* and *Tricorythodes* and the crayfish *Procambarus*, while Spring Run 3 was dominated by the caddisfly *L. sarita*, the water penny *P. texanus*, and Chironomidae. *Baetis* was almost six times more abundant in Spring Run 1 than in Spring Run 3 and the caddisfly *L. sarita* was three times more abundant in Spring Run 3 as compared to Spring Run 1. Hydroptilids, or purse case-makers, often attach their pupal retreats to submerged rocks and stones and larvae commonly live on the upper surfaces of rocks and graze on surrounding periphyton (Wiggins 1996). The general absence of macrophytes in Spring Run 3 prevents taxa that commonly utilize or are associated with macrophytes from dominating the invertebrate community, thus allowing those taxa that thrive on open cobble substrate, such as *L. sarita* and *P. texanus*, to dominate. Similarly, the presence of macrophytes in Spring Run 1 offers ample refuge and attachment space for burrowers, swimmers, and climbers such as *Baetis*, *Tricorythodes*, and *Procambarus*.

Chironomidae dominated the drift in Spring Run 3 in the late summer of 2000, during which flows in the Comal River reached their lowest observed levels during this study. The large number of chironomids collected in Spring Run 3 on

these dates appeared to be related to the amount of red algae contained in those samples. This algae was only collected from Spring Run 3 and is believed to have been the red algae *Batrachospermum* (Beth Davis, pers. comm., 2001), although no samples were retained for positive identification. The fact that chironomids were only collected in large numbers when red algae was present suggests it was a preferred habitat and contributed to their increased abundance in Spring Run 3.

-- *Composition of the Drift*

The insect orders Coleoptera, Ephemeroptera, Trichoptera, and Diptera accounted for 88 % of the invertebrates collected in the drift at Comal Springs. Of these taxa, Ephemeroptera, Trichoptera, and Diptera are commonly among the numerically dominant species in swift-flowing temperate streams (Waters 1972, Brittain and Eikeland 1988, Ward 1992, Allan 1995), while coleopterans generally constitute a small portion of the drift (Cover 1980, Scullion and Sinton 1983, Bowles and Short 1988).

Most of the coleopterans collected in our study were members of the family Elmidae, of which *M. pusillus* was the most abundant (96%). Several studies in the Guadalupe River basin (Cover 1980, Bowles and Short 1988) and elsewhere (Reisen and Prins 1972, Hynes 1975, Allan 1987) have reported low numbers of Elmidae in the drift. However, similar to our findings, Tolley (2000) reported that Elmidae comprised a large component of the drift in the Guadalupe River. Larvae formed a very small percentage of the elmids collected by Tolley

(2000), whereas larval forms comprised a large percentage (87%) of the elmids collected in our study.

Elmidae larvae, many of which were later instars, and exuviae were collected on all sampling dates and pupae were collected on seven of the nine sampling dates in both spring runs. Larval drift in elmids is a mechanism by which poor environmental conditions and overcrowding can be avoided and pupation sites can be located. Brown (1987) suggested that the presence of air sacs only in later instars of elmids was indicative that they function to aid in transport (i.e. drifting) to pupation sites. Most of the elmid larvae collected were later instars, indicating they possessed air sacs, thus it may be that elmid larvae are to some degree drifting as a means of locating pupation sites. Because *M. pusillus* constituted the vast majority of elmids, the aforementioned explanation may only hold true for this species.

The majority of the life stages collected for all taxa in Comal Springs were larval and nymph forms. While the majority of elmid larvae were later instars, larvae of other taxa such as *Baetis* were more commonly earlier instars. Various life stages of aquatic insects have been recorded in the drift at different times of the year; nevertheless, larvae and nymphs often constitute the majority of the drifting invertebrates (Brittain and Eikeland 1988). The size group and life stage most likely to drift varies with species and may indicate different strategies in relation to the function of drift. Several studies have suggested that drift may be a function of the degree to which the carrying capacity of the benthos tends to be exceeded (Waters 1966, Dimond 1967), while other studies showed that drift

increased in relation to periods of rapid growth and subsequent increased activity (Stoneburner and Smock 1979, Kohler 1983). As such, the drift of some taxa may be due to overcrowding or excess productivity within the spring runs, while the drift of other taxa, may be more closely related to pupation or emergence.

In general, as more individuals of a taxa were collected the number of exuviae collected for that taxa increased. *Baetis*, *P. texanus*, *L. sarita*, and *M. pusillus* exuviae were the most commonly encountered. Cloud and Stewart (1974) found that drift of exuviae in the Brazos River, Texas was an accurate indicator of mayfly emergence patterns. The abundance of exuviae observed in Comal Springs may also be the result of emergence or life history patterns. As multiple generations per year are common, especially in thermally constant environments (Ward 1992), the presence of exuviae throughout the year is not unusual. The large number of exuviae collected in the late winter, spring, and fall months may indicate peaks in pupation or emergence, especially among the dominant taxa as these dates roughly correspond to peaks in the number of invertebrates collected. Further research into the life history, benthic densities, and drift rate of the dominant taxa are warranted to illuminate such relationships.

-- *Seasonal Comparisons of Total Drift*

Graphical analysis of our data showed a seasonal pattern in total drift rates in both spring runs where drift rates were generally highest from late winter to early spring and declined from late summer through early winter (Fig. 8). Seasonal patterns or variations in the drift fluctuate with changes in life stage, growth rate, population density, and physical attributes of the stream (Bishop and

Hynes 1969, Elliot 1968, Waters 1972). The vast majority of studies investigating drift rate and its relation to biotic and abiotic factors have been done in temperate streams, thus drift rates are usually reported to be lowest during the cold winter months (Waters 1962, 1966, Clifford 1972), with increases in numbers through the spring and summer months (Waters, 1962, 1966, Pearson and Franklin 1968, Bishop and Hynes 1969). Studies of drift rates and patterns in other regions of the world have found different seasonal patterns than those found in temperate areas. Similar to our results, drift in a subtropical Florida stream was greatest from winter to spring and lowest in the summer (Cowell and Carew 1976). The differences in environmental conditions (i.e. water temperature, photoperiod, allochthonous input, etc.) between northern and southern streams that led to different life history patterns were implicated for the differences in seasonal drift patterns. Temperature does not explain the seasonal pattern observed in Comal Springs because of the thermal stability. Thus, the presence of a similar seasonal pattern in drift between the two subtropical streams suggests that life history patterns related to the photoperiod associated with subtropical regions may be a factor (Sweeney 1984). Studies of life history characteristics, especially emergence patterns, for the dominant taxa in Comal Springs would aid in the corroboration of this hypothesis.

To our knowledge no seasonal drift studies have been performed in subtropical spring systems, so the seasonal patterns and variations observed in this study may be the first report of its kind. Total drift rates in each spring run were negatively correlated with Julian day (Spring Run 1, $R=-0.79$; Spring Run 3,

$R=-0.62$), indicating that drift rates in each spring run declined as the year progressed. The relationship between drift rate and Julian day was significant ($p=0.01$) in Spring Run 1 and almost significant ($p=0.07$) in Spring Run 3. It is possible that the seasonal drift pattern we observed is attributable to the coarse temporal sampling schedule of roughly 3 months between collecting. A smaller, more frequent sampling interval would have provided a more definitive characterization of drift patterns, but the nine sampling dates over the 21 months of this study at least reveals broad seasonal patterns in drift. A study with more frequent sampling intervals would better clarify the seasonal patterns.

-- Diel Patterns of Total Drift

Drift rates in both spring runs were generally greater (2x) by night than by day, indicating behavioral drift, and Spring Run 1 exhibited a distinct crepuscular peak associated with sunset on five of the sampling dates. In contrast to Spring Run 1, Spring Run 3 lacked marked crepuscular peaks and drift rate tended to peak in the middle of the night or close to sunrise. The majority of drift studies have reported increased drift rates at night (Waters 1962, Elliot 1967, Reisen and Prins 1972, Cowell and Carew 1976, Bowles and Short 1988, Brittain and Eikeland 1988). There are two primary explanations for increased drift at night, these are; 1) predator avoidance (Chaston 1969, Kroger 1974) and 2) increased activity levels by invertebrates due to endogenous rhythms associated with changes in light intensity (Waters 1962, Elliot 1968, Bishop 1969).

It is unlikely that the avoidance of predation is a factor affecting the daily drift of invertebrates in Comal Springs. The avoidance of predation has been

implicated as a cause of increased nocturnal drift by many authors (Allan 1978, Skinner 1985, Flecker 1992). Flecker (1992) studied a high Andean stream where drift-feeding fish do not occur and a foothill stream where drift-feeding fish are abundant to assess the presence/absence of a predator on diel drift patterns. Diel drift was aperiodic in the high Andean stream lacking drift-feeding fish, while the stream with trout displayed nocturnal increases. The only fish observed in the spring runs at Comal Springs were *Etheostoma fonticola* (fountain darter), *Gambusia affinis* (western mosquitofish) and one madtom species, which was collected from Spring Run 1. It seems unlikely that predation by these fishes is heavy enough to induce the diel changes in drift observed, as other studies have all implicated larger, drift-feeding fish as important predators. As such, endogenous rhythms related to changes in light intensity are a more likely cause of increased nocturnal drift in Comal Springs.

Various aspects of the behavioral responses of aquatic insects to changes in light factors have been studied. Bishop (1969) found that artificially induced light patterns altered endogenous activity rhythms. Several other studies show that light intensity, rather than wavelength, is the most critical factor responsible for daily activity patterns (Bishop 1969). Waters (1972) found artificially darkening and illuminating a section of natural stream virtually switched on and off a large portion of the drift. A major environmental difference between the two spring runs is difference in light intensity. The lower, denser overhanging vegetation combined with the shading escarpment that runs along the northwest edge of Spring Run 3, mutes diurnal changes in light intensity. The presence of

a diel drift pattern with crepuscular peaks in Spring Run 1 indicates changes in drift in relation to changes in light intensity, while the lack of such crepuscular peaks in Spring Run 3 suggests that drift is not as strongly affected by changes in light intensity. It is likely that the difference in changes in light intensity between the spring runs affects the activity and drift patterns of the invertebrate community, resulting in different diel patterns and crepuscular peaks between the spring runs.

-- *Drift of Selected Taxa*

Baetis sp.- *Baetis* displayed a similar seasonal pattern in both spring runs, although abundances were much greater in Spring Run 1. Drift rates were highest in February 2002 in both spring runs and *Baetis* displayed the highest 24-hour drift rate observed for any taxa in Spring Run 1 over the course of the study on this date. Interestingly, 63% of the seasonal variability in *Baetis* drift rates in both spring runs was explained by Julian day, indicating that season has a large effect on *Baetis* drift rates. This supports the findings of Pearson and Franklin (1968) who also reported that Julian day accounted for a significant amount of the variability in drift rates of *Baetis*. Thus, seasonal drift rates of *Baetis* likely influenced seasonal patterns of total drift in Spring Run 1 and had little influence on seasonal drift in Spring Run 3 because *Baetis* was more dominant in Spring Run 1.

Our study showed that *Baetis* drifted in higher numbers at night than by day in both spring runs, thus suggesting behavioral drift. Diel patterns for *Baetis* varied greatly between spring runs and marked crepuscular peaks were apparent

in Spring Run 1 and were absent in Spring Run 3. Results from studies on the causes of increased nocturnal drift among *Baetis* spp. vary and include accidental dislodgement during increased activity levels associated with changes in light intensity (Ploskey and Brown 1980, Waters 1962, Pearson and Franklin 1968), the avoidance of predation (Kroger 1974), and the search for more suitable habitat (Corkum et al 1978, Allan et al. 1986). The search for more suitable habitat seems an unlikely cause for increased nocturnal drift in Comal Springs because of the chemical and physical stability of the spring system. As mentioned previously in relation to total drift, the general lack of fish predators in the spring runs makes the avoidance of predation an unlikely cause of increased nocturnal drift for *Baetis*.

Changes in light intensity appear to be the proximate cause of increased nocturnal drift rates in both spring runs and the crepuscular peaks associated with sunset in Spring Run 1. Similar to our results, Waters (1962) reported a diel pattern for *Baetis vagans* with marked crepuscular peaks about 1 hour after sunset that decreased during the night and then fell sharply at about sunrise and implicated changing light conditions as a possible mechanism for the observed pattern. The same diel drift pattern occurred for *Baetis intercalaris* in a subtropical Florida stream, although no mechanism was inferred (Cowell and Carew 1976). Increased nocturnal drift rates for *Baetis* in both springs runs is likely due to the photoperiod experienced and changes in light intensity between night and day. The marked differences in shading between the spring runs likely explains the differences in the magnitude of change between day and night drift

rates and the presence of crepuscular peaks in Spring Run 1 and lack of such in Spring Run 3.

Leucotrichia sarita- The family Hydroptilidae, also known as microcaddisflies, comprised the majority of the Trichopterans collected from both spring runs, as has been observed in studies across the world where hydroptilids have been collected (Flint, 1970). *Leucotrichia sarita* constituted the majority of the hydroptilids collected in this study in both spring runs. McAuliffe (1982) showed that over 75% of *Leucotrichia pictipes* in a Montana stream occupied abandoned pupal retreats. Most *L. sarita* collected had the extreme lateral distention of abdominal segments, which indicates larvae were later instars and were possibly drifting as a result of searching for an abandoned pupal retreat (Wiggins 1996). Passive entry into the drift cannot be discounted though, as McAuliffe (1982) also noted that larvae of *L. pictipes* lived on the upper surfaces of rocks and grazed on surrounding periphyton and other matter by extending the anterior portion of the body from its retreat. Therefore, it is possible that *L. sarita* were accidentally swept downstream while feeding.

In general, *L. sarita* displayed an increased propensity to drift during the day as compared to night, and this relationship was more frequent in Spring Run 3. Fjellheim (1980) reported changes in the major diel drift pattern for a trichopteran during their life cycle, whereby young stages were more nocturnal in their drift pattern than later stages. The developmental stage of larvae is an unlikely cause for the difference in drift rate between spring runs observed in this study, as the majority of instars collected in both spring runs were late instars.

Differences in drift patterns between spring runs could be attributable to shifts in dominance throughout the year and the low numbers of *L. sarita* collected in September and November of 2000 and 2001, as these dates appear to have produced some of the more unusual diel patterns. However, increased shade in Spring Run 3 may also be the proximate cause of the contrasting diel patterns displayed by *L. sarita* between spring runs.

Psephenus texanus- In this study, *P. texanus* drift rates in Spring Run 3 were greatest in the spring of 2001 and 2002 and were greatest in Spring Run 1 on 14 September 2000 and in spring 2001. Mature Psephenidae larvae crawl to moist niches above the edge of the water line to pupate. Bosse (1979) reported that *P. texanus* pupation in Comal Springs takes 10-12 days and that adults emerged in March. Thus, the peaks in seasonal drift during the spring are likely due to increased activity levels associated with seeking pupation sites.

Nocturnal increases in drift of *P. texanus* were displayed on several dates in Spring Run 1, but were not observed on a consistent basis. The most consistent pattern observed in Spring Run 1 was a peak in drift shortly after midnight observed on two-thirds of the sampling dates. A similar peak associated with the sampling intervals around midnight was observed in Spring Run 3 on seven of nine sampling dates. The observed similarities in diel patterns between spring runs despite differences in seasonal patterns may indicate that the daily patterns of drift in *P. texanus* are more affected by behavioral characteristics (i.e. increased activity at night) than changes in light intensity and photoperiod.

Procambarus sp.- Drift rates were generally low in both spring runs, with the exception of three sampling dates in Spring Run 1, when a large number of juvenile crayfish were collected during one three-hour sampling period.

Members of the Cambaridae family often migrate into lotic habitats from lentic habitats to search for spawning sites (Hobbs 1991). As juvenile crayfish grow larger, they abandon riffle areas (Spring Run 1) and move to deeper waters (i.e. Landa Lake) in search of the best food and shelter available (Hobbs 1991). The well-developed macrophyte community and associated fine sediments in Spring Run 1 likely provide an ideal habitat for burrowing to brood eggs and also offers juveniles abundant shelter and a relatively predator-free foraging habitat. An overwhelming majority of the *Procambarus* collected were juveniles, thus it is likely that the spring runs are used as a spawning site. The large quantities of *Procambarus* collected in August and September of 2000 and May of 2002 is also consistent with the Spring and Fall spawns reported by Hobbs (1991). The low numbers of *Procambarus* reported in Spring Run 1 on other dates are likely the result of declines in reproduction or sampling error.

Diel drift patterns of *Procambarus* further support the hypothesis that the spring runs are used as spawning grounds. Marked crepuscular peaks associated with sunset were observed in Spring Run 1 in August and September 2000 and again in May 2002. On all three sampling dates few *Procambarus* were collected for the rest of the sampling period, indicating that changes in light intensity triggered the drift of these crayfish. The lack of such a pattern in Spring

Run 3 is likely either due to differences in light intensity or habitat characteristics between the two spring runs.

Chironomidae- Anderson and Lemkuhl (1967) and Brooker and Hemsworth (1978) found that Chironomidae drift greatly increased in response to freshets. Anderson and Lemkuhl (1967) suggested this was an example of catastrophic drift as defined by Waters (1965b), whereby the Chironomidae drifted in greater numbers in response to the downstream flushing of leaf debris with which the chironomids were associated. Similarly, the drift of Chironomidae during low flows in Fall 2000 could be categorized as catastrophic as defined by Waters (1965b) because the presence of the Chironomidae in the drift resulted from the dislodgement of the red algae with which they were associated.

Unfortunately, the proposed catastrophic drift from this study occurred on the first two sampling dates, so the habitat conditions and drift behavior prior to this in the presence of red algae are not known. Also, a major flood occurred in the Guadalupe River Basin in early November, which may also have caused the removal of the red algae from the system, although a much larger flood occurred 3 years previously and apparently did not impact the red algae. The impact of the loss of red algae from the system to the Chironomidae population in Spring Run 3 cannot be assessed from this study and would be difficult to study further as the red algae is greatly reduced in abundance or no longer appears to be present.

The drift of Chironomidae in both spring runs displayed no seasonal pattern and several different diel patterns within each spring run. This is similar

to the finding of Bowles and Short (1988), who found that Chironomidae drift in a small spring-fed stream (also within the Guadalupe River Basin) showed considerable variation among sampling dates. They also reported Chironomidae displayed a less pronounced periodicity than other dominant taxa examined, which is also consistent with this study. Chironomids are often reported as a major component of the drift (Hynes 1975, Scullion and Sinton 1983, Bowles and Short 1988) and numerous studies have reported aperiodic drift behavior (Anderson and Lemkuhl 1967, Brooker and Hemsworth 1978, Allan 1995), which may indicate that a positive phototactic response exists among Chironomidae.

-- *Elmidae in the Drift*

Unlike adults of *H. comalensis* and *M. pusillus*, adult *P. clavicornis* are terrestrial and only enter the water accidentally or when ovipositing (Brown 1972). The 13 adults collected in Spring Run 3 in May 2001 accounted for the majority (65%) of adult *P. clavicornis* and may be indicative of an active period of oviposition. Bosse (1979) reported finding *P. clavicornis* in the San Marcos River, but did not find any in Comal Springs. *Phanocerus clavicornis* has also been reported from the Devil's River and San Felipe Creek in Del Rio (Burke 1963, Brown 1972) and to our knowledge this is the first account of *P. clavicornis* in Comal Springs.

Adults of *H. comalensis* were not collected in either spring run in August 2000, September 2001, and November 2001 and were also not collected from Spring Run 1 in February 2002. Similarly, Bosse (1979) reported not collecting adult *H. comalensis* in August and September, but also reported their absence in

June, December, and January and suggested this may indicate a normal cycle within the population. Because of the differences in sampling schedule and sampling technique, it is difficult to correlate the results of the two studies. For example, Bosse (1979) sampled each station with a hand-held net, dislodging specimens from the substrate and examining submerged rocks and wood, specifically targeting adult elmids, while drift sampling was employed in this study. Additionally, the sampling schedule and sampling interval used was different between the two studies and Bosse (1979) collected all specimens of *H. comalensis* from Spring Run 2, which was dropped from analysis in this study because current velocities proved insufficient for drift sampling. However, given the endangered status of *H. comalensis* and the similarity in findings between the two studies in regards to the absence of adults, more research on life history patterns is warranted.

-- *Seasonal Drift of Elmidae*

No distinct seasonal pattern was apparent for Elmidae at the family or species level of resolution. There are several explanations for the lack of a seasonal drift pattern among Elmidae taxa; 1) the frequency of sampling, 2) the presence of a multivoltine life cycle, and 3) the low overall number of specimens collected. Sampling occurred at roughly 3-month intervals, thus gaps exist in the data acquired. A more frequent sampling schedule would provide a better characterization of seasonal drift patterns, additionally, it would aid in assessing life cycle patterns for individual taxa, including the Elmidae.

Life cycle characteristics of Elmidae may also explain the lack of a distinct seasonal pattern. The large number of Elmidae larvae and exuviae collected throughout the year coupled with the presence of pupae on most sampling dates suggests a multivoltine life cycle. The number of instars (5-8) and duration of larval stage (6-36 months) is affected by temperature, as well as body size and food availability (Brown 1987). Development is generally faster at higher temperatures and in species with smaller body sizes as these tend to exhibit fewer larval instars than larger species (Brown 1972). The relatively small body size of *M. pusillus* in relation to other Elmidae suggests that development may be faster for this species. The constant thermal regime of Comal Springs and subsequent winter-warm habitat combined with a faster developmental rate would likely be conducive to a multivoltine life cycle for *M. pusillus*.

A multivoltine life cycle would explain the presence of later instars throughout the year and would likely affect seasonal drift patterns for *M. pusillus*. However, the lack of a seasonal pattern may also be due to an extended period of reproduction whereby pupation occurs throughout the year. Brown (1987) reported Elmidae pupation occurs throughout the year in tropical regions with no pronounced dry season, while pupation commonly occurs from late spring through summer in temperate areas. Either an extended reproduction period or a multivoltine life cycle would explain the lack of a distinct seasonal pattern for *M. pusillus*, however, more detailed research on its life history characteristics is required. It is difficult to associate life history characteristics with seasonal drift

patterns of *H. comalensis* and *P. clavicornis* because of the relatively low numbers collected.

-- Relationship of Drift to Flow Rate

Drift rate, the number of individuals drifting past a point within a given time interval, and drift density, the number of individuals collected per volume of water (generally 100 m³), are the two most commonly reported quantitative values for drift. Elliot (1970) suggested drift density may be more useful for comparisons between streams, while drift rate is preferable if the objective is to study losses from the benthic population and is often dependent upon variation in discharge. Since discharge is related primarily to water depth and current velocity, these two variables were included in the multiple regression and correlation analysis and drift rate was used to assess the effects of variations in current velocity, water depth, and Julian day on invertebrate drift in each spring run and drift density was used to make comparisons between the spring runs.

-- Drift Rate in Relation to Variable Flows

Multiple regression analysis showed that current velocity was not significantly correlated with total drift rate in either spring run, however, correlation analysis showed significant ($p < 0.05$) relationships between current velocity and the drift rate of several individual taxa in both spring runs (Table 8). Drift theoretically is a function of factors such as density and current velocity, but because of different modes of existence, behavioral patterns, life history characteristics, and morphological adaptations, different insects have different drift potentials (Brittain and Eikeland 1988, Rader 1997). The lack of a significant

relationship between total drift and current velocity in both spring runs likely reflects the influence of other factors, such as season (*Baetis*) and life history characteristics (*M. pusillus*) on the drift of dominant taxa.

The relationships between the drift rates of individual taxa and current velocity were generally negative in Spring Run 1 and positive in Spring Run 3, indicating that habitat differences in the spring runs may cause different responses to variable flows. The drift rate of three invertebrates in Spring Run 1, the odonate *Perithemis* sp., the caddisfly *Helicopsyche* sp., and the crayfish *Procambarus*, showed a significant negative relationship to both current velocity and water depth. Studies show reductions in discharge and current velocity cause an increase in drift rate (Minshall and Winger 1968, Pearson and Franklin 1968, Radford and Hartland-Rowe 1971, Armitage 1977, Hemsworth and Brooker 1981, Corrarino and Brusven 1983), as did we. Most of these studies have attributed increased drift rates to factors related to water depth, such as the dewatering of habitat and/or the reduction of available habitat resulting in overcrowding.

Drift is commonly used as a dispersal mechanism to avoid unfavorable conditions (Ciborowski et al. 1977, Corkum and Pointing 1979), however, the conditions that induce drift vary according to requirements of the organism. Elliot (1967) implicated reductions in current velocity as causing a reversal of the positive thigmotaxis of stream invertebrates and inducing swimming. This may explain the relationship of current velocity and water depth to drift rate of the sprawler *Perithemis*, as swimming may be induced when current velocity

decreases. Additionally, Merritt and Cummins (1996) classify *Perithemis* as a sprawler that commonly inhabits floating macrophytes and fine sediments. Assuming *Perithemis* in Comal Springs has the same mode of existence as described by Merritt and Cummins (1996), it is likely that drift is induced during low flows as the result of loss of suitable habitat. A similar argument can be made for the caddisfly *Helicopsyche* and the crayfish *Procambarus*.

The strong negative relationships of current velocity and water depth to the drift rate of *Helicopsyche* are likely due to changes in flow dynamics at the water-substrate interface. As current velocities change, flow is altered at the water-substrate interface (Newbury 1996). Minshall and Winger (1968) suggested that drift of invertebrates in response to decreased current velocities was initiated by respiratory stress as a result of altered relationships at the water-substrate interface that interrupt diffusion gradients surrounding organisms. Assuming diffusion gradients surrounding organisms are negatively affected by reductions in stream flow in Comal Springs, invertebrates requiring well-oxygenated waters, such as *Helicopsyche*, would likely be induced to search for more suitable habitat. Whether entry into the drift is active or the result of dislodgement while searching for more suitable habitat is not known. As Allan (1995) points out, there is a need for better understanding of the hydrodynamic conditions that organisms experience as techniques currently used are inadequate. While the effect of reduced current velocities on processes at the water-substrate interface is unclear, the dewatering of habitat certainly has a marked effect on the suitability of habitat.

While the near dewatering of habitat in Spring Run 1 during periods of low flow likely induced organisms to drift, a similar relationship was not apparent in Spring Run 3. In contrast to Spring Run 1, significant ($p < 0.05$) positive relationships between current velocity and drift rate were present for five taxa in Spring Run 3 and only one taxa (*Atopsyche* sp.) showed a significant ($p = 0.05$) relationship to water depth. These taxa included two riffle beetles (*H. comalensis* and *P. texanus*), a caddisfly (*Atopsyche* sp.), a lepidopteran (*Petrophila* sp.), and a cave-dwelling amphipod (*Stygobromus* sp.). Many studies have reported that increased discharge or current velocity leads to increased drift under flood conditions (Elliot 1967, Anderson and Lemkuhl 1968, Crisp and Robson 1979, Bird and Hynes 1981, Scullion and Sinton 1983). When current velocities increase the scouring effect on the benthos also increases (Newbury 1996); thus increasing the number of invertebrates drifting, generally through dislodgement (Bird and Hynes 1981, Brittain and Eikeland 1988). With the exception of *Stygobromus* sp., all of the invertebrates showing a significant relationship to current velocity in Spring Run 1 are classified as clingers, meaning they have behavioral (i.e. fixed retreats) or morphological (i.e. long, curved tarsal claws, ventral gills arranged as suckers) adaptations for attachment to surfaces in swift-flowing waters (Merritt and Cummins 1996). The morphological and behavioral differences among taxonomic divisions greatly affect the amount of shear stress required to induce drift by accidental dislodgement (Brittain and Eikeland 1988). The feeding characteristics associated with several of the taxa may explain their vulnerability to dislodgement under higher current velocities. The riffle beetles *H.*

comalensis and *P. texanus* and the lepidopteran *Petrophila* are characterized as scrapers (Merritt and Cummins 1996) that graze on the tops of stones, thus their feeding activities make them more susceptible to being dislodged during increased current velocities. Similarly, *Atopsyche* is reported as a free-ranging predator that may also be more susceptible to accidental dislodgement while searching for prey on the tops of stones.

The increased drift of the cave-dwelling *Stygobromus* sp. in response to increased current velocities may be the result of more water forcing its way through the spring openings, which in turn results in the dislodgement of more amphipods. No other studies on the downstream drift of cave-dwelling invertebrates were discovered, so causes for the displacement of *Stygobromus* sp. are not known.

-- *Drift Density in Relation to Variable Flows*

In this study, drift densities in Spring Run 1 ranged from 9 to 73 per 100 m³ and from 13 to 56 per 100 m³ in Spring Run 3. Reported estimates of drift densities for other streams are commonly between 10 and 500 per 100 m³ during normal flow conditions (Armitage 1977, Allan 1987). Drift density is reported to be more useful as a comparison of stream size than drift rate (Waters 1972), thus the low drift densities reported from the spring runs at Comal Springs in relation to other studies is likely due to their relatively smaller size.

The highest drift density in each spring run occurred on 14 September 2000, during the lowest recorded flows, suggesting that reductions in current velocity and subsequent decreases in water depth may result in an increase in

the density of drifting organisms. Drift density estimates during periods of floods are generally much greater than during normal flow conditions (Allan 1995, Brittain and Eikeland 1988). Pearson and Franklin (1968) estimated individual densities for the mayfly *Baetis* during spates as high as 17,260 per 100 m³. In contrast, other studies (Minshall and Winger 1968) show that drift density greatly increases for some taxa during periods of decreased flows. Most of the increase in drift density in each spring run in September 2000 is explained by increases in the abundance of a few taxa, the most pronounced of which was Chironomidae in Spring Run 3.

Multiple regression analysis showed the relationship of current velocity to drift density was different between the spring runs, much like the relationship to drift rate. In Spring Run 1, current velocity showed a significant relationship ($p=0.03$) to total drift density, while no significant ($p<0.5$) relationship was found in Spring Run 3. The same taxa in Spring Run 3 showing a significant relationship between drift rate and current velocity also showed a significant relationship between drift density and current velocity (Tables 8 and 9). The same was not true in Spring Run 1 as twice as many taxa showed a significant relationship between current velocity and drift density as did between drift rate and current velocity. Interestingly, none of the taxa in Spring Run 3 showed a significant relationship to water depth, while several taxa in Spring Run 1 showed significant relationships between water depth and both drift rate and drift density.

The strong relationships between drift (rate and density) and water depth in Spring Run 1 and lack of such a relationship in Spring Run 3 indicates that

fluctuations in current velocity may have a larger impact on water depth in Spring Run 1 than in Spring Run 3. The increased affect of current velocity on water depth in Spring Run 1 in relation to Spring Run 3 is further supported by the significant ($p=0.04$) relationship between current velocity and water depth in Spring Run 1. The physical conditions of the stream (i.e. substrate, width, depth, presence or absence of macrophytes, etc...) influence the degree of change to habitats within the system in relation to changes in flow conditions (Ward 1992). Because the spring runs in Comal Springs have been channelized, changes in current/discharge do not appreciably change the width of the stream but do alter the depth and subsequently alter current velocities at the water substrate interface and within macrophytes. It appears as though changes in water depth have a greater affect on drift in Spring Run 1, with a general trend toward increased drift at lower water levels.

-- Assessment of Low Flows

Assessing the effects of low flow events on invertebrate drift is difficult considering that flows were low only on the first two sampling dates and were high for all subsequent sampling dates. A major drought was taking place in Central Texas during the first two sampling dates in the late summer/early fall of 2000. As a result, discharge for the Comal River was well below the monthly annual mean in August (259 fcs) and September (277 cfs), with daily mean flows of 167 cfs and 154 cfs on 28 August 2000 and 14 September 2000, respectively (USGS 2002). Drift rate was relatively low on 28 August 2000 and greatly increased on 14 September 2000, most pronounced in Spring Run 3.

Differences in habitat and flow patterns as a result of changes in water depth were noted in Spring Run 1 between these first two sampling dates. On 28 August 2000, macrophytes upstream of the sampling site were partially exposed although water still flowed across the entire channel. Two weeks later after a 2.0 cm decrease in water depth, many of the stands of macrophytes were further exposed and flow was primarily confined to channels with gravel/cobble substrate. Similar changes in habitat and flow patterns were not observed in Spring Run 3. However, a slightly larger decrease (2.5 cm) in water depth and a larger increase in drift rate was observed in Spring Run 3 than in Spring Run 1 between 28 August 2000 and 14 September 2000. Similar changes in habitat in Spring Run 1 were not observed for the remainder of the study.

A major flood occurred before our third sampling date in November 2000 and flows on subsequent sampling dates were all above the reported daily mean of 8.0 cms (284 cfs) for Comal Springs. The lack of low flows for the remainder of the study makes assessing low flow conditions difficult. The observation of changes in habitat and the general inverse relationship of current velocity and water depth to the drift of several taxa in Spring Run 1 suggest that low flow conditions have a marked affect on invertebrate drift in Spring Run 1. Similarly, the fact that drift rates in September 2000 were 54% greater in Spring Run 1 and 265% greater in Spring Run 3 (despite a general trend among taxa toward positive relationships to current velocity in Spring Run 3) than in September 2001 indicates that low flows may cause an increase in invertebrate drift. Pearson and Franklin (1968) noted that artificial reduction in current velocity affected virtually

all benthic forms in a large river and the catastrophic drift of organisms in response to reduced stream discharge has been implicated in many studies (Anderson and Lemkuhl 1968, Minshall and Winger 1968, Pearson and Franklin 1968, Corrarino and Brusven 1983). Studies on regulated rivers (Radford and Hartland-Rowe 1971, Corrarino and Brusven 1983) have shown that the frequency of changes in flow can also affect drift. Irvine (1985) and Perry and Perry (1986) show that changes in flow after a long period of stability had a greater effect on the number of drifting invertebrates than did frequent fluctuations in flow. Thus, decreases in flow at Comal Springs, which historically has not happened in an abrupt or sudden manner because of the dependability of the spring system, are likely to cause an increase in the number of drifting invertebrates. To the degree that this applies to all of the fauna, being below take/jeopardy levels could cause an increased propensity to drift and have a marked effect on the *H. comalensis* population, especially in Spring Run 1 as *H. comalensis* showed a significant negative relationship to water depth. More data on invertebrate drift during low flows are needed to determine if reductions in stream flow have a marked effect on the benthic community in Comal Springs.

-- Indicator Insects

Because of the size of the spring runs and the fact that they are home to several endangered species, traditional benthic sampling to determine instream flows (Bovee et al 1978) would have a marked disturbance on habitat. Thus, our objective was to determine if sampling the drift community could be used to determine instream flow needs. Gore (1978) commented that the results of

studies examining the relationship between current velocity and/or depth in relation to the biology of an organism is difficult to translate into hydrologic terms, thus making the prediction of optimum streamflow requirements for the benthic community as a whole difficult. The concept of indicator species for instream flow evaluations is based on the fact that some organisms have a narrower range of tolerances than others to changes in flow.

Many of the taxa in Comal Springs are noted as indicators of good water quality and are known to require swift-flowing water, while drift is known to be a common dispersal mechanism to avoid unfavorable conditions and recolonize new areas (Minshall and Winger 1968, Townsend and Hildrew 1976, Williams and Hynes 1976). Because studies (Minshall and Winger 1968, Pearson and Franklin 1968, Radford and Hartland-Rowe 1971) show a strong connection between the drift community structure and the benthic community structure, we assumed changes in the drift community in relation to changes in flow reflect changes in the benthic community. By investigating the response of the invertebrate community to changes in current velocity and water depth, we hoped to identify those organisms most likely to be indicators of changing flow conditions in Comal Springs according to the following criteria:

- 1) should be widely distributed within the riffle-spring runs,
- 2) occur in large enough numbers that significant changes in their abundance due to changes in current velocity and/or water depth are detectable,
- 3) be present through much of the year, and

- 4) published literature describing life history characteristics and biological requirements of candidate insects are available.

In Spring Run 1, the drift rate and density of *Perithemis*, *Helicopsyche*, and *Procambarus* showed strong relationships to current velocity and water depth and were not significantly influenced by Julian day (Tables 8 and 9). This suggests that drift of these taxa is not as influenced by season as it is by flow regime. Abundance varied greatly among the three taxa, although all taxa are assumed to be widely distributed within the spring runs. *Procambarus* was the most abundant of the three taxa and was present on all but one sampling date, while *Helicopsyche* was second in abundance and was present on all sampling dates. The odonate *Perithemis* was the least abundant and was absent on the three sampling dates with the highest recorded flows in Spring Run 1. Analysis of life history characteristics showed *Procambarus* is likely a poor choice as an indicator species because of life cycle and behavior, thus *Perithemis* and *Helicopsyche* are proposed as indicators of hydrologic change in Spring Run 1 because the drift rate and drift density of these taxa showed significant negative relationships to current velocity and water depth in Spring Run 1. Additionally, the drift rate for both taxa showed a significant negative relationship to discharge of the Comal River (Table 8).

In Spring Run 3, the drift rate and density of *Stygobromus*, *H. comalensis*, *Petrophila*, *P. texanus*, and *Atopsyche* all displayed significant relationships to current velocity. *Atopsyche* was the only taxa whose drift rate was significantly affected by water depth, however, absence on three sampling dates combined

with the overall low numbers collected makes *Atopsyche* a poor choice as an indicator species. Although *Stygobromus* and *H. comalensis* were less abundant in the drift than *Petrophila* and *P. texanus*, significant changes in their drift rate and density due to changes in current velocity were detected, thus these four taxa appear to be good indicators of hydrologic change in Spring Run 3.

SUMMARY AND CONCLUSIONS

Drift sampling was used to assess the taxonomic composition of the invertebrate community in the spring runs of Comal Springs, as well as the drift rates, densities, and patterns of selected invertebrates, and the affects of changes in season, water depth, and current velocity on the abundance of drifting invertebrates, especially Elmidae. By investigating the response of the invertebrate community to changes in current velocity and water depth, we hoped to identify organisms that can be used as indicators of changing flow conditions in Comal Springs.

The composition, abundance, and diel patterns of drifting invertebrates were different between spring runs and the drift rate of individual taxa in relation to changes in flow regime also differed between spring runs. The taxonomic richness of invertebrates collected in Spring Run 1 (55 taxa) was greater than that of Spring Run 3 (44 taxa) and is likely due to differences in habitat complexity between the spring runs. Spring Run 1 has a well-developed macrophyte community and associated fine sediments, while Spring Run 3 is generally lacking macrophytes. Thus, the diverse macrophyte community in Spring Run 1 and resultant increased habitat complexity supports a greater number of invertebrates in relation to Spring Run 3 due to the greater number of available niches. Similarly, differences in the dominant taxa between spring runs can also be explained by differences in habitat complexity between spring runs. The dominant taxa in Spring Run 1 included taxa (*Baetis*, *Tricorythodes*, *Procambarus*) that are commonly associated with macrophytes and fine

sediments, while Spring Run 3 was dominated by taxa (*L. sarita*, *P. texanus*, *M. pusillus*) commonly associated with open cobble substrate.

Seasonal patterns in drift were similar between the spring runs, while diel patterns differed between the spring runs. Drift rates in our study, with the exception of September 2000, were greatest from winter to spring and lowest in the summer. A similar pattern in seasonal drift was reported in a subtropical Florida stream lacking in springs (Cowell and Carew 1976), thus life history characteristics related to the photoperiod associated with subtropical regions might explain the similarity in seasonal patterns. Analysis of seasonal drift patterns for selected taxa (*M. pusillus*, *L. sarita*, *Procambarus*, *P. texanus*, *Baetis*) further supported the effect of life history characteristics on the seasonal drift pattern of some taxa.

Drift rates in both spring runs were generally greater (2x) by night than by day, although Spring Run 1 exhibited distinct crepuscular peaks and Spring Run 3 did not. Muted changes in light intensity due to increased shading in Spring Run 3 as compared to Spring Run 1 were implicated as the proximate cause for the lack of crepuscular peaks in Spring Run 3. The diel drift patterns for several individual taxa (*Baetis*, *Procambarus*, *L. sarita*) further supported the effect of muted changes in light intensity on diel drift patterns, while the daily drift patterns of other taxa (Chironomidae, *P. texanus*) were not effected by changes in light intensity.

Although total drift in both spring runs showed no significant relationship to current velocity, the drift rate of several taxa were significantly related to current

velocity. The relationships between the drift rates of individual taxa and current velocity were generally negative in Spring Run 1 and positive in Spring Run 3, indicating that habitat differences in the spring runs may cause different responses to variable flows. Changes in current velocity had a greater effect on water depth in Spring Run 1 than in Spring Run 3 and the drift rate of taxa in Spring Run 1 that showed a significant negative relationship to current velocity also showed significant negative relationships to water depth. In contrast, the drift rate of taxa in Spring Run 3 that showed significant positive relationships to current velocity were not significantly related to water depth. Interestingly, Spring Run 3 showed a much larger increase in drift rate than Spring Run 1 in September 2000, during the period of lowest observed flows, as compared to September 2001.

Because low flows occurred on the first two sampling dates and flows were relatively high for the remainder of the study, it is difficult to assess the effects of low flows on the invertebrate community. However, the negative relationships between the drift rate of several taxa to current velocity and water depth in Spring Run 1 and the abundance of invertebrates in the drift in Spring Run 3 in September 2000 suggests that reductions in flow regime cause an increase in the drift of certain taxa. The extent to which reductions in flow would affect the invertebrate community, especially the *H. comalensis* population, is not clear. Thus, more research on the drift community during periods of low flows is necessary.

The following *a priori* criteria were used to select candidate invertebrates

for further study as indicator flow species for Comal Springs: 1) should be widely distributed within the riffle-spring runs, 2) occur in large enough numbers that significant changes in their abundance due to changes in current velocity and/or water depth are detectable, 3) be present through much of the year, and 4) published literature describing life history characteristics and biological requirements of candidate insects are available. Based on these criteria, two taxa (*Perithemis* and *Helicopsyche*) in Spring Run 1 and four taxa (*P. texanus*, *Petrophila*, *Stygobromus*, and *H. comalensis*) in Spring Run 3 were proposed as indicators of hydrologic change in Comal Springs.

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Table 1. Current velocity, water depth, discharge, drift rate, and drift density for spring run 1 for all sampling dates.

Date	Mean current velocity (m/s)	Mean depth (m)	Discharge (cms)	Drift rate (#/24 hr)	Drift density (#/100 m ³)
28 August 2000	0.44	0.15	4.7	899	36.7
14 September 2000	0.39	0.13	4.4	1418	72.9
21 November 2000	0.79	0.30	9.6	779	8.6
20 March 2001	0.69	0.35	10.1	2071	22.3
23 May 2001	0.53	0.39	10.4	1806	22.6
12 September 2001	0.66	0.33	9.3	918	10.8
5 November 2001	0.71	0.33	9.6	835	9.4
19 February 2002	0.69	0.36	11.0	1623	16.9
20 May 2002	0.52	0.32	9.0	1165	18.5
Overall Mean	0.6	0.29	8.7	1279	24.3
Standard Deviation	± 0.13	± 0.09	± 2.3	± 444	± 19.0

Table 2. Current velocity, water depth, discharge, drift rate, and drift density for spring run 3 for all sampling dates.

Date	Mean current velocity (m/s)	Mean depth (m)	Discharge (cms)	Drift rate (#/24 hr)	Drift density (#/100 m ³)
28 August 2000	0.37	0.27	4.7	799	20.5
14 September 2000	0.30	0.26	4.4	1633	55.8
21 November 2000	0.53	0.29	9.6	785	13.4
20 March 2001	0.49	0.31	10.1	1503	38.8
23 May 2001	0.46	0.36	10.4	1540	36.8
12 September 2001	0.39	0.32	9.3	448	13.9
5 November 2001	0.26	0.27	9.6	400	14.4
19 February 2002	0.47	0.28	11.0	1403	25.9
20 May 2002	0.44	0.27	9.0	1294	26.6
Overall Mean	0.41	0.29	8.7	1089	27.3
Standard Deviation	± 0.08	± 0.03	± 2.3	± 484	± 14.2

Table 3. Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 1 on 28 August 2000, 14 September 2000, 21 November 2000, 20 March 2001, and 23 May 2001.

Taxa	August 28, 2000		September 14, 2000		November 21, 2000		March 20, 2001		May 23, 2001	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Coleoptera										
Elmidae										
<i>Heterelmis comalensis</i> Adult/Larvae	0/3	0/0 34	2/3	0.14/0.21	1/10	0.13/1.3	2/3	0.10/0.15	2/4	0.11/0.22
<i>Microcyloepus pusillus</i> Adult/Larvae	4/36	0.4/4.0	21/151	1.5/10.7	14/128	1.8/16.5	24/254	1.2/12.3	67/208	3.7/11.5
<i>Phanocerus</i> Adult/Larvae	0/1	0/0 11	0/2	0/0 14	0/6	0/0 77	0/0	0/0	4/0	0.22/0
Elmidae Pupae	3	0.33	3	0.21	2	0.26	24	1.2	21	1.2
Psephenidae										
<i>Psephenus texanus</i> Adult/Larvae	7/47	0.78/5.3	18/105	1.3/7.4	3/69	0.4/8.9	10/100	0.48/4.8	45/93	2.5/5.1
Dytiscidae Adult/Larvae	0/1	0/0 11	0	0	0/0	0/0	0/0	0/0	0/0	0/0
Staphylinidae										
<i>Bledius</i>	0	0	0	0	0	0	0	0	0	0
Helophoridae										
<i>Helophorus</i>	0	0	0	0	0	0	0	0	1	0.06
Hydrophilidae										
<i>Berosus</i>	0	0	0	0	0	0	1	0.05	1	0.06
Ptilodactylidae										
<i>Anchytars</i>	0	0	2	0.14	0	0	0	0	0	0
Halplidae										
<i>Haliplus</i>	0	0	0	0	0	0	0	0	0	0
<i>Peltodytes</i>	0	0	0	0	0	0	0	0	0	0
Gyrinidae										
<i>Gyrinus</i>	0	0	0	0	0	0	0	0	0	0
Curculionidae	0	0	0	0	0	0	1	0.05	14	0.78
Ephemeroptera										
Baetidae										
<i>Baetis</i>	260	29.1	121	8.5	199	25.6	294	14.2	423	23.4

Table 3 (continued). Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 1 on 28 August 2000, 14 September 2000, 21 November 2000, 20 March 2001, and 23 May 2001.

Taxa	August 28, 2000		September 14, 2000		November 21, 2000		March 20, 2001		May 23, 2001	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
<i>Baetodes</i>	3	0.33	6	0.42	1	0.13	22	1.1	65	3.6
Tricorythidae										
<i>Tricorythodes</i>	23	2.6	124	8.8	121	15.6	234	11.3	146	8.1
<i>Leptohyphes</i>	5	0.56	21	1.5	20	2.6	22	1.1	21	1.2
Trichoptera										
Helicopsychidae										
<i>Helicopsyche</i>	19	2.1	118	8.3	5	0.64	4	0.19	15	0.83
Hydroptilidae										
<i>Leucotrichia sarita</i>	62	6.9	7	0.49	21	2.7	347	16.8	269	14.9
<i>Ochrotrichia</i>	8	0.89	31	2.19	18	2.3	495	24.0	83	4.6
<i>Oxyethura</i>	0	0	1	0.07	0	0	0	0	0	0
Leptoceridae										
<i>Nectopsyche</i>	1	0.11	1	0.07	0	0	4	0.19	3	0.17
Hydrobiosidae										
<i>Atopsyche</i>	0	0	0	0	0	0	0	0	1	0.06
Hydropsychidae										
<i>Smicridea</i>	0	0	0	0	1	0.13	0	0	0	0
Phlopotamidae										
<i>Wormaldia</i>	1	0.11	0	0	0	0	0	0	0	0
Odonata										
Libellulidae										
<i>Brechmorhoga</i>	0	0	1	0.07	1	0.13	0	0	0	0
<i>Perithemus</i>	30	3.4	28	1.9	0	0	1	0.05	15	0.83
Cordulidae	3	0	0	0	5	0.64	0	0	0	0
Coenagrionidae										
<i>Argia</i>	9	1.0	20	1.4	46	5.9	7	0.34	80	4.4

Table 3 (continued). Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 1 on 28 August 2000, 14 September 2000, 21 November 2000, 20 March 2001, and 23 May 2001.

Taxa	August 28, 2000		September 14, 2000		November 21, 2000		March 20, 2001		May 23, 2001	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Gomphidae	0	0	8	0.56	2	0.26	0	0	0	0
Aeshnidae										
<i>Anax</i>	0	0	0	0	1	0.13	0	0	0	0
Hemiptera										
Gerridae										
<i>Metrobates</i>	8	0.89	23	1.6	17	2.2	0	0	9	0.50
<i>Trepobates</i>	0	0	0	0	0	0	0	0	0	0
Velidae										
<i>Rhagovelia</i>	12	1.3	63	4.4	6	0.77	4	0.19	4	0.22
Mesovelidae										
<i>Microvelia</i>	0	0	2	0.14	0	0	0	0	9	0.50
Notonectidae										
<i>Notonecta</i>	0	0	0	0	0	0	0	0	0	0
Lepidoptera										
Pyrallidae										
<i>Petrophila</i>	6	0.67	26	1.83	2	0.26	67	3.2	99	5.5
<i>Parapoynx</i>	1	0.11	2	0.14	0	0	0	0	0	0
Diptera										
Chironomidae Larvae/Pupae	133/18	14.9/2.0	38/65	2.7/4.6	40/18	5.2/2.3	87/36	4.2/1.7	56/28	3.1/1.6
Empididae										
<i>Hemerodromia</i>	5	0.56	10	0.71	5	0.64	6	0.29	14	0.78
Ceratopogonidae										
<i>Forcipomyia</i> Larvae/Pupae	0/1	0/0.11	6/0	0.42/0	2/0	0.26/0	0/3	0/0.14	0/0	0/0
<i>Culicoides</i>	0	0	0	0	0	0	0	0	0	0
<i>Dasyelea</i>	0	0	0	0	0	0	0	0	0	0
Culicidae										
<i>Anopheles</i>	3	0.33	3	0.21	0	0	0	0	0	0

Table 3 (continued). Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 1 on 28 August 2000, 14 September 2000, 21 November 2000, 20 March 2001, and 23 May 2001.

Taxa	August 28, 2000		September 14, 2000		November 21, 2000		March 20, 2001		May 23, 2001	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Psychodidae										
<i>Pericoma</i>	0	0	5	0.35	0	0	0	0	0	0
Stratiomyidae										
<i>Myxosargus</i>	0	0	3	0.21	0	0	0	0	5	0.28
<i>Caloparyhus</i>	0	0	0	0	0	0	0	0	0	0
Simuliidae										
<i>Simulium</i>	0	0	3	0.21	0	0	0	0	0	0
Muscidae	0	0	0	0	1	0.13	7	0.34	1	0.06
Collembola	1	0.11	3	0.21	0	0	2	0.10	0	0
Amphipoda										
Cambaridae										
<i>Procambarus</i>	180	20.1	364	25.7	9	1.2	1	0.05	0	0
Hyalellidae										
<i>Hyalella</i>	0	0	2	0.14	5	0.64	1	0.05	0	0
Crangonyctidae										
<i>Stygobromus</i>	2	0.11	0	0	0	0	3	0.14	0	0
Hirudinea	3	0.33	5	0.35	0	0	1	0.05	0	0
Oligochaeta	0	0	0	0	0	0	4	0.19	0	0
Nematoda	0	0	0	0	0	0	0	0	0	0
Total	899		1418		779		2071		1806	
# Taxa	29		34		27		27		26	

Table 4. Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 1 on 12 September 2001, 5 November 2001, 19 February 2002, and 20 May 2002.

Taxa	September 12, 2001		November 5, 2001		February 19, 2002		May 20, 2002		Total	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Coleoptera										
Elmidae										
<i>Heterelmis comalensis</i> Adult/Larvae	0/1	0/0 11	0/4	0/0 50	0/5	0/0 31	1/0	0 08/0	8/33	0 07/0.2
<i>Microcylloepus pusillus</i> Adult/Larvae	18/252	2 0/27.5	34/248	4 1/29 9	31/346	1 9/21 3	19/131	1 6/11 2	232/1754	2 0/15 2
<i>Phanocerus</i> Adult/Larvae	0/0	0/0	0/1	0/0 12	0/0	0/0	0/0	0/0	4/10	0.03/0.09
Elmidae Pupae	0	0	0	0	3	0 18			59	0 5
Psephenidae										
<i>Psephenus texanus</i> Adult/Larvae	0/47	0/5 1	0/66	0/8 0	5/39	0 31/2 4	7/57	0 60/4 9	95/623	0 8/5.4
Dytiscidae Adult/Larvae	0/0	0/0	0/0	0/0	1/0	0 06/0	0/0	0/0	2/4	0 02/0 03
Staphylinidae										
<i>Bledius</i>	0	0	1	0 12	0	0	0	0	1	0.009
Helophoridae										
<i>Helophorus</i>	0	0	0	0	0	0	0	0	1	0 009
Hydrophilidae										
<i>Berosus</i>	0	0	0	0	0	0	0	0	2	0 02
Ptilodactylidae										
<i>Anchytars</i>	0	0	0	0	0	0	0	0	2	0.02
Halplidae										
<i>Halplus</i>	0	0	0	0	3	0 18	0	0	3	0 03
<i>Peltodytes</i>	0	0	0	0	3	0 18	0	0	3	0 03
Gyrinidae										
<i>Gyrinus</i>	0	0	0	0	1	0.06	0	0	1	0 009
Curculionidae	0	0	0	0	1	0.06	0	0	18	0.2
Ephemeroptera										
Baetidae										
<i>Baetis</i>	179	19 5	216	26 1	828	51.0	207	17 8	2727	23.7

Table 4 (continued). Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 1 on 12 September 2001, 5 November 2001, 19 February 2002, and 20 May 2002.

Taxa	September 12, 2001		November 5, 2001		February 19, 2002		May 20, 2002		Total	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
<i>Baetodes</i>	1	0.11	8	0.96	9	0.55	11	0.94	126	1.1
Tricorythidae										
<i>Tricorythodes</i>	309	33.7	136	16.4	44	2.7	102	8.8	1239	10.8
<i>Leptohyphes</i>	14	1.5	2	0.24	7	0.43	9	0.77	121	1.1
Trichoptera										
Helicopsychidae										
<i>Helicopsyche</i>	1	0.11	1	0.12	10	0.62	18	1.5	69	0.6
Hydroptilidae										
<i>Leucotrichia sarita</i>	37	4.03	19	2.3	119	7.3	51	4.4	935	8.1
<i>Ochrotrichia</i>	2	0.22	15	1.8	52	3.2	17	1.5	678	5.9
<i>Oxyethira</i>	0	0	0	0	0	0	0	0	1	0.009
Leptoceridae										
<i>Nectopsyche</i>	0	0	0	0	6	0.37	7	0.6	22	0.2
Hydrobiosidae										
<i>Atopsyche</i>	0	0	0	0	0	0	0	0	1	0.009
Hydropsychidae										
<i>Smicridea</i>	0	0	0	0	0	0	0	0	1	0.009
Philopotamidae										
<i>Wormaldia</i>	0	0	0	0	0	0	0	0	1	0.009
Odonata										
Libellulidae										
<i>Brechmorhoga</i>	0	0	0	0	0	0	0	0	2	0.02
<i>Perithemus</i>	1	0.11	0	0	0	0	9	0.77	84	0.7
Cordulidae	0	0	0	0	0	0	0	0	8	0.07
Coenagrionidae										
<i>Argia</i>	14	1.5	43	5.2	4	0.25	33	2.8	191	1.7

Table 4 (continued). Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 1 on 12 September 2001, 5 November 2001, 19 February 2002, and 20 May 2002.

Taxa	September 12, 2001		November 5, 2001		February 19, 2002		May 20, 2002		Total	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Gomphidae	0	0	0	0	0	0	0	0	10	0.09
Aeshnidae										
<i>Anax</i>	0	0	0	0	0	0	0	0	1	0.009
Hemiptera										
Gerridae										
<i>Metrobates</i>	0	0	2	0.24	0	0	4	0.34	42	0.4
<i>Trepobates</i>	0	0	0	0	0	0	0	0	42	0.4
Velidae										
<i>Rhagovelia</i>	9	0.10	3	0.36	0	0	4	0.34	53	0.5
Mesovelidae										
<i>Microvelia</i>	0	0	0	0	0	0	0	0	11	0.1
Notonectidae										
<i>Notonecta</i>	0	0	0	0	0	0	0	0	0	0
Lepidoptera										
Pyrallidae										
<i>Petrophila</i>	4	0.44	4	0.50	25	1.5	19	1.6	252	2.2
<i>Parapoynx</i>	6	0.65	2	0.24	0	0	0	0	11	0.1
Diptera										
Chironomidae Larvae/Pupae	15/0	1.64/0	16/0	1.9/0	55/9	3.4/0.55	22/2	1.9/0.17	358/176	3.1/1.5
Empididae										
<i>Hemerodromia</i>	0	0	2	0.24	5	0.31	2	0.17	35	0.3
Ceratopogonidae										
<i>Forcipomyia</i> Larvae/Pupae	0	0	3/0	0.36/0	0/0	0/0	3/0	0.26/0	14/4	0.1/0.03
<i>Culicoides</i>	1	0.11	0	0	0	0	0	0	1	0.009
<i>Dasyhelea</i>	0	0	1	0.12	0	0	0	0	1	0.009
Culicidae										
<i>Anopheles</i>	0	0	0	0	0	0	0	0	6	0.05

Table 4 (continued). Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 1 on 12 September 2001, 5 November 2001, 19 February 2002, and 20 May 2002.

Taxa	September 12, 2001		November 5, 2001		February 19, 2002		May 20, 2002		Total	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Psychodidae										
<i>Pericoma</i>	0	0	0	0	1	0.06	0	0	6	0.05
Stratiomyidae										
<i>Myxosargus</i>	0	0	0	0	1	0.06	0	0	9	0.08
<i>Caloparyhus</i>	1	0.11	0	0	0	0	0	0	1	0.009
Simuliidae										
<i>Simulium</i>	0	0	0	0	0	0	0	0	3	0.03
Muscidae	0	0	0	0	0	0	0	0	9	0.08
Collembola	0	0	2	0.24	0	0	0	0	8	0.07
Amphipoda										
Cambaridae										
<i>Procambarus</i>	4	0.44	3	0.36	4	0.25	427	36.7	992	8.6
Hyalellidae										
<i>Hyaella</i>	1	0.11	3	0.36	1	0.06	0	0	4	0.03
Crangonyctidae										
<i>Stygobromus</i>	1	0.11	0	0	2	0.12	0	0	8	0.07
Hirudinea	0	0	0	0	0	0	0	0	9	0.08
Oligochaeta	0	0	0	0	3	0.18	0	0	7	0.06
Nematoda	0	0	0	0	0	0	0	0	0	0
Total	918		835		1623		1165		11514	
# Taxa	21		24		26		20			

Table 5. Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 3 on 28 August 2000, 14 September 2000, 21 November 2000, 20 March 2001, and 23 May 2001.

Taxa	August 28, 2000		September 14, 2000		November 21, 2000		March 20, 2001		May 23, 2001	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Coleoptera										
Elmidae										
<i>Heterelmis comalensis</i> Adult/Larvae	0/1	0/0.1	1/3	0.06/0.2	3/9	0.38/1.1	5/13	0.33/0.86	3/13	0.2/0.84
<i>Microcyloepus pusillus</i> Adult/Larvae	11/63	1.4/7.9	30/178	1.8/11.0	19/150	2.4/19.1	34/246	2.3/16.4	58/243	3.8/15.8
<i>Phanocerus</i> Adult/Larvae	0/1	0/0.1	0/0	0/0	3/0	0.38/0	0/1	0/0.06	13/0	0.84/0
Elmidae Pupae	7	0.9	20	1.2	23	2.9	24	1.6	28	1.8
Psephenidae										
<i>Psephenus texanus</i> Adult/Larvae	7/29	0.9/3.6	6/68	0.4/4.2	12/143	1.5/18.2	16/220	1.1/14.6	14/224	0.9/14.5
Dytiscidae Adult/Larvae	0/0	0/0	3/0	0.2/0	0/0	0/0	0/0	0/0	2/3	0.1/0.2
Staphylinidae										
<i>Thinobus</i>	1	0.1	0	0	0	0	0	0	0	0
Helophoridae										
<i>Helophorus</i>	0	0	1	0.06	0	0	0	0	1	0.06
Hydrophilidae										
<i>Berosus</i>	0	0	0	0	0	0	0	0	1	0.06
Gyrinidae										
<i>Gyrinus</i>	0	0	0	0	0	0	0	0	0	0
Curculionidae	2	0.25	0	0	0	0	1	0.07	3	0.20
Ephemeroptera										
Baetidae										
<i>Baetis</i>	24	3.0	38	2.3	12	1.5	36	2.4	107	6.9
<i>Baetodes</i>	17	2.1	13	0.80	42	5.4	67	4.5	30	1.9
Tricorythidae										
<i>Tricorythodes</i>	19	2.4	37	2.3	1	0.13	49	3.3	5	0.32
<i>Leptohyphes</i>	1	0.1	4	0.24	0	0	0	0	2	0.13
Ephemeridae	0	0	0	0	0	0	1	0.07	0	0

Table 5 (continued). Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 3 on 28 August 2000, 14 September 2000, 21 November 2000, 20 March 2001, and 23 May 2001.

Taxa	August 28, 2000		September 14, 2000		November 21, 2000		March 20, 2001		May 23, 2001	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Trichoptera										
Helicopsychidae										
<i>Helicopsyche</i>	3	0.4	3	0.2	8	1.02	3	0.20	1	0.06
Hydroptilidae										
<i>Leucotrichia sarita</i>	147	18.4	190	11.6	96	12.2	386	25.7	507	33.0
<i>Ochrotrichia</i>	0	0	23	1.4	23	2.9	164	10.9	57	3.7
<i>Agraylea</i>	0	0	0	0	0	0	0	0	0	0
Hydrobiosidae										
<i>Atopsyche</i>	0	0	0	0	2	0.25	11	0.73	31	2.0
Hydropsychidae										
<i>Cheumatopsyche</i>	0	0	0	0	0	0	0	0	0	0
Philopotamidae										
<i>Wormaldia</i>	0	0	0	0	0	0	0	0	7	0.50
Odonata										
Libellulidae										
<i>Perithemus</i>	10	1.3	3	0.2	2	0.25	0	0	6	0.40
Coenagrionidae										
<i>Argia</i>	2	0.25	1	0.06	5	0.64	3	0.20	4	0.30
Gomphidae	0	0	0	0	0	0	0	0	0	0
Hemiptera										
Gerridae										
<i>Metrobates</i>	5	0.6	22	1.3	44	5.6	3	0.20	13	0.84
<i>Trepobates</i>	0	0	0	0	0	0	0	0	0	0
Velidae										
<i>Rhagovelia</i>	5	0.6	16	0.98	10	1.3	0	0	12	0.80
Mesovelidae										
<i>Microvelia</i>	0	0	0	0	0	0	0	0	0	0

Table 5 (continued). Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 3 on 28 August 2000, 14 September 2000, 21 November 2000, 20 March 2001, and 23 May 2001.

Taxa	August 28, 2000		September 14, 2000		November 21, 2000		March 20, 2001		May 23, 2001	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Notonectidae										
<i>Notonecta</i>	0	0	0	0	0	0	0	0	2	0.13
Lepidoptera										
Pyrallidae										
<i>Petrophila</i>	32	4.0	26	1.6	37	4.7	76	5.0	31	2.0
<i>Parapoynx</i>	0	0	0	0	0	0	1	0.07	1	0.06
Diptera										
Chironomidae Larvae/Pupae	344/55	43.1/6.9	773/112	47.3/6.8	64/10	8.2/1.3	41/37	2.7/2.5	59/13	3.8/0.8
Empididae										
<i>Hemerodromia</i>	2	0.25	13	0.80	4	0.50	3	0.20	9	0.60
Ceratopogonidae										
<i>Forcipomyia</i> Larvae/Pupae	0/0	0/0	0/2	0/0.12	0/0	0/0	2/3	0.1/0.20	0/0	0/0
Tipulidae										
<i>Tipula</i>	0	0	0	0	0	0	0	0	0	0
Collembola	0	0	10	0.6	0	0	3	0.20	7	0.50
Amphipoda										
Cambaridae										
<i>Procambarus</i>	6	0.8	5	0.3	28	3.6	5	0.33	8	0.52
Hyalellidae										
<i>Hyalella</i>	5	0.6	31	1.9	17	2.2	30	2.0	15	1.0
Crangonyctidae										
<i>Stygobromus</i>	0	0	1	0.6	16	2.0	19	1.3	7	0.50
Hirudinea	0	0	0	0	0	0	0	0	0	0
Oligochaeta	0	0	0	0	0	0	0	0	0	0
Nematoda	0	0	0	0	2	0.25	0	0	0	0
Total	799		1633		785		1503		1540	
# Taxa	21		24		22		24		30	

Table 6. Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 3 on 12 September 2001, 5 November 2001, 19 February 2002, and 20 May 2002.

Taxa	September 12, 2001		November 5, 2001		February 19, 2002		May 20, 2002		Total	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Coleoptera										
Elmidae										
<i>Heterelmis comalensis</i> Adult/Larvae	0/2	0/0 45	0/1	0/0 2	2/9	0 14/0 64	5/8	0 39/0 62	19/59	0 2/0 6
<i>Microcyloepus pusillus</i> Adult/Larvae	14/129	3 1/29 0	18/84	4 5/21 0	26/143	1 9/10 2	17/248	1 3/19 2	227/1484	2 3/15 1
<i>Phanocerus</i> Adult/Larvae	0/0	0/0	0/0	0/0	0/1	0/0 07	0/0	0/0	16/3	0 2/0.03
Elmidae Pupae	0	0	0	0	28	2 0	3	0.23	133	1.4
Psephenidae										
<i>Psephenus texanus</i> Adult/Larvae	0/62	0/13 8	0/52	0/13 0	14/74	1 0/5 3	9/199	0 70/15 4	78/1071	0.8/10.9
Dytiscidae Adult/Larvae	0/0	0/0	0/0	0/0	4/0	0 29/0	0/2	0/0 15	9/5	0 09/0.05
Staphylinidae										
<i>Thinobus</i>	0	0	0	0	0	0	0	0	1	0.01
Helophoridae										
<i>Helophorus</i>	0	0	0	0	6	0.43	0	0	8	0 08
Hydrophilidae										
<i>Berosus</i>	0	0	1	0 2	1	0 07	0	0	3	0 03
Gyrinidae										
<i>Gyrinus</i>	0	0	0	0	1	0 07	0	0	1	0.01
Curculionidae	0	0	0	0	1	0 07	2	0 15	9	0 09
Ephemeroptera										
Baetidae										
<i>Baetis</i>	13	2 9	4	1 0	207	14 8	33	2 6	474	4 8
<i>Baetodes</i>	38	8 5	25	6.3	28	2 0	19	1 5	279	2 8
Tricorythidae										
<i>Tricorythodes</i>	0	0	2	0.5	23	1 6	7	0 54	143	1 5
<i>Leptohyphes</i>	6	1 34	1	0 25	4	0 29	2	0 15	20	0 2
Ephemeridae			0	0	0	0	0	0	1	0 01

Table 6 (continued). Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 3 on 12 September 2001, 5 November 2001, 19 February 2002, and 20 May 2002.

Taxa	September 12, 2001		November 5, 2001		February 19, 2002		May 20, 2002		Total	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Trichoptera										
Helicopsychidae										
<i>Helicopsyche</i>	1	0.22	0	0	0	0	0	0	19	0.2
Hydroptilidae										
<i>Leucotrichia sarita</i>	117	26.1	132	33.0	632	45.0	549	42.4	2756	28.1
<i>Ochrotrichia</i>	1	0.22	4	1.0	40	2.9	46	3.6	358	3.7
<i>Agraylea</i>	4	0.90	11	2.8	0	0	0	0	15	0.1
Hydrobiosidae										
<i>Atopsyche</i>	2	0.45	0	0	11	0.78	8	0.62	65	0.7
Hydropsychidae										
<i>Cheumatopsyche</i>	1	0.22	0	0	0	0	0	0	1	0.01
Philopotamidae										
<i>Wormaldia</i>	0	0	0	0	1	0.07	2	0.15	10	0.1
Odonata										
Libellulidae										
<i>Perithemus</i>	1	0.22	0	0	0	0	3	0.23	25	0.3
Coenagrionidae										
<i>Argia</i>	1	0.22	1	0.25	0	0	3	0.23	20	0.2
Gomphidae			0	0	0	0	0	0	0	0
Hemiptera										
Gerridae										
<i>Metrobates</i>	0	0	1	0.25	9	0.64	4	0.31	101	1.0
<i>Trepobates</i>	0	0	1	0.25	0	0	0	0	1	0.01
Velidae										
<i>Rhagovelia</i>	6	1.34	8	2.0	1	0.07	0	0	58	0.6
Mesovelidae										
<i>Microvelia</i>	0	0	0	0	0	0	17	1.3	17	0.2

Table 6 (continued). Taxonomic composition and richness, and absolute and relative abundance of macroinvertebrates collected at Comal Springs run 3 on 12 September 2001, 5 November 2001, 19 February 2002, and 20 May 2002.

Taxa	September 12, 2001		November 5, 2001		February 19, 2002		May 20, 2002		Total	
	Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Notonectidae										
<i>Notonecta</i>	0	0	0	0	0	0	0	0	2	0.02
Lepidoptera										
Pyrallidae										
<i>Petrophila</i>	15	3.3	11	2.8	42	3.0	40	3.1	310	3.2
<i>Parapoynx</i>	0	0	2	0.5	0	0	0	0	4	0.04
Diptera										
Chironomidae Larvae/Pupae	17/0	3.8/0	23/0	5.7/0	37/15	2.6/1.1	32/6	2.5/0.46	1390/248	14.2/2.5
Empididae										
<i>Hemerodromia</i>	0	0	0	0	19	1.4	6	0.46	56	0.6
Ceratopogonidae										
<i>Forcipomyia</i> Larvae/Pupae	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	2/5	0.02/0.05
Tipulidae										
<i>Tipula</i>	1	0.22	0	0	0	0	0	0	1	0.01
Collembola	0	0	1	0.25	1	0.07	2	0.15	24	0.2
Amphipoda										
Cambaridae										
<i>Procambarus</i>	11	2.5	10	2.5	6	0.43	5	0.39	84	0.9
Hyalellidae										
<i>Hyalella</i>	3	0.7	6	1.5	13	0.93	13	1.0	132	1.3
Crangonyctidae										
<i>Stygobromus</i>	2	0.45	1	0.25	4	0.29	4	0.31	54	0.6
Oligochaeta	1	0.22	0	0	0	0	0	0	1	0.01
Nematoda	0	0	0	0	0	0	0	0	2	0.02
Total	448		400		1403		1294		9805	
# Taxa	22		22		26		24			

Table 7. Multiple regression analysis of drift rate and density against Julian day, current velocity, and water depth for both spring runs. Standard correlation coefficient, R, and p-value in parentheses. Multiple R² presented for all independent variables against drift rate and density for each spring run.

	Julian day	Current velocity	Water depth	Multiple R ²
Spring run 1				
Drift rate	-0.72 (0.05)	-0.47 (0.23)	0.27 (0.50)	0.72
Drift density	-0.38 (0.06)	-0.71 (0.03)	-0.46 (0.09)	0.90
Spring run 3				
Drift rate	-0.55 (0.22)	0.23 (0.62)	-0.18 (0.65)	0.43
Drift density	-0.58 (0.25)	-0.29 (0.58)	-0.01 (0.98)	0.25

Table 8. Simple linear correlation coefficients, R, and p-value in parentheses of selected taxa in both spring runs for drift rates against Julian day, flow rate, and water depth. * indicates no significant ($p \leq 0.05$) relationship was present.

Taxa	Julian day	Current velocity	Water depth	Discharge
Spring Run 1				
All taxa	-0.79 (0.01)	-0.18 (0.6)	0.27 (0.5)	0.20 (0.7)
<i>Baetis</i> sp.	-0.80 (0.01)	*	*	*
<i>Nectopsyche</i> sp.	-0.86 (0.003)	*	*	*
<i>Stygobromus</i> sp.	-0.74 (0.02)	*	*	*
<i>Leucotrichia sarita</i>	-0.74 (0.02)	*	*	*
<i>Petrophila</i> sp.	-0.68 (0.04)	*	*	*
<i>Perithemis</i> sp.	*	-0.97 (0.000)	-0.65 (0.05)	-0.74 (0.02)
<i>Helicopsyche</i> sp.	*	-0.82 (0.006)	-0.65 (0.05)	-0.67 (0.05)
<i>Procambarus</i> sp.	*	-0.69 (0.04)	-0.78 (0.01)	-0.75 (0.02)
<i>Microcyloepus pusillus</i>	*	*	-0.73 (0.03)	0.72 (0.03)
<i>Rhagovelia</i> sp.	*	*	-0.79 (0.01)	-0.82 (0.006)
Spring Run 3				
All taxa	-0.62 (0.07)	0.42 (0.3)	0.02 (0.9)	-0.09 (0.9)
<i>Baetis</i> sp.	-0.80 (0.01)	*	*	*
<i>Leucotrichia</i> sp.	-0.87 (0.003)	*	*	*
<i>Psephenus texanus</i>	*	0.66 (0.05)	*	*
<i>Petrophila</i> sp.	*	0.75 (0.02)	*	*
<i>Heterelmis comalensis</i>	*	0.81 (0.008)	*	*
<i>Stygobromus</i> sp.	*	0.82 (0.006)	*	0.67 (0.05)
<i>Atopsyche</i> sp.	*	0.73 (0.03)	0.67 (0.05)	0.69 (0.04)
<i>Baetodes</i> sp.	*	*	*	0.72 (0.03)
<i>Chironomidae</i>	*	*	*	-0.90 (0.003)

Table 9. Simple linear correlation coefficients, R, and p-value in parentheses of selected taxa in both spring runs for drift density against Julian day, flow rate, and water depth. * indicates no significant ($p \leq 0.05$) relationship was present.

Taxa	Julian day	Current velocity	Water depth	Discharge
Spring Run 1				
All taxa	-0.10 (0.8)	-0.88 (0.002)	-0.72 (0.03)	0.19 (0.7)
<i>Stygobromus</i> sp.	-0.74 (0.02)	*	*	-0.70 (0.04)
Chironomidae	*	-0.68 (0.04)	-0.80 (0.01)	*
<i>Psephenus texanus</i>	*	-0.80 (0.01)	-0.83 (0.006)	*
<i>Helicopsyche</i> sp.	*	-0.77 (0.02)	-0.82 (0.006)	*
<i>Procambarus</i> sp.	*	-0.86 (0.003)	-0.85 (0.004)	*
<i>Hemerodromia</i> sp.	*	-0.80 (0.01)	-0.77 (0.02)	*
<i>Perithemis</i> sp.	*	-0.88 (0.002)	-0.93 (0.000)	-0.67 (0.05)
<i>Rhagovelia</i> sp.	*	*	-0.84 (0.005)	-0.70 (0.04)
<i>Microcylloepus pusillus</i>	*	*	*	0.72 (0.03)
<i>Heterelmis comalensis</i>	*	*	-0.78 (0.014)	*
Spring Run 3				
All taxa	-0.44 (0.2)	-0.001 (0.99)	-0.01 (0.97)	-0.1 (0.8)
<i>Baetis</i> sp.	-0.77	*	*	0.75 (0.02)
<i>Leucotrichia</i> sp.	-0.78	*	*	*
<i>Psephenus texanus</i>	*	0.66 (0.05)	*	*
<i>Petrophila</i> sp.	*	0.75 (0.02)	*	*
<i>Atopsyche</i> sp.	*	0.73 (0.03)	*	*
<i>Heterelmis comalensis</i>	*	0.81 (0.008)	*	*
<i>Stygobromus</i> sp.	*	0.82 (0.007)	*	0.74 (0.03)
<i>Tricorythodes</i> sp.	*	*	*	0.74 (0.03)
<i>Perithemis</i> sp.	*	*	*	0.74 (0.03)
<i>Hyallela</i> sp.	*	*	*	-0.87 (0.003)
<i>Leptohyphes</i> sp.	*	*	*	0.74 (0.03)

Table 10. Simple linear correlation coefficients (R) for drift rate of Elmidae and selected Elmidae species against Julian day, current velocity, and water depth in both spring runs.

Taxa	Julian day	Current velocity	Water depth
Spring Run 1			
Elmidae	-0.41	0.59	0.62
<i>Microcylloepus pusillus</i>	-0.44	0.51	-0.73
<i>Heterelmis comalensis</i>	0.02	0.29	-0.02
Spring Run 3			
Elmidae	-0.48	0.54	0.4
<i>Microcylloepus pusillus</i>	-0.47	0.51	0.39
<i>Heterelmis comalensis</i>	-0.62	0.81	0.34

Table 11. Simple linear correlation coefficients (R) for drift density of Elmidae and selected Elmidae species against Julian day, current velocity, and water depth in both spring runs.

Taxa	Julian day	Current velocity	Water depth
Spring Run 1			
Elmidae	0.01	-0.49	-0.44
<i>Microcylloepus pusillus</i>	-0.37	-0.41	-0.25
<i>Heterelmis comalensis</i>	-0.51	-0.51	-0.78
Spring Run 3			
Elmidae	-0.23	0.04	0.32
<i>Microcylloepus pusillus</i>	-0.23	0.03	0.02
<i>Heterelmis comalensis</i>	-0.62	0.69	0.42

Table 12. Categorization of aquatic insect habits (modes of existence), with representative taxa from Comal Springs. Adapted from Merritt and Cummins (1996).

Category	Description	Representative Taxa
Skaters	Adapted for "skating" on the surface where they feed as scavengers on organisms trapped in the surface film.	<i>Rhagovelia</i> , <i>Metrobates</i> , <i>Trepobates</i> , <i>Microvelia</i>
Planktonic	Inhabit open water limnetic zone of standing waters (lentic habitats); representatives float and swim about in the open water.	<i>Anopheles</i>
Divers	Adapted for swimming by "rowing" with hind legs in lentic habitats and lotic pools; representatives come to surface to obtain oxygen and may cling to or crawl on submerged objects such as macrophytes.	adult Dytiscidae, <i>Gyrinus</i>
Swimmers	Adapted for "fish-like" swimming in lotic or lentic habitats; representatives usually cling to submerged objects, such as rocks or macrophytes between short bursts of swimming.	<i>Baetis</i> ,
Clingers	Representatives have behavioral (i.e., fixed retreat construction) and morphological (i.e., long, curved tarsal claws, dorsoventral flattening, and ventral gills arranged as suckers) adaptations for attachment to surfaces in stream riffles.	<i>M. pusillus</i> , <i>H. comalensis</i> , <i>P. texanus</i> , <i>Leucotrichia</i> , <i>Ochrotrichia</i> , <i>Helicopsyche</i> , <i>Baetodes</i> , <i>Leptohyphes</i>
Sprawlers	Inhabit the surface of floating leaves of macrophytes or fine sediments, usually with modifications for staying on top of the substrate and maintaining the respiratory surfaces free of silt.	<i>Tricorythodes</i> , <i>Perithemis</i> , <i>Forcipomyia</i>
Climbers	Adapted for living on macrophytes or detrital debris (i.e., overhanging branches, roots, and vegetation along streams) with modifications for moving vertically on stem-type surfaces.	<i>Halipilus</i> , <i>Nectopsyche</i> ; <i>Parapoynx</i>
Burrowers	Inhabit the fine sediments of streams and lakes. Some construct discrete burrows with sand grain tubes extending above surface of substrate or may ingest their way through sediments.	<i>Culicoides</i> , <i>Pericoma</i> , <i>Procambarus</i>

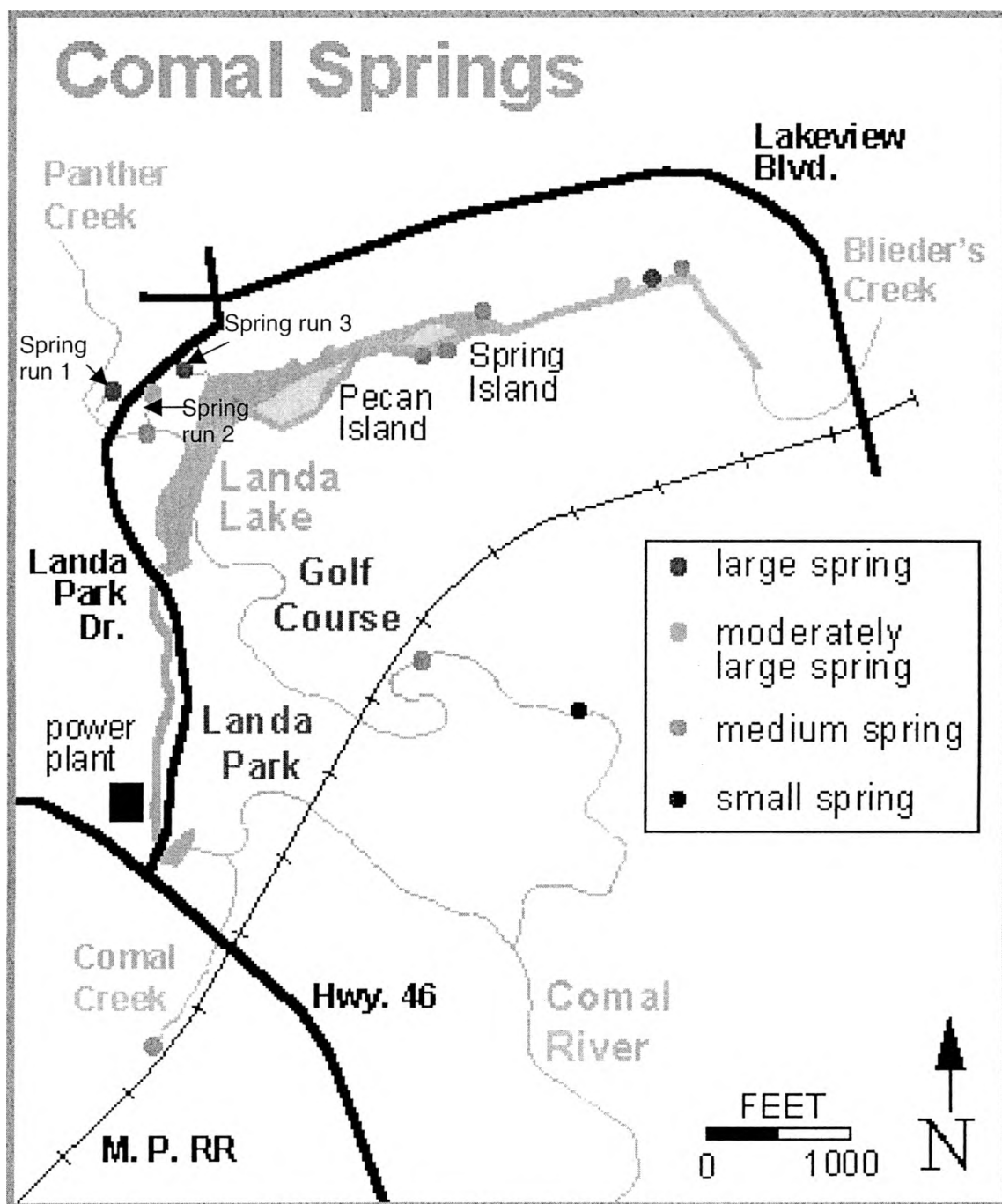


Figure 1. Map of Comal Springs with selected spring openings and spring runs labeled. Spring location from Brune (1981). Map courtesy of Gregg Eckhardt.

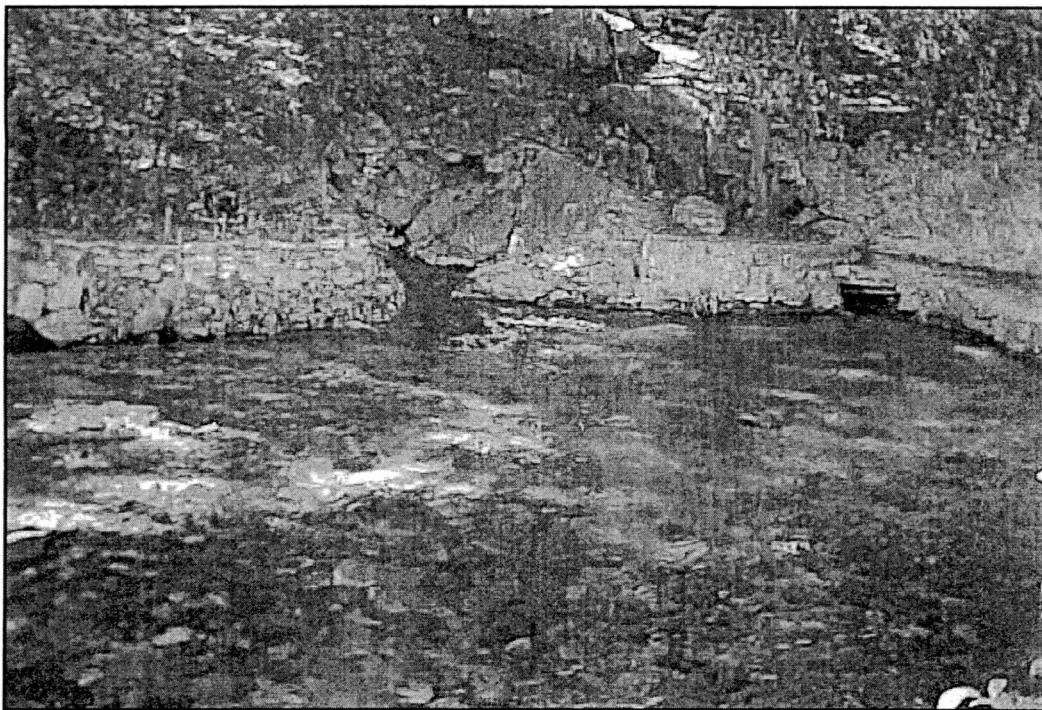


Figure 2. Spring openings in spring run 1 at Landa Park, New Braunfels, TX.

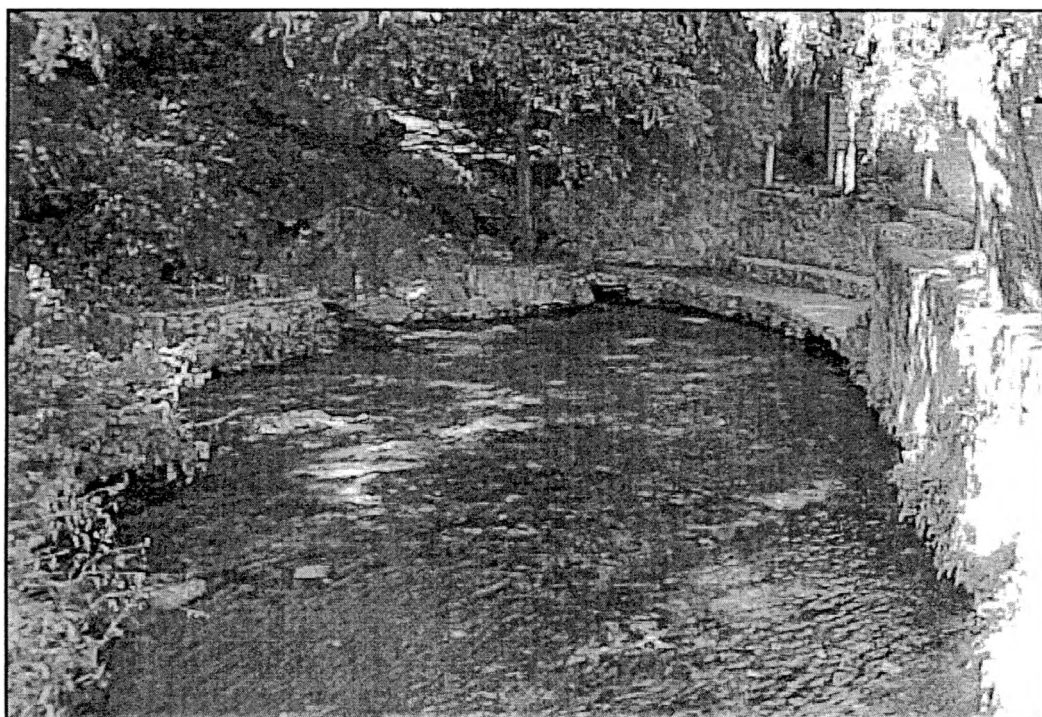


Figure 3. Headwaters of spring run 1 at Landa Park, New Braunfels, TX.



Figure 4. Downstream view of spring run 1 at the sampling site.



Figure 5. Upstream view of spring run 2 at the sampling site.



Figure 6. Spring opening along the escarpment in spring run 3.



Figure 7. Upstream view of spring run 3 with the escarpment on the right.

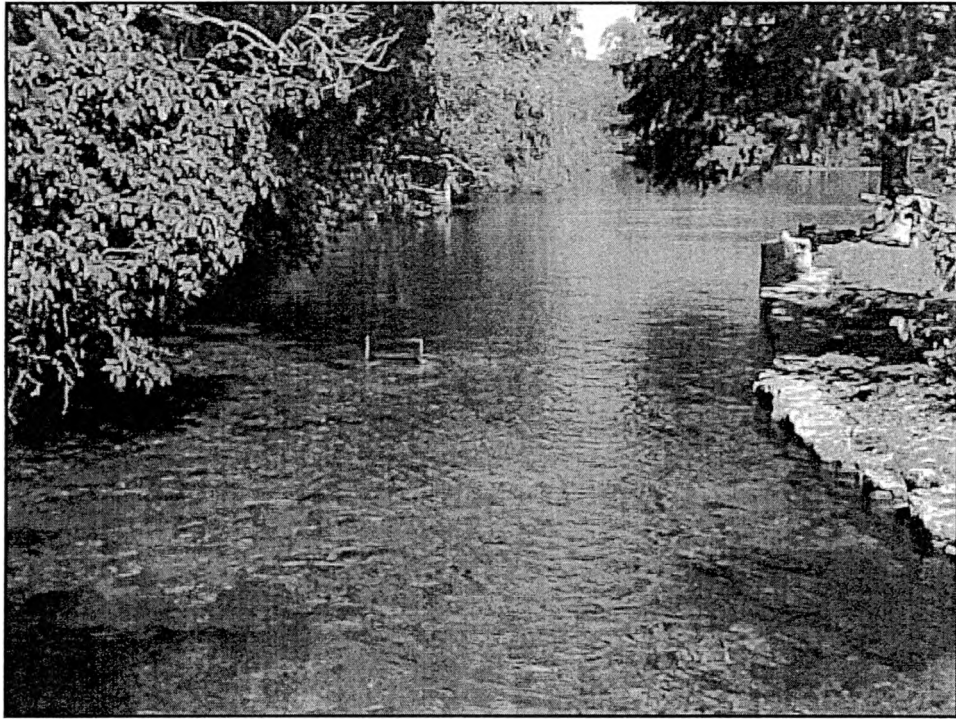


Figure 8. Downstream view of spring run 3 above the confluence with Landa Lake.

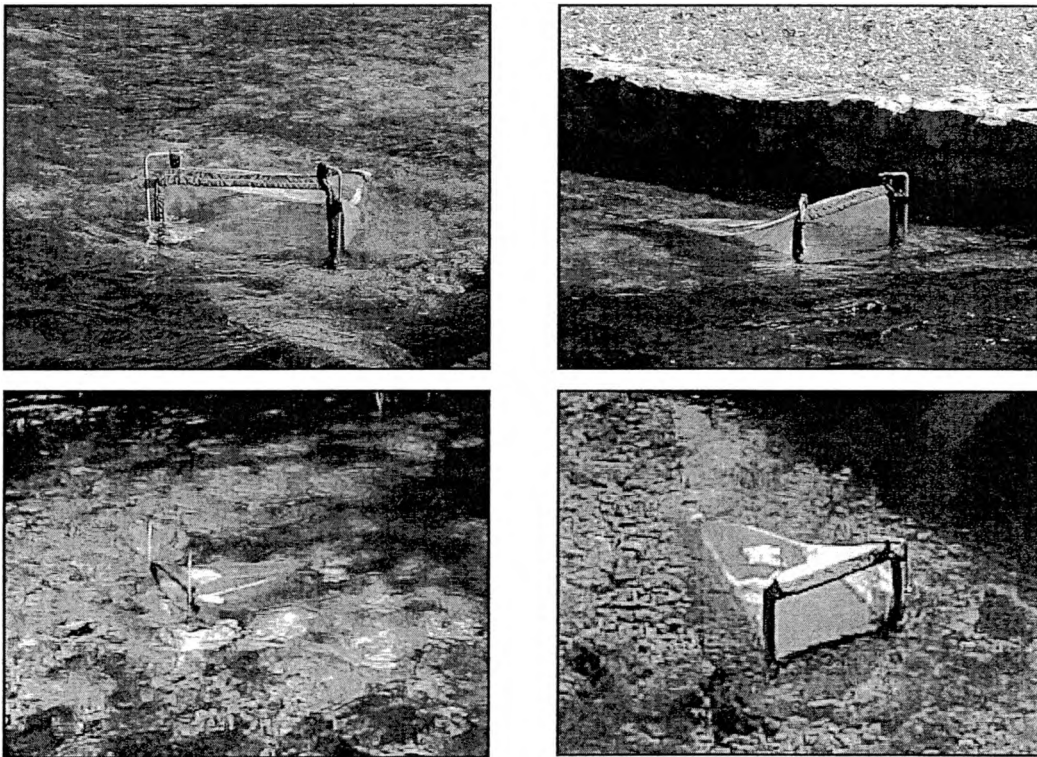


Figure 9. Examples of drift net placement.

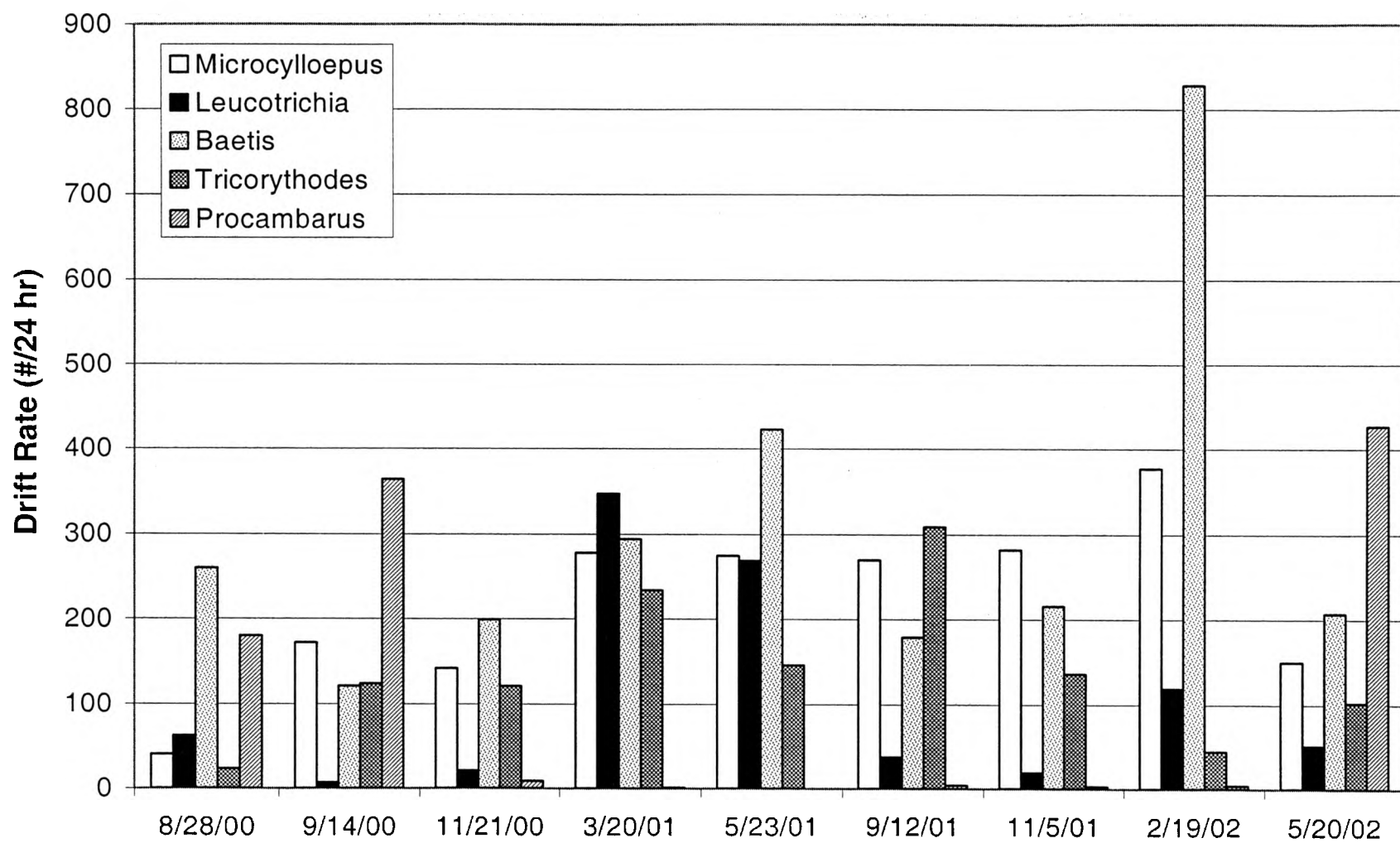


Figure 10. Drift rate for dominant taxa across sampling dates for spring run 1.

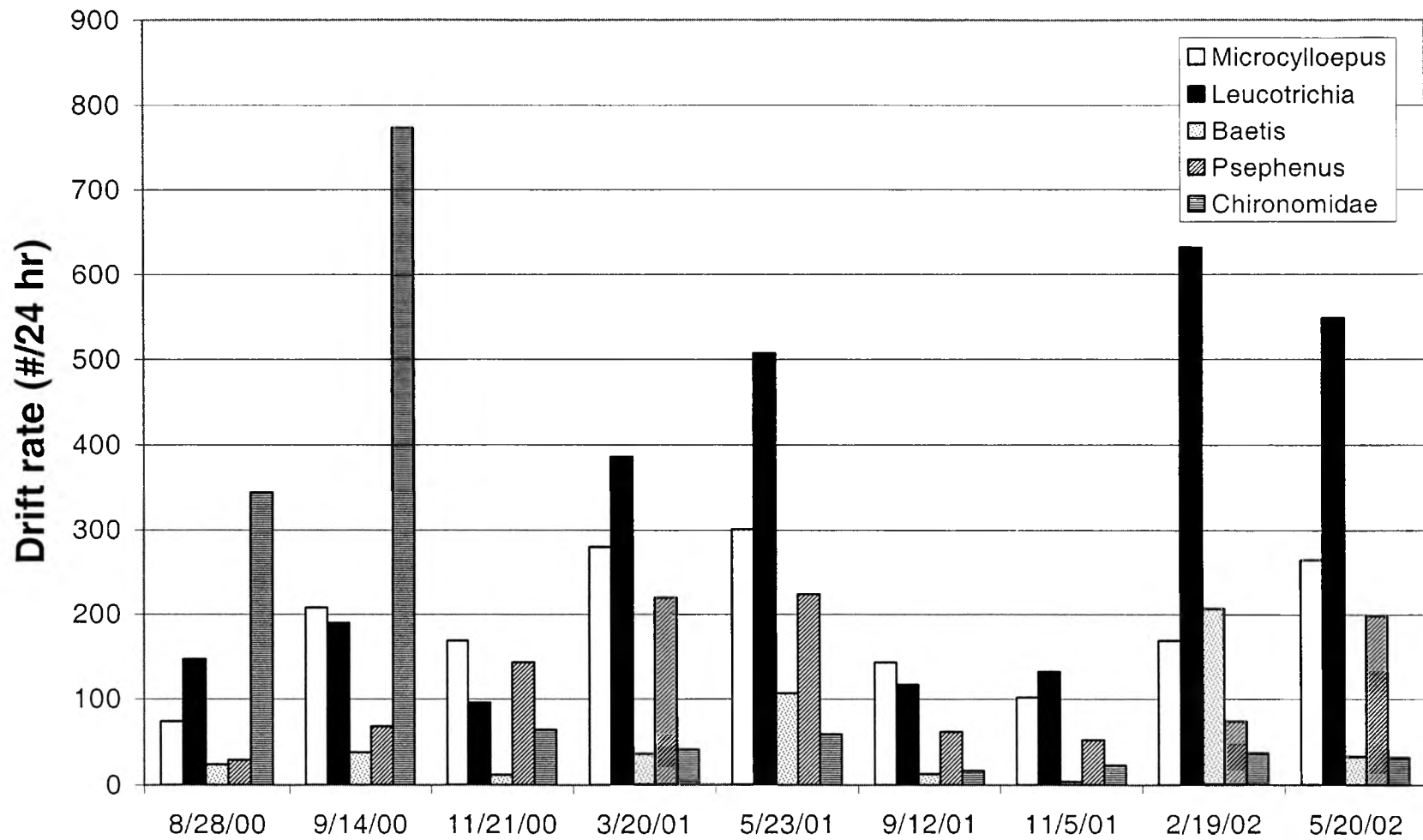


Figure 11. Drift rate for dominant taxa across sampling dates for spring run 3.

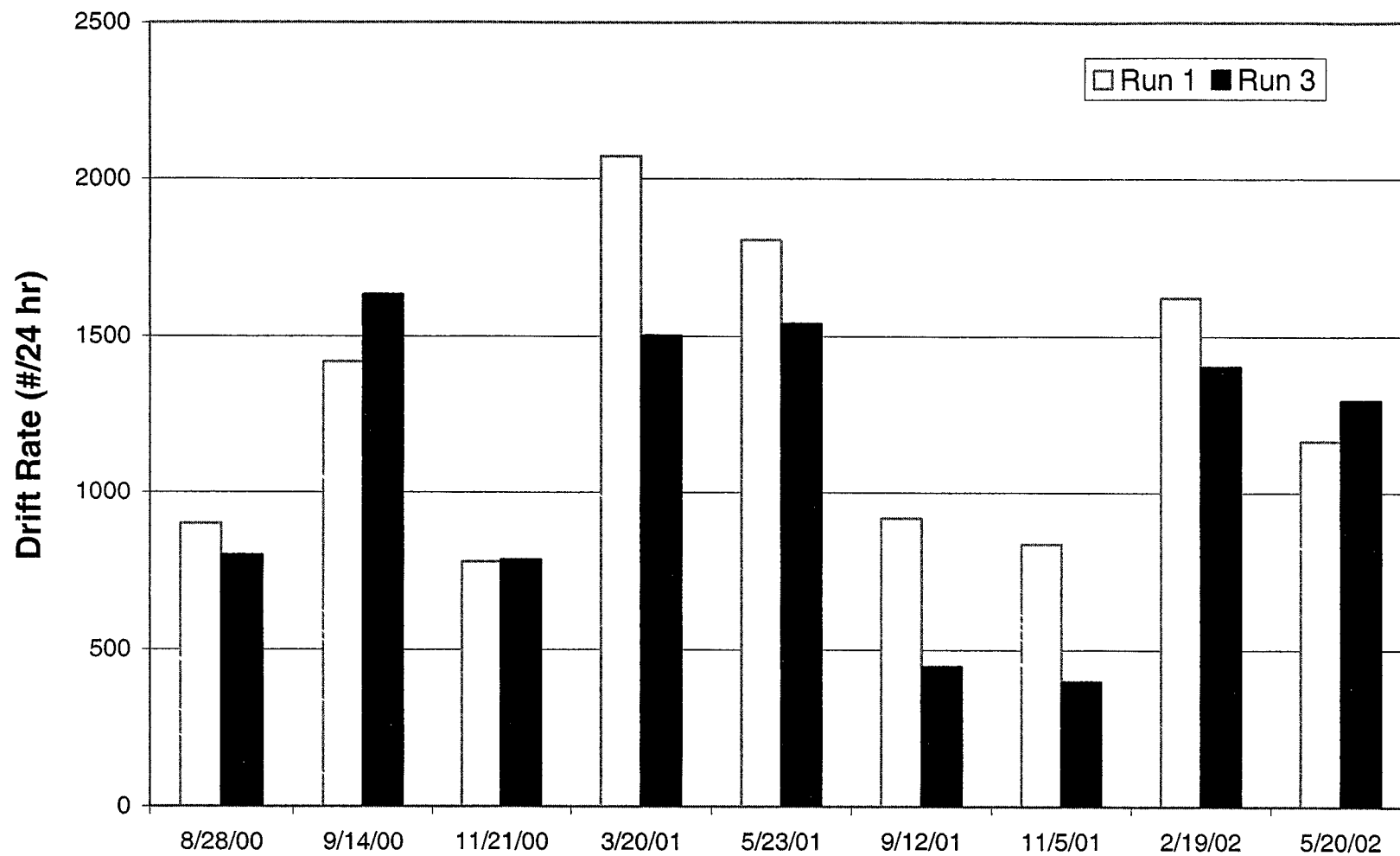


Figure 12. Drift rate for both spring runs across all sampling dates.

Drift rate (#/3 hr)

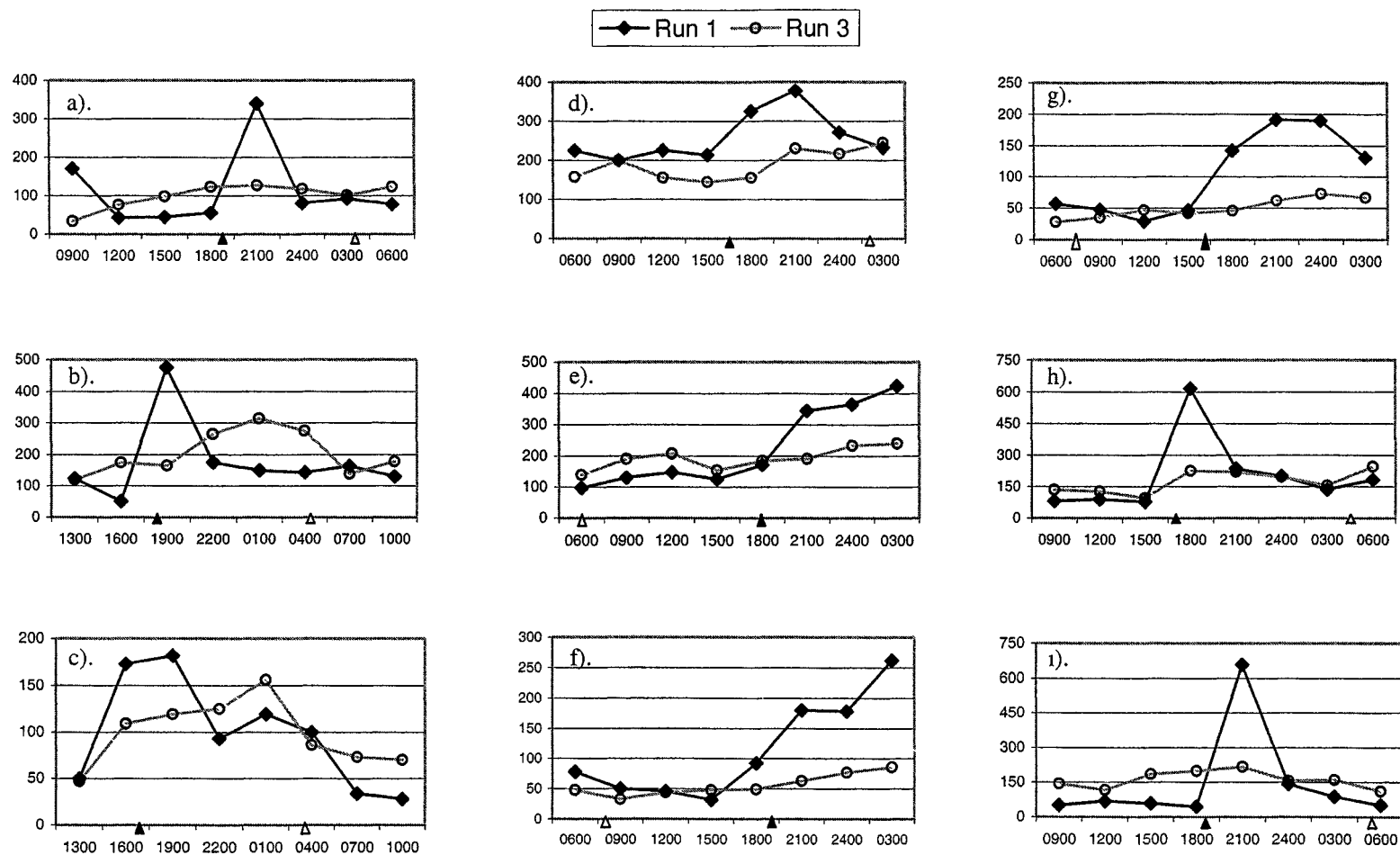


Figure 13. Diel drift rate for both spring runs on (a) 28 August 2000, (b) 14 September 2000, (c) 21 November 2000, (d) 20 March 2001, (e) 23 May 2001, (f) 12 September 2001, (g) 5 November 2001, (h) 19 February 2002, and (i) 20 May 2002. ▲ - indicates sunset, △ - indicates sunrise.

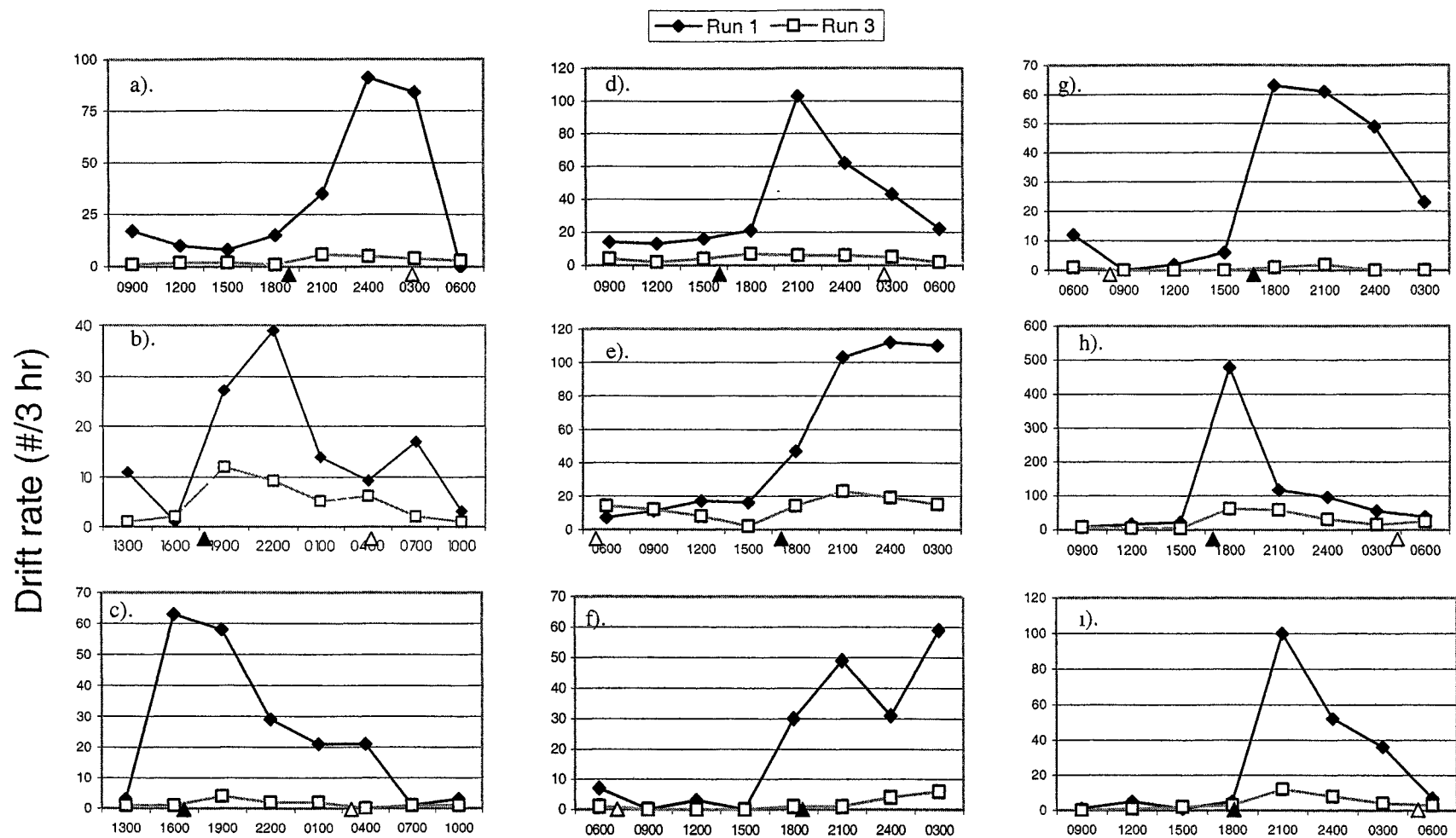


Figure 14. Diel drift rates for the mayfly *Baetis* on (a) 28 August 2000, (b) 14 September 2000, (c) 21 November 2000, (d) 20 March 2001, (e) 23 May 2001, (f) 12 September 2001, (g) 5 November 2001, (h) 19 February 2002, and (i) 20 May 2002. ▲ - indicates sunset, △ - indicates sunrise.

Drift rate (#/3 hr)

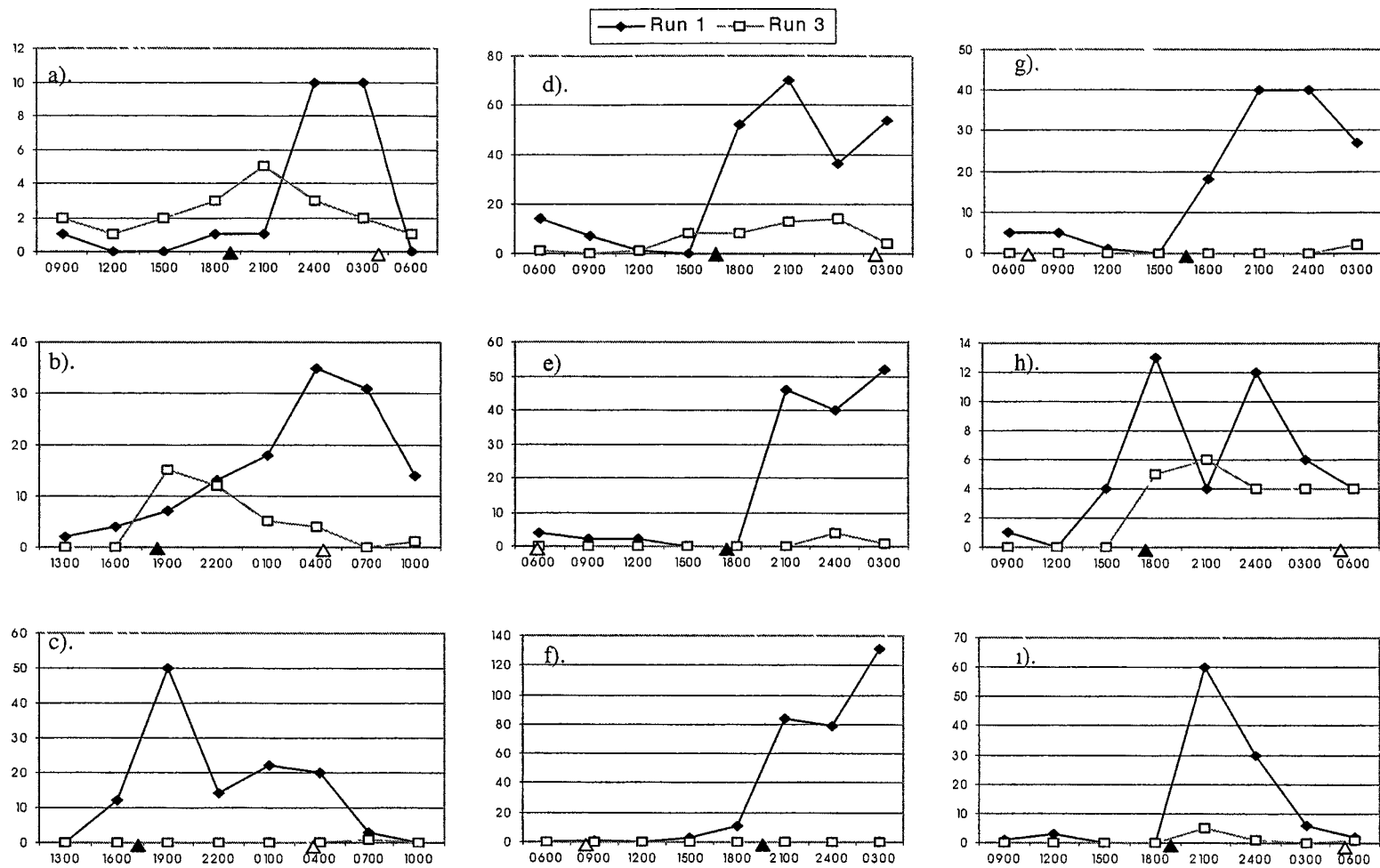


Figure 15. Diel drift rates for *Tricorythodes* on (a) 28 August 2000, (b) 14 September 2000, (c) 21 November 2000, (d) 20 March 2001, (e) 23 May 2001, (f) 12 September 2001, (g) 5 November 2001, (h) 19 February 2002, and (i) 20 May 2002. ▲ - indicates sunset, △ - indicates sunrise.

Drift rate (#/3 hr)

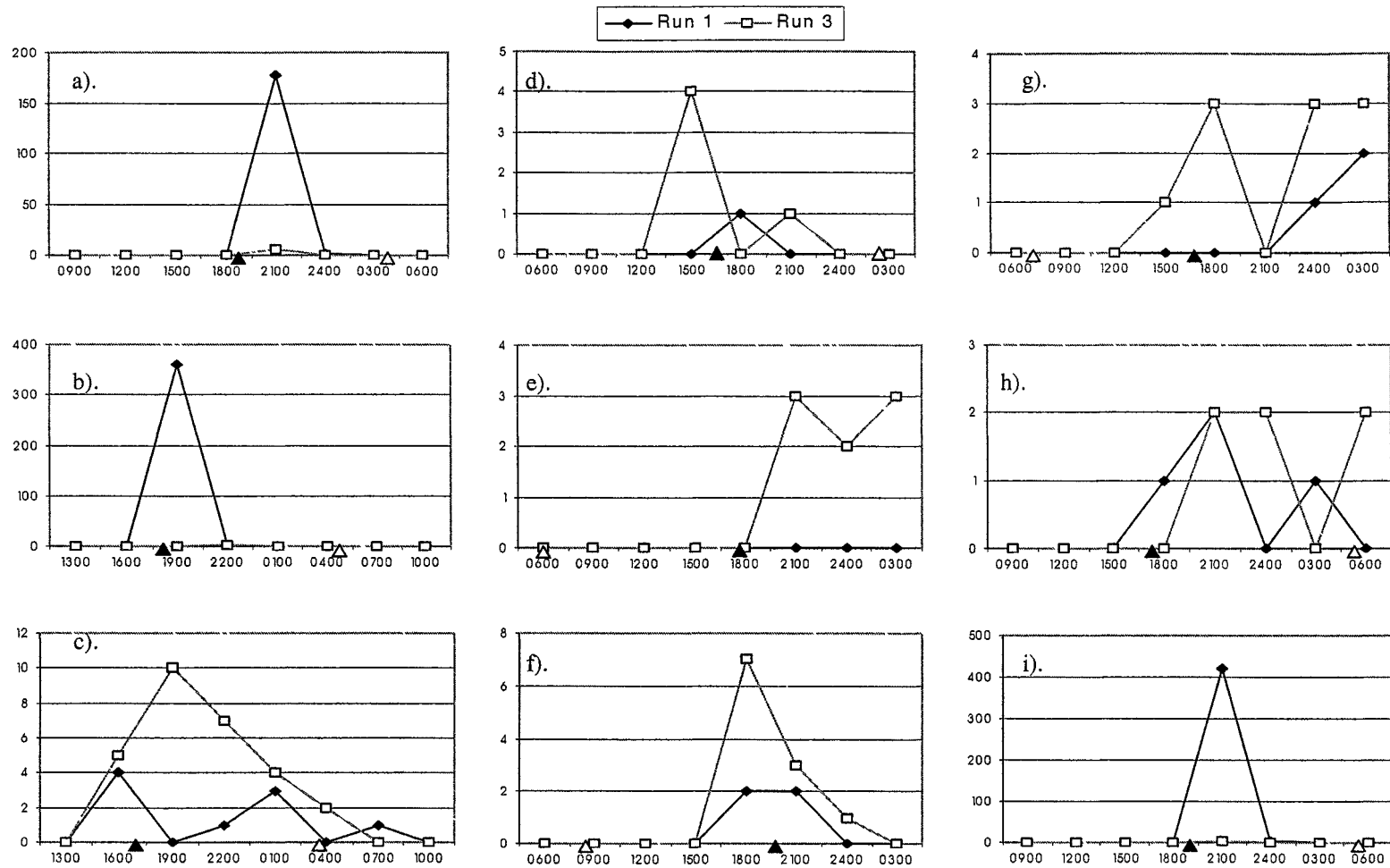


Figure 16. Diel drift rates for *Procambarus* on (a) 28 August 2000, (b) 14 September 2000, (c) 21 November 2000, (d) 20 March 2001, (e) 23 May 2001, (f) 12 September 2001, (g) 5 November 2001, (h) 19 February 2002, and (i) 20 May 2002. ▲ - indicates sunset, △ - indicates sunrise.

Drift rate (#/3 hr)

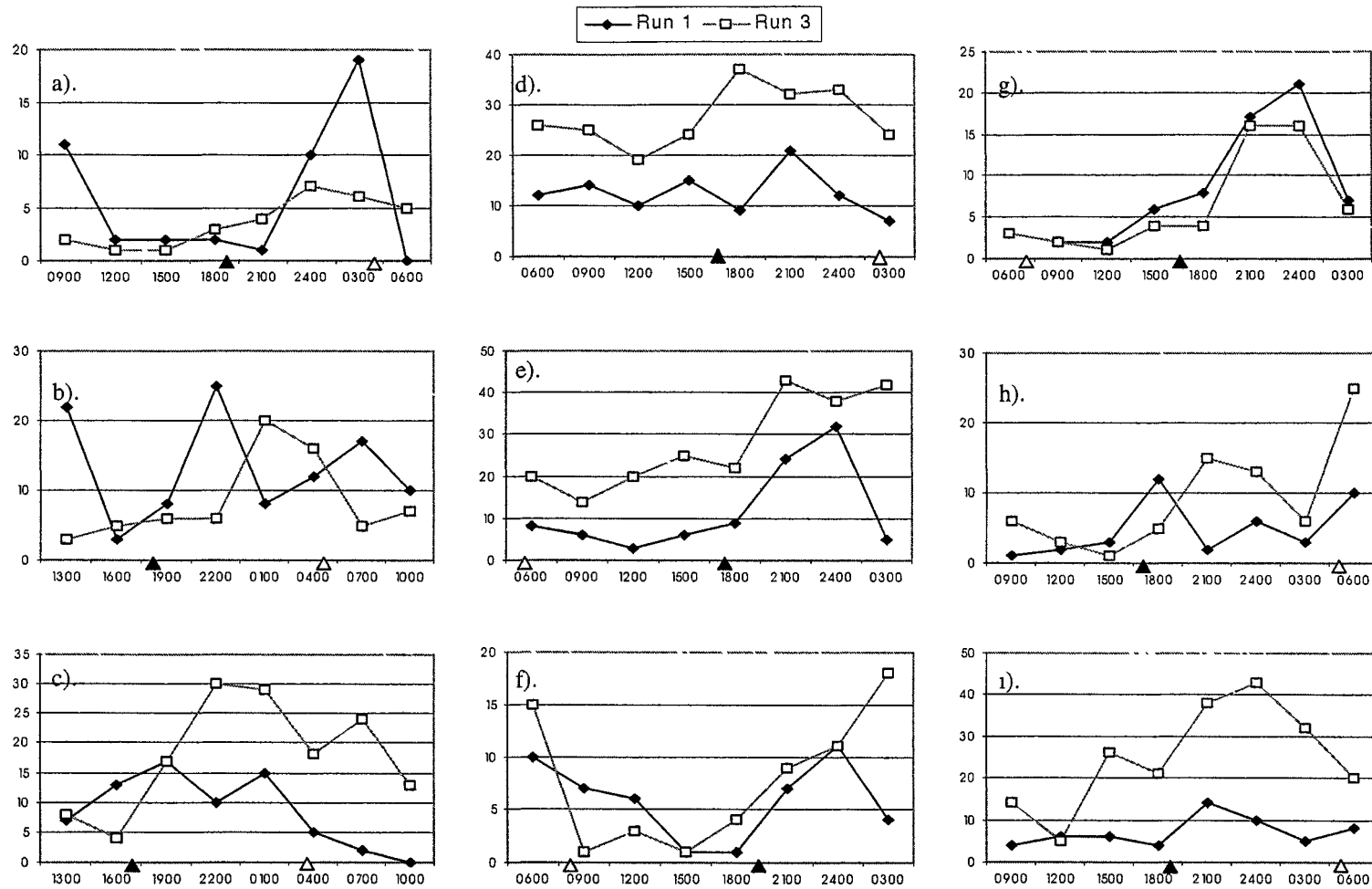


Figure 17. Diel drift rates for *P. texanus* on (a) 28 August 2000, (b) 14 September 2000, (c) 21 November 2000, (d) 20 March 2001, (e) 23 May 2001, (f) 12 September 2001, (g) 5 November 2001, (h) 19 February 2002, and (i) 20 May 2002. ▲ - indicates sunset, △- indicates sunrise.

Drift rate (#/3 hr)

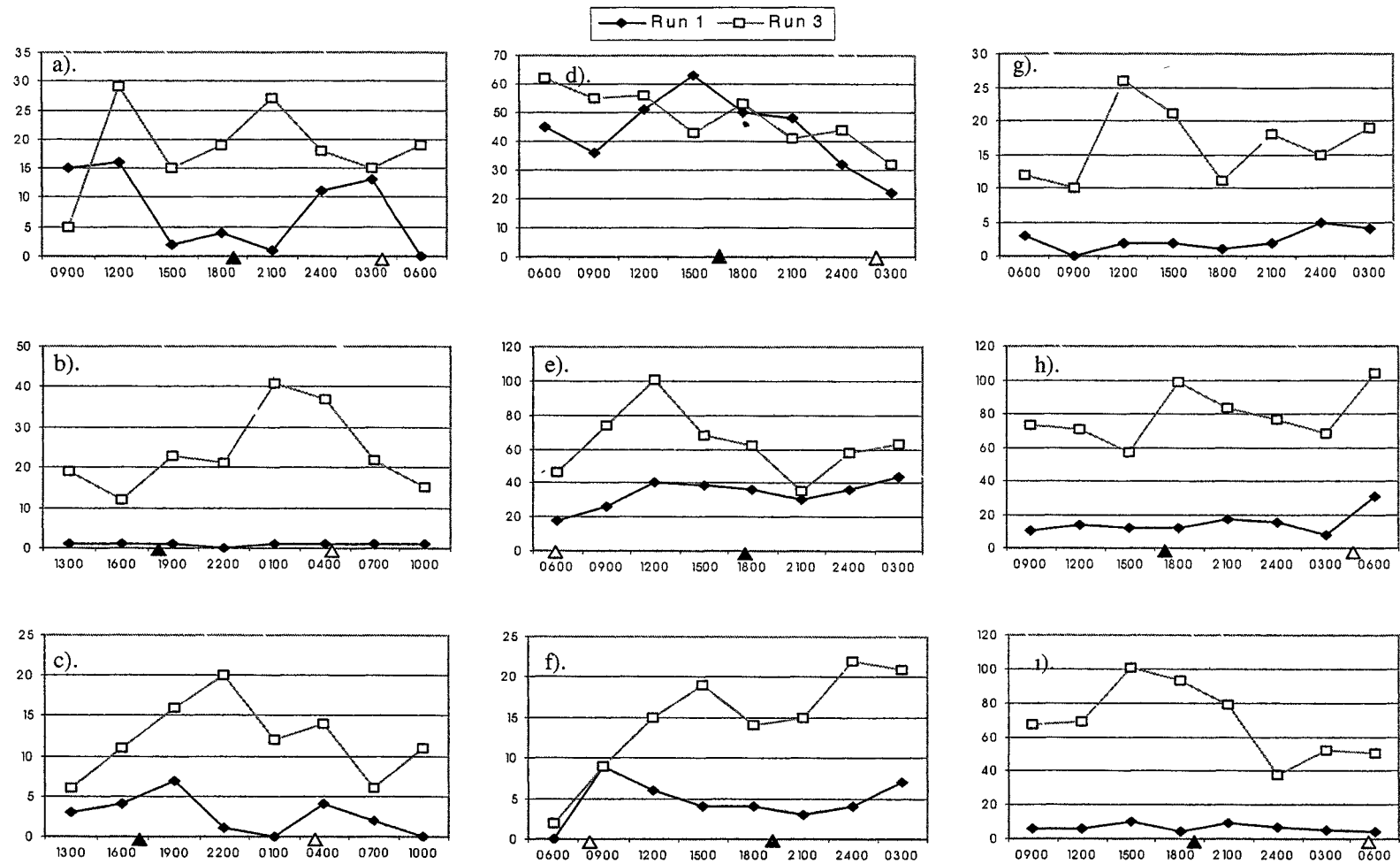


Figure 18. Diel drift rates for *L. sarita* on (a) 28 August 2000, (b) 14 September 2000, (c) 21 November 2000, (d) 20 March 2001, (e) 23 May 2001, (f) 12 September 2001, (g) 5 November 2001, (h) 19 February 2002, and (i) 20 May 2002. ▲ - indicates sunset, △ - indicates sunrise.

Drift rate (#/3 hr)

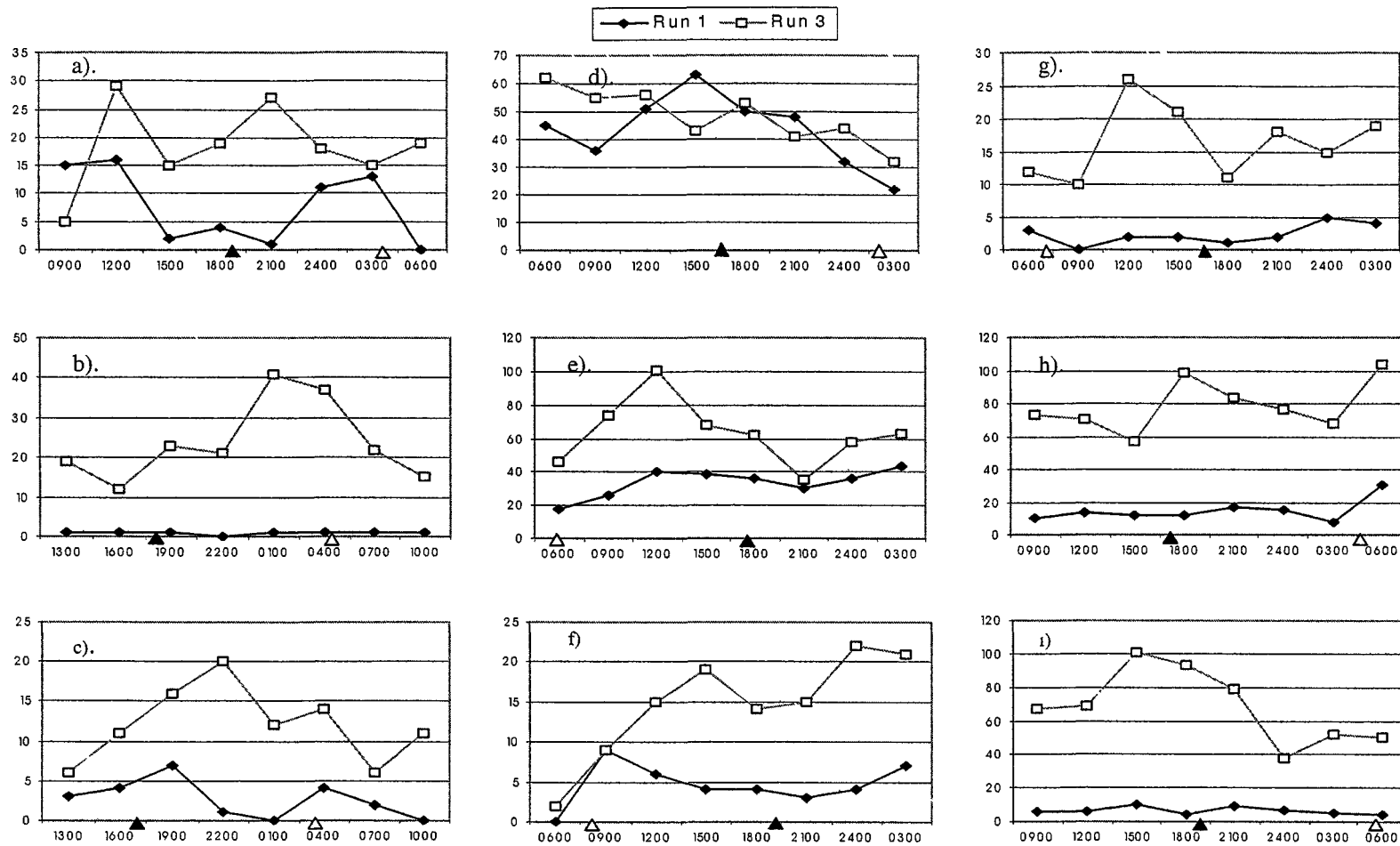


Figure 19. Diel drift rates for *L. sarita* on (a) 28 August 2000, (b) 14 September 2000, (c) 21 November 2000, (d) 20 March 2001, (e) 23 May 2001, (f) 12 September 2001, (g) 5 November 2001, (h) 19 February 2002, and (i) 20 May 2002. ▲ - indicates sunset, Δ- indicates sunrise.

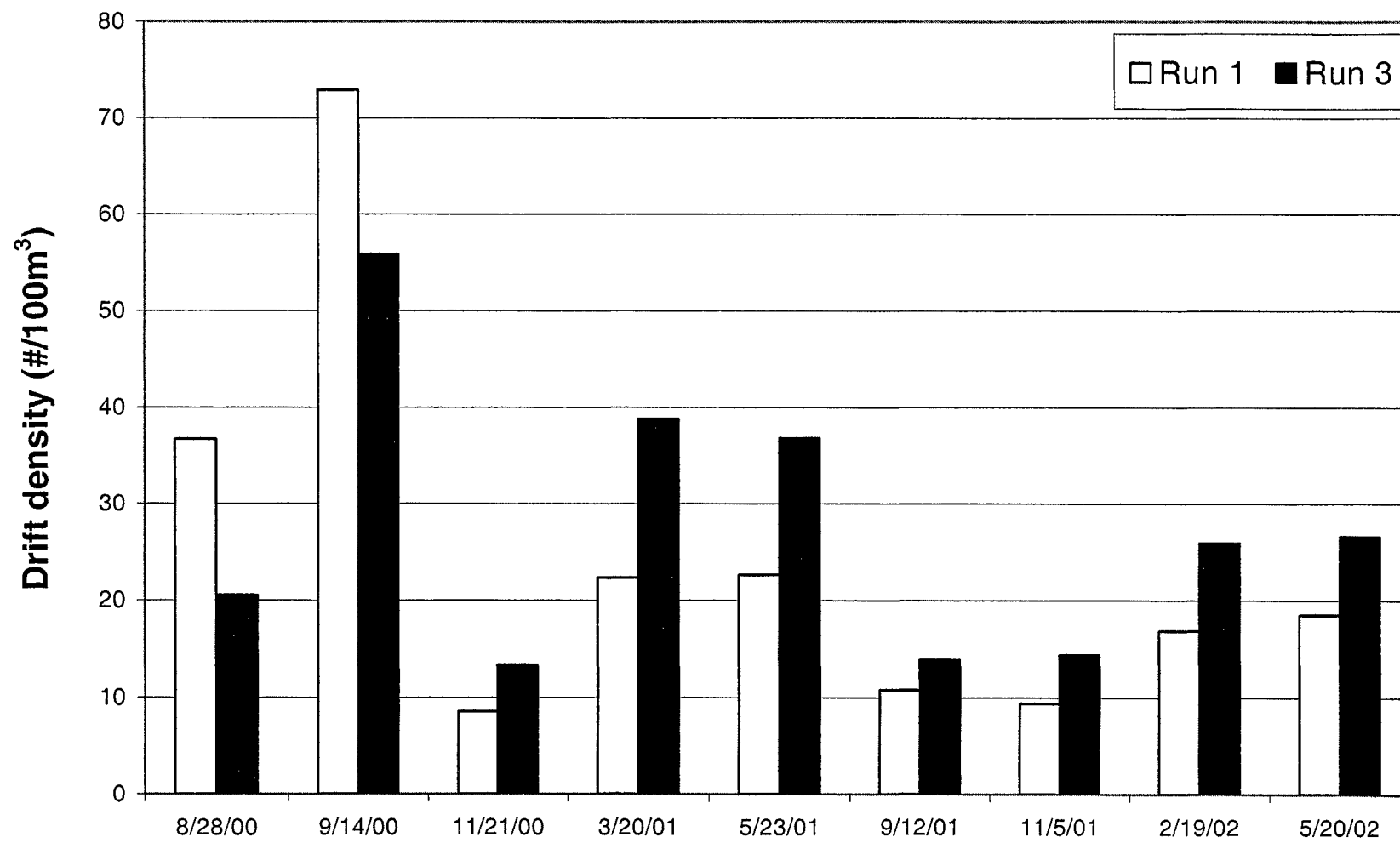


Figure 20. Drift density for both spring runs across all sampling dates.

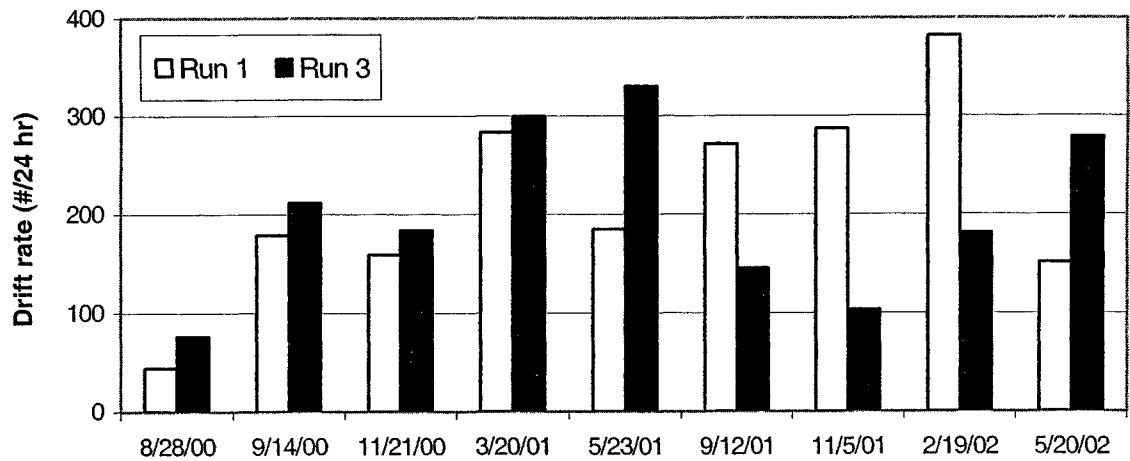


Figure 21. Drift rate for Elmidae adults and larvae in both spring runs across all sampling dates.

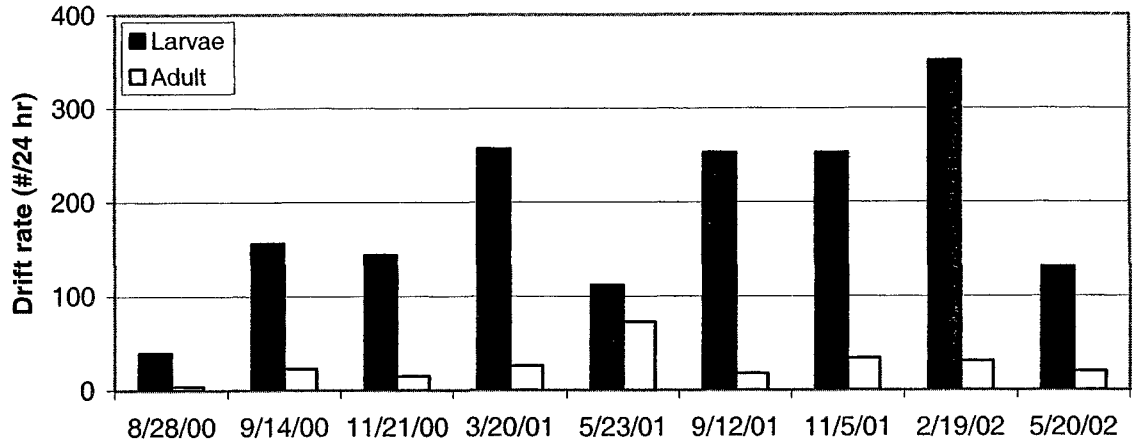


Figure 22. Drift rate for Elmidae adults and larvae in spring run 1 across all sampling dates.

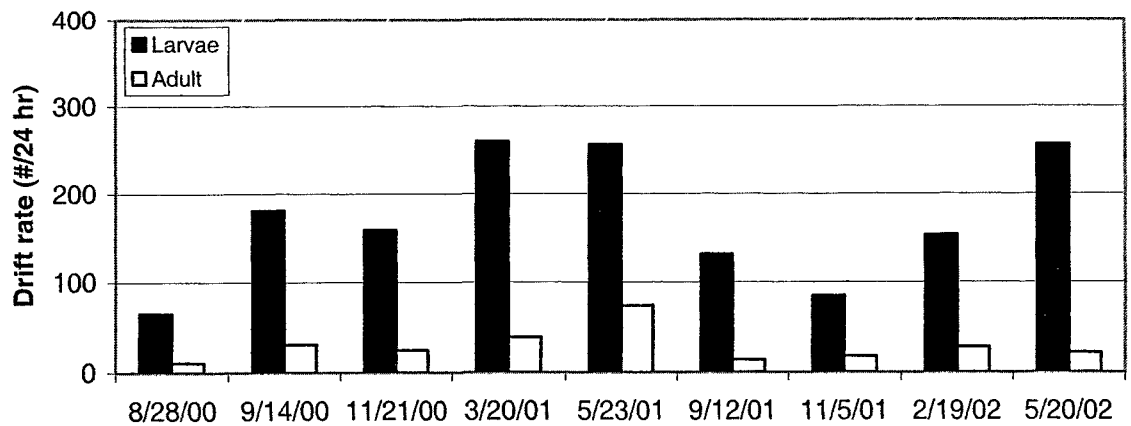


Figure 23. Drift rate for Elmidae adults and larvae in spring run 3 across all sampling dates.

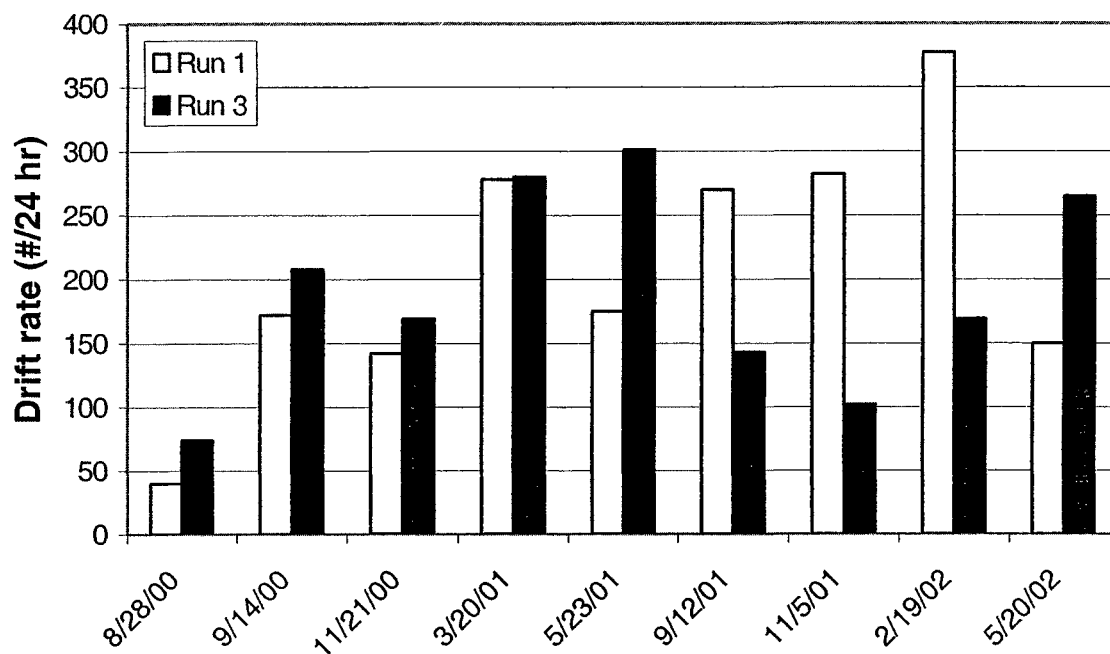


Figure 24. Drift rate of *M. pusillus* for both spring runs across all sampling dates.

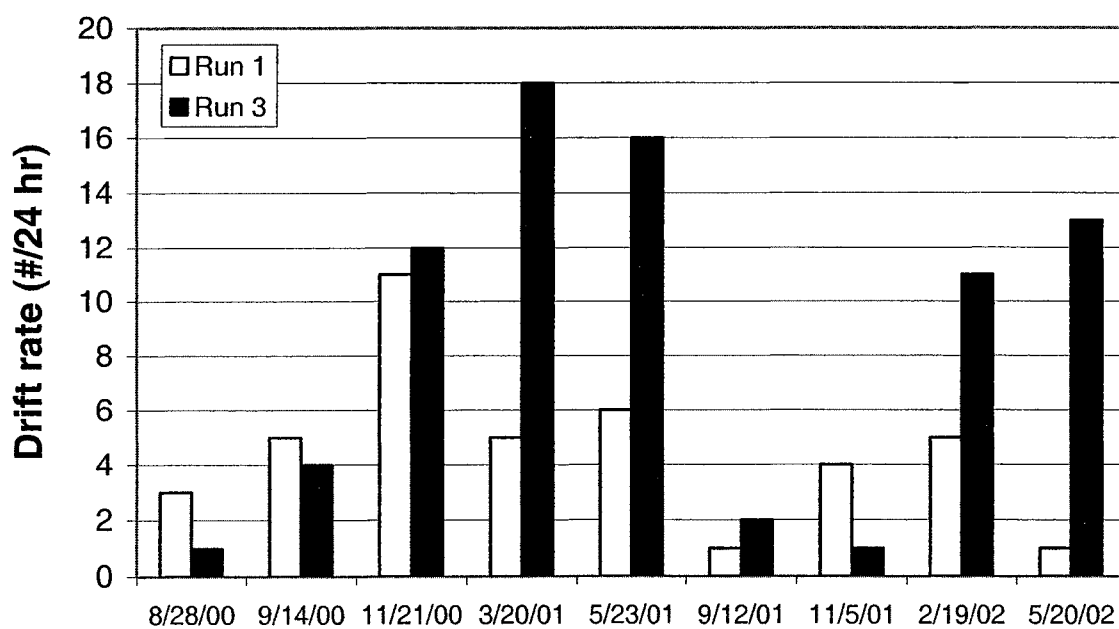


Figure 25. Drift rate of *H. comalensis* for both spring runs across all sampling dates.

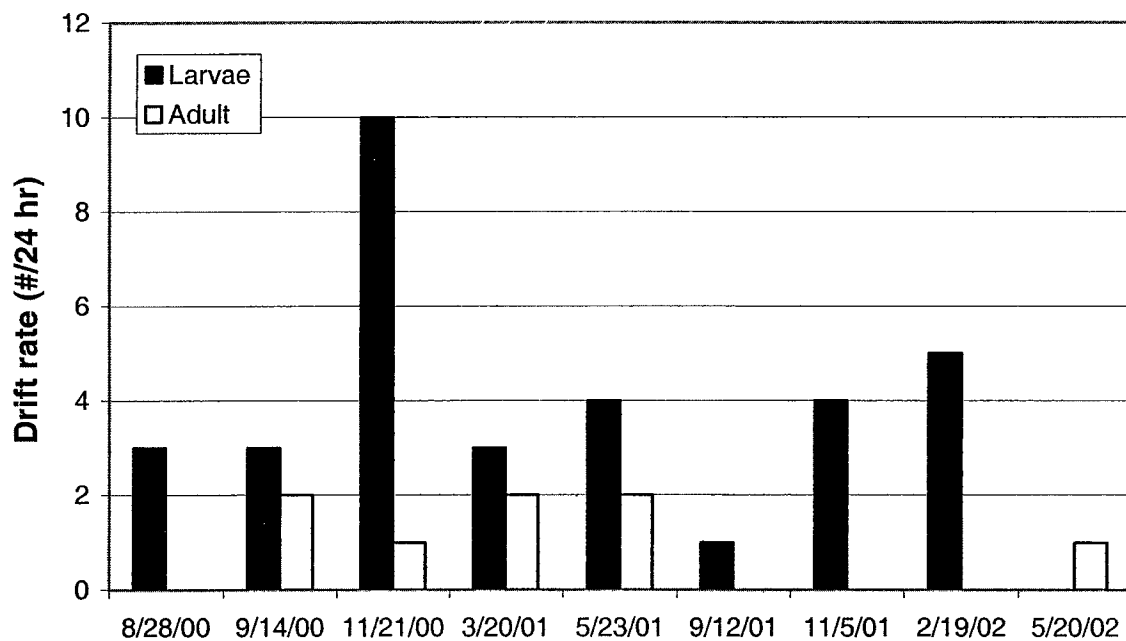


Figure 26. Drift rate for *H. comalensis* larvae and adults in spring run 1 across all sampling dates.

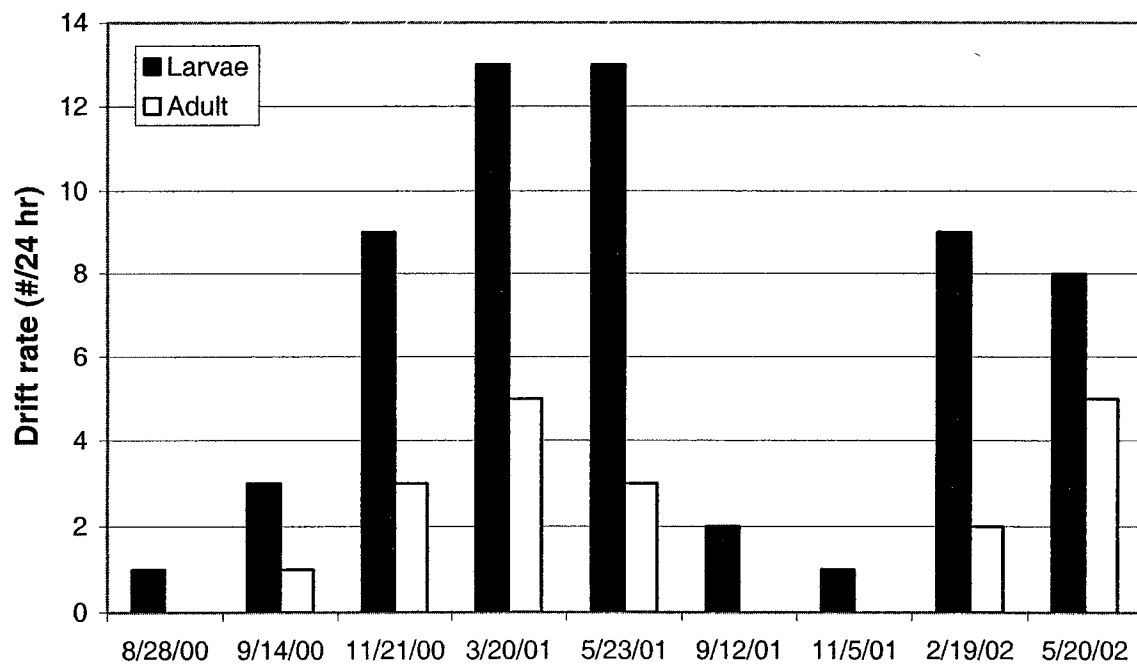


Figure 27. Drift rate for *H. comalensis* larvae and adults in spring run 3 across all sampling dates.

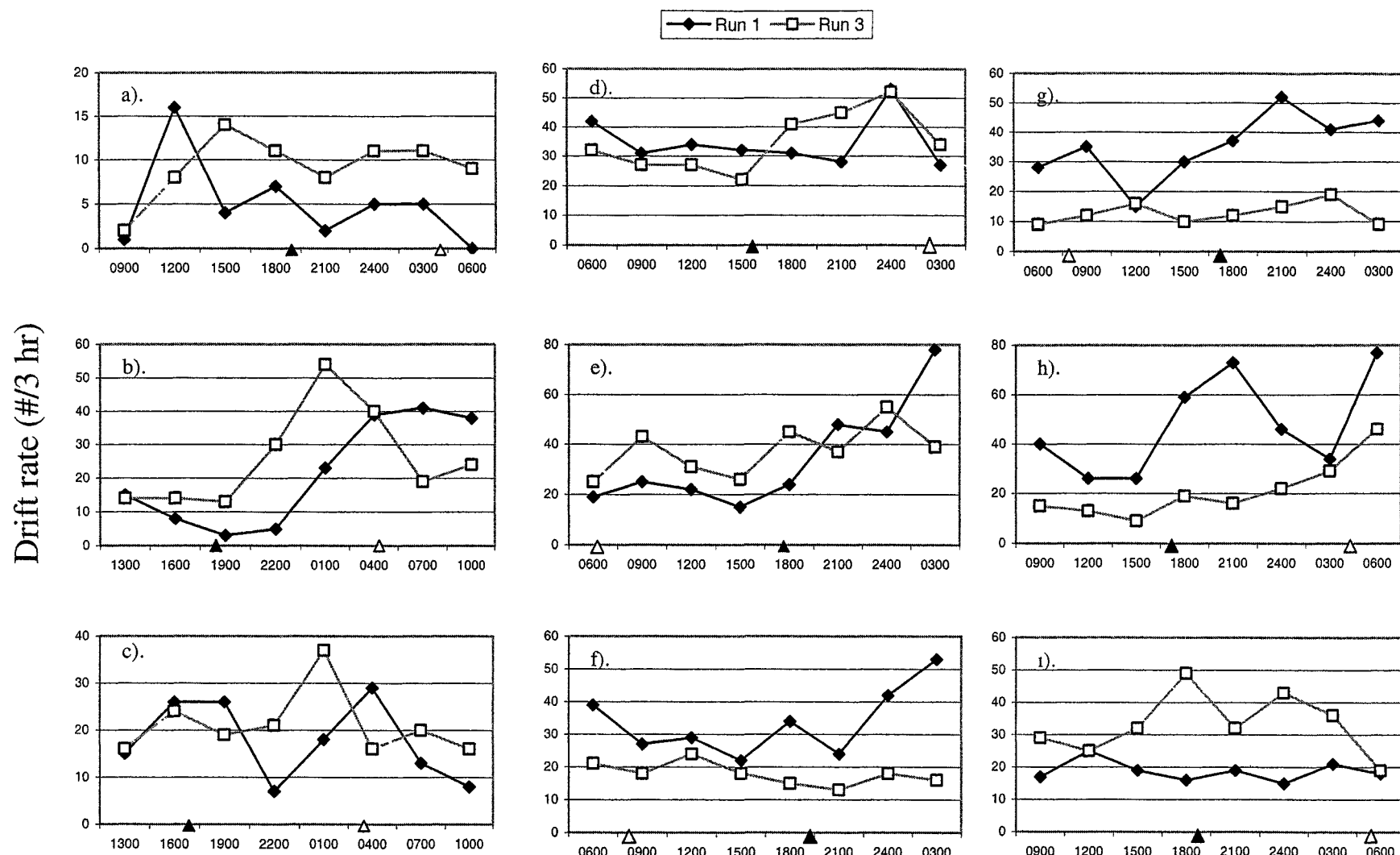


Figure 28. Diel drift rate for *M. pusillus* in both spring runs on (a) 28 August 2000, (b) 14 September 2000, (c) 21 November 2000, (d) 20 March 2001, (e) 23 May 2001, (f) 12 September 2001, (g) 5 November 2001, (h) 19 February 2002, and (i) 20 May 2002. ▲ - indicates sunset, △ - indicates sunrise.

VITA

Chad Norris was born in Richmond, Virginia, on September 30, 1971, the son of Faith Ann Norris and Robert William Norris Jr. He attended the University of Houston and graduated summa cum laude with a Bachelor's degree in Environmental Science in 1999. In 1998 he began working for the Texas Parks and Wildlife Department performing various forms of sampling and maintaining water quality instruments along the Upper and Central Texas Coast. While attending graduate school at Southwest Texas State University, he worked both as a research assistant for Dr. Arsuffi and for the Water Resources Branch of the Texas Parks and Wildlife Department in Austin.

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