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Mikel J. Shakarjian
The University of Montana

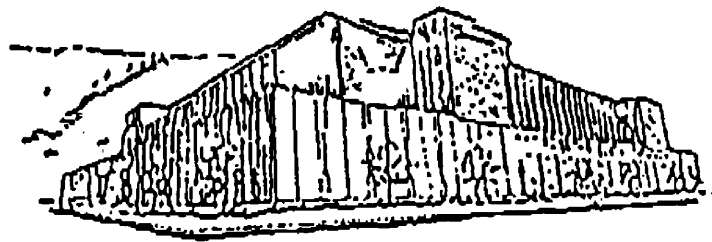
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**LIFE HISTORY AND DISTRIBUTION OF A RARE STONEFLY,
*ISOGENOIDES ZIONENSIS (PLECOPTERA: PERLODIDAE),***

**IN RELATION TO
EXTREME ENVIRONMENTAL VARIATION**

By

Mikel J. Shakarjian

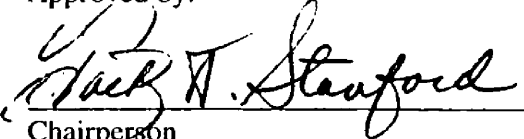
B.S. State University of New York, College of Environmental Science and Forestry

Presented in partial fulfillment of the requirements
for the Master of Science

UNIVERSITY OF MONTANA

1997

Approved by:


Chairperson


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Life History and Distribution of a Rare Stonefly (*Isogenoides zionensis*) in Relation to Extreme Environmental Variation

Committee Chair: J.A. Stanford



Isogenoides zionensis can be collected throughout the southwest; however, it is rarely reported in abundance. Within the N. F. Virgin River, *I. zionensis* was found in densities up to 110/m². Water development projects planned upstream of Zion National Park stimulated research on this species and its relationship to temperature and discharge, variables likely to be altered by regulation. The objectives of this study were to: i.) determine the life history of *I. zionensis* in relation to temperature and discharge, ii.) evaluate the role of temperature as an emergence cue, and iii.) characterize the distribution within the upper Virgin River basin and identify differences in the thermal regime, growth or abundance among sites.

Monthly collections revealed *I. zionensis* has a univoltine life cycle, no egg diapause and an extremely synchronized emergence. Discharge is unpredictable on both an annual and daily basis, as influenced by annual snowpack and flashfloods. The highly synchronized emergence suggests discharge does not have a direct observable influence on the life cycle. Discharge is likely related as it may influence instream temperatures.

The response of mature nymphs reared at constant temperatures showed the emergence cue for this species is not related to the average daily temperature, the accumulation of degree-hours or an absolute temperature. Experimental results and emergence under ambient conditions suggest emergence synchrony was related to diel periodicity.

The distribution of *I. zionensis* in the upper Virgin River extends from the headwaters through the rhitron-potomon transition, which encompasses a wide range of biophysical conditions. Sites exhibited similar average daily temperatures and seasonal heat accumulation; however, diel amplitudes varied among sites (range: 16.8-5.0°C).

Longitudinal differences in abundance was likely related to substratum, productivity and other factors including the thermal regime. Differences in growth rates of *I. zionensis* between sites was related to diel variation. Temperature duration curves illustrated differences in the thermal regima associated with the diel periodicity. The downstream distribution of this species was related to the cumulative effect of time spent at potentially lethal or metabolically costly temperatures.

Reservoirs in the headwaters of the N.F. Virgin River and subsequent flow regulation would have altered the thermal regimes that control the emergence, growth and distribution of *I. zionensis*. Partly as a result of this research, *I. zionensis* and the riverine resources of Zion National Park are protected in perpetuity by a Federal Reserve Water Right (1997)

PREFACE

Water is considered one of our most valuable resources. In the United States, nowhere is this resource more coveted than in the desert environment of the southwest. The human legacy includes silt-filled reservoirs, dewatered rivers, and declining biodiversity (Minckley and Deacon 1991). The smaller drainages that until recently have remained largely intact, are now coveted for their water. The Virgin River system in southwestern Utah is a good example. Many of the tributaries to the lower Virgin River already have dams in place and the mainstem is heavily diverted in several locations. Because localized growth is predicted for the headwaters region and alternative water sources are lacking, the North and East Forks of the Virgin River are at risk of flow manipulation.

The problems associated with river regulation have been extensively studied. Dams and diversions disrupt the continuity of a river ecosystem and can serve to alter every physical, chemical and biological characteristic of a lotic system (Ward and Stanford 1979). In the Virgin River system, the impacts of past mistakes are clear. Many native fish species have been extirpated and the populations that remain are fragmented (Deacon 1993). However, the North Fork of the Virgin River in the vicinity of Zion National Park, is minimally affected by anthropocentric change and native species dominate the fish assemblage (Deacon 1993). In addition, a rare stonefly, *Isogenoides zionensis* (Plecoptera) inhabits the North and East Forks of the Virgin River. Insects as

well as other aquatic biota, are extremely sensitive to changes in river conditions, especially temperature, one of the major variables that may be affected by river regulation.

Negotiations to adjudicate a Federal Reserve Water Right for Zion National Park (ZNP) began in 1993. The issue was contentious because the State of Utah proposed to construct several reservoirs at the upstream end of the Park boundary. Construction of the impoundments would help satisfy the increasing demand for water by the growing city of St. George, almost 128 kilometers (80 miles) downstream, by using the N.F. Virgin River through ZNP as a conduit. The boundary of Zion National Park does not extend to the headwaters and water rights predating the park existed upstream. The combination of the ever growing demand for water and its scarcity in this region, coupled with the existence of senior water rights above the Park's boundary, provided the backdrop for a legal battle between the state and the federal government over water.

In order to evaluate the potential impacts of water regulation on the terrestrial and aquatic resources of ZNP, many scientific experts, including Dr. Jack Stanford, my advisor, were gathered together by the Park Service to present their opinions and empirical data on the State's proposal. Based on the information provided by the scientific review panel, it was determined that proposed reservoirs would have a significant impact on the Park's resources.

The strength of the federal case was based on strong scientific information and an out-of-court settlement was reached. Negotiations concluded with the adjudication of a Federal Reserve Water Right for ZNP (1997), that allowed the construction of several

very small impoundments on the East Fork of the Virgin River. These small impoundments will have no measurable effect on flow or other important biophysical attributes of ZNP.

Stoneflies are widely recognized for their usefulness as biological indicators due to their sensitivity to environmental conditions. The rarity of *I. zionensis* throughout its range and its abundance within the N.F. Virgin River suggested that conditions within the Park are optimal for this species. Research on *I. zionensis* began in 1994, in an effort to provide Zion National Park with basic information of the life history of this species and its response to temperature and discharge, two critical variables that would be altered by water regulation. Based on the results of my research, water regulation, due to its influence on temperature would have risked the viability of this rare population. The Federal Water Rights Agreement for Zion National Park signed in 1996, will serve to protect this unique system and the biotic life associated with it.

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INTRODUCTION

The upper Virgin River watershed lies within the canyonlands of the southern Rocky Mountain region, an area characterized by abrupt environmental gradients and a high level of endemism. The variation in topography creates distinct lotic environments associated with the high desert plateau and deep narrow canyons. Covering an altitudinal gradient of 1140m (3740ft.), conditions in the North Fork of the Virgin River would be considered extreme by most biotic standards. Organisms must cope with dynamic regimes including intense flashfloods that can alter streamflow by several orders of magnitude and drastic temperature fluctuations as high as 16.8°C in a single day. Within this unique environment, in the vicinity of Zion National Park, a rare stonefly with broad zoogeographical distribution, *Isogenoides zionensis* (Plecoptera: Perlodidae), exists in the canyon influenced environment

The life history characteristics of aquatic insects can vary among individuals or populations in response to environmental factors (Butler 1984). The most significant factor may be the thermal regime, which can influence distribution and abundance on both local and geographical scales (Ward and Stanford 1982). Insects as well as other aquatic biota are extremely sensitive to changes in river conditions, especially temperature, one of the major variables that may be affected by river regulation. Water development projects planned upstream of Zion National Park stimulated this study on the life history, distribution and abundance of *Isogenoides zionensis* in relation to

temperature and discharge in the upper Virgin River, the variables most likely to be significantly altered by water regulation.

Widely distributed, members of the family Perlodidae demonstrate the ability to adapt and sustain populations in a vast array of environments. This family includes species that inhabit subalpine lakeshores in Norway, spring brook streams in Michigan, montane streams, large silty rivers and desert streams in the southwest USA (Sheldon 1972, Baumann et al. 1977, Brittan 1983, Haro and Wiley 1992). Twenty-two out of the 27 Perlodid genera found in North America are considered endemic, and many are purely eastern or western in distribution (Hynes 1988).

Members of genera *Isogenoides* exhibit continentality (distributed across North America) suggesting that this genus may be derived from ancient invaders. Many species in this genus appear to be restricted to the east or west coast, indicating speciation may have resulted from isolation during or since the Pleistocene glaciation (Stewart et al. 1974, Hynes 1988). The Colorado cordillera region has been identified as part of a southwestern refugia for Plecoptera during glaciation, after which many populations became isolated (Stewart et al. 1974). Of the three Rocky Mountain species, only *I. zionensis* appears to be confined to the southern Rocky Mountains of the Colorado cordillera.

The rarity of *I. zionensis* within its range (Ward and Kondratieff 1992) suggests this species became geographically isolated as the post-Pleistocene climate became increasingly warmer and dryer. As the proportion of favorable habitat within its range

decreased, the limited dispersal capabilities of *I. zionensis* may have assisted localized specialization and adaptation to the native regime.

Plecoptera are widely recognized for their use as biological indicators due to their sensitivity to environmental conditions. Because Plecoptera are considered such sensitive representatives of the aquatic fauna, rarely does one expect to find these taxa in areas experiencing severe environmental variation. In the upper N. F. Virgin River, *I. zionensis* was found in abundant numbers (up to 110/m²), exhibiting a patchy distribution in the Virgin River watershed (Fox and Eddy 1977, Boyle et. al 1993), highly associated with the canyon influenced environment. Populations of this species are rare, but widely distributed across the Colorado Cordillera region (Ward and Kondratieff 1992). The abundance of *I. zionensis* in the N.F. Virgin R. watershed suggests that current conditions are optimal for perpetuation of this species in the canyon influenced environment.

The environmental variability experienced by aquatic insects acts as a selective pressure influencing the life history and distribution of a species. The response of aquatic insects to their environment includes life history traits that are advantageous within a particular habitat and promote species persistence under the conditions at which they evolved. For example, droughts and flashfloods commonly occur in desert streams. Life history adaptations to desiccation and scour include nondiapausing eggs, rapid development and continuous reproduction (Gray 1981). Life history traits can also vary

intraspecifically among populations in response to localized environmental conditions (Lillehammer 1987, Sweeney 1984, Frutigar 1996). For this reason, the variability of environmental regimes is often thought of as a driving factor in the life history of aquatic insects (Ward and Stanford 1982, Sweeney 1984, Power et al. 1988, Resh 1988).

Of the ecologically significant environmental factors that influence aquatic insects, the most important may be the thermal regime¹(Ward and Stanford 1982). A wide range of responses to temperature have been identified for a number of plecopterans, usually under constant, experimental conditions. This literature suggests that temperature can influence any phase of the life cycle; the success and timing of embryogenesis, nymphal growth, adult development and emergence (see Nebeker and Gaufin 1967, Markarian 1980, Lillehammer et al. 1989, Marten 1991, Marten and Zwick 1989). Some insects respond to absolute temperature units (i.e. degree days or specific temperature) while others appear to exhibit temperature independence during embryogenesis or nymphal development (Khan 1965, Mutch and Pritchard 1986). Recent evidence suggests that fluctuating thermal regimes may also influence the life cycle processes at various stages (Sweeney and Schnack 1977, Lillehammer et al. 1991, Frutigar 1996). However, very little research has focused on the temporal variability of the thermal regime and its consequences for life cycle strategies or adaptation.

¹ Thermal regime is used in this paper as defined by Ward and Stanford (1982): a composite of patterns including absolute temperatures, diel and seasonal amplitudes, rates of change and all phase relationships.

The response of insects reared under constant versus fluctuating temperature environments is usually found to be different (Hagstrum and Hagstrum 1970, Ratee 1985). Enhanced growth and development under a fluctuating thermal regime appears to be species-specific and may differ among populations. Unfortunately, the majority of experiments incorporating a fluctuating regime in the design, fail to describe the native thermal regime of the experimental population (Humpesch 1982, Elliott 1988, Zwick 1996). Without this information, it is impossible to determine if the thermal history of the organism or population includes exposure to a dynamic temperature regime. Experienced on a predictable basis, temperature fluctuations could provide a selective pressure prompting a life history response or adaptation (Newell 1973). The thermal history of an organism may help explain the varied responses of a species or population to a fluctuating temperature regime.

Thermal variability, both seasonal and diel, may be incorporated into an organisms' response to temperature, providing a thermal cue for specific life history stages or events (Ward and Stanford 1982). The response of an organisms to either temporal scale may be influenced by the thermal history of the organism (Peters et al. 1987). For example, in an environment where temperatures fluctuate dramatically on a daily basis, this level of variability may be incorporated into a species-specific thermal cue. Furthermore, the mean temperature of a thermally dynamic environment may represent the temperature insensitive phase for organisms adapted to a fluctuating regime (Hoffmann 1985). Hence, physiological cues and metabolic adaptations to dynamic

temperature regimes may manifest at the extreme ends of the variation (daily or seasonal) (Hoffmann 1985, Huey and Bennett 1990).

Within the canyonlands of the Virgin River, temperature patterns are highly influenced by the climate and topography. Seasonal and diel temperature fluctuations within the range of *I. zionensis* are dramatic and may be incorporated into this species response to temperature. Virtually nothing is known about the life history of *I. zionensis* or the environmental factors that influence its longitudinal distribution in the upper Virgin River system.

Lotic characteristics of the river continuum are often utilized to differentiate between the unique and ecologically significant rhithron and potomon environments within the longitudinal profile (See Illies and Botosaneanu 1963, Ward 1986, Ward and Stanford 1991, Stanford and Ward 1993, Stanford 1994). The rhithron environment typically includes low to mid-order streams with coarse substratum, cool temperatures (<20°C) and high water velocities. Potomon reaches are characterized by warmer (>20°C), lower velocity waters with small substrate and often turbid waters (Ward and Kondratieff 1992). These habitat characteristics vary as a function of environmental gradients, creating ecologically significant spatial variations that may influence the longitudinal distribution of species.

The purpose of this paper is to evaluate the role and consequences of natural environmental variability, especially the thermal regime, on the distribution and life history of *I. zionensis* in the upper Virgin River basin. The phenology of *Isogenoides*

zionensis, in relation to temperature and discharge, was evaluated at a single location, Big Bend, in Zion National Park (Fig. 1). The distribution and relative densities of *I. zionensis* throughout the Upper Virgin River Basin were determined by quantitative sampling at sites along the elevational gradient. The relationship between distribution and the thermal regime was evaluated using temperature data gathered at several locations including sites within and outside the range of this species. Two experiments were conducted on mature nymphs near emergence to determine the role of temperature on this event. In the first experiment, nymphs were exposed to a constant temperature simulating the mean daily temperature during emergence in the field. In a second experiment, nymphs were exposed to a constant temperature simulating the daily minimum temperature at time of collection. I assumed this temperature would mask any further thermal cues associated with seasonal or daily temperature fluctuation.

STUDY AREA

The North and East Forks of the Virgin River originate in the high desert plateau country of southwestern Utah, forming the headwaters region of the Virgin River (Fig. 1). At their confluence, the North and the East Forks are fourth order streams (*sensu* Strahler 1957) that drain large watersheds, 569.7 km² and 658.2 km² (354 mi² and 409 mi²), respectively (Diaz 1992).

The study area is considered semiarid; however, local precipitation patterns vary significantly as influenced by topography and climate (Heilweil and Freethey 1992). Precipitation patterns in the study area follow a central north-south orientation of decreasing precipitation from 68.5 to 25.4 cm (27 to 10 inches) annually, following the topographic gradient as the high desert mesas dominating the north central region give way to the lower elevation alluvial valleys in the canyons of the southern portion.

The high desert plateau is characterized by colder and wetter seasons, with average air temperatures near or below freezing from mid-November through March (-3.2-0.9°C) reaching an annual high of 17-19°C during July and August (Alton Weather Station, NCDC420086, U.S. Historical Climatology Network 1997). In contrast, in Zion Canyon the valley floor rarely experiences winter temperatures below 4°C (Zion N.P. Weather Station, NCDC429717, U.S. Historical Climatology Network 1997) and receives significantly less snowfall, due to the low elevation and surrounding topography. Summer air temperatures in the valley regularly fluctuate 20°C daily, with maximum

daily temperatures from June through September of over 38°C (100°F).

Seasonal stream temperatures within the study area reflect both the altitudinal gradient, climate and topography. During the winter, the exposed, high elevation sites on the North Fork may experience temperatures at or near freezing for several months, whereas in the valley, temperature data indicates stream temperature rarely fluctuates below 5°C. Vernal warming may also occur sooner in the valley, delayed at higher elevations due to the cooler climate and snowmelt.

A snowmelt hydrograph may dominate the discharge pattern of the N.F. Virgin River in some years; however, in low water years, a snowmelt event may not occur (Fig. 2). The magnitude and duration of the spring runoff event is dependent upon annual snowpack and the rate of vernal warming. The spring runoff period can occur from late March through early June, providing the bulk of the mean annual flow (96.9hm³/yr or 78,600 ac-ft/yr) and transporting 80% of the average annual sediment load (Andrews 1994, Hereford et al. 1995).

The annual peak flood can occur any time of the year and equal or exceed the magnitude of the spring runoff event. The annual flood most frequently occurs in the summer and is of short duration (Hereford et al. 1995). Seasonal precipitation events during the summer, fall or winter may determine a high water year and have significantly declined during the period of record (Hereford et al. 1995). It appears that the frequency of these seasonal events has declined over time, rather than the magnitude of individual storms.

The N.F. Virgin River originates from a spring at approximately 2295m (7,530ft.) in elevation, flowing a total of 40 km (35.6 miles) through the rhyolite-potomian transition before its confluence with the East Fork at approximately 1149m (3770ft.) in elevation (Pacific Southwest Inter-Agency Committee 1974). The watershed of the North Fork is relatively undisturbed. For most of its length, the North Fork is within the boundaries of Zion National Park, excluding the first 16 kilometers (10 miles) where ownership is a composite of Bureau of Land Management, Forest Service and private lands. Below the park, the river is surrounded by the town of Springdale. One impoundment exists on a small tributary, Kolob Creek; however, it does not affect the historic discharge regime (Hereford et al. 1995) and its effect on streamflow in the North Fork appears negligible under normal dam operating conditions. Small diversions above and below the Park account for 3.7% of the mean annual flow (Diaz and Hansen 1994).

For the majority of its length, the North Fork exhibits rhyolite characteristics, as it flows through a deeply incised canyon, commonly known as the "Virgin River Narrows" (Fig. 1). Within the Narrows, the vertical canyon walls reach approximately 304m (1000ft.) overhead. Areas exist where the river is completely bound by canyon walls only 10-30 meters apart and stream gradients are in excess of 10%. As the North Fork meanders through wider areas, riparian vegetation is present on high terraces.

Substratum in the canyon is highly variable, influenced by stream gradient and valley width. Riffles are dominated by sandstone cobbles (20-30cm) with some gravel. Large boulders (1-6m) broken free from the canyon walls, create deep pools. In the

narrowest sections of the canyon, long, deep glides of sand substrate are created. Stream gradient is steep (28.7m/km) and high intensity, short duration flashfloods are common. The deep canyon provides significant shade, creating a cool environment at a low elevation.

The canyon walls gradually begin to widen in an area known as "Zion Canyon" (RM12.2), 0.8 river kilometers (0.5 river miles) upstream of the main study site at Big Bend (RM11.7, Fig. 1.). The floodplain at Big Bend is approximately 500m wide and well shaded due to the height of the canyon walls. The active channel is approximately 20m wide with stabilized segments on the east side to support Zion Canyon Drive. To the west of the active channel lie historic channels and terraces. Substratum at Big Bend is mostly large cobble (25 cm) with some gravel. A large spring, known as Menu Falls, is approximately 60m upstream and groundwater seeps are common along the margins of a midstream island. The Big Bend site is located 19 river kilometers (11.7 river miles) upstream of the confluence with the East Fork Virgin River.

Under baseflow conditions the North and East Forks are relatively clear, indicating that sediment transport at this time is low. However, both streams carry a high silt load during spring runoff and flashflood events, causing the water to become very turbid rather unpredictably, due to abrupt changes in discharge. In addition, the Narrows and Zion canyons are composed of highly erodible sandstone that occasionally sloughs off, depositing large quantities of rock in the river channel. Within Zion Canyon, approximately 2.4 river kilometers (1.5 river miles) downstream from the Big Bend site,

an active landslide area exists. Historically, this area was responsible for the creation of a lake after a large rockfall dammed the North Fork forcing water to back up into the canyon past the Big Bend site (Hereford et al. 1995). Within the last 100 years, at least 3 major rock slides have occurred in this area (Cline 1995). The most recent slide occurred in April of 1995, depositing over 7079 cubic meters (250,000 cubic-feet) of material in the riverbed. This slide temporarily dammed the river to a depth of approximately 12.1m (40ft.), forcing the river to break through the debris flow, and washing out over 182m (200 yards) of roadway (Cline 1995).

The East Fork of the Virgin River starts at an elevation of approximately 2,500m (8202ft.) in elevation and flows 76km (46 miles) through agricultural, urban and residential lands in an unconfined valley for the majority of its length (Fig. 1). The East Fork enters Zion National Park just 16 river kilometers (10 river miles) upstream from the confluence with the North Fork, as it flows through the constricting Parunaweap Canyon. Agricultural, domestic and municipal water demands result in extensive dewatering upstream from the Park at Mount Carmel (Fig. 16) (B. Hansen, Pers. Comm 1995). Much of the flow downstream from this point is attributable to groundwater accretion associated with the Navajo Aquifer, contained in the Navajo Sandstone Formation.

The Navajo Sandstone Formation is a porous and fractured formation confined by the less permeable overlying Carmel Formation and the underlying Kayenta Formation. As a result, vertical groundwater movement is impeded and discharge from the Navajo Aquifer is associated with exposed outcrops and deep canyons throughout the study area

(Heilweil and Freethey 1992). Navajo Sandstone is the dominate rock surface in the Narrows, Zion and Parunaweap Canyons, providing baseflow for each river from numerous springs and seeps (Hereford et al. 1995).

METHODS

FIELD STUDY

Discharge: North Fork Virgin River at Visitor Center (RM5.0)

Discharge data for the N.F. Virgin River was obtained from a U.S. Geological Survey gauge installed at Visitor Center site (USGS 09405500) within Zion National Park. Discharge data was used to characterize the hydrologic regime of the N.F Virgin River and the Big Bend site during the study period. Due to the lack of any major tributaries between the Big Bend site and the Visitor Center discharge station, any increase in flow was considered insignificant.

Thermal Regime: North Fork Virgin River

Temperature data from the Big Bend (RM11.7) site was collected using StowAway temploggers (Onset Instruments®) placed in the stream to continuously monitor ambient conditions. Dataloggers recorded temperatures every 45 to 120 minutes and were downloaded every 4-6 months. Data was then interpolated to give estimates of hourly temperatures at the site. Harsh flow conditions at Big Bend resulted in the loss of a datalogger during Spring 1995, limiting the temperature data to July 1995 - October

1996.

In April 1996, StowAway temploggers were installed at two additional locations on the North Fork: North Fork above Narrows (RM26.8) and the Visitor Center (RM5.0) sites. Continuous temperature data were collected from these sites, April 11-August 31, 1996 and interpolated to estimate hourly temperatures at each site. Total degree-hours (dhrs) were calculated for Big Bend, N.F. above Narrows and the Visitor Center sites by summing the average hourly temperature for each day.

FIELD STUDY

Life History of Isogenoides zionensis at Big Bend

The life history of *Isogenoides zionensis* was evaluated at a single location, Big Bend (RM11.7), in Zion Canyon (Fig. 1). This site was chosen due to the abundance of *I. zionensis* at this location, ease of access and the availability of discharge records from a nearby location.

Benthic organisms were collected by Park Service employees at approximately monthly intervals from November 1993 to July 1996 using a hand held dip net. Collected specimens were preserved in 10% formalin and ethyl alcohol and shipped to the University of Montana Flathead Lake Biological Station for evaluation. Interocular

distance (to nearest .05mm) was measured to evaluate growth and approximate the hatch time of *I. zionensis* at Big Bend. Emergence timing was determined by checking the site frequently near the expected time of emergence activity.

A total of 459 *I. zionensis* adults (231 female, 228 male) were collected from the Big Bend site on May 8, 1996 and shipped to the Biological Station. Adults were placed in screened cages for observation, with vegetation and petri dishes filled with water.

A reference collection of all benthic organisms found during this study within Zion National Park has been provided to the park and voucher specimens stored in a permanent collection at the Flathead Lake Biological Station.

Distribution, Density and Size of Isogenoides zionensis within North Fork Virgin River.

In September 1995, quantitative sampling at twelve sites throughout the North and East Forks was completed to determine the distribution and relative abundance of *Isogenoides zionensis* in the basin. Riffles representative of each site location were chosen and zoobenthos were collected from a 0.25m² area by dislodging the organisms with hand and foot action into a modified Nitex (240um pore size) kicknet held downstream (after Hauer and Stanford 1981). A total of three replicate samples were collected from each site and preserved in 10% formalin and ethyl alcohol. *Isogenoides zionensis* were removed from each sample, enumerated and interocular distance measured, to reveal any significant difference in abundance or size among sites. Students

t-test was used to determine the significance of seasonal size differences among sites on various sampling dates. Observations from each site include stream width and depth, periphyton biomass and benthic community characteristics (Table 1).

LABORATORY STUDY

*Effect of Temperature on the Emergence of *Isogenoides zionensis**

Late stage nymphs were collected 4 weeks prior to emergence, on April 10, 1996, from the Big Bend site and transferred to the wet laboratories at the University of Montana Flathead Lake Biological Station. Nymphs were divided between two artificial lotic microcosms, acclimated and then exposed to experimental temperatures within the diel range of variation normally experienced by this species. Temperature data and monitoring of emergence activity at Big Bend provided a reference under ambient conditions.

The experimental troughs were approximately 2.0 x 0.3 x 0.3m (7x1x1ft.) in dimension and lined with a natural cobble substrate. Styrofoam pieces, woody debris and exposed cobbles provided potential terrestrial habitat for emergence. Troughs were enclosed by screen mesh and fashioned with sealable hatches, used to collect adults and add food. Benthic organisms and allochthonous matter from nearby Yellow Bay and Roy's Creeks provided the main food source for each trough. To ensure food was

abundant and favorable, additions were made at least every other day and feeding activity was observed at night using a red light source.

Water for the troughs was supplied using untreated, potable water piped into the laboratory from a spring on the Biological Stations grounds. The spring provides a thermally stable water source with dissolved oxygen levels at or above saturation year round (Stanford 1975). In each trough, a continuous flow-through of water was maintained at a depth of 12.5cm (5in.) from an water inlet at the upper end of the trough and a screened drain at the opposite end.

Water temperature in each trough was recorded every 15 minutes using Hobo temploggers (Onset Instruments®) and adjusted using hot and cold taps. Photoperiod in the wet lab was regulated at 12 hour light and dark intervals. Each trough was checked daily for behavioral activity, signs of nymph emergence (exuvia), adults and mortalities. Nymphs were carefully observed for four days to ensure acclimation to the trough environment prior to the experimental manipulation of temperature.

Once the nymphs were acclimated, two separate experiments were performed. In Experiment A, two hundred and sixty two nymphs were exposed to a gradually increasing constant temperature simulating the average daily temperature during emergence at Big Bend ($14.5 \pm 0.5^{\circ}\text{C}$) in 1996. I assumed this temperature regime would provide the proper emergence cue. In Experiment B, one hundred and eighty nymphs were exposed to a relatively constant temperature ($8.7 \pm 1.0^{\circ}\text{C}$) simulating the daily minimum

temperature experienced at Big Bend at the time of collection. The constant cold temperature was assumed to mask any further environmental cue associated with vernal warming. Total degree hour accumulation at the time of 50% emergence was calculated for both the experimental population and the control population at Big Bend.

RESULTS AND DISCUSSION

Hydrograph of the North Fork Virgin River 1995-1996

Water years 1995 and 1996 encompass the extreme flow variability that can occur within the N.F. Virgin River on both an annual and daily basis. A snowmelt hydrograph dominated the discharge pattern of 1995, with high flows occurring from early May through June (Fig. 2). In addition, several short duration, high magnitude flashfloods occurred. The most notable flashflood during the 1995 water year occurred on February 14, 1995, increasing the flow from 63 cfs ($1.78 \text{ m}^3/\text{s}$) on the previous day to 665 cfs ($18.83 \text{ m}^3/\text{s}$). In contrast, the hydrograph for the 1996 water year shows almost no spring runoff event and only one conspicuous flashflood, also occurring in February and of similar magnitude. Because the bulk of the annual flow was provided by the spring snowmelt event, the annual discharge for 1996 ($56,495 \text{ m}^3/\text{yr}$; $45,780 \text{ ac-ft/yr}$) was only 32% of the total volume discharged in 1995 ($172,192 \text{ m}^3/\text{yr}$; $139,540 \text{ ac-ft/yr}$). The discharge patterns from the 1995 and 1996 water years are significantly different; however, this level of variability is not uncommon in the N.F. Virgin River (Fig.3). Water years 1996 and 1996 are characteristic of typical high and low water years on the N.F. Virgin River.

A possible explanation for the variation in flows observed during the study period may be the influence of global climate patterns. Annual climatic patterns in the

southwestern U.S are influenced by the El Nino Southern Oscillation, which increase precipitation during the winter. These events are highly correlated with the spring runoff period, and have been shown to increase seasonal discharge by as much two to three orders of magnitude in some southwestern rivers (Molles and Dahm 1990). The longest duration El Nino event ever recorded occurred during 1990-1995, influencing weather patterns throughout western North America (Trenberth and Hoar 1996). In contrast, 1996 was not influenced by an El Nino event and may have been influenced by the opposite climatic event known as a La Nina. La Nina events have also been shown to be highly correlated with streamflow, significantly decreasing the spring runoff in the southwest (Molles and Dahm 1990).

Thermal Regime of Sites on North Fork Virgin River

From April to August 1996, the average daily temperatures at Big Bend (RM11.7), N.F. above Narrows (RM26.8) and the Visitor Center (RM5.0) sites showed only slight seasonal differences, despite an altitudinal difference of 680m (2230ft.) between the sites (Fig. 4). The daily average at the Above Narrows site was consistently lower than both downstream sites, as would be expected due to the difference in elevation (Table 1). However, during the study period, the Above Narrows site on average was only 1.5°C colder than the Big Bend site. A similar difference was observed at the Visitor Center site, where the daily temperatures averaged 1.3°C warmer than those at Big Bend.

Based on the spring and late summer temperatures from 1996, it appears these sites exhibit the least difference during July and August, the warmest months of the year.

Although the Above Narrows site was consistently colder on average, this site also experienced the highest maximum stream temperatures (Fig. 5). Daily maximum temperatures at the Above Narrows site normally exceeded those at Big Bend, and equaled or exceeded temperatures at the Visitor Center site (Fig. 5). During July and August 1996, maximum temperatures at the Above Narrows site averaged 23.9°C, in comparison to 20.9°C and 22.9°C at Big Bend and the Visitor Center sites.

Much of the difference in thermal regime observed among these three sites occurred as a result of diel fluctuations as influenced by elevation and the surrounding topography (Fig. 6). The lack of shade from steep canyon walls at the Above Narrows site allows direct insolation to raise stream temperatures rapidly during the day, while the high elevation results in night time cooling, resulting in a high average diel amplitude for the summer months (June 11 - August 31) of 12.1°C (Fig. 6). The maximum amplitude experienced at any site in a 24 hour period was a change of 16.8°C, at the exposed, high elevation Above Narrows site on July 27, 1996.

In contrast, as the North Fork flows downstream through the Narrows Canyon, temperatures are moderated by shading provided by canyon walls. This canyon-cool environment is reflected in the diel variation experienced at Big Bend (Fig. 6). The Big Bend site located just downstream 0.8 river kilometers (0.5 river miles) from where the canyon walls begin to widen, experiences the lowest of diel amplitudes of the three sites,

averaging 5.1°C during the summer season. In contrast, the Visitor Center, located only 10.7 river kilometers (6.7 river miles) downstream from Big Bend, exhibits an average diel amplitude almost 2°C greater (6.7°C) than Big Bend. Canyon walls still provide some shading at this location; however, the floodplain is much wider, exposing the channel to direct insolation for the majority of the day, allowing stream temperatures to rise accordingly. Due to the low elevation and greater volume of water at this location, night time cooling does not offset the high daytime temperatures, resulting in the highest average daily temperature among the sites and a reduced diel variation when compared with the exposed, high elevation site (Fig.4 and 6).

The variation in thermal regime among sites can be clearly illustrated using a frequency distribution, showing the duration or the total number of hours, spent at each temperature from April through August 1996 (Figs. 7 and 8). As would be expected because of the moderating influence of the canyon, Big Bend exhibits the narrowest range of temperatures ($6\text{-}25^{\circ}\text{C}$), with the majority of hours spent at or below 20°C . At both the Above Narrows and Visitor Center sites temperatures regularly fluctuate above this threshold. However, these sites exhibit completely different temperature patterns over time as influenced by diel variation. During the summer months when the daily average temperatures exhibit the least between site difference, they also display the greatest within site variation, due to the temporal pattern of the thermal regime at each location (Fig. 8). The majority of hours at the Visitor Center site are spent at stream temperatures above 20°C . In contrast, the variation in temperature and duration experienced at the

Above Narrows and Big Bend sites result in the majority of hours being spent at temperatures below 20°C.

Total degree-hour accumulations at each site also reflect the variability of the thermal regime among these sites (Fig. 9). Total degree hours accumulated at the Above Narrows site (49645dhrs) were almost 10% less than at the Big Bend site (55027dhrs). The Visitor Center site had the highest cumulative degree hours (59353dhrs) among the sites, almost 8% more than that of Big Bend.

Life History of Isogenoides zionensis at Big Bend, North Fork Virgin River

Isogenoides zionensis at the Big Bend site (RM11.7) had a univoltine life cycle (Fig. 10). This species did not exhibit egg diapause and growth was rapid immediately after the eggs hatched in May or June. Differentiation of the sexes could not be established until December or January, when wing pad development easily distinguished the sexes. Males were brachypterous and significantly smaller than the females. During the winter, as the growth of both sexes slowed, female wing development continued.

Newly hatched nymphs were very difficult to find during the first 12 weeks of growth (June, July, August). The density of *I. zionensis* at Big Bend seemed to increase over time, maximizing just prior to emergence in the spring. When sampling at Big Bend in April 1996, 3 weeks prior to emergence, a total of 64 individuals were collected from beneath a single cobble.

During 1995, rapid growth of *I. zionensis* occurred at Big Bend during the warmest time of the year (Fig. 11). Emergence was nocturnal and highly synchronized, from approximately May 5 - May 15, 1996 at the Big Bend site (Fig. 11). The average daily temperature during the emergence period of *I. zionensis* at Big Bend was 12.6-15.8°C (Fig. 11). In the lab, I observed the newly emerged adults drinking water and mating in vegetation or under litterfall in the cages. After mating for approximately 4-6 hours, females displayed avoidance behavior, placing their wings over their backs to discourage males from mounting. As air temperature in the observation room reached the daily maximum (approximately 23°C), females began flight patterns in the cages, ovipositing eggs for 2-3 hours. This behavior continued for 3-4 days until the female's egg supply was exhausted. The duration of the adult stage of *I. zionensis* was approximately 9 days, based on laboratory observations.

The univoltine life cycle, male brachyptery and sexual dimorphism exhibited by *I. zionensis* in the N.F. Virgin River are characteristics commonly reported among the Perlodidae (Minshall and Minshall 1966, Sheldon 1972, Cather and Gaufin 1975, Stanford 1975, Oberndorfer and Stewart 1977, Short and Ward 1980). Egg hatch followed by a period of rapid larval growth and the overwintering of near to full grown nymphs, has also been displayed by other members of this family. Most Perlodid species appear to have very slow, but continuous growth during the colder seasons.

The average daily temperature during the emergence period of *I. zionensis* at Big Bend was similar to that reported for several North American Perlodidae (*e.g.*

Arcynopteryx curvata, *A. picticeps*, *A. aurea*, *Diurna knowltoni*, *Hydroperla crosbyi*, *Megarcys signata*, *Isoperla clio*)(Minshall and Minshall 1966, Cather and Gaufin 1975, Sheldon 1972, Oberndorfer and Stewart 1977) . This species displayed a highly synchronized emergence at Big Bend, with emergence of upstream populations occurring progressively later. The delayed emergence of upstream populations is a common phenomenon among aquatic insects that is usually associated with an decrease in thermal units accumulated at each location (Sweeney 1984).

Emergence at Big Bend in 1996 preceded the time period when sustained high flows of the spring snowmelt would be expected in years with regular snowpack. Emergence prior to this seasonal event has distinct advantages; therefore, the timing of this event may be the result of long term selective pressures on the life history of this organism. The sustained flows in the spring are responsible for the majority of geomorphic change in the river (Hereford et al. 1995). During these events, the stability of the substratum is significantly reduced, creating a hostile environment for large nymphs. Floods that equal or exceed the magnitude of the spring runoff may occur any month of the year (Fig. 2) likely alter substratum characteristics substantially. However , the relative predictability of the springtime flows may have allowed for a long term evolutionary response (Resh et al. 1988, Poff and Ward 1989).

The long term discharge records for the North Fork indicate that in most years, high springtime flows are a normal occurrence (Fig. 3). However, the annual flow pattern is highly variable among years, as illustrated by the extremely different regimes

experienced during this study (Fig. 2). This suggests that a long term response to spring flows may play an evolutionary role in the seasonal timing of emergence, but the extreme flow variability among years indicate that the annual emergence cue for *I. zionensis* is unlikely to be correlated with this highly unpredictable event.

Extreme temperatures of the summer may also provide a selective pressure influencing the phenology of *I. zionensis*. Plecoptera have been described as being to alpine or densely forested streams, mainly due to their intolerance of warmer waters (Hynes 1976). For this reason, high temperatures during the summer are more likely lethal than cold temperatures experienced during the winter.

Due to the limited dispersal capability and univoltine life cycle of *I. zionensis*, synchronized emergence for successful reproduction is essential for population viability. The spring runoff period and extreme summer temperatures may provide a certain level of annual predictability to the system; however, the timing, magnitude and duration of these events vary annually. Confined to a relatively brief period dictated by vernal warming and in some years, discharge patterns, the successful reproduction of this population may depend upon its ability to respond to environmental variation at various temporal scales, by means of a precise environmental cue (Ward and Stanford 1982, Huey and Bennett 1990).

Experiment A: Response of Mature Nymphs Exposed to the Average Daily Temperature
During Ambient Emergence

Egg development, length of hatch, larval growth rates and emergence timing of Plecoptera have all been related to temperature (See Nebeker 1971, Schraer 1971, Stanford 1975, Brittian 1983, Lillehammer et al. 1989, Marten and Zwick 1989, Marten 1991). For many aquatic organisms, the success and timing of life cycle phenomena exhibit a species-specific temperature dependence where environmental cues may serve to initiate and synchronize the event. For organisms living in highly variable or dynamic systems, such as *I. zionensis*, reproductive success and population viability may be dependent upon a life history strategy that incorporates natural variation on a daily and seasonal basis into a thermal cue.

In the N.F. Virgin River, thermal fluctuations occur on annual and diel scales with some predictability; however, extremely unpredictable flashfloods can result in large, instantaneous changes in temperature and discharge (Figs 2 and 4). Exposed to this level of variability, an advantageous life history would include rapid response upon cue initiation. Several investigators have concluded that exposure to a thermal cue 24 to 48 hours prior to an event may initiate the emergence response (Peters et al. 1987), while for other organisms precise temperature thresholds can exist (Macan and Maudsley 1965, Danks and Oliver 1972, Trottier 1973, Wartinbee 1979). Very little research has been conducted to determine cues initiating emergence in stoneflies; however, the sensitivity

of this group to temperature suggests that for some species, a distinct thermal cue may exist. In a study of emergence patterns in Sagehen Creek, Sheldon (1972) attributed delayed emergence, followed by increased emergence intensity of several perlotidid species to short term temperature variation associated with a cold spell followed by a warm day. For my experimental purposes, I assumed that a thermal emergence cue for *I. zionensis* in the N.F. Virgin River to be associated with the average daily temperature during the time of emergence.

Late stage *I. zionensis* nymphs transferred from Big Bend (RM11.7) to the wet laboratory experienced very little mortality (n=3) during the five day acclimation period, and behavior appeared normal. The nymphs were influenced by photoperiod, moving to the surface only during dark hours. At night, nymphs were active feeding on live prey and other food items. No aggressive or competitive behavior among the nymphs was observed. Clusters of males seemed to form small groups (2-5) assembling around individual females. Similar behavior has been reported for near emergent Perlodidae (Cather and Gaufin 1975).

Experimental manipulation began on April 16, when the temperature was increased 5°C over a 6 hour period, to a final temperature of 12°C for 24 hours (Fig.12). On April 17, the temperature was increased 1.5°C over 12 hours to 13.5°C. No mortality was experienced and changes in the behavior or morphology of the nymphs was not observed.

On April 18, the temperature was increased by 1°C, to 14.5°C. (Fig. 12) Several hours later, during the light period, a drift response was initiated resulting in the majority of nymphs at one end of the trough, near the drain. During the dark hours, nymphs seemed to reposition themselves by spreading out, but most remained in hiding and those that did come out were very slow moving. No morphological changes were observed and three mortalities occurred.

On April 19, the temperature increased 0.5°C, from 14.5 to 15.0°C (Fig. 12). The nymphs were very stressed and no longer influenced by photoperiod. Drifting continued and the numbers of nymphs around the drain increased. Very little activity was observed and no morphological changes were observed. Two mortalities occurred.

From April 20-28, the temperature ranged from 14.5 to 15.5°C. Behavior continued to show signs of stress. Many nymphs began to crawl out of the water. The wing pads of a few individuals had blackened tips, but none attempted to emerge. During this period, mortality increased significantly, eventually resulting in 100% mortality.

Mature nymphs did not emerge in response to the constant experimental temperatures (12-15.0°C) simulating the daily average during the emergence period (12.6-15.8°C) of the native population in the field at Big Bend (Fig. 12). These results illustrate that exposure to a constant temperature within the range of ambient conditions normally experienced by mature nymphs, even the average daily temperature, only three weeks prior to natural emergence can result in 100% mortality. These data suggest that a thermal cue for *I. zionensis* is more complex than the average daily temperature at time of

emergence. Moreover, the range of temperatures experienced at Big Bend on a daily basis expose *I. zionensis* nymphs to potentially lethal temperatures for several hours a day as a result of diel fluctuations.

The response of Plecoptera to an increase in temperature is species-specific, and accelerated development and emergence has been observed for a number of species (Nebeker 1971, Schraer 1972, Lillehammer et al. 1989). However, long term exposure to chronic nonlethal temperatures can also result in mortality (Schraer 1972). Since the experimental individuals seemed to have acclimated to the troughs, it seems they died as a result of constant exposure to temperatures within the range of conditions they would experience in the wild. Therefore, it is likely that these temperatures are stressful, but can be tolerated for many hours a day, day after day.

The natural range of variation experienced in lotic habitats includes stressful events. However, it is the duration, magnitude and predictability of these events that may manifest a life history response or adaptation. Daily averages represent the composite of temperatures experienced over a 24 hour period. For many hours during the day, temperatures at Big Bend are much lower or higher than the average daily temperature. Hence, it is plausible that temperatures above 14.5°C, or an unknown threshold, induce heat stress under constant conditions, whereas, exposure for a short period of time at or above this threshold is not harmful. Furthermore, temperatures above this threshold may be incorporated into a thermal emergence cue, based on the duration or magnitude of the

high temperatures experienced or the transition between the maximum and minimum daily temperatures as influenced by diel periodicity. In this experiment, I did not allow for the diel fluctuations that would occur in the field. All emergence at Big Bend was nocturnal, suggesting that if emergence is associated with the thermal regime, it may incorporate ends of the daily thermal variation to correctly time the event with favorable terrestrial conditions.

The thermal history of an organism, particularly its previous exposure to fluctuating temperatures, may dictate its response to acute (short term) or chronic (long term) temperatures (Huey and Bennett 1990). Some organisms that are exposed to a high level of thermal variability, such as intertidal animals, have developed metabolic adaptations to acute temperatures and exhibit short term temperature independence (Newell and Northcroft 1967). This phenomenon has also been shown for some Perlodidae that inhabit dynamic thermal regimes (Schrear 1972). Another possible explanation includes a short term response of thermal resistance known as heat hardening, as a result of previous exposure or acclimation to sublethal temperatures (Cossins and Bowler 1987). Although no examples are available for stoneflies, Brown and Feldmeth (1971) demonstrated heat hardening in the desert pupfish (*Cyprinodon nevadensis*), where increased thermal tolerance was associated with acclimation temperatures.

It is impossible from the results of this experiment to determine the exact mechanism incorporated by *I. zionensis* to survive potentially lethal temperatures in their

native habitat. However, it is clear that the favorable temperature range of an organism under constant conditions can not be derived from the average daily temperature on site, especially for species whose native thermal regime is dynamic. Short term physiological adaptations or acclimation responses may exist that modify the effects of potentially lethal temperatures based on exposure time. However, these short term responses may provide only limited protection under potentially lethal circumstances, at the expense of other ecologically important parameters, such as growth and development.

Experiment B: Response of Mature Nymphs to the Daily Minimum Temperature at Time of Collection.

Similar to the nymphs in the warm water experiment, *I. zionensis* experienced very little mortality (n=1) during the acclimation period. Behavior patterns were responsive to photoperiod and activity levels appeared normal. Water temperatures during this experiment simulated the daily minimum temperature experienced in the field at the time of collection (Fig. 13). During the emergence period at Big Bend (May 5-15, 1996), the daily minimum temperatures ranged from 11.4-13.4°C (Fig. 13). In contrast, the constant temperatures during the experimental emergence (May 2-June 3) were 7.8-9.7°C.

The emergence period (30 days) of experimental individuals was extended (May 2-June 2), relative to the ten day synchronized emergence experienced from the population at Big Bend. Fifty percent of the experimental population successfully emerged, while the same proportion died (Fig. 14). Fifteen percent of all mortalities occurred during unsuccessful ecdysis. Emergence and mortality under experimental conditions displayed a similar relationship with time, maximum mortality and emergence occurring on May 19 and May 20, respectively (Fig. 14).

The wings of experimental females indicated adult tissue development was problematic. Forty percent of successfully emerged females exhibited signs of incomplete wing formation while, sixty percent of emerged females (n=18) experienced complete wing formation. (Fig.14). In contrast, the wings of adult females (n=231) that emerged under ambient conditions at Big Bend were individually checked and did not show any signs of incomplete wing formation.

As a result of the uniform cold temperatures, 11% fewer degree hours were accumulated by the experimental population prior to 50% emergence (6726.2 dhrs) than required by the Big Bend population (7559.5 dhrs). Time at 50% emergence was May 17 for experimental individuals, and May 10, at Big Bend.

Constant temperature experiments and distributional studies on members of the Perlodidae have found that species with limited distributions (e.g. *Dinocras cephalotes*, *Isoperla grammatica*, *Isogenoides frontalis*) or those occupying a fluctuating thermal environment (e.g. *Hydroperla crosbyi*, *Isogenus decisus*) often exhibit restrictive

temperature ranges for growth, development and emergence (Nebeker 1971, Lillehammer et al. 1989, Minshall and Minshall 1966, Oberndorfer and Stewart 1977). The response of *I. zionensis* exposed to the constant cold temperature (7.8-9.7°C) suggests that 8-9°C is near the minimum temperature required for complete metamorphosis and emergence of *I. zionensis*. Perhaps a slightly warmer constant temperature (10-11°C) would have resulted in lower mortality and higher percentage of females with normal wings. However, nymphal response to a constant temperature of 14.5°C included catastrophic drift, eventually resulting in complete mortality. Based on the results of both experiments, under constant temperature conditions, *I. zionensis* requires a very narrow temperature range to complete its life cycle.

Exact temperature thresholds for ecdysis have been reported for some aquatic insects (Macan and Maudsley 1966, Danks and Oliver 1972, Trottier 1973, Peters and Peters 1977); however, 50% of the individuals attempted to emerge, suggesting that this species does not require an absolute temperature cue and these conditions were within a favorable range for emergence. Although 50% of the population successfully emerged under the constant cold conditions, reproductive success was cut in half due to mortality and 40% of the females displayed abnormal adult tissue development. This temperature may have provided the minimum required physiologically, but these conditions were less than ideal for metamorphosis and emergence.

Survival of an organism can be directly affected by absolute temperatures or exposure time; however, secondary, sublethal effects may influence normal activity and

development, altering the reproductive success and future viability of the species. For example, small changes in the thermal regime of a first order stream in Ontario altered the phenology and significantly reduced the adult body size of the stonefly, *Nemoura trispinosa* (Hogg et al. 1995). The relationship between adult body size and fecundity has been clearly established (Vannote and Sweeney 1980) and although the altered thermal regime did not extirpate the population of *N. trispinosa*, it reduced the potential reproductive capacity of the population. For aquatic organisms that rely upon particular aspects of the thermal regime for an environmental cue (e.g. embryogenesis or metamorphosis), the effect on a population may be more direct. Lehmkuhl (1974) found that the mayfly, *Ephoron album*, was completely eliminated from a regulated river due to the loss of annual thermal variability required as stimuli during several phases of its life cycle.

The constant cold thermal regime was not absolutely lethal to the experimental individuals. However, removal of seasonal and diel temperature fluctuations, only three weeks prior to emergence, resulted in sublethal effects, influencing mortality, emergence synchrony and female adult tissue development. These sublethal effects illustrate the extreme sensitivity of this species to temperature. Sweeney and Vannote (1980) hypothesized that there is a distinct difference between larval and adult tissue development, and the latter is less likely to be influenced by temperature. This hypothesis was based on observations of decreasing adult size during the emergence period indicating that a given temperature threshold may exist simulating adult tissue

development for all individuals regardless of nymphal size (Sweeney and Vannote 1981). Data on the size of newly emerged adults was not collected for this study; however, emergence was highly synchronized under ambient conditions and the females examined from Big Bend showed no signs of incomplete wing formation. Therefore, the removal of the seasonal or diel fluctuations may have affected proper wing formation, despite the propensity for complete adult tissue development under nonlethal temperatures. Similar findings by Wright and Mattice (1981) illustrate that at a nonlethal temperature, body size of *Hexagenia bilineata* was maximized, but the emergence period was prolonged and metamorphosis problematic, resulting in significant mortality. Wright and Mattice (1981) concluded the loss of thermal variability was responsible for the asynchronous emergence and mortality.

Synchronized emergence is often thought of as a reproductive advantage (Vannote and Sweeney 1980), initiated by a thermal cue. Emergence timing and the degree of synchrony has been related to temperature in many studies and appears to be a species-specific response associated with degree-day accumulations or a particular aspect of the thermal regime (e.g. minimum or maximum temperature). For example, the emergence timing of *P. badia* has been directly correlated to degree-day accumulations, whereas the intensity of the emergence may be attributed to nearshore temperatures or, under experimental conditions, warmer waters (Stanford 1975). Some species may respond to both absolute temperatures and the variability of the thermal regime. Danks and Oliver (1972) found the emergence timing of some Chironomids to be directly related to

absolute water temperatures, whereas the degree of synchrony was negatively correlated to the magnitude of diel fluctuations. The degree of emergence synchrony differed for populations of *Megarcys signata* in Mill Creek, Utah. The shortest emergence period was less than 14 days occurring at an exposed, high elevation site (Cather and Gaufin 1975), suggesting diel fluctuations may influence emergence intensity. Still other research has shown that an absolute water temperature may be responsible for initiating a cue to emerge, but daily emergence intensity was species-specific and associated with diel fluctuations and/or photoperiod (Danks and Olivier 1972, Wartinbee 1979).

Several studies have attributed the asynchronous emergence of aquatic insects at constant temperatures to the loss of natural thermal variability (Wright and Mattice 1981, Marten 1991), while others have attributed a synchronized response to short term temperature fluctuations (Sheldon 1972, Peters et al. 1982). It is plausible that the cue required for emergence of *I. zionensis* incorporates both degree-hour accumulation and diel fluctuations in temperature. The emergence period of experimental individuals was lengthened by the cold, constant temperatures, but 50% of the nymphs successfully emerged within 1 week of the population at ambient conditions, and required 11% less thermal units (dhrs) to do so. Furthermore, the time of 50% emergence was not temporally distinct from the Big Bend population (May 17 vs. May 10). This suggests that emergence timing (cue) may be independent of temperature and degree-hour accumulations, or vernal warming experienced prior to removal from ambient conditions had provided nymphs with some aspect of an thermal emergence cue.

Based on the temperature sensitivity of mature nymphs, it is highly unlikely that the emergence timing of *I. zionensis* is independent of the thermal regime. The influence of seasonal warming in the N.F. Virgin River would force nymphs from the water in order to survive. This was observed in the constant warm water experiment where many nymphs exited the unsuitable water, crawling back in only when disturbed by activity in the laboratory. The difference in degree-hours coupled with peak emergences nearly coinciding under drastically different thermal regimes (Experiment B vs. Big Bend) suggests emergence timing for *I. zionensis* is not solely dependent upon thermal demand. A potential explanation for the synchrony in emergence timing may be associated with exposure at ambient conditions prior to experimental manipulation. The mature nymphs were only 3 weeks away from natural emergence and vernal warming *a priori* may have provided a cue for adult maturation processes to begin. If a cue had been initiated prior to experimental manipulation this would explain the similarity in timing, but not the prolonged emergence period.

The extended emergence suggests that a second thermal cue, potentially short term in nature, may be required for synchronous emergence. The correlation between short term temperature fluctuations and emergence has been demonstrated for only a few species (Trottier 1973, Wartinbee 1979, Peters et al. 1987); however, there are benefits to a short term response in a dynamic system. Diel temperature fluctuations reflect the environmental conditions of a site, both terrestrial and aquatic. Incorporating daily fluctuations into a life history response would allow nymphs to correctly time

synchronous emergence with favorable environmental conditions for ecdysis and reproduction.

Stream temperatures reflect favorable atmospheric conditions, providing a mechanism to avoid potentially lethal temperatures (too cold or hot) or extremely dry conditions. Under ambient conditions emergence was nocturnal and early morning observations suggest that the majority of nymphs that emerged over night had completed ecdysis and moved into vegetation by sunrise, leaving only their skins behind exposed on the river bank. Based on behavior in the field and the experimental results, it seems plausible that emergence synchrony is a short term response to temperatures experienced below at least 14.5°C and above 8-9°C. Figure 15 illustrates the time period for May 10-11, 1996 at Big Bend during which emergence could occur based on the results of these experiments.

Isogenoides zionensis proved extremely sensitive to temperature, despite the thermal variability experienced on both an annual and diel basis within its native habitat. Although this species is very responsive to temperature, it is a time dependent adaptation where the rate and magnitude of the variability is not of lethal consequence, only the duration. These results indicate that *I. zionensis* has invoked a life history strategy more complex than the summing of degree-hours, an absolute temperature, or even the average daily temperature, which may be linked at several temporal scales to the timing and synchrony of emergence.

Distribution of Isogenoides zionensis in the North and East Forks Virgin River

Sampling sites covered an altitudinal gradient of 2261m to 1158m (7420-3798ft.) on the North and East Forks of the Virgin River. The location of sampling sites and the range of *I. zionensis* are shown in Figure 16. Site descriptions and observations are located in Table 1.

The distribution of *I. zionensis* in the East Fork Virgin River was limited to the upper watershed above 1800 m, at the Glendale site (RM186.6). Although *I. zionensis* was found at this location, the community appeared to be dominated by *Hydropsyche* spp.. Fox and Eddy (1977) report similar findings from this location.

The distribution of *I. zionensis* in the North Fork drainage was much more extensive, extending from the headwaters around 2261 m to 1310 m (7420-4296ft.). Sampling revealed that the distribution of *I. zionensis* did not extend as far downstream as the Springdale site (RM2.0). The Visitors Center site (RM5.0), located between the Big Bend site and the Springdale site, was not quantitatively sampled, due to unsuitable substratum. Qualitative sampling at the Visitor Center in September 1995, April 1996 and September 1996 failed to find *I. zionensis* at this location. Further attempts to narrow the range of *I. zionensis* in April 1996 determined that the distribution of *I. zionensis* extended less than 1 kilometer downstream of Big Bend.

Determining the role of abiotic controls, such as substratum, discharge and

temperature, on the distribution and abundance of aquatic organisms is often a central theme in ecological studies (e.g. Ward and Stanford 1982, Statzner and Higler 1986, Death 1995). Correlations are often used to explain observations. However, rarely are they corroborated by experimental studies (Power et. al. 1988) or undertaken at the population level in different habitats (Sweeney 1984). For the majority of aquatic species, basic life history information is lacking (Power et al. 1988, Naiman et al. 1995), let alone which abiotic variables may be most influential.

In the upper Virgin River watershed, lotic attributes vary both spatially and temporally within the distributional range of *I. zionensis* (Table 1). Heterogeneous channel characteristics include exposed, first order streams, canyon confined sections and wide alluvial valleys. The entire spectrum of substrate can be encountered from sand to very large boulders, and the physical characteristics of elevation, climate and topography modify aspects of the thermal regime at each location. Hence, the longitudinal distribution of *I. zionensis* includes a wide range of ecologically significant factors (i.e. substratum, discharge, temperature).

In the North Fork of the Virgin River longitudinal variation in community composition can be associated with altitudinal zonation and the canyon attributes of the system. Data from Fox and Eddy (1976) and Boyle et al. (1993) indicate that several species (*Suwallia* spp., *Rhithrogena* spp.) are restricted to the headwaters region (above 2133m or 7000 ft) whereas others (*Atherix* spp., *Taenionema nigripenne*, *P. badia*) exhibit a distinct zonation downstream, restricted to the middle-lower rhithron segments.

The rhithron-potomon transition appears to delineate the upstream boundary for *Corydalis* spp. and *Petrophilia* spp. (Boyle et al. 1993, Addley and Hardy 1993), species commonly associated with potomal habitats in the Southern Rocky Mountain Region (Ward 1986, Ward and Stanford 1991).

The distribution of *I. zionensis* and longitudinal changes in community composition (Fox and Eddy 1977, Boyle et. al. 1993, Addley and Hardy 1993), suggest the distribution of *I. zionensis* extends from the headwaters downstream into the rhithron-potomon transition zone. Faunal composition of sites farthest downstream include the typical potomal species, *Corydalis* spp. and *Petrophilia* spp., in addition to *I. zionensis* (Boyle et al. 1993, Addley and Hardy 1993). Although I did not collect water quality data for this study, results from earlier studies do not indicate any limiting parameters for aquatic biota within the N.F. Virgin River. Fox and Eddy (1977) conducted a complete water quality analysis within the study area and found all parameters met water quality standards. Similar findings were reported from a study conducted in 1993, adding that seasonal differences among sites were correlated with discharge (Boyle et al. 1993).

The thermal regimes of sites on the N.F. Virgin River vary as a function of elevation and other physical attributes. Variation in the thermal regime among sites may explain longitudinal changes in community composition. For example, several studies have shown cold stenotherms generally dominate the rhithron community (Ward and Kondratieff 1992) and often exhibit a discontinuous distribution, dropping out of the benthos prior to potomal conditions (Ward 1986, Ward et al. 1986, Ward and Stanford

1991, Ward et al. 1994). Few Plecoptera are tolerant of temperatures above 25°C (Hynes 1976) limiting the distribution of most species to the rhithron environment.

Shifts in faunal composition can be associated with longitudinal gradients, especially temperature, within the river continuum. The Above Narrows site consistently exhibited lower average temperatures than both downstream sites for the period of April 10- August 31, 1996 (Fig. 4), although the daily maximum temperatures experienced at this location generally exceeded the maximum temperatures at Big Bend, and equaled or exceeded that experienced at the Visitor Center site (Fig. 5). In addition, the Above Narrows site experienced the most extreme diel variation (Fig. 6). The average daily temperatures (Fig. 4) remained well below 20°C, indicating rhithral characteristics.

Due to the moderating influence of the Narrows and Zion canyons, average daily temperatures at Big Bend indicate the rhithron segment is extended on the North Fork (Fig.4). Qualitative sampling downstream from this site revealed that *I. zionensis* drops out almost 5 river miles upstream from the Visitor Center (RM5.0). Although there is only a slight difference in both average daily temperatures and degree-hours between the Visitor Center and Big Bend sites, the thermal regime experienced at both sites differ due to diel fluctuations. Many more hours are spent above 20°C at the Visitor Center, than at either Big Bend or Above Narrows sites (Fig 7 and 8). Hence, the distribution of *I. zionensis* may be influenced by slight differences in the thermal regime associated with the duration of exposure to marginally stressful temperatures, as a result of diel fluctuations.

Longitudinal Density of *Isogenoides zionensis* in the N.F. Virgin River

Sampling in the N.F. Virgin River revealed differences in the density of *I. zionensis* among sites during the September 1995 sampling period (Fig. 17, Table 1). The distribution of *I. zionensis* included four within canyon sites on Deep Creek, a major tributary to the North Fork: Virgin Flats (RM5.6), Hogs Heaven (RM4.0), Box Canyon (RM1.8) and Above NF Confluence (RM0.1)(Fig. 16). The density (average \pm 1std) of *I. zionensis* at each of the Deep Creek sites ranged from $18.7\pm 18.0/m^2$ to $9.3\pm 2.3/m^2$. These densities are most similar to those of the canyon-influenced sites on the North Fork, Big Spring (RM17.0) and Big Bend ($34.7\pm 14.0/m^2$ and $36.0\pm 14.0/m^2$).

At the Headwaters site, the density of *I. zionensis* ($22.0\pm 18.9/m^2$) was comparable to the other North Fork and Deep Creek sites. However, *I. zionensis* was not the most abundant species at this location. *Pteronarcella badia* ($88.0\pm 53.0/m^2$) dominated the community at the Headwaters site, far exceeding the numbers of *I. zionensis* at this location. The exposed, high elevation Above Narrows site (RM26.8), exhibited the highest density of *I. zionensis* ($68.0\pm 25.7/m^2$), in comparison to the canyon-influenced sites. Although each site exhibited a high within site variability, this data suggest that longitudinal differences in the density of *I. zionensis* in the N.F. Virgin River may be associated with canyon-influenced lotic characteristics, including the thermal regime.

Seasonal Size Differences Among Sites: Above Narrows (RM26.8) vs. Big Bend(RM11.7)

Seasonal collections at the Above Narrows site during September 1995 and 1996 revealed size differences among *I. zionensis* in the N.F. Virgin River basin. *Isogenoides zionensis* collected from the Above Narrows site (RM26.8) in both September 1995 and 1996 were significantly larger than those collected from Big Bend (Student's t-test, $p < .001$, $p < .0001$), respectively (Fig. 18). However, no significant difference in size was found among individuals from the Above Narrows and Big Bend sites in April 1996 (Fig. 18).

These results illustrate the different growth rates of *I. zionensis* at these sites during the period of rapid growth (June-September 1996). This result was surprising because it was the opposite of what would be expected based on longitudinal emergence patterns; individuals at Big Bend emerged earlier than those at the Above Narrows site. This suggests that the greater nymphal size achieved by individuals at the Above Narrows site, occurred in a shorter period of time.

During the summer months, the Above Narrows and Big Bend sites experienced very similar average daily temperatures (Fig. 4), suggesting that the observed size differences among sites are not correlated to this parameter. Numerous studies have illustrated a difference in the growth rate of Plecoptera under various constant temperatures (See Branham et al. 1975, Heiman and Knight 1975, Lillehammer 1985,

Lillehammer 1987, Lillehammer et al. 1989). However, I am not aware of any studies that have examined the difference in nymphal growth rates under experimentally fluctuating conditions. This phenomena has been observed for several species experiencing different thermal regimes in the field (Cather and Gaufin 1975, Oblad 1991, Haro and Wiley 1992); however, the temporal variation of the thermal regime was not examined.

Despite their similarity in average daily temperatures, significant differences in the thermal regime exist between the Above Narrows and Big Bend sites that may explain the observed differences in nymph size. Thermal accumulation is usually calculated based on the mean daily temperature and reported as degree-days (Sweeney 1984). For this study, degree-hours were used as a measurement of thermal accumulation at each site. During the summer growing season, Big Bend accumulated almost 10% more degree-hours (55027 dhrs) than at the Above Narrows site (49645dhrs), indicating more time on an hourly basis may be spent at unfavorable growing conditions at the lower elevation site (Fig. 8).

During the summer growing season, the majority of time at the Big Bend site is spent at high temperatures, between 16-22°C (Fig. 8). In contrast, the Above Narrows site may reach a higher maximum daily temperature, but less hours are spent at high temperatures on a daily and seasonal basis due to night-time cooling (Fig. 7 and 8). These results indicate that an absolute temperature threshold may exist, above which the energetic cost of metabolic processes may reduce the energy available for growth

(Vannote and Sweeney 1980). Increased rates of growth observed under fluctuating thermal regimes suggest that the metabolic rate is not independent of the temperature fluctuations (Sweeny and Schnack 1977, Hoffmann 1985). Therefore, the pattern of temperatures experienced at the Above Narrows site may provide a metabolic advantage during the summer due to more time spent under favorable conditions for growth (below a critical threshold associated with metabolic costs) as a result of diel periodicity.

Although *I. zionensis* may experience a growth advantage during the summer at the Above Narrows site, it is a seasonal phenomenon. No significant differences in the size among late stage nymphs (males or females) from the Above Narrows and Big Bend sites were found in April 1996 (Student's t-test, $p=.603$, $p=.927$). These results indicate that temperature patterns during the winter and spring seasons at Big Bend allow these individuals to increase in size by late spring, eliminating the difference in size observed at the end of the previous summer growing season.

A possible explanation associated with the thermal regime may explain the lack of seasonal size differences observed among the sites in April 1996. Unfortunately, I do not have winter or early spring temperature data from the Above Narrows site. However, the climate, elevation and emergence in 1996, suggest this site experiences harsher winter conditions and delayed vernal warming, when compared to the low elevation site at Big Bend. Therefore, the differences in elevation and climate may result in significantly warmer winter or spring temperatures at Big Bend. Minimum temperatures required for growth have been identified for a number of species, including Plecoptera (Markarian

1980). This suggests slightly warmer conditions at Big Bend may allow growth to occur during the winter or spring, whereas the colder temperatures at the high elevation site may retard the growth of *I. zionensis* during these seasons.

SUMMARY AND CONCLUSIONS

The phenology and distribution of *I. zionensis* in the N.F. Virgin River is highly associated with the thermal regime as illustrated by both field data and experimental results in this study.

The annual and daily discharge pattern of the N.F. Virgin River is highly variable, influenced by seasonal snowpack, global climatic conditions and the unpredictable occurrence of flashfloods. Spring snowmelt events can occur and seasonal emergence prior to this event has distinct advantages, which may manifest as a long term selective pressure influencing the life history of this organism. Discharge was not directly associated with the timing of emergence in 1996 and probably plays only a secondary role in the life cycle of *I. zionensis* because of its relationship with temperature. Stream temperatures are, in part, a function of volume. In low flow years such as 1996, the stream probably warmed sooner than in 1995 due to the lack of spring runoff which likely moderates the effect of vernal warming on water temperatures. Therefore, discharge plays an indirect role on the life cycle of *I. zionensis*, as it may influence temperature and the timing of thermally controlled physiological cues.

Despite the range of temperatures experienced on a daily basis by this species, *I. zionensis* proved to be extremely sensitive to this variable as a function of the duration of exposure, even when only a few weeks away from emergence. Experimental results using late stage nymphs under constant temperature conditions simulating the average

daily temperature during ambient emergence resulted in 100% mortality. These results illustrate the chronic effect of exposure to sublethal temperatures normally experienced only for short periods of time, as a result of diel fluctuations.

The sensitivity of this species to the fluctuating thermal regime was also illustrated experimentally by removing the diel periodicity and exposing late stage nymphs to a constant thermal regime simulating the daily minimum temperature experienced at the time of collection. Although conditions were not ideal, 50% of the population emerged, indicating the experimental temperature was within the range of favorable conditions necessary for the completion of the life cycle. However, reproductive success was cut in half due to mortality (50%). Likewise, 40% of the emerged females exhibited signs of abnormal wing development. In addition, the emergence period was prolonged under experimental conditions and emergence timing was temporally indistinct. These results can not be explained by degree-hour accumulation, suggesting the adult maturation process had begun *a priori* and that a second thermal cue is required to synchronize emergence. Therefore, exposure at the constant cold temperature provided the minimum temperature necessary, physiologically, but these conditions were less than ideal for metamorphosis and recruitment.

The results from these experiments suggest that the emergence cue is not associated with the composite value of the average daily temperature, and instead is likely related to the transition between the maximum and minimum daily temperature or the duration and magnitude of these extremes. Hence, *I. zionensis* has invoked a life history

strategy more complex than the summing of degree-hours, an absolute temperature, or even the average daily temperature, which is linked at several temporal scales to the timing and synchrony of emergence.

The extreme sensitivity of *I. zionensis* to temporal aspects of thermal variability, may also serve to limit the range of this species within the upper Virgin River watershed. Within the North and East Forks many ecologically significant abiotic factors vary as a function of elevation and topography influencing the thermal regime and the location of the rhithron-potomon transition.

The distribution of *I. zionensis* in the North and East Forks extends from the headwaters to the rhithron-potomon transition characterized by community composition and temperature. Within the range of this species, substratum characteristics, the thermal regime and the aquatic community shift as influenced by elevation and canyon shading. On the East Fork, the distribution of *I. zionensis* is limited to above 1798m (5900ft.), below this point the river flows through an exposed, unconfined valley dropping in elevation, inhabited by potomon species. In contrast, rhithral characteristics on the North Fork are shifted downstream due to the influence of canyon shading, extending favorable habitat for many species, including *I. zionensis*.

The range of *I. zionensis* on the North Fork extends from 2261m (7420 ft.) in elevation to less than 1280m (4200 ft.), including exposed areas on the high desert plateau and a wide alluvial valley at the most downstream end. Substratum includes sand, boulders and deep pools; and riffles can be composed of small gravel to large

cobbles. Stream characteristics of the North Fork are highly influenced by the canyon environment, as is the thermal regime.

Sites within and outside of the distributional range of *I. zionensis* on the North Fork have only slight differences in average daily temperatures ($<2^{\circ}\text{C}$), and less than 10% difference in degree-hours. Similar to the emergence cue for this species, the distribution may not be explained by thermal variability between these sites based on these parameters. Large diel fluctuations and the highest maximum temperatures are experienced at the site where *I. zionensis* appears to be most abundant and attains the largest body size after the summer growing season. These results may illustrate the cumulative effect of environmental conditions as they influence the energy balance of this species (Hall et al. 1992).

Within the range of *I. zionensis*, aspects of the thermal regime vary which may cause energetic costs at some locations to be greater than at others, resulting in variations in the size and abundance of a species at different locations. These results indicate that the thermal regime, particularly diel fluctuations, may provide a growth and reproductive advantage under favorable conditions along a gradient. Similarly, diel fluctuations may also serve to limit the downstream distribution of this species as influenced by the duration of time spent above a critical temperature, by increasing maintenance costs or sublethal effects at a critical temperature.

The role of the thermal regime in the life history and distribution of aquatic organisms is central to understanding the ecological significance of natural environmental

variability. The range of natural variability undoubtedly includes potentially lethal effects that may manifest at various temporal and spatial scales (Frissel and Bayles 1996). As the results of this study illustrate, the relatively predictable pattern of the thermal regime as described by the temporal variability on a daily basis includes critical aspects for life cycle processes and the distribution of *I. zionensis*. Therefore, it is not enough to describe the critical habitat characteristic of temperature by convenient measures such as a daily average, when some species respond to the entire range of temperatures and temporal patterns.

A Federal Reserve Water Rights Agreement (1997) for Zion National Park will preserve the dynamic integrity of the N.F. Virgin River and serve to protect *I. zionensis* and many other species, associated with the canyonlands in Zion National Park.

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FIGURES

Figure 1. North Fork Virgin River study area.

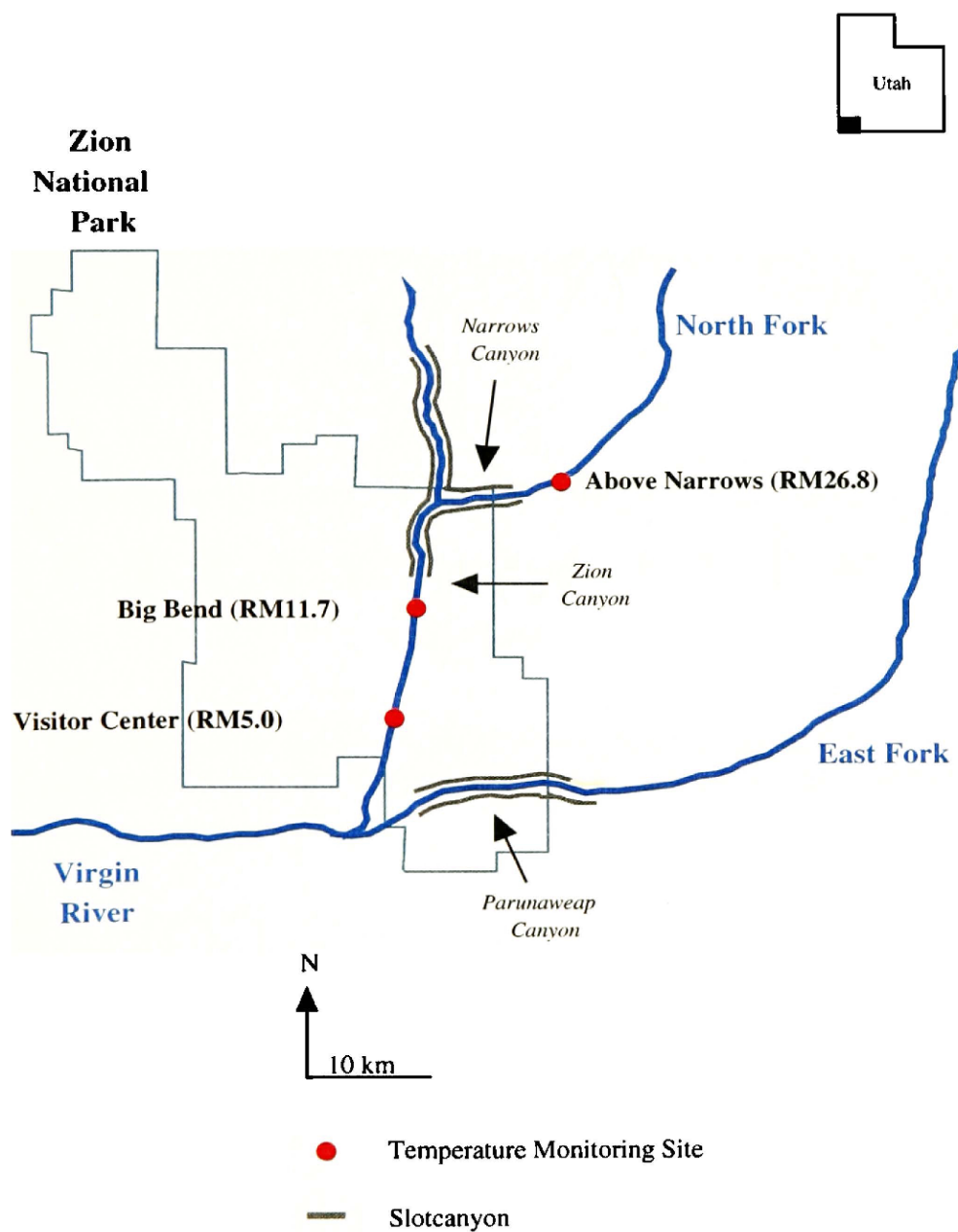


Figure 2. Hydrographs of water years 1995 and 1996 for the North Fork Virgin River at the Visitor Center (RM5.0) site. Mean daily discharge shown in in cubic feet per second.

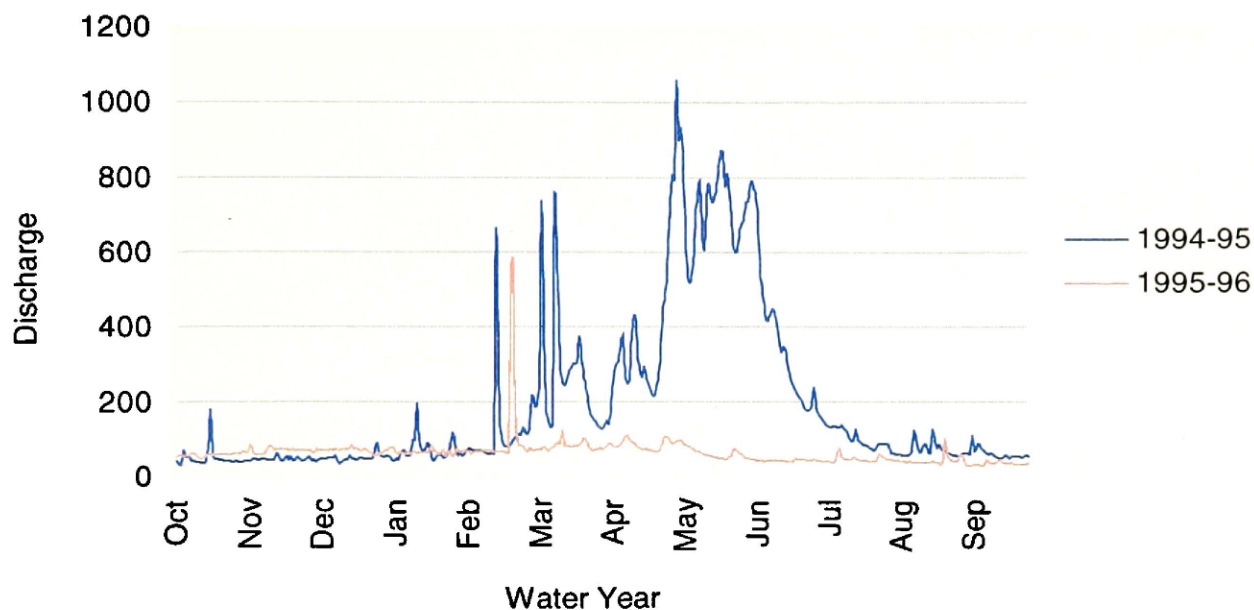


Figure 3. Hydrographs of the North Fork Virgin River at the Visitor Center (RM5.0) site for water years 1977-1993. Mean daily discharge in cubic feet per second.

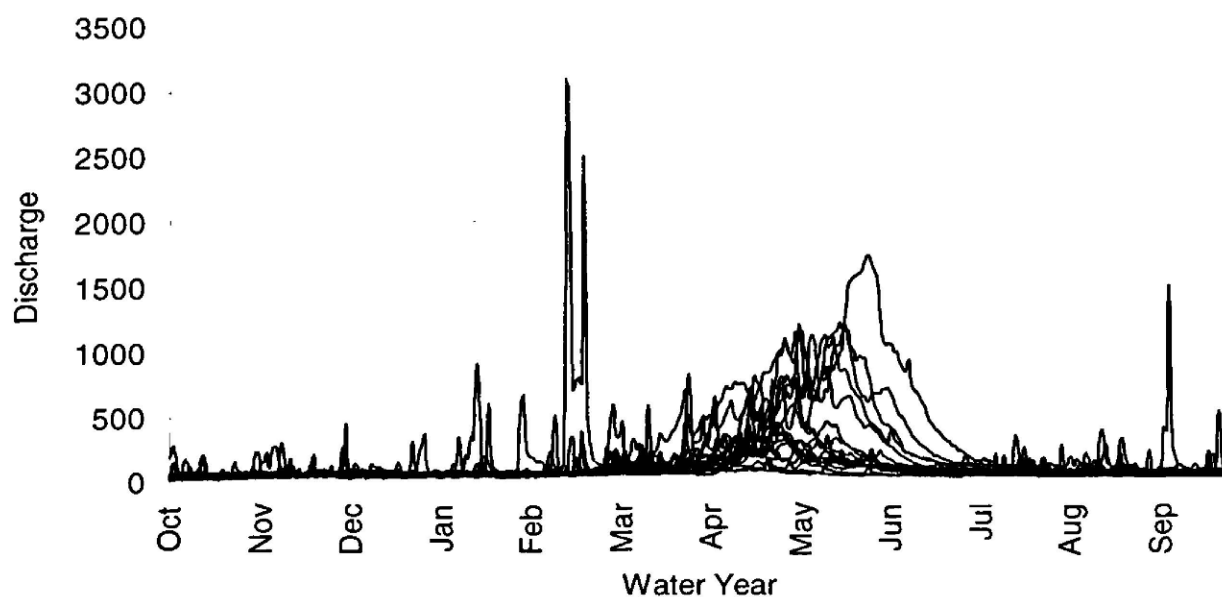


Figure 4. Average daily temperatures at the Above Narrows (RM26.8), Big Bend (RM11.7) and Visitor Center (RM5.0) sites, April 10-August 31, 1996.

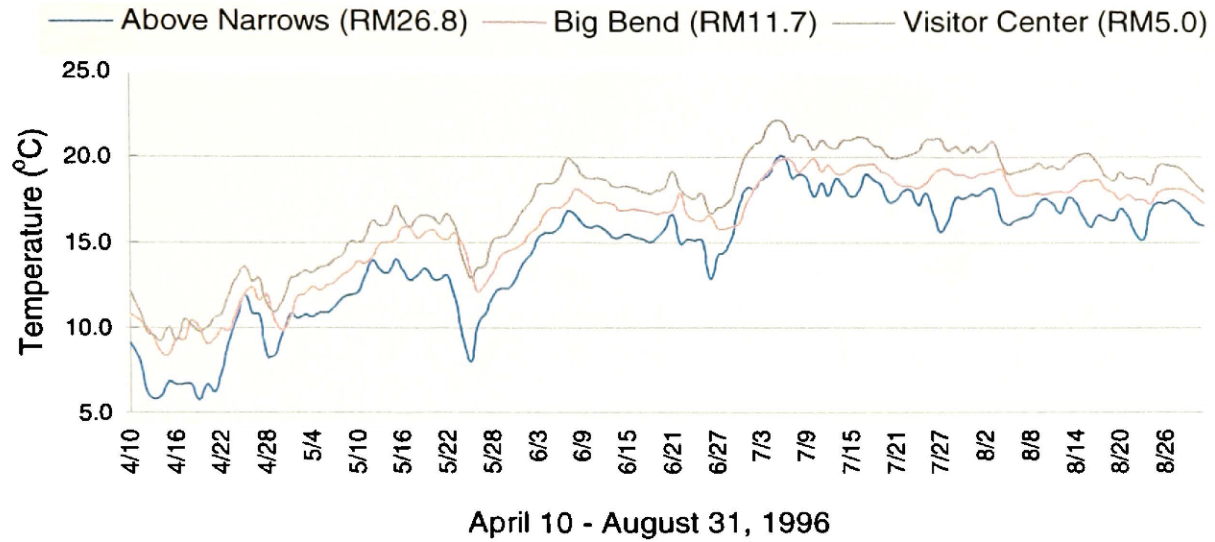


Figure 5. Maximum daily temperature at the Above Narrows (RM26.8), Big Bend (RM11.7) and Visitor Center (RM5.0) sites, April 10- August 30, 1996.

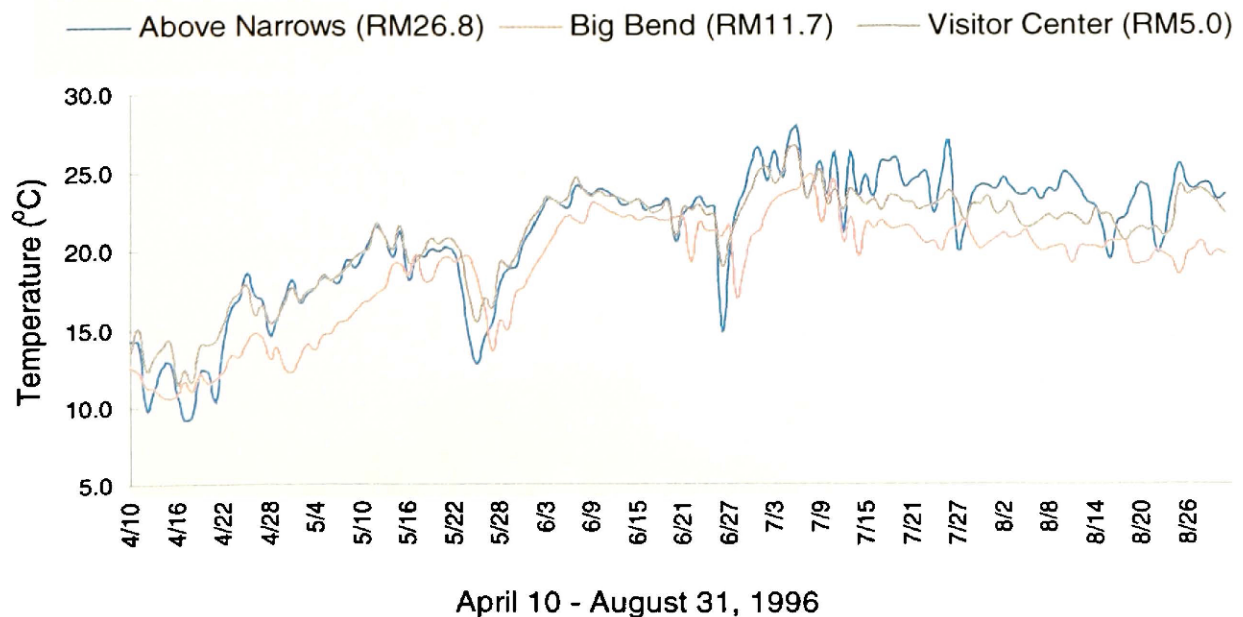


Figure 6. Diel amplitude at sites on the North Fork Virgin River.

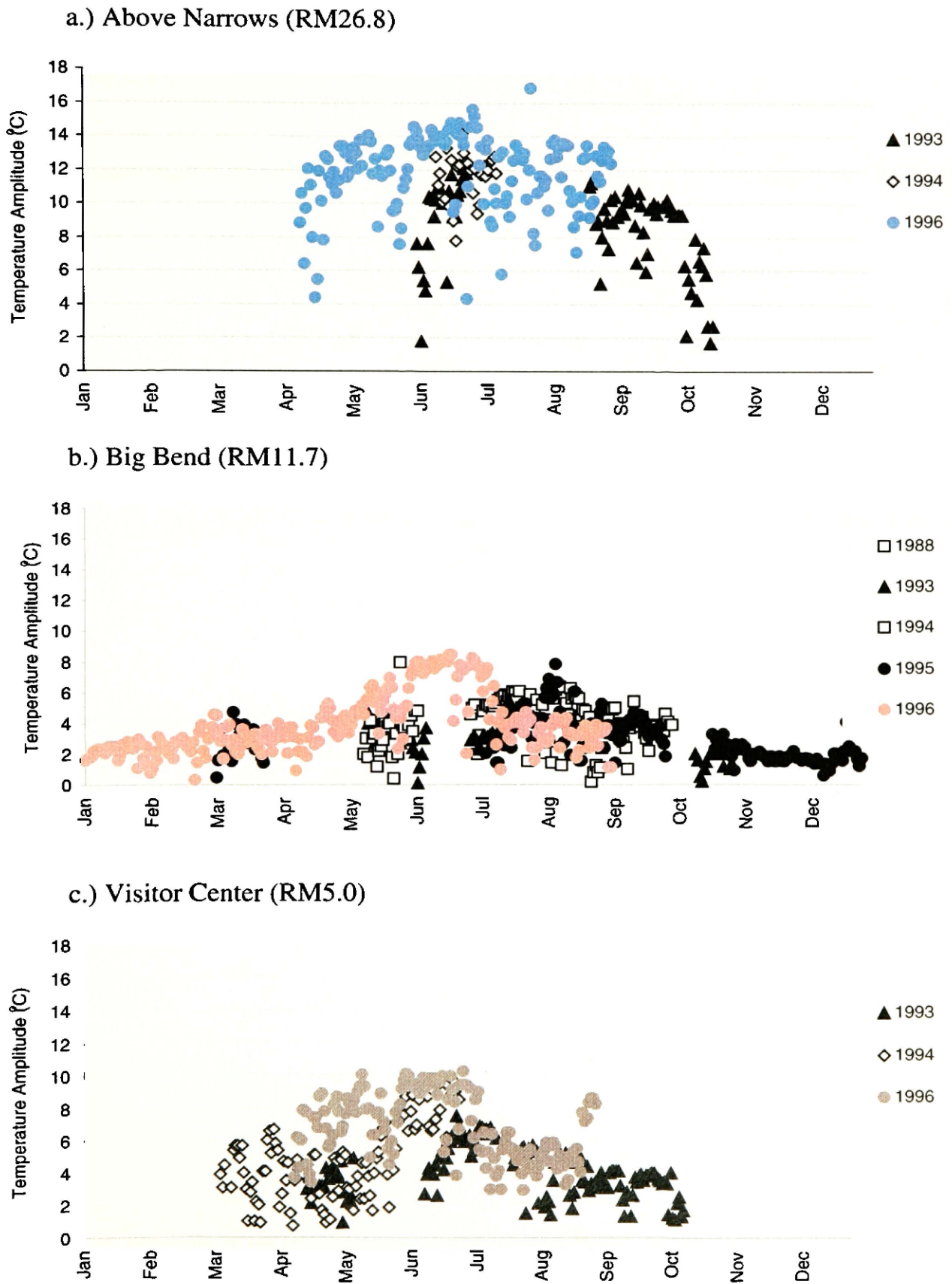


Figure 7. Temperature duration curves illustrating the number of hours spent at each temperature interval, April 11 - August 31, 1996, at the Above Narrows (RM26.8), Big Bend (RM11.7) and Visitor Center (RM5.0) sites.

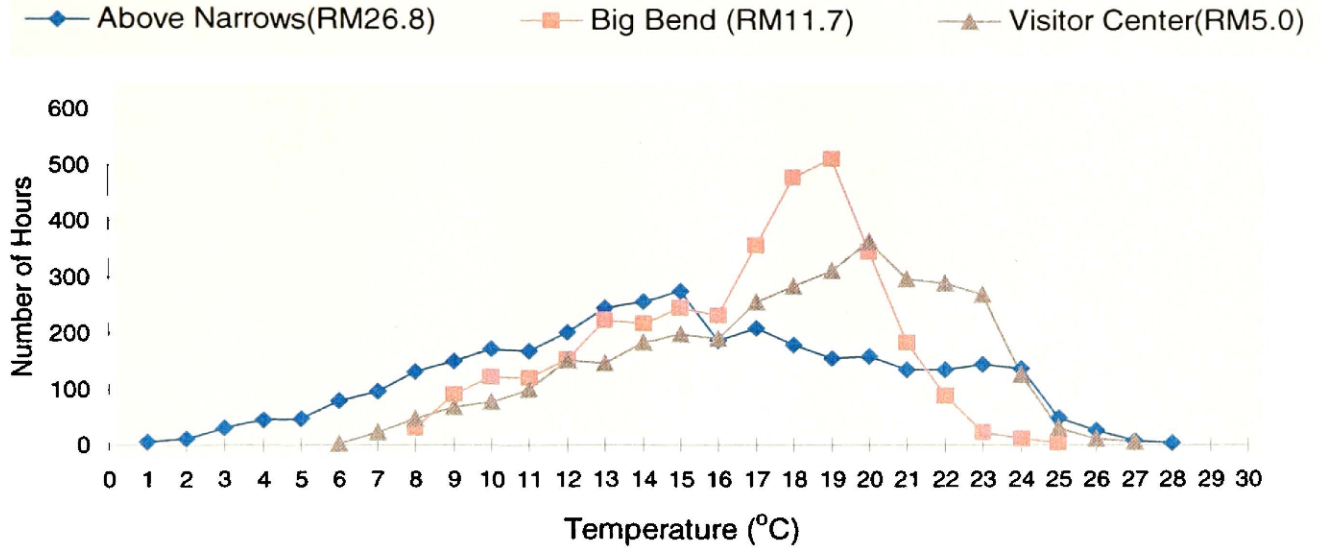


Figure 8. Temperature duration curve illustrating the number of hours spent at each temperature interval, June 1 - August 31, 1996, at the Above Narrows (RM26.8), Big Bend (RM11.7) and Visitor Center (RM5.0) sites.

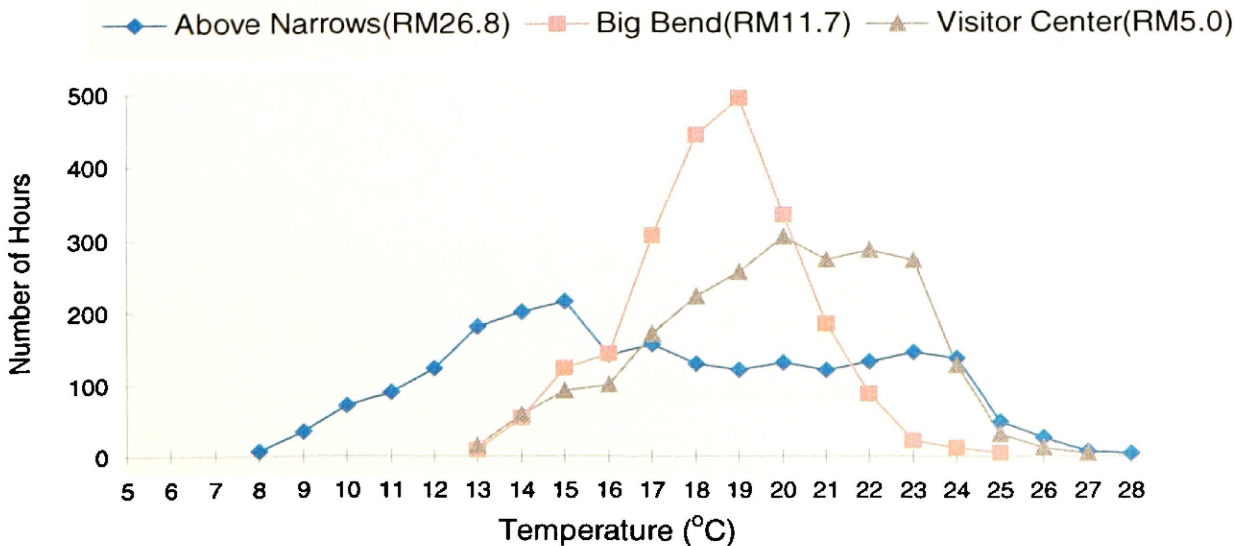


Figure 9. Heat accumulation, shown as total degree-hours, for the North Fork Virgin River at the Above Narrows(RM26.8), Big Bend (RM11.7) and Visitor Center (RM5.0) sites, April 11 - August 31, 1996.

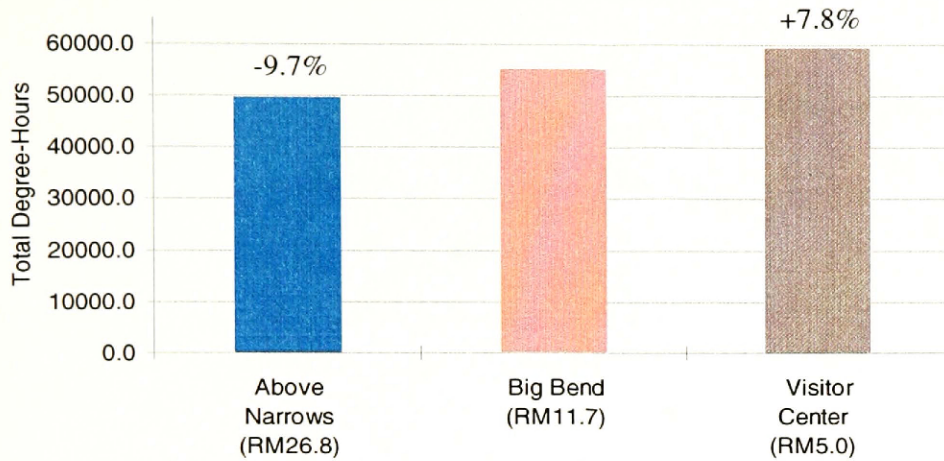


Figure 10. Growth, measured using interocular width (mm), of *Isogenoides zionensis* nymphs at Big Bend (RM11.7) from November 1993 through April 1996. Average size of all nymphs shown by blue bars. Average size of males (■) and females (▲) denoted.

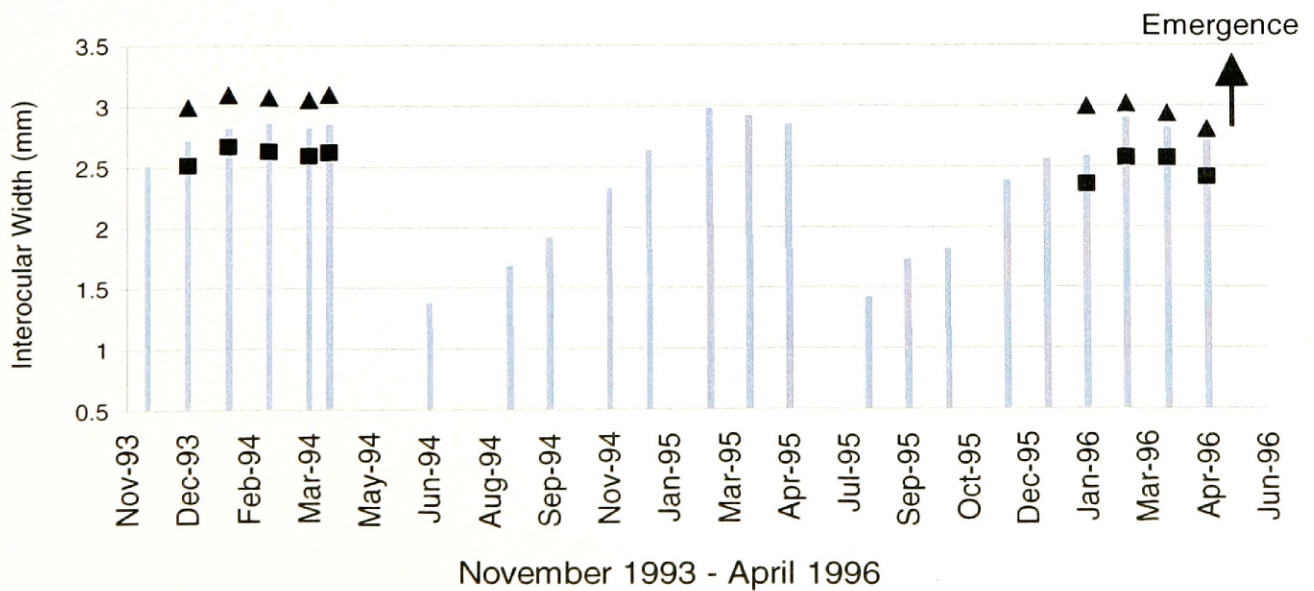


Figure 11. Growth and emergence of *Isogenoides zionensis* at the Big Bend (RM11.7) site, July 1995-August 1996, in relation to the thermal regime (average daily temperature). Average daily temperature at Big Bend shown in blue. Average size of all nymphs indicated by triangles (black), average size of male and female nymphs shown as squares (dark blue) and circles (pink), respectively.

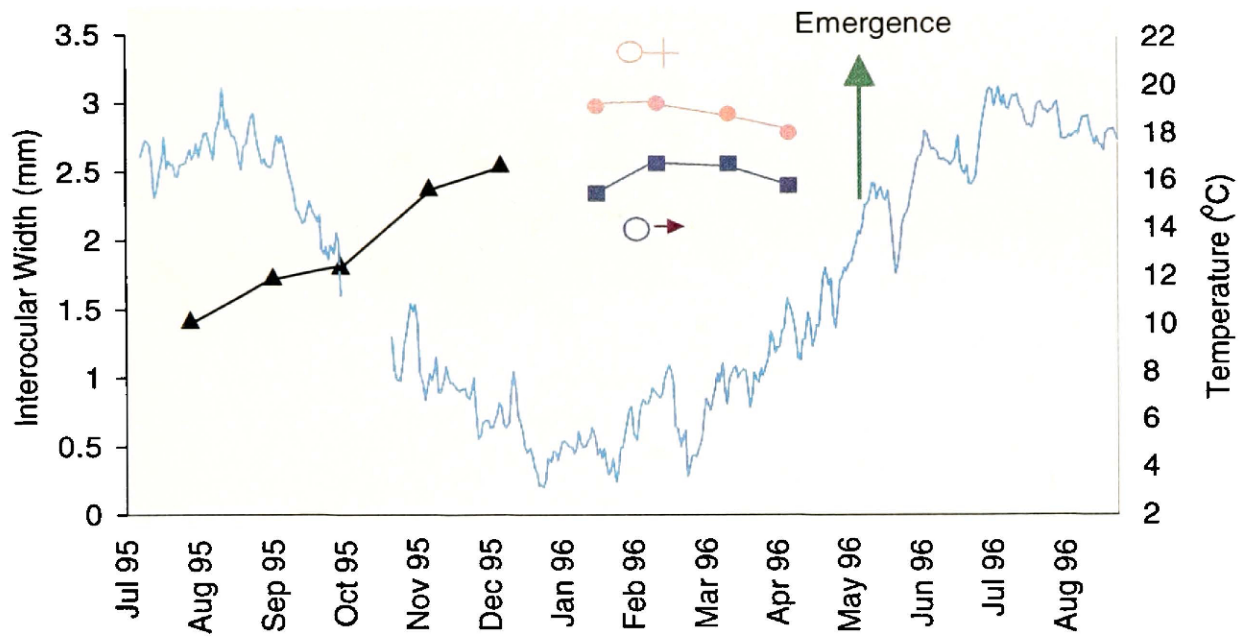


Figure 12. Experiment A: Mature nymphs from Big Bend (RM11.7) exposed to the average daily temperature in the field during natural emergence. Hourly temperatures during experiment (April 11-April 28, 1996) shown in green. Hourly temperatures at Big Bend under ambient field emergence conditions (May 4-21, 1996) shown in black. Response of nymphs to experimental temperatures indicated.

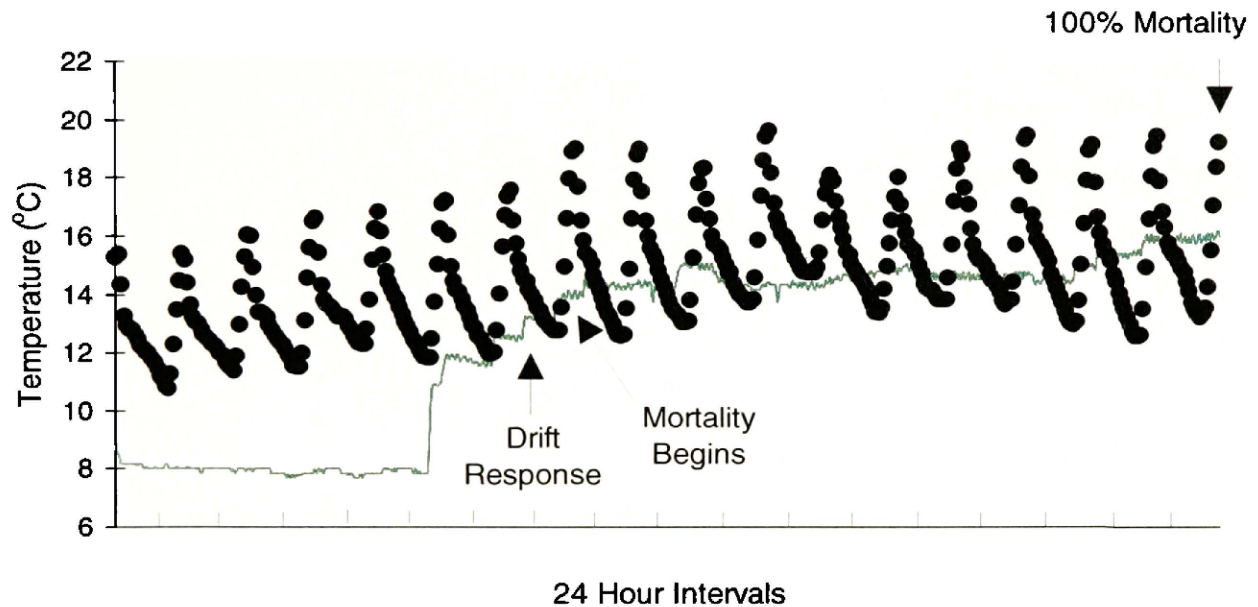


Figure 13. Experiment B: Mature nymphs from Big Bend (RM11.7) exposed to the minimum daily temperature at time of collection (April 10, 1996). Green dots illustrate the daily average experimental temperature. Hourly temperatures in the field at Big Bend shown in black. Emergence period under ambient and experimental period illustrated.

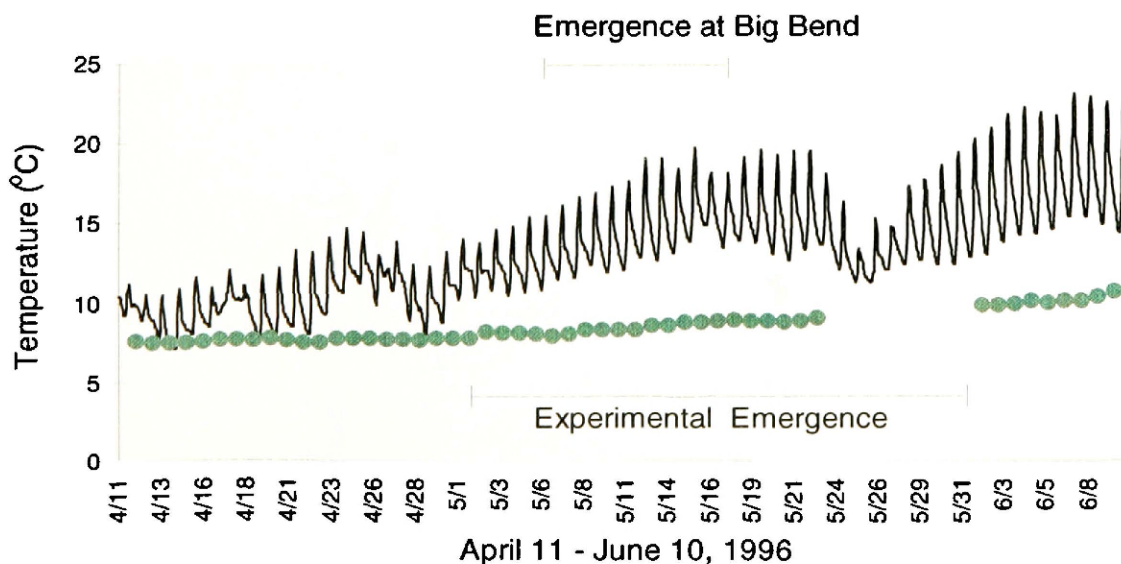


Figure 14. Results from Experiment B: total mortality, emergence and female wing development.

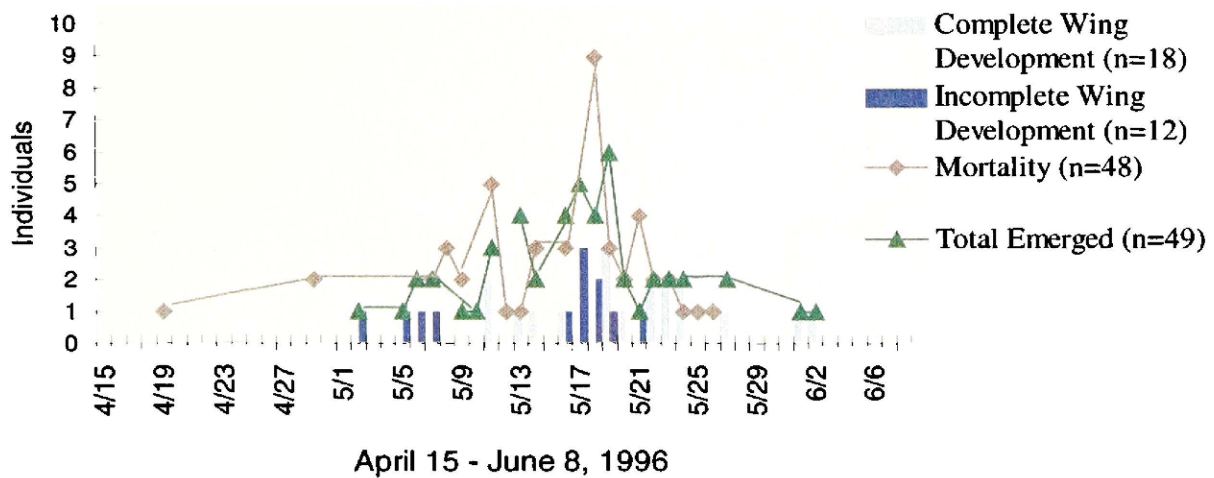


Figure 15. Ambient conditions experienced in a 24 hour period during the emergence at Big Bend (RM11.7). Favorable temperatures range for emergence illustrated.

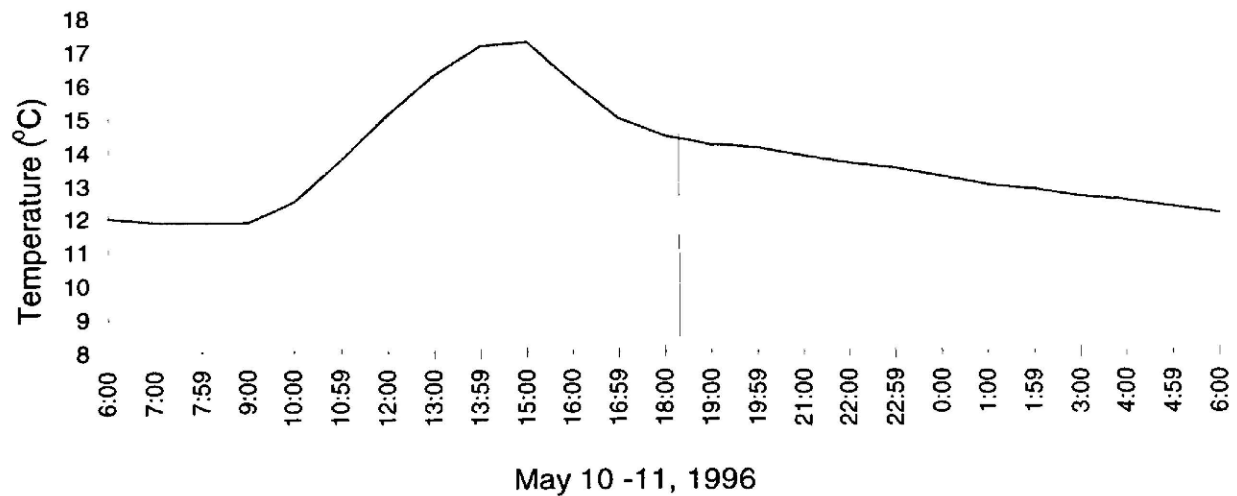


Figure 16. Distribution of *Isogenoides zionensis* and sampling sites in the upper Virgin River watershed.

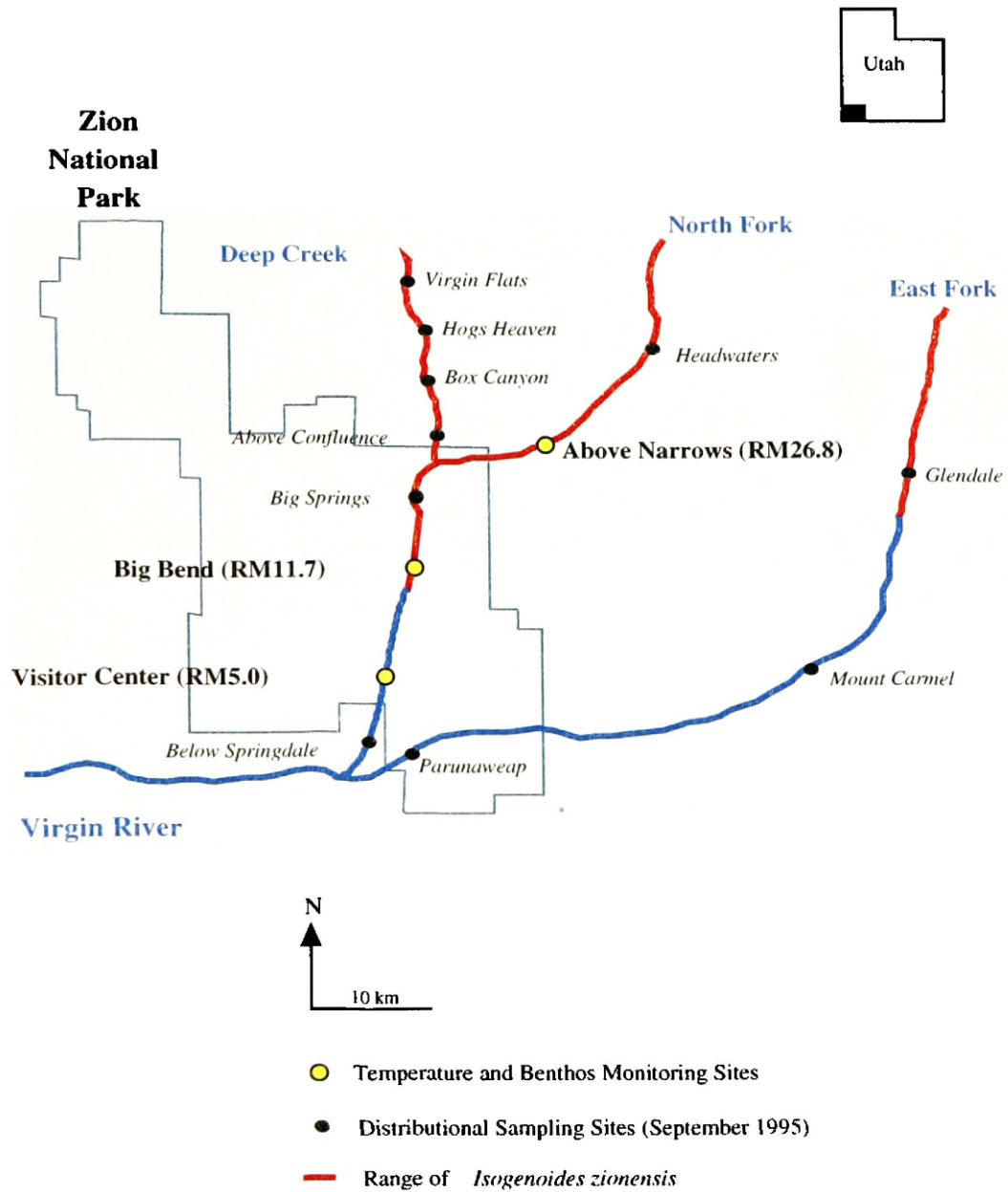


Figure 17. Longitudinal density of *Isogenoides zionensis* within the North Fork Virgin River basin. Error bars ± 1 standard deviation.

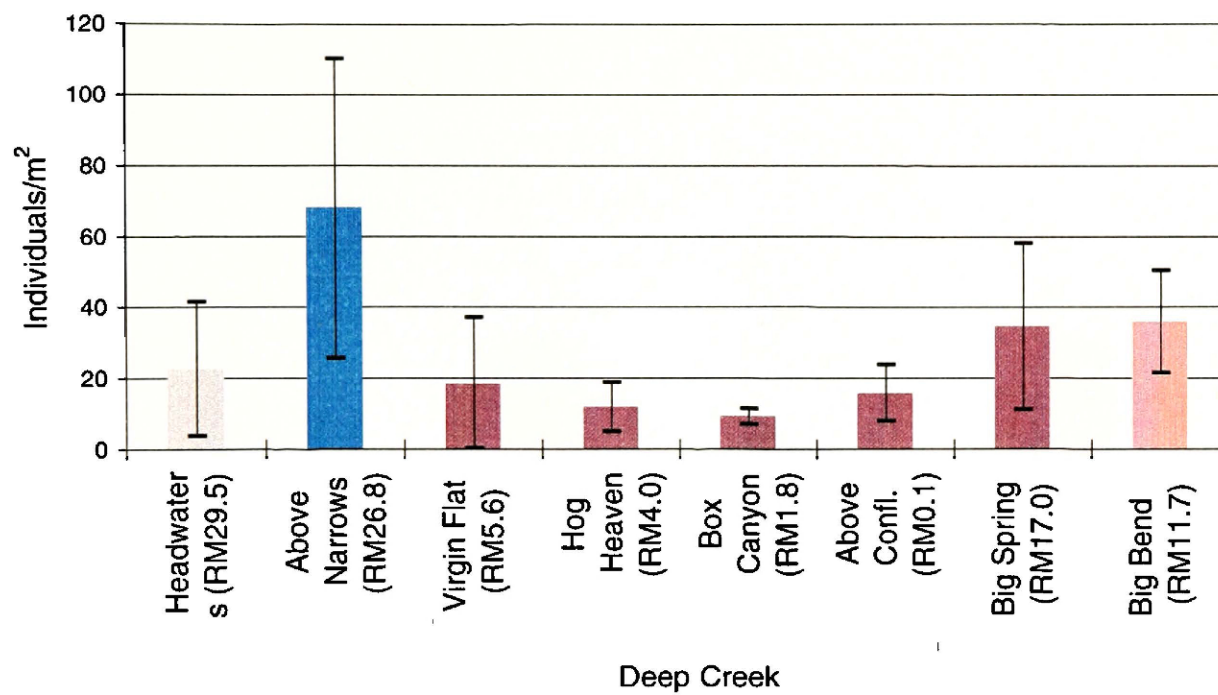


Figure 18. Size of *Isogenoides zionensis* from the Above Narrows (RM26.8, blue) and Big Bend (RM11.7, pink) in September 1995 and 1996. Significant differences in size are denoted by asterisks ($P < .001 = *$ and $P < .0001 = **$). Error bars indicate ± 1 standard deviation.

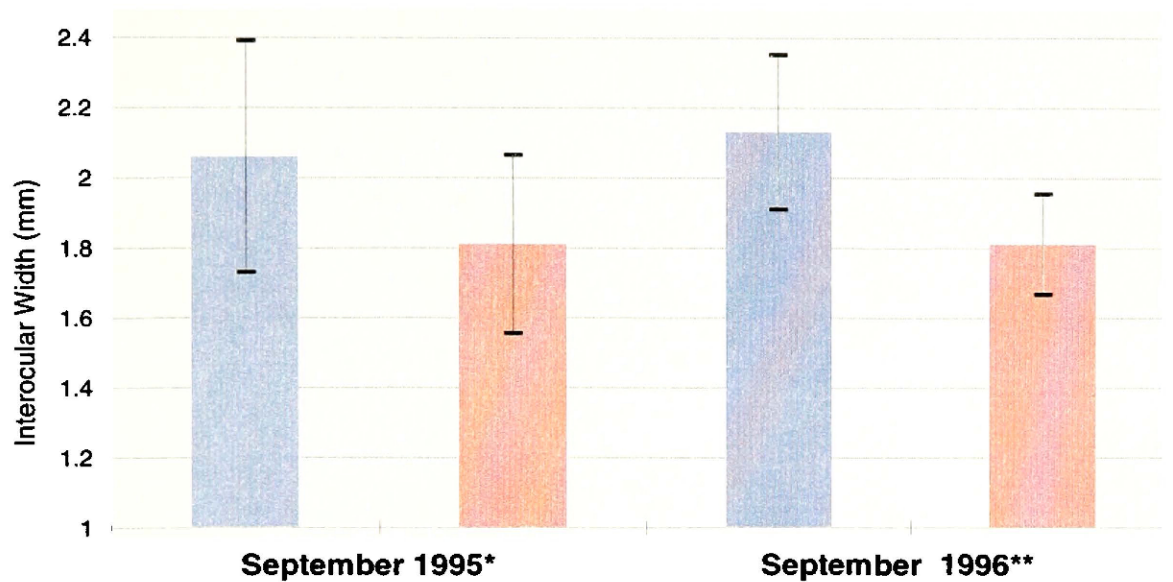


Figure 19. Size of *Isogenoides zionensis* females and males from Above Narrows (blue) and Big Bend (pink) sites. No significant difference in size of either sex between sites ($P = .9217$ and $P = .6032$). Error bars indicate ± 1 standard deviation.

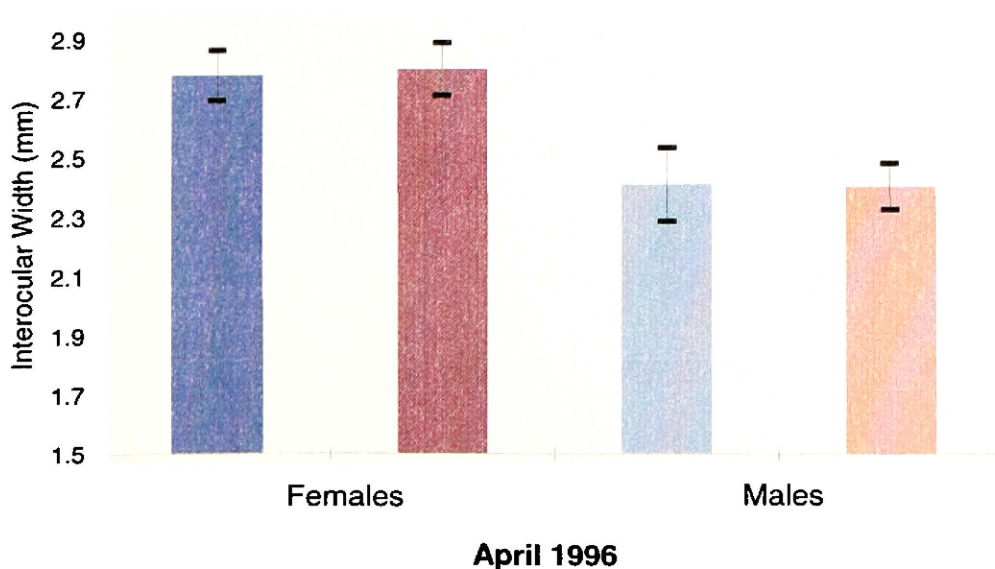


Table 1: Site Descriptions and Density of *Isogenoides zionensis* in the Upper Virgin River Basin: September 1995

<u>East Fork Virgin River</u>	<u>Elevation</u> (m, ft.)	<u>Channel</u> <u>Width (m)</u>	<u>Depth</u> (cm)	<u>Periphyton</u>	<u>Density of</u> <u><i>I. zionensis</i> (m²)</u> (Mean± STD)
EF at Glendale (RM186.6)	1974 (5900)	1.5	30.0	moderate	13.3 ± 6.1
Mt. Carmel (RM176.9)	1562 (5140)	10.6	15.0	low	0
Parunaweap (RM157.3)	1200 (3950)	12.1	30.0	low	0
<u>Deep Creek</u>					
Virgin Flats (RM5.6)	1763 (5800)	7.6	30.0	low	18.7 ± 18.0
Hogs Heaven (RM4.0)	1690 (5560)	7.6	30.0	low	12.0 ± 6.0
Box Canyon (RM1.8)	1629 (5360)	7.6	30.0	low	9.3 ± 2.3
Above NF Confluence (RM0.1)	1602 (5270)	7.6	30.0	low	16.0 ± 8.0
<u>North Fork Virgin River</u>					
Headwaters (RM29.5)	2256 (7420)	1.1	12.0	low	22.0 ± 18.9
Above Narrows (RM26.8)	1885 (6200)	4.6	15.0	low	68.0 ± 42.3
Big Spring (RM17.0)	1581 (5200)	7.6	30.0	low	34.7 ± 14.0
Big Bend (RM11.7)	1307 (4300)	12.1	25.0	low	36.0 ± 14.0
Visitor Center (RM5.0)	1207 (3970)	4.5	60.0	moderate	0*
Springdale (RM2.0)	1155 (3800)	7.6	45.0	moderate	0

* Quantitative sampling was not conducted due to unsuitable substrate.