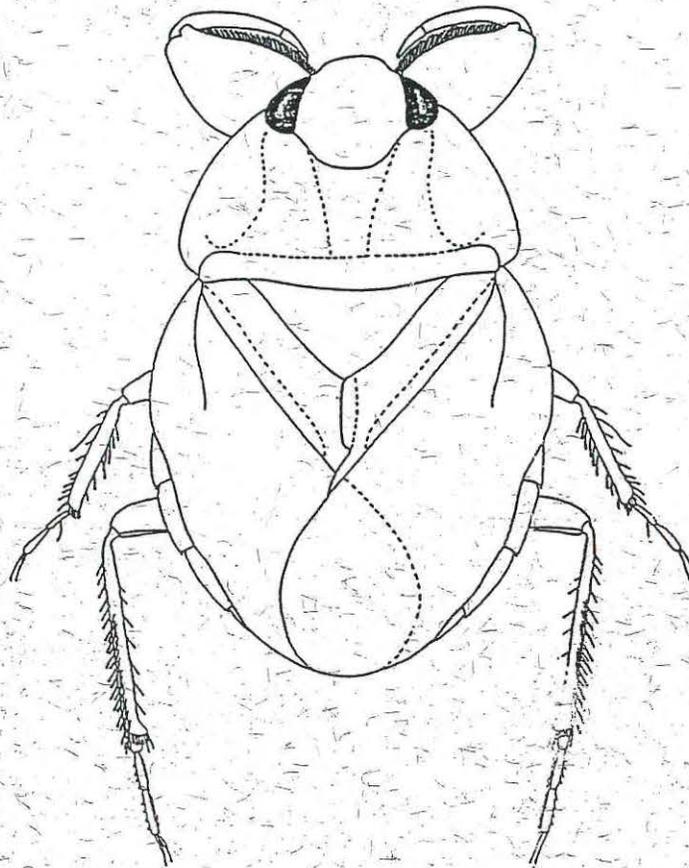


Ecological Investigation of Two Naucorid Species  
(*Ambrysus amargosus* and *A. relictus*) Endemic to  
Thermal Springs of the Ash Meadows  
National Wildlife Refuge.



Michael S. Parker  
G. Gary Scoppettone  
M. Bridget Neilsen

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by:

Michael S. Parker  
Department of Biology  
Southern Oregon University  
Ashland, OR

G. Gary Scoppettone & Bridget Neilsen  
U. S. Geological Survey  
Biological Resources Division  
Reno Field Station  
Reno, NV

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This project was completed with the assistance of numerous individuals and agencies. Cynthia Martinez (U.S. Fish & Wildlife Service, Southern Nevada Field Office) provided logistical and technical support and assisted with sample collection on numerous occasions. Matt Frantz, Steve Lydick, Chris Mace, Stewart Reinbold, and Sean Shea (U.S. Geological Survey, Reno Field Office) assisted with field sampling and Dionne Ybarra assisted with sample sorting in the laboratory. Joseph Kiernan and Deidre Deen, students at Southern Oregon University, sorted and identified a major portion of the benthic invertebrate samples and assisted in conducting feeding trials and microhabitat sampling. Finally, personnel of Ash Meadows National Wildlife Refuge, particularly David St. George, David Ledig and Eric Hopson, provided important logistical support, and David St. George provided much valuable assistance with various aspects of the field work.

## Abstract

A two-year study was undertaken to describe important ecological relationships determining the distributions and abundances of two endemic naucorid species, *Ambrysus amargosus* and *A. relictus*, inhabiting springs within the Ash Meadows National Wildlife Refuge. Aspects of naucorid biology that were studied included: (1) seasonal variation in abundance, and abundances of co-occurring benthic invertebrates, within and among springs, (2) life history characteristics, (3) physical habitat requirements and microhabitat selection, and (4) diet and feeding. In addition, this study documented the successful introduction and establishment of *A. amargosus* into a portion of its former range. Results of monthly population monitoring showed that naucorid populations vary considerably among spring systems, and that populations within most springs fluctuate seasonally. Naucorid abundance peaks during summer, when reproduction is greatest, and is lowest during the winter, the period of lowest productivity. Associated macroinvertebrate populations fluctuated following a similar pattern. Hydrobiid snails were consistently the most abundant invertebrate species within and among springs.

Among springs inhabited by *A. relictus*, North Skruggs and Marsh springs had higher population densities than North Indian Spring, with Skruggs having the largest population. Within the Point-of-Rocks system, *A. amargosus* populations were very small and restricted to the upper-most (10-15 M) sections. The population of *A. amargosus* introduced into the Kings Pool outflow during late summer 1997 grew steadily during the study period, reaching its peak abundance in June 1998. This population is currently the largest population of *A. amargosus* within the Point-of-Rocks system. This result suggests that restoration of other springs would likely benefit naucorid, and other endemic invertebrate, populations.

An experimental analysis of the effects of substrate size and current velocity on naucorid abundance, and sampling within diverse microhabitats, revealed that naucorids prefer

microhabitats with gravel-pebble size substrates and relatively high flows (>30 cm/s). They do not use microhabitats with silt or sand substrates. Naucorid nymphs had higher relative abundances within aquatic vegetation, and the greatest number of naucorid eggs was also found on vegetation and within gravel-pebble substrates, showing that different microhabitats are used by different life stages. To provide the necessary habitat diversity, restoration efforts should focus on reestablishing connections between spring outflow channels and natural drainage networks to facilitate transport of larger substrates into these channels during flash floods.

Life histories of both species are typical of most aquatic and semi-aquatic heteroptera. They are univoltine, with 5 nymphal instars. Reproduction takes place from spring through summer, and they over-winter as late instar nymphs or adults. Fecundity is relatively low (approximately 7 eggs per female) and egg size is large relative to female body size.

Feeding trials and direct observation revealed that among macroinvertebrate taxa common within most spring systems, "soft-bodied" forms (amphipods, mayfly nymphs, elmids beetle larvae and caddisfly larvae) were preferred over those with shells or thick exoskeletons (snail and adult elmids beetles). The amphipod *Hyalella* is typically the most abundant of the preferred taxa, and therefore probably makes the greatest contribution to *Naucorid* diets.

## Acknowledgments

This project was completed with the assistance of numerous individuals and agencies. First, and foremost, Gary Scoppettone (U.S. Geological Survey, Reno Field Station) was the driving force behind the study and was the primary source of logistical, scientific and technical support. He also spent considerable time in the field assisting with sample collection and setting up field experiments. Cynthia Martinez (U.S. Fish & Wildlife Service, Las Vegas Field Office) also provided logistical and technical support and assisted with sample collection on numerous occasions. Bridget Neilsen (U.S.G.S. Reno Field Station) coordinated much of the field sampling and was assisted at various times by Matt Fransz, Steve Lydick, Chris Mace, Cynthia Martinez, Stewart Reinbold, and Sean Shea. In addition, Bridget put in considerable time sorting and identifying invertebrate samples, along with Dionne Ybarra. Joseph Kiernan and Deidre Deen, students at Southern Oregon University, sorted and identified a major portion of the benthic invertebrate samples and assisted in conducting feeding trials and microhabitat sampling. Finally, personnel of Ash Meadows National Wildlife Refuge, particularly David St. George, David Ledig and Eric Hopson, provided important logistical support, and David St. George provided much valuable assistance with various aspects of the field work.

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## INTRODUCTION

Ash Meadows, an area defined by its high concentration of thermal springs, within the Amargosa River drainage, has long been recognized as harboring some of the most diverse local assemblages of endemic plants, fish, and invertebrates in North America (e.g. Hershler and Sada 1987; Soltz and Naiman 1978). Due to extensive modification of most springs and their outflows throughout Ash Meadows, however, many species of aquatic organisms have suffered severe population declines and have been eliminated from portions of their former ranges (e.g. Shepard 1993; Williams et al. 1985). Among these are two species of creeping water bugs, the Ash Meadows and relict naucorids (*Ambrysus amargosus* and *A. relictus* respectively). The historic distribution of the Ash Meadows naucorid was a series of springs and their outflows at Point-of-Rocks, near the southeast margin of Ash Meadows. In the original description of *A. amargosus*, LaRivers (1953) described collecting them "in large quantities" from one of the outlet streams draining a large spring pool. By 1985, however, Ash Meadows naucorid populations were so reduced, and their range restricted to a small fraction of their historic distribution, that the species was listed as threatened and provided protection under the federal Endangered Species Act (U.S. Fish and Wildlife Service 1985). In 1987, surveys of other Ash Meadows springs resulted in the discovery of additional naucorid populations (G. G. Scopettone, personal communication), originally thought to be

*A. amargosus*, but later identified as a new species, *A. relictus* (Polhemus and Polhemus 1994).

With the exception of taxonomic descriptions, and brief descriptions of their habitats at the time of discovery (LaRivers 1953; Polhemus and Polhemus 1994), nothing is known about the biology of these two species. The goal of this study, therefore, was to describe important ecological relationships determining the distribution and abundance of naucorids within and among the springs they inhabit, and to thus provide information valuable in the effort to restore and conserve these environments.

Specifically, we addressed the following areas of naucorid biology: (I) seasonal variation in naucorid abundance, and abundances of co-occurring benthic invertebrates, within and among springs (II) life history characteristics; (III) physical habitat requirements and microhabitat selection; and (IV) diet and feeding.

## METHODS

### Study Sites

#### *Point-of-Rocks*

This site consists of a series of springs and seeps emerging approximately 50 m upslope from the base of a limestone ridge, near the southeast border of the Refuge (Fig. 1). Historically, the discharge from these springs collected in a large pool at the base of the ridge (estimated to be approximately 10 X 5 M;

[LaRivers 1953]), the discharge of which became a braided channel that flowed approximately 3 km to the southwest. It was from this channel that LaRivers (1953) first collected *A. amargosus*. At the time of this study, only the upper-most portions of the spring outlets remained intact, the lower spring pool and channel having been eliminated during construction of several large ponds at the base of the hill. Removal of the ponds in 1996 left behind a gently sloping expanse of fine sediments through which three artificial channels were dug to accept the discharge of these springs. These channels were continuations of the major spring sources within the system. The substratum within these lower channels was primarily mud and silt, with dense patches of the macroalga *Nitella* sp. and cattails growing throughout. Extensive sampling within these lower channels, prior to and throughout our study, failed to capture any naucorids; their distribution apparently ending where the spring channels leave the hill slope and begin to traverse the former pond sediments.

We focused our sampling efforts within the upper reaches of the three main spring sources within this system, all of which had discreet channels, and were known to be inhabited by *A. amargosus*. From W to E, these springs were Grindstone (named for depressions carved in limestone outcroppings nearby), Middle, and Refugium (which is the source of water for the Devils Hole pupfish refugium, located downslope to the E). All three springs are quite small, ranging from approximately 0.2 to 0.8 m wide and 1 to 10 cm deep. Refugium Spring had the greatest and Grindstone the least discharge. The substratum in the upper reaches of all three

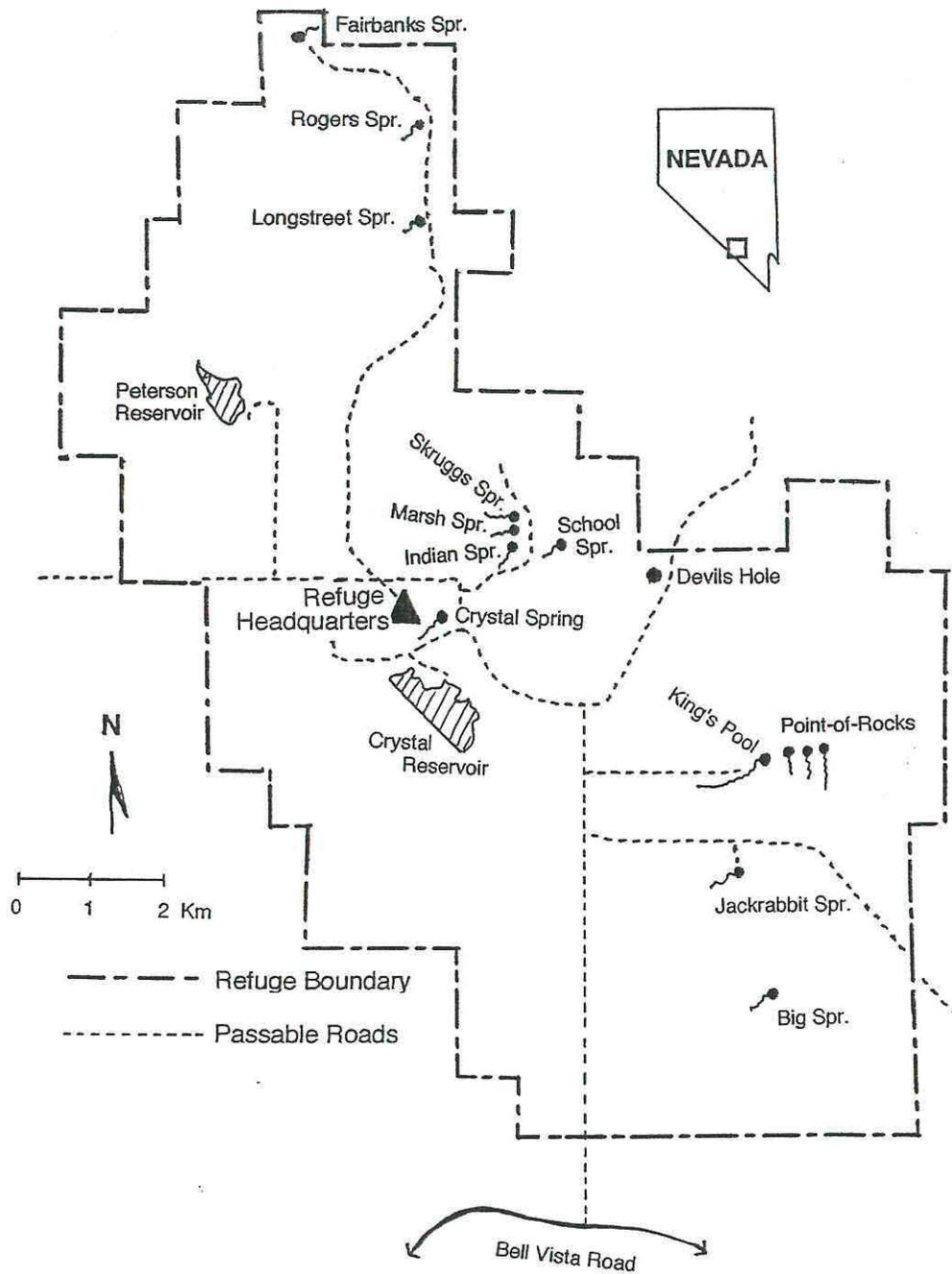


Figure 1. Map of Ash Meadows National Wildlife Refuge showing approximate locations of major springs.

springs consisted of gravel to pebble size stones overlying coarse sand, with extensive travertine deposits throughout. A large number of small cobbles had been placed in the channel of upper Refugium Spring by refuge personnel during summer 1996, in an attempt to increase naucorid habitat (David Ledig, personal communication). Water temperatures ranged from 31°C to 33.1°C among these springs throughout the period of the study. Temperatures in the lower, altered reaches fluctuated more widely, both daily and seasonally, with temperatures as low as 25.8°C being recorded in January 1998.

#### *Kings Pool Outflow*

Kings Pool is the largest and western-most spring within the Point-of-Rocks system (Fig. 1), and consists of a large spring pool with a single discharge channel. Both the pool and channel were modified numerous times in the past, primarily to provide water for irrigation and domestic use. The historic outflow channel was relocated several times and the entire discharge was piped or carried through a concrete-lined canal to distant agricultural fields. During these massive alterations, *A. amargosus* was apparently extirpated from the system, and distributions of many of the other endemic species were restricted to a small area near the point of discharge from the pool (e.g. Hershler and Sada 1987).

A large-scale restoration effort, initiated in 1995, re-established the outflow, which now carries the spring discharge through a single, highly sinuous channel that flows for several

hundred M. This channel carries several times the discharge of any of the other Point-of-Rocks springs, with a width that varies from 0.9 to 2.0 M and depth that ranges from approximately 0.10 to nearly 1 M. The substratum is a complex of substrate patches consisting of coarse to fine sediments, with numerous large boulders dispersed throughout the upper 50 M. Substrate particle size diminishes with distance downstream. Native riparian vegetation (*Prosopis* spp. and *Fraxinus velutina*) was planted and is naturally colonizing channel banks along the upper portion of the channel, as are *Tamarisk* and cattails. Long-term monitoring of this channel should provide valuable information about restoration and recovery of these types of desert spring systems and their associated biota.

During late summer and fall 1997 Ash Meadows naucorids were introduced into the Kings Pool outflow in an attempt to re-establish a viable population. Between August and September, twenty two individuals, removed from the outflow of the pupfish refugium, were released into the channel approximately 5-10 m below Kings Pool (David St. George, U.S. Fish & Wildlife Service, personal communication). On 29 May 1998, 12 additional naucorids were introduced; 3 (2 adult, 1 nymph) from the refugium outflow, 3 (2 adult, 1 nymph) from Middle spring, and 6 (5 adult, 1 nymph) from a small spring at the base of the hill between Middle and Refugium springs. On 07 August 1998, 5 additional naucorids were introduced; 1 late instar nymph from the pupfish refugium outflow and 2 (1 adult and 1 nymph) from Refugium spring channel, 1 adult from Middle Spring and 1 adult from the area between Middle and

Refugium springs. From these initial introductions a large naucorid population became established (see Results), which allowed us the opportunity to monitor the recovery of this population in response to habitat restoration.

#### *Skruggs, Marsh and Indian Springs*

This group of small springs is located approximately 5 km northeast of the Point-of-Rocks system (Fig. 1). These springs are inhabited by the only known populations of *A. relictus*. All three spring systems have been channelized, re-routed and, in some areas, impounded. At many sites, the channels have been overgrown by terrestrial or phreatophytic vegetation. Little if any habitat resembling historical conditions remains.

Skrugg springs consists of two spring sources (North and South Skruggs) and their outflows, and both are inhabited by *A. relictus*. Our study site was on North Skruggs and included the open reach downstream of the road crossing to where the channel spreads out into a large cattail marsh approximately 30-35 M downstream. The marsh is the result of a former impoundment. The upper portion of this reach consisted of a narrow (20-35 cm wide), rapidly flowing (35-70cm/s) channel with a substratum dominated by large, complex travertine deposits interspersed with loose gravel to pebble size substrate particles. The lower section, above the cattail marsh, had a wider channel, slower flow velocities (<20cm/s), and a substratum dominated by silt and sand. In addition, emergent vegetation, primarily *Carex* sp., was abundant within and adjacent to the channel. Temperature at the spring

source was consistently 34.0°C, at the road crossing it was 32.0-33.0°C, and at the lower end it varied from 31.0-32.2 °C.

Marsh Spring is located approximately 0.5 km S of South Skruggs. The spring emerges from a single source and flows in a SW direction approximately 50 M before disappearing into a former impoundment, now a dense cattail marsh. Our sample site was the 30 M reach downstream of the metal V-notch weir. The upper portion of this reach was a relatively open channel with rapid flow (30-50cm/s) and a substratum consisting of travertine deposits, and travertine-derived gravel overlying silt and sand. Very little emergent vegetation is present in this section of the channel. In contrast, the lower portion of the reach has a dense growth of emergent *Carex* and is heavily shaded by terrestrial vegetation. The channel is wider and more spread out, current velocities are much lower (0-10 cm/s) and the substratum is dominated by silt and sand. Temperature at the spring source was 31°C and at the lower end of the reach ranged from 28.2-30.8°C.

North and south Indian springs are located several hundred M south of Marsh Spring. Our sample site was within the upper 60 M of North Indian Spring. Within this reach the channel is deeply incised, narrow (<30cm) and overgrown by terrestrial and phreatophytic vegetation. The substratum throughout the reach is primarily sand and silt. Temperature at the spring source was 27.0-27.8°C.

## Population Monitoring of Naucorids and Associated Invertebrates

To monitor macroinvertebrate populations we used artificial substrate samplers that mimicked small patches of pebble-size substrate. Samplers were constructed of heavy-duty plastic mesh (19 mm openings), folded to make 17 X 17 cm square pouches, filled with approximately 20 large pebbles (28-35 mm diameter). Sampler tops and sides were closed with plastic cable ties, creating substrate-filled mesh "pillows" which could be placed on, and removed from, the streambed with minimal disturbance to the existing substrate. There are a number of advantages to sampling benthic invertebrates using artificial substrates, including standardization and repeatability of sampling effort among sites and sample collectors, smaller sample number required to achieve desired precision, and, perhaps most importantly in our study, reduced disturbance to the stream environment relative to standard, destructive sampling methods (e.g. Surber, Hess or dredge samplers) that disrupt or remove portions of the natural streambed (Rosenberg and Resh 1982).

Samplers were deployed by placing them directly on the streambed within shallow depressions created by displacing small amounts of streambed sediments. They were collected after a minimum colonization period of 28 days, which allowed invertebrate populations to reach an equilibrium with the surrounding environment. Naucorid populations were sampled at approximately monthly intervals, and the entire macroinvertebrate assemblage at bi-monthly intervals, from September 1997 through August 1998.

downstream reaches. The downstream reaches were channelized sections flowing over deposits of silt and mud left behind after several large, artificial ponds were drained and the ground leveled. In the restored outflow channel of King's Pool, six samplers were placed within 10 m of the outflow and six 35-50 downstream of the outflow. Habitat conditions (depth, flow, substrate and cover) were similar between these two sites.

At both South Skruggs and Marsh springs, five samplers were placed within upper and lower reaches. The upper reaches had higher current velocities and larger, more complex substrate materials than the lower reaches, which had silty sediments and considerable vegetation along the channel banks and emerging from the streambed within the channel. At Indian Spring, a total of six samplers was placed along the length of the spring outflow, in relatively open sections or sections where the overhanging vegetation could be parted to allow access to the channel.

#### Life History Analyses

The population monitoring just described yielded important information on changes in size distribution and population structure. From size distribution data, and relative proportions of juvenile and adult life stages, we could determine important aspects of naucorid life histories, including periods of peak reproduction, voltinism, and number and size ranges of larval instars. Combined with data from our habitat selection analyses (see below) we could determine habitat requirements for different

populations to reach an equilibrium with the surrounding substratum. During retrieval, a D-frame dip net was placed directly downstream from an individual basket to retain dislodged organisms as it was lifted from the streambed. Basket contents, and the contents of the D-net, were emptied into a large, white pan and the substrate particles were rinsed and removed. The remaining material was searched, all naucorids removed, and the number of naucorids per sample recorded. Life stage and body length measurements were also recorded for each individual. Naucorids were held in separate containers until all the baskets at a site were retrieved and were then returned, unharmed, to the stream. The remainder of the sample was preserved (70% ethyl alcohol) and returned to the laboratory, where all invertebrates were sorted from the remaining sediment and debris under 10X magnification, identified to the lowest practical taxonomic level, and enumerated. Differences in naucorid abundance, and the abundances of common macroinvertebrates, were analyzed by two-way Analysis of Variance (ANOVA), with substrate size and current velocity as main factors. Since differences in naucorid abundances between springs were not significantly different (three way ANOVA, site effect  $p = 0.245$ ) data from the two springs were combined in the final analysis.

#### *Microhabitat Sampling*

To compare naucorid densities among different microhabitats, we collected replicate samples within discreet substrate patches using a 15 X 15 cm square template. Substrate within the template

04-07 August 1998, with *A. amargosus* as predator. The general procedure was to place a known number of individuals of common prey species into small, flow-through chambers, with and without naucorid predators, and compare the number of surviving prey after 12 to 24 hr. The difference between the number of prey remaining in predator-present versus predator-absent (control) chambers was considered a measure of prey susceptibility. Significant differences were detected using t-tests.

Chambers used in Marsh Spring feeding trials were 30.0 X 7.5 X 5.0 cm (Length, width, depth respectively) plastic trays with three 2-cm diameter holes covered with 0.33 mm mesh nylon screening in each end. The screens retained introduced naucorids and prey organisms, prevented movement of invertebrates into the chamber, and allowed water to pass longitudinally through it (average velocity = 21 cm/sec; range = 18 - 33 cm/sec). Eight pebble size stones were placed into each chamber to mimic natural substrates on which predator-prey interactions take place. Three trays were placed into the stream channel at sites with depths less than 5 cm and flow velocities ranging from 25-42 cm/sec. To each tray was added thirty individuals each of the most common potential prey found in Marsh Spring, including adults of two elmids beetle species, (*Microcylloepus similis* and *Stenelmis calida*), elmidae larvae, spring snails (*Pyrgulopsis pisteri*), and amphipods (*Hyaella* sp.). Approximately 1 hr after prey were introduced, each tray received 2 adult naucorids. Naucorids were introduced between 1800-1830 hr and the trial was terminated 12 hr later, between 0600-0630 hr, when the naucorids were removed. No

naucorids escaped during the trial. Numbers of surviving prey were determined by emptying the contents of the tray into a shallow, white pan and thoroughly searching for, and recording the number of live individuals with the aid of a hand lens (4-8X magnification) or dissecting microscope (10-20X magnification). After determining the number of surviving prey, additional individuals were added as needed to restore the number to 30 within each tray, and the trays were placed back into the stream without naucorids. Twelve hr later the number of remaining individuals was determined. These predator-free trays served as controls.

Springs within the Point-of-Rocks system, including the Kings Pool outflow, are inhabited by a greater diversity of potential prey taxa. In addition, the greater size and flow of the Kings Pool outflow provided greater opportunity to conduct a larger number of feeding trials examining susceptibility of a wider range of prey. Chambers used in Kings Pool feeding trials were constructed of 10 X 10 cm square plastic boxes (9 cm deep) with screen-covered windows on two sides (7.5 X 9.5 cm openings; 0.33 mm mesh screen) and a screened top. Chambers were placed into floating racks (0.5 X 0.4 M), constructed of 1.9 cm diameter pvc pipe, and held in place with elastic cords. Their screened sides were oriented perpendicular to the flow, allowing water to pass directly through them (current velocity = 8-10 cm/sec). Each rack held eight chambers, and five racks were placed into the stream during each feeding trial. Three pebbles were added to each chamber to mimic the natural substrate. All chambers within a

rack received 10 individuals of a single prey species and 5 were randomly selected to receive an individual naucorid predator (either 5th-instar nymph or adult), the remaining 3 chambers did not receive naucorids and thus served as controls. Prey taxa used in these feeding trials were the most abundant potential prey among springs of the Point-of-Rocks system and included (1) Baetid mayfly nymphs (genus *Baetis*), (2) amphipod crustaceans (*Hyaella* sp.), (3) riffle beetle larvae (family Elmidae), (4) adults of two elmidae beetle species (*S. calida* and *M. similis*), (6) case-building caddisfly larvae (*Helicopsyche borealis*), (7) pebble snails (*Pyrgulopsis erythropoma*), (8) small individuals (9-15 mm shell length) of the exotic red-rim melania snail (*Melanoides tuberculata*), and (9) flatworms (Order Turbellaria). Predators were introduced into their respective chambers 1-2 hr after prey were added, and the trials were terminated 24 hr later, at which time naucorids were removed and remaining live prey were counted.

These trials differed from the Marsh Springs trials by presenting a single prey species to the predator. Therefore, results of these trials do not assess prey selection directly, but reveal relative susceptibilities of the different prey to naucorid predation, which is a strong indicator of which prey are likely to be most important to naucorid diets in their natural environment.

In addition to performing feeding trials, direct observations were made, using a clear Plexiglas view box or mask and snorkel, in an attempt to describe details of naucorid foraging behavior and mechanisms responsible for prey selection. Although we were unable to directly quantify components of the predation cycle

(e.g. encounter rates, attack, capture, and ingestion efficiencies) for each prey taxon, our observations provide a general description of naucorid foraging behavior. A total of 2.5 hr of observation was accumulated on 4 *A. relictus* individuals during feeding trials within Marsh Spring, and approximately 2.0 hr on 7 *A. amargosus* individuals foraging among natural substrates within the Kings Pool outflow on 07 August 1998.

## RESULTS & DISCUSSION

### Population Variation Within and Among Springs

#### *Naucorids*

Monitoring results show considerable variation in naucorid population densities, both within a given spring over time and among springs. Among *A. relictus* populations, densities were consistently greatest in Skruggs Spring and lowest in Indian Spring (Fig. 2). Within all three *A. relictus* populations there appeared to be a bimodal pattern in population density, with densities increasing during the spring and reaching a peak in the summer. A secondary peak is evident in late Autumn (Fig. 2). This pattern is most likely a response to the timing and intensity of reproduction, which occurs during the spring and summer (see below), and recruitment of early instars into the over wintering population. Although our sampling technique was effective at tracking overall population patterns, it was biased towards larger nymphal instars and adults. Due to their small size and lower

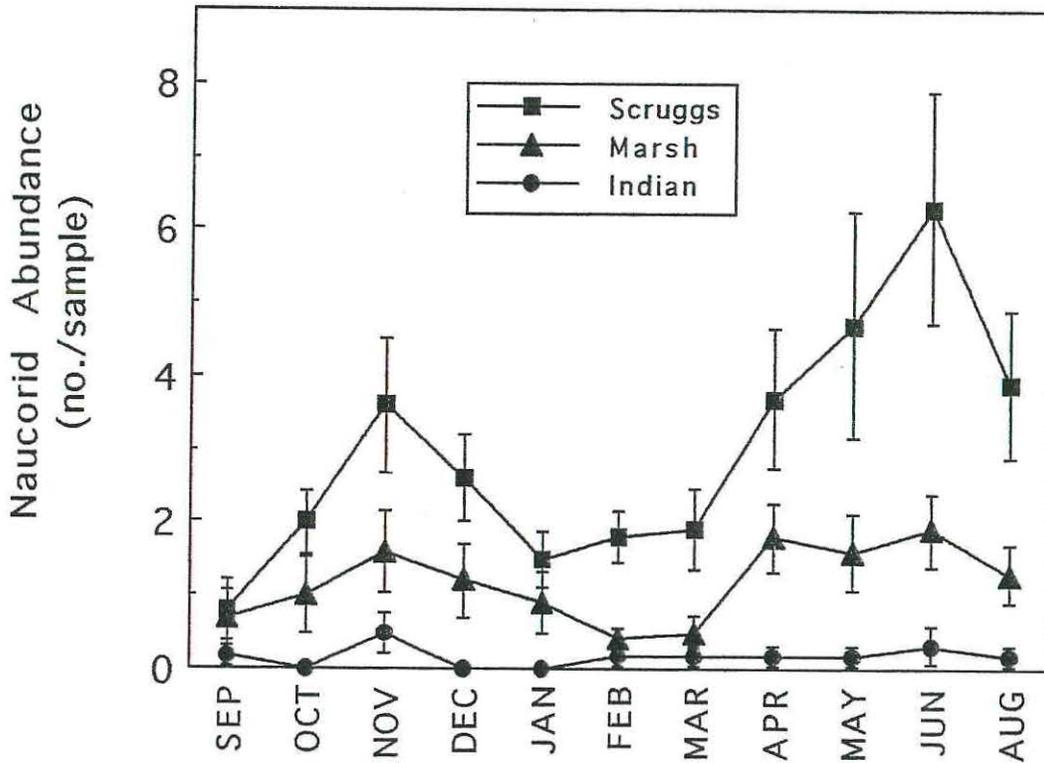


Figure 2. *Ambrysus relictus* abundance showing seasonal differences within and among springs. Values are means  $\pm 1$  SE (n=10).

activity levels, some instar I and II individuals likely went undetected during sample processing in the field. For example, a number of early instar individuals that went undetected during field processing were removed from preserved samples when they were sorted under magnification in the laboratory. Therefore, the

increase in population density observed during the late summer and autumn may be due in part to sampling bias. Earlier instars that were under-represented in spring and summer samples entered larger instars that were detected in autumn samples. In addition, peak abundances observed in the spring and summer likely under estimate total abundance due to early instars being under-represented.

Consistent declines in naucorid abundance during winter correspond to the periods of lowest productivity within these systems, and are probably the result of increased mortality and reduced activity. Therefore, these small populations are most susceptible to disturbances during the winter, prior to the onset of reproduction, and care should be taken in sampling them, or manipulating their habitats, at this time.

Differences in naucorid abundance among these three springs is most likely due to differences in habitat conditions and prey availability. Indian spring has a deeply-incised channel that is largely overgrown with dense terrestrial vegetation. Moreover, for most of its length the substrate is made up entirely of silt and sand, which is unsuitable naucorid habitat (see discussion of habitat requirements below). Among the three springs, the naucorid's primary prey, *Hyaletta* sp., was consistently most abundant within Skruggs Spring (Table 1).

Populations of *A. amargosus* within two of the three springs of the Point-of-Rocks system (Middle and Refugium springs) followed a pattern similar to that observed for *A. relictus* populations, with peak abundances occurring in spring and summer and lowest abundances occurring early autumn and winter (Fig. 3).

Overall, however, naucorid abundances were quite low in all three headwater springs sampled and observed population trends were quite weak. Although present within the Grindstone spring (personal observation), no naucorids were collected in our artificial substrates on any date. In addition, no naucorids were

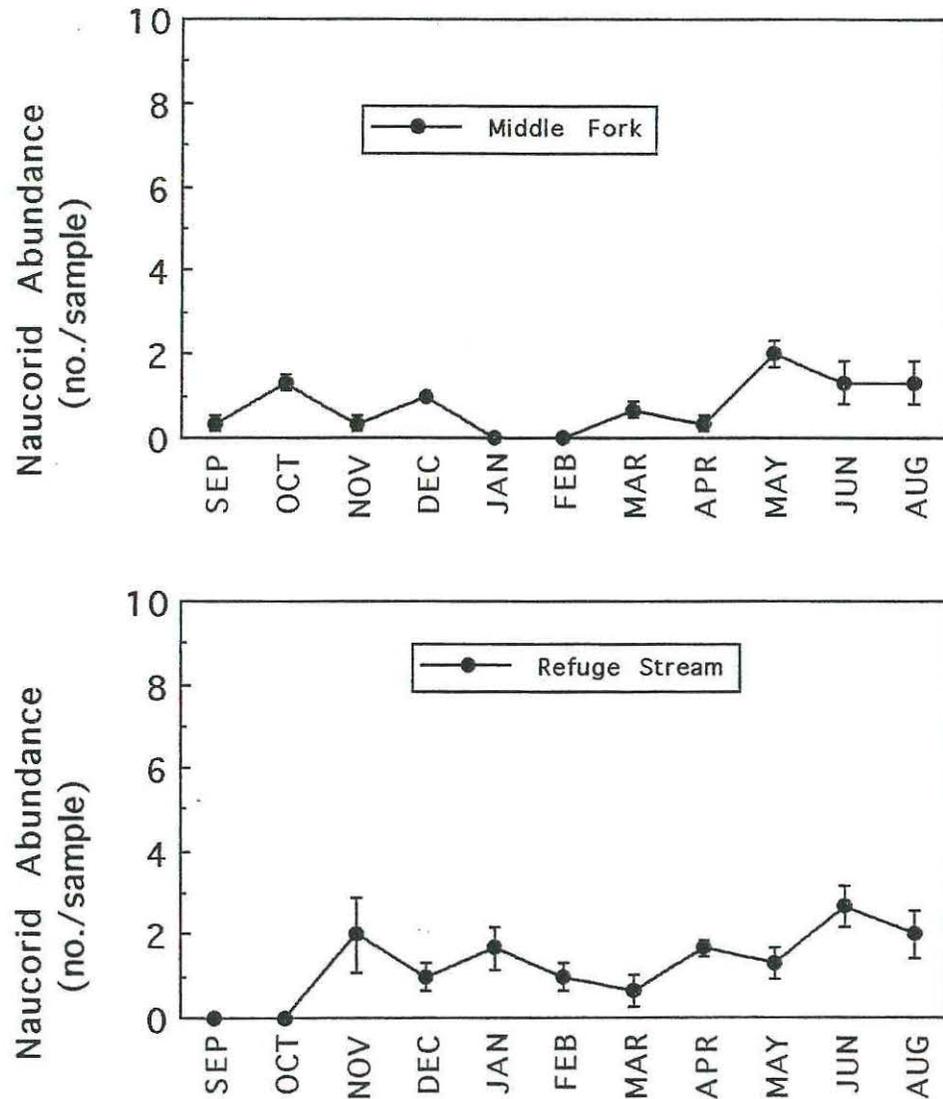


Figure 3. *Ambrysus amargosus* abundance within and between two springs of the Point-of-Rocks system. Values are means  $\pm$  1SE (n=3).

collected in the highly-altered lower reaches of any of the Point-of-Rocks springs, and these samples are omitted from this analysis. Due to the very restricted amount of habitat available to naucorids within the upper-most reaches of these spring sources, and their extremely low population densities, these populations remain in jeopardy of going extinct. Restoration of the lower reaches of these channels, to increase available naucorid habitat, should thus be a priority in the recovery of this species.

The *A. amargosus* population within the Kings Pool outflow followed a much different pattern (Fig. 4). The initial

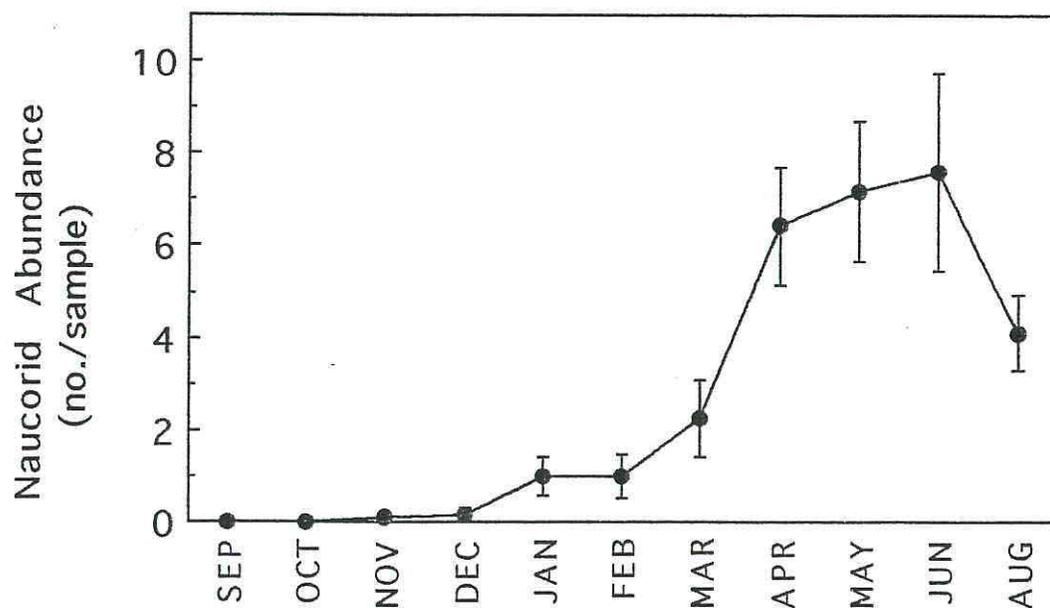


Figure 4. *Ambrysus amargosus* abundance within Kings Pool outflow illustrating establishment and growth of a population introduced into a restored spring system.

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introduction of naucorids into this stream took place in late August and September 1997. No naucorids were collected in our samplers in September or October. A single, late instar nymph was collected in November 1997 followed by one late instar nymph and one adult in December, 3 late instar nymphs in January and 3 adults in February 1998. The population increased dramatically during the spring, reaching peak abundance in June, corresponding to the period of peak reproduction (see Life History below). In addition, peak *A. amargosus* densities were much higher in the Kings Pool outflow than the other Point-of-Rocks springs, and higher than *A. relictus* peak densities. This discrepancy is due to differences in the amount and quality of suitable naucorid habitat, which is much greater within the Kings Pool outflow than any of the other springs inhabited by naucorids of either species. These results clearly demonstrate that naucorid populations have the capacity for rapid increase provided appropriate habitat conditions, and further suggest that drastically reduced populations in the remaining altered spring systems could experience substantial recovery following appropriate habitat restoration. However, careful, long-term monitoring will be required to determine the ultimate outcomes of populations within restored systems.

#### *Associated Benthic Invertebrates*

Abundances of associated benthic invertebrates (Figs. 5-7), and composition of invertebrate assemblages (Tables 1-3), also varied considerably within and among springs. With the exception

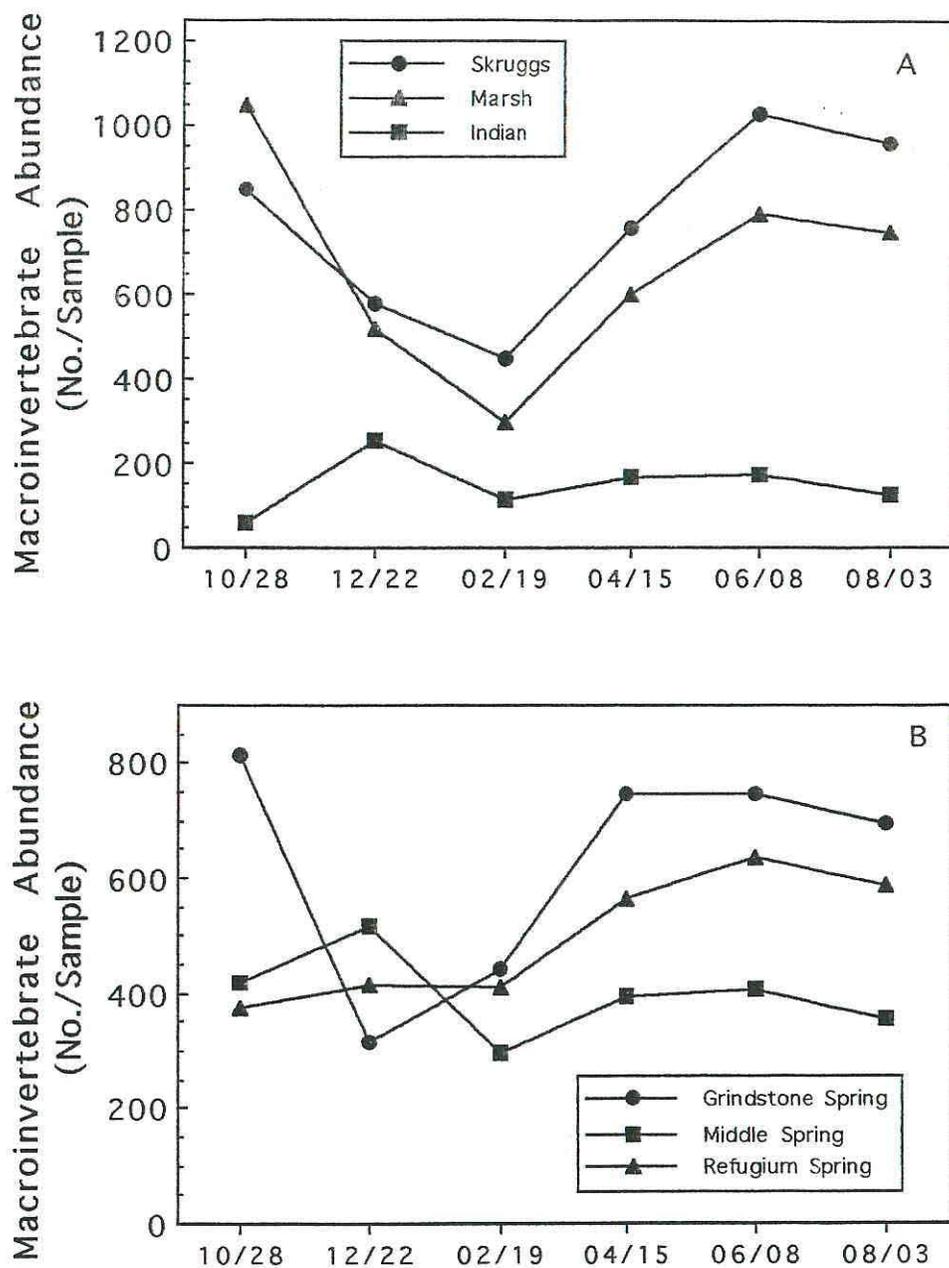


Figure 5. Total macroinvertebrate abundance within and among springs (A) inhabited by *Ambrysus relictus*, and (B) inhabited by *A. amargosus*. Error bars omitted for clarity (See tables 1 & 2 for SD of individual taxa)

of the Kings Pool outflow, most springs experienced the highest total invertebrate densities during spring and summer (April and June) and lowest densities in December or February (Fig. 5a and b). In contrast, total invertebrate densities within Kings Pool

outflow showed a continuous and dramatic increase over the duration of our study (Fig. 6). The pattern observed in most springs is likely due to invertebrate population responses to seasonal changes in productivity. The Kings Pool pattern is likely due to the ongoing process of recolonization of the restored channel. Since most common taxa lack an aerial adult stage (e.g. elmids beetles, hydrobiid snails, amphipods), recolonization of this newly-created channel could take up to several months before an equilibrium is approached and populations demonstrate marked fluctuations in response to productivity.

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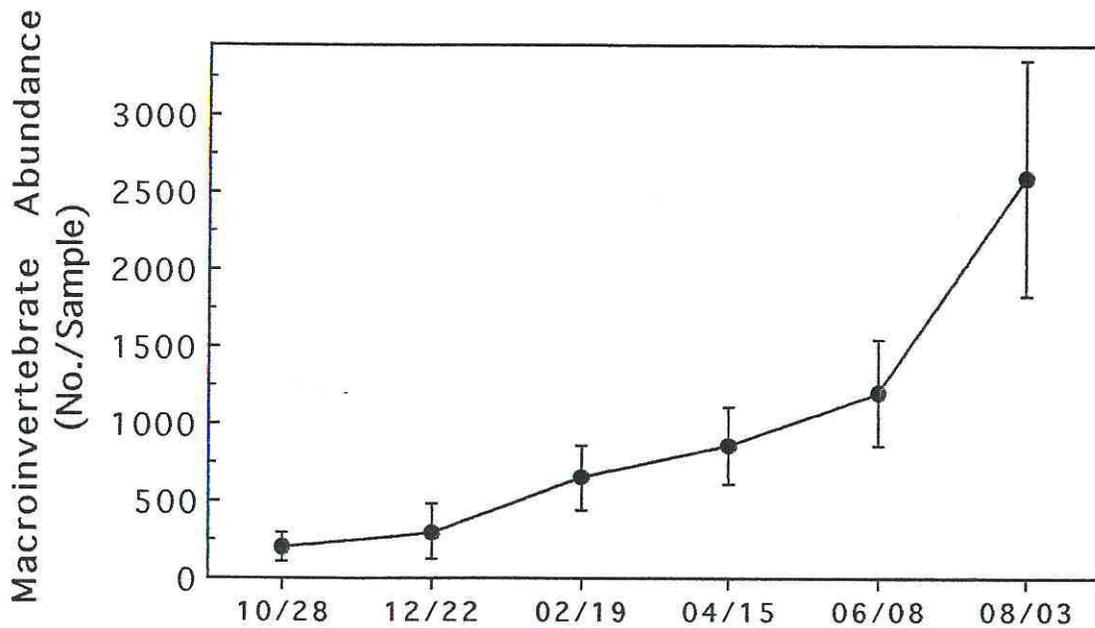


Figure 6. Total macroinvertebrate abundance within Kings Pool outflow. Values are means  $\pm$  1SE (n=6)

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Table 1. Seasonal abundances of macrorinvertebrates among springs inhabited by *Ambrysus relictus*. Values are mean number of individuals per artificial substrate sampler with 1 SD in parentheses. N = 6 on each date for Skruggs and Marsh springs; N = 3 for Indian Spring.

**SKRUGGS SPRING**

Taxon	10/28/97	12/22/97	02/19/98	04/15/98	06/08/98	08/03/98
ODONATA						
<i>Argia</i> sp.	0.3( 0.5)	1.0( 1.7)	0.5( 0.8)	0.5( 0.8)	0.5( 2.3)	1.3( 2.3)
Gomphidae	0.0	0.2( 0.4)	0.0	0.0	0.8( 1.0)	0.3( 0.8)
EPHEMEROPTERA						
<i>Baetis</i> sp.	0.0	0.0	0.0	0.0	3.0( 5.4)	0.0
TRICHOPTERA						
<i>Nectopsyche</i> sp.	0.0	0.0	0.0	0.0	0.5( 1.0)	0.0
COLEOPTERA						
<i>Stenelmis calida</i>	3.7( 1.9)	2.7( 2.0)	8.7( 7.1)	28.0( 37.2)	14.0( 11.5)	1.2( 1.6)
<i>Microcylloepus similis</i>	24.5( 13.9)	49.2( 46.4)	34.0( 38.5)	41.0( 45.9)	67.0( 47.0)	23.5( 25.1)
Elmidae larvae	20.3( 8.6)	59.3( 60.5)	64.7( 53.4)	137.8( 59.4)	102.3( 54.3)	48.3( 21.8)
DIPTERA						
Chironomidae	3.3( 2.9)	13.5( 20.1)	15.3( 20.6)	14.0( 16.8)	18.3( 15.1)	18.7( 13.7)
Ceratopogonidae	0.0	1.8( 2.6)	1.5( 2.3)	0.8( 0.8)	0.8( 1.0)	1.5( 2.1)
CRUSTACEA						
<i>Hyallela</i> sp.	37.5( 30.7)	129.5(161.0)	104.0(175.1)	195.7(162.0)	412.3(323.3)	272.5(351.7)
Ostracoda	0.2( 0.4)	0.2( 0.4)	0.0	0.0	0.0	0.0
MOLLUSCA						
<i>Pyrgulopsis pisteri</i>	685.8(283.8)	248.5(154.3)	195.0( 44.6)	300.3(148.5)	372.3( 65.2)	403.5(214.1)
<i>Tryonia</i> spp.	175.9( 99.6)	133.8(212.2)	20.8( 16.1)	34.0( 25.0)	28.8( 22.1)	151.0(163.3)
<i>Melanoides tuberculata</i>	0.5( 0.8)	0.0	0.0	6.3( 10.8)	0.8( 1.5)	1.8( 2.2)
OTHERS						
Turbellaria	2.2( 1.6)	11.0( 10.3)	4.2( 6.9)	0.5( 0.8)	3.5( 5.2)	7.3( 5.3)
Oligochaeta	0.2( 0.4)	15.8( 24.6)	1.3( 2.8)	0.2( 0.4)	2.3( 3.9)	23.5( 37.1)
Acarina	0.0	0.2( 0.4)	0.0	0.0	0.0	0.0

Table 1 continued.

## MARSH SPRING

Taxon	10/28/97	12/22/97	02/19/98	04/15/98	06/08/98	08/03/98
ODONATA						
<i>Argia</i> sp.	0.0	1.6( 3.0)	1.2( 1.9)	4.3( 3.2)	3.8( 1.0)	1.7( 2.0)
Gomphidae	0.0	0.2( 0.4)	0.0	0.0	1.0( 0.8)	0.0
EPHEMEROPTERA						
<i>Baetis</i> sp.	0.0	0.0	0.2( 0.4)	0.3( 0.5)	1.0( 0.0)	0.2( 0.4)
TRICHOPTERA						
<i>Nectopsyche</i> sp.	1.2( 1.5)	0.2( 0.4)	0.0	0.0	6.3( 2.2)	0.7( 0.8)
COLEOPTERA						
<i>Stenelmis calida</i>	2.7( 3.6)	1.4( 1.1)	7.2( 8.9)	8.8( 6.2)	7.3( 6.2)	8.3( 17.0)
<i>Microcylloepus similis</i>	80.3( 82.4)	50.8( 37.0)	39.7( 45.5)	50.8( 41.4)	53.5( 39.4)	38.6( 40.1)
Elmidae larvae	18.7( 6.1)	54.4( 28.4)	29.3( 12.7)	137.8( 38.9)	163.5( 59.6)	42.5( 5.1)
DIPTERA						
Chironomidae	3.8( 2.7)	1.4( 3.1)	5.5( 4.5)	9.5( 2.9)	7.8( 3.8)	4.5( 5.1)
Ceratopogonidae	0.2( 0.4)	0.4( 0.8)	0.0	1.0( 0.6)	4.3( 1.7)	0.2( 0.4)
CRUSTACEA						
<i>Hyalolella</i> sp.	30.6( 16.5)	60.2( 54.0)	16.8( 10.6)	43.3( 15.0)	90.5( 4.2)	41.7( 25.9)
MOLLUSCA						
<i>Pyrgulopsis pisteri</i>	791.8(409.7)	272.8(149.3)	186.7(120.7)	281.0(225.0)	337.8(163.0)	571.7(310.2)
<i>Tryonia</i> spp.	88.0( 73.4)	48.6( 56.1)	10.5( 10.9)	26.5( 36.2)	73.8( 36.4)	14.5( 24.9)
<i>Melanoides tuberculata</i>	0.7( 0.8)	0.0	1.6( 2.1)	33.5( 50.8)	34.3( 32.2)	0.2( 0.4)
OTHERS						
Turbellaria	19.7( 10.9)	17.2( 18.0)	0.7( 1.2)	0.8( 1.0)	1.0( 0.8)	22.2( 11.6)
Oligochaeta	10.2( 19.9)	7.0( 10.5)	0.0	5.0( 2.2)	2.0( 2.4)	0.0
Acarina	0.0	1.2( 1.3)	0.2( 0.4)	0.0	0.0	0.0

Table 1 continued.

## INDIAN SPRING

Taxon	10/28/97	12/22/97	02/19/98	04/15/98	06/08/98	08/03/98
ODONATA						
<i>Argia</i> sp.	0.0	3.09 ( 2.7)	2.3( 1.5)	7.3( 3.1)	8.7( 2.5)	10.0( 1.7)
Gomphidae	0.0	0.3( 0.5)	0.0	0.0	1.0( 1.0)	0.0
EPHEMEROPTERA						
<i>Baetis</i> sp.	2.0( 2.0)	0.3( 0.5)	0.0	2.7( 3.8)	16.7( 4.4)	30.7( 10.7)
COLEOPTERA						
<i>Stenelmis calida</i>	0.0	0.3( 0.6)	0.7( 0.6)	1.0( 1.0)	1.0( 1.0)	0.3( 0.6)
<i>Microcylloepus similis</i>	0.7( 0.6)	11.0( 11.3)	4.3( 4.0)	7.0( 2.0)	7.7( 3.5)	3.3( 2.5)
Elmidae larvae	2.3( 5.8)	10.3( 3.5)	18.3( 5.3)	55.7( 28.4)	30.0( 15.1)	11.7( 7.6)
DIPTERA						
Chironomidae	3.3( 2.9)	16.7( 26.3)	13.3( 14.6)	7.7( 5.1)	22.3( 7.6)	28.0( 27.1)
Ceratopogonidae	0.3( 0.6)	0.7( 1.2)	0.0	0.0	2.0( 2.7)	1.3( 1.5)
CRUSTACEA						
<i>Hyalolella</i> sp.	41.3( 32.6)	185.7(113.1)	45.0( 5.2)	48.3( 35.9)	46.7( 12.5)	33.0( 12.1)
MOLLUSCA						
<i>Pyrgulopsis pisteri</i>	1.0( 1.7)	14.0( 12.5)	30.0( 52.0)	30.3( 35.9)	24.3( 35.4)	1.0( 1.7)
<i>Tryonia</i> spp.	0.0	0.0	1.7( 1.2)	0.0	0.0	0.0
OTHERS						
Turbellaria	0.0	0.3( 0.6)	0.0	0.3( 0.6)	1.0( 1.0)	0.0
Oligochaeta	6.7( 7.2)	18.0( 16.5)	2.3( 4.0)	5.0( 4.6)	10.0( 5.6)	2.7( 2.5)

Table 2. Seasonal abundances of macroinvertebrates among Point-of-Rocks springs inhabited by *Ambrysus amargosus*. Values are mean number of individuals per artificial substrate sampler with 1 SD in parentheses. N=3, and includes only samples from upstream sites.

POINT-OF-ROCKS: GRINDSTONE SPRING

Taxon	10/28/97	12/22/97	02/19/98	04/15/98	06/08/98	08/03/98
ODONATA						
<i>Argia</i> sp.	3.7( 2.5)	3.0( 2.7)	1.0( 1.0)	2.3( 1.5)	1.7( 0.6)	1.7( 2.9)
Gomphidae	0.0	0.3( 0.6)	0.0	0.0	0.0	0.0
EPHEMEROPTERA						
<i>Baetis</i> sp.	0.3( 0.6)	0.7( 0.6)	0.3( 0.6)	0.3( 0.6)	1.0( 1.0)	0.3( 0.6)
COLEOPTERA						
<i>Stenelmis calida</i>	0.0	0.0	0.7( 0.6)	2.0( 1.0)	3.7( 3.8)	1.7( 2.1)
<i>Microcyloopus similis</i>	110.0( 57.3)	77.0( 12.3)	60.3( 18.2)	41.3( 24.6)	66.0( 30.5)	56.0( 23.3)
Elmidae larvae	2.7( 0.6)	6.3( 0.6)	18.7( 9.3)	41.7( 18.9)	60.3( 58.8)	20.7( 20.6)
DIPTERA						
Chironomidae	2.0( 3.5)	6.3( 5.5)	0.7( 0.6)	1.0( 1.0)	1.7( 0.6)	1.7( 2.1)
Ceratopogonidae	0.3( 0.6)	0.3( 0.6)	0.0	0.0	0.0	0.0
CRUSTACEA						
<i>Hyalolella</i> sp.	106.0( 77.9)	132.0( 17.5)	185.0( 49.9)	387.0(219.3)	385.3( 81.5)	388.3(157.5)
MOLLUSCA						
<i>Pyrgulopsis erythropoma</i>	581.3(354.1)	93.3( 19.4)	172.0( 75.4)	255.0(220.2)	225.3(142.3)	221.7(119.8)
<i>Tryonia</i> spp.	0.0	0.0	1.7( 2.9)	0.0	0.0	0.0
<i>Melanoides tuberculata</i>	0.0	0.0	0.0	1.0( 1.7)	0.0	0.0
OTHER TAXA						
Turbellaria	5.3( 2.5)	1.7( 2.1)	1.0( 1.0)	2.0( 1.7)	0.7( 0.6)	1.5( 2.1)
Oligochaeta	0.0	0.0	0.0	1.0( 1.7)	0.0	0.0

Table 2 continued.

## POINT-OF-ROCKS: MIDDLE SPRING

Taxon	10/28/97	12/22/97	02/19/98	04/15/98	06/08/98	08/03/98
ODONATA						
<i>Argia</i> sp.	1.7( 2.9)	5.7( 5.1)	0.7( 0.6)	10.0( 3.0)	5.0( 2.6)	0.7( 1.2)
EPHEMEROPTERA						
<i>Baetis</i> sp.	0.3( 0.6)	0.0	0.0	0.0	0.0	0.0
TRICHOPTERA						
<i>Helicopsyche borealis</i>	16.0(14.7)	14.0( 9.5)	3.7( 4.0)	14.7( 8.5)	27.3( 5.7)	12.0( 8.7)
COLEOPTERA						
<i>Stenelmis calida</i>	0.0	0.7( 1.2)	0.0	0.0	0.0	0.0
<i>Microcylloepus similis</i>	19.0( 10.4)	29.0( 9.5)	12.0( 2.7)	8.7( 4.7)	22.7( 7.6)	13.0( 5.6)
Elmidae larvae	10.7( 7.4)	30.0( 27.9)	17.3( 4.0)	61.0( 20.2)	65.0( 3.5)	19.3( 6.0)
DIPTERA						
Chironomidae	1.3( 1.5)	4.3( 5.8)	2.3( 2.5)	5.7( 3.5)	4.0( 3.6)	0.0
Ceratopogonidae	0.0	2.3( 3.2)	0.3( 0.6)	0.0	0.0	0.0
<i>Pericoma</i> sp.	0.0	1.7( 1.5)	0.0	0.0	0.0	0.0
<i>Stratiomys</i> sp.	0.3( 0.6)	0.0	0.0	0.0	0.3( 0.6)	1.3( 2.3)
CRUSTACEA						
<i>Hyalolella</i> sp.	55.7( 35.9)	266.3(123.1)	190.7(106.5)	172.0( 81.7)	204.0( 70.7)	218.0( 70.4)
MOLLUSCA						
<i>Pyrgulopsis erythropoma</i>	303.7( 35.9)	134.0( 26.2)	63.3( 36.9)	113.3( 68.3)	76.7( 50.3)	86.3( 32.7)
<i>Tryonia</i> spp.	0.0	18.39 18.9)	4.3( 4.0)	0.0	0.0	0.0
<i>Melanoides tuberculata</i>	0.0	2.0( 3.5)	0.7( 0.6)	4.0( 6.9)	0.0	0.0
OTHER TAXA						
Turbellaria	10.0( 8.7)	9.3( 8.1)	1.3( 1.5)	2.7( 3.1)	1.0( 1.0)	5.0( 2.7)
Oligochaeta	0.0	0.0	0.0	2.0( 3.5)	0.0	0.0
Acarina	0.0	1.0( 1.0)	0.3( 0.6)	0.7( 1.2)	0.0	0.0

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Table 2 continued.

## POINT-OF-ROCKS: REFUGIUM SPRING

Taxon	10/28/97	12/22/97	02/19/98	04/15/98	06/08/98	08/03/98
ODONATA						
<i>Argia</i> sp.	0.7( 1.2)	0.3( 0.6)	1.0( 1.0)	0.3( 0.6)	2.0( 1.7)	2.0( 0.0)
Gomphidae	0.0	0.0	0.0	0.0	0.3( 0.6)	0.3( 0.6)
EPHEMEROPTERA						
<i>Baetis</i> sp.	0.0	0.3( 0.6)	0.3( 0.6)	0.3( 0.6)	1.0( 1.0)	0.0
TRICHOPTERA						
<i>Helicopsyche borealis</i>	5.3( 2.5)	14.3( 11.6)	13.0( 7.0)	20.7( 6.4)	38.7( 15.3)	75.3( 31.7)
COLEOPTERA						
<i>Stenelmis calida</i>	0.0	0.0	0.0	3.0( 2.7)	2.3( 3.2)	3.7( 6.4)
<i>Microcylloepus similis</i>	26.7( 22.3)	69.0( 13.1)	25.0( 6.1)	23.3( 3.1)	22.3( 11.2)	22.0( 10.5)
Elmidae larvae	10.7( 7.4)	3.0( 4.4)	6.0( 4.4)	16.0( 5.0)	20.3( 17.0)	9.0( 6.6)
DIPTERA						
Chironomidae	0.0	0.7( 0.6)	2.0( 1.0)	1.3( 1.2)	2.7( 2.1)	2.3( 2.5)
Ceratopogonidae	0.0	0.0	0.0	0.0	0.0	0.7( 0.6)
CRUSTACEA						
<i>Hyalolella</i> sp.	31.3( 26.6)	85.0( 28.1)	102.7( 59.7)	244.0( 102.4)	185.3( 38.9)	169.0( 37.2)
MOLLUSCA						
<i>Pyrgulopsis erythropoma</i>	301.0( 177.3)	215.3( 138.0)	243.3( 17.6)	250.3( 119.0)	358.3( 140.2)	297.7( 90.3)
<i>Tryonia</i> spp.	0.0	0.0	0.0	0.0	0.0	0.3( 0.6)
<i>Melancoides tuberculata</i>	0.0	0.0	0.0	0.0	0.7( 0.6)	0.0
OTHER TAXA						
Turbellaria	0.0	25.0( 6.6)	15.7( 4.0)	5.7( 2.5)	3.0( 2.7)	6.7( 2.1)
Acarina	1.0( 1.7)	0.3( 0.6)	0.0	0.0	0.0	0.0

Table 3. Seasonal abundances of macroinvertebrates within the recently restored Kings Pool outflow. Values same as in Tables 1 and 2 (N=6)

KING'S POOL OUTFLOW

Taxon	10/28/97	12/22/97	02/19/98	04/15/98	06/08/98	08/03/98
ODONATA						
<i>Argia</i> sp.	2.3( 1.9)	3.2( 3.3)	2.0( 3.6)	6.0( 2.6)	6.8( 4.1)	8.7( 10.7)
Gomphidae	0.2( 0.4)	0.2( 0.4)	0.3( 0.5)	0.7( 0.8)	1.3( 1.5)	0.5( 1.2)
EPHEMEROPTERA						
<i>Baetis</i> sp.	6.2( 3.9)	0.8( 1.6)	0.3( 0.5)	4.0( 5.2)	4.7( 4.6)	12.8( 5.8)
TRICHOPTERA						
<i>Helicopsyche borealis</i>	0.0	0.2( 0.4)	0.0	0.0	0.0	0.0
imm. Hydroptilidae	0.2( 0.4)	0.2( 0.4)	0.2( 0.4)	3.8( 4.6)	2.5( 2.2)	6.2( 6.9)
<i>Oxyethira</i> sp.	0.0	0.0	0.0	0.3( 0.5)	0.2( 0.4)	0.0
<i>Stactobiella</i> sp.	0.0	0.0	0.0	0.0	0.0	2.2( 3.2)
COLEOPTERA						
<i>Stenelmis calida</i>	0.2( 0.4)	0.0	0.0	0.3( 0.5)	3.2( 3.1)	0.0
<i>Microcylloepus similis</i>	0.0	4.7( 10.9)	0.2( 0.4)	0.2( 0.4)	1.5( 1.2)	0.6( 1.3)
Elmidae larvae	0.0	1.5( 3.2)	0.2( 0.4)	15.0( 10.8)	40.3( 44.9)	2.6( 1.1)
DIPTERA						
Chironomidae	34.7( 23.6)	10.0( 9.9)	10.3( 14.2)	13.2( 11.9)	15.7( 7.5)	10.6( 5.0)
Ceratopogonidae	0.5( 0.8)	0.3( 0.8)	0.3( 0.5)	0.0	1.0( 1.3)	1.8( 0.8)
CRUSTACEA						
<i>Hyallolella</i> sp.	53.5( 45.4)	51.8( 44.5)	59.3( 63.8)	182.7(268.2)	161.8(113.9)	105.0( 31.7)
MOLLUSCA						
<i>Pyrgulopsis erythropoma</i>	101.8( 64.1)	220.3(116.1)	572.5(231.1)	571.3(244.8)	904.3(350.4)	2409.4(749.3)
<i>Tryonia</i> spp.	0.0	0.0	0.0	0.0	0.0	1.8( 1.5)
<i>Melanoides tuberculata</i>	2.8( 3.1)	1.5( 1.6)	0.5( 0.8)	52.2( 43.4)	46.7( 35.0)	4.2( 4.3)
<i>Physella</i> sp.	1.7( 1.9)	0.5( 0.8)	0.2( 0.4)	0.5( 0.8)	0.0	0.4( 0.6)
OTHER TAXA						
Turbellaria	0.5( 0.8)	5.7( 10.1)	1.7( 2.3)	1.3( 1.5)	8.3( 8.9)	21.4( 17.0)
Oligochaeta	0.0	0.0	0.0	9.3( 7.7)	3.8( 3.7)	0.0

With the exception of Indian Spring, springsnails (genus *Pyrgulopsis*) were consistently the most abundant taxa within all the springs sampled. Other taxa abundant in all springs included amphipods (*Hyalella* sp.) and elmids beetles (Tables 1-3). Of the elmids beetles, *Stenelmis calida* was much rarer than *Microcyllloepus similis*. Although the introduced snail *Melanoides tuberculata* is common, to very abundant, in all of these springs, its abundance was consistently low in our samples on all dates. Rare taxa that were collected in only a subset of the springs included the leptocerid caddisfly *Nectopsyche* sp. in Marsh and Skruggs springs, the helicopsychid caddisfly *Helicopsyche borealis* in the Point-of-Rocks system, and micro-caddisflies (family Hydroptilidae) in the Kings Pool outflow.

#### Life History Characteristics

Monthly sampling and size-frequency analyses revealed that Ash Meadows *Ambrysus* species are univoltine, reproduce from early spring through mid-summer, have five nymphal instars, and over winter as late instar nymphs or adults. These life history details are typical of the majority of aquatic and semiaquatic heteroptera (Hilsenhoff 1991; Williams and Feltmate 1992), including *Ambrysus* and other Naucoridae (Usinger 1946; Polhemus 1979).

Mean body length of naucorid nymphs was shortest and range in body lengths, and thus number of instars present, was greatest from April through August (Table 4), clearly demonstrating the seasonal timing of reproduction. Combining monthly body length

Table 4. Body lengths of naucorid nymphs from Skruggs Spring and Kings Pool outflow illustrating increases in nymph abundance, and range of nymphal instars, during spring and summer.

Date	<i>A. relictus</i> (Skruggs Sp.)		<i>A. amargosus</i> (Kings Pool)	
	Mean (SD) (n)	Range	Mean (SD) (n)	Range
30 Sept	4.78 (0.55) (n=5)	3.8-5.1	--	--
28 Oct	5.00 (0.10) (n=3)	4.9-5.1	--	--
25 Nov	4.60 (0.47) (n=4)	3.9-4.9	4.10 (0.00) (n=1)	--
29 Dec	4.74 (0.25) (n=9)	4.1-4.9	4.80 (0.00) (n=1)	--
22 Jan	4.57 (0.49) (n=3)	4.0-4.9	4.21 (0.83) (n=8)	3.1-5.5
19 Feb	4.77 (0.32) (n=3)	4.4-5.0	5.00 (0.87) (n=8)	3.3-5.5
18 Mar	4.45 (0.47) (n=4)	4.0-4.9	4.35 (0.71) (n=13)	3.0-5.5
16 Apr	4.08 (0.87) (n=12)	2.0-4.9	3.90 (0.85) (n=62)	2.1-5.5
12 May	4.24 (0.65) (n=12)	3.1-5.3	4.07 (1.03) (n=57)	1.8-5.5
08 June	4.15 (0.71) (n=32)	2.3-5.1	4.48 (0.76) (n=52)	2.5-5.9
03 Aug	4.10 (1.02) (n=14)	1.8-5.2	4.32 (0.88) (n=20)	3.1-5.5

measurements of all juvenile naucorids into composite length-frequency histograms revealed five relatively distinct instars (Figs. 7 and 8). Instar lengths were similar between species with

the exception that V-instar nymphs of *A. amargosus* were larger than V-instar of *A. relictus* (Table 5). In addition, mean body lengths of adults were somewhat larger in *A. amargosus* (mean=6.05; range=5.7-6.3; n=21) than *A. relictus* (mean = 5.71 mm; range = 5.3-6.1 mm; n=46). A similar size difference is revealed by comparing descriptions of type specimens of *A. amargosus* in LaRivers (1953) with *A. relictus* in Polhemus and Polhemus (1994). Monthly sample sizes were too small to allow estimates of, or seasonal variation in, growth rates. Some of the overlap among instar lengths may therefore be due to combining data from all dates which would incorporate slight seasonal differences in growth rates within instars.

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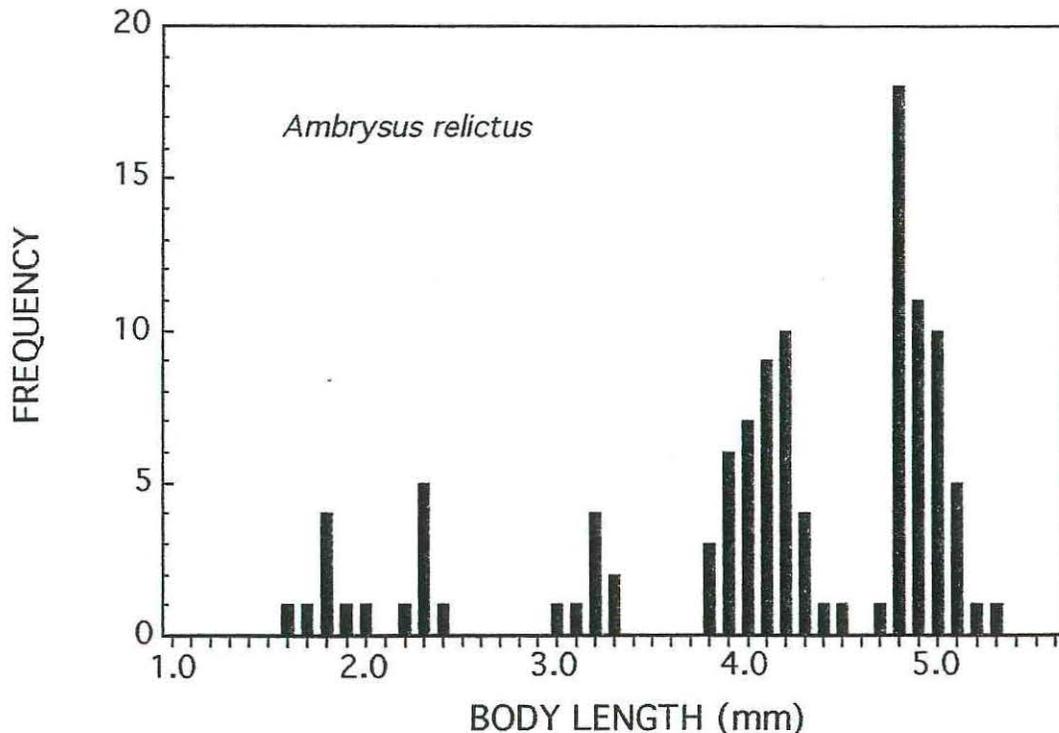


Figure 7. Length-frequency histogram of nymphal instars of *Ambrysus relictus*. Measurements include all nymphs collected within artificial substrate samplers between 30 September 1997 and 03 August 1998 from Skruggs Spring.

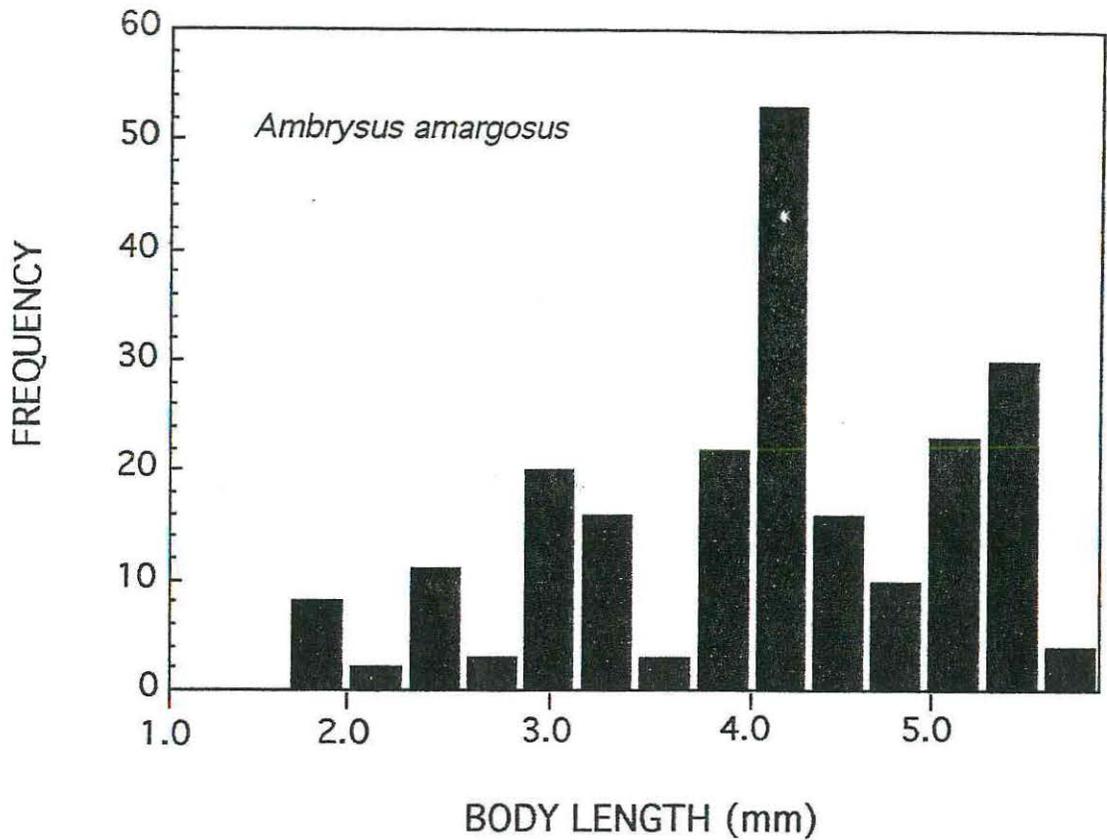


Figure 8. Length-frequency histogram illustrating nymphal instars of *Ambrysus amargosus* from Kings Pool outflow.

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All three gravid female naucorids had seven eggs within their abdomens, which is probably indicative of fecundity for both species. The eggs were all of similar size and appeared to completely fill the abdominal cavity. This pattern suggests that both species trade-off egg number for egg size by producing a relatively small number of large eggs. Eggs were cream-colored, ovoid in shape, 1.04 mm long by 0.60 mm in diameter.

Table 5. Modal body lengths of nymphal instars of *Ambrysus relictus* and *A. amargosus* (ranges in parentheses).

Instar	<i>A. relictus</i>	<i>A. amargosus</i>
I	1.8 (1.6-2.0)	1.8 (1.8-2.1)
II	2.3 (2.2-2.4)	2.4 (2.2-2.6)
III	3.2 (3.0-3.3)	3.2 (2.9-3.4)
IV	4.2 (3.8-4.5)	4.2 (3.8-4.6)
V	4.8 (4.7-5.3)	5.3 (4.8-5.7)

After determining the characteristics of naucorid eggs, several were observed among debris within our invertebrate samples, particularly in samples collected during April, June, and August. These eggs possessed remnants of a short stalk at the micropylar end, indicating that they are attached singly to suitable substrates, as is typical for most *Ambrysus* (Usinger 1946). In addition, scanning electron microscopy revealed species-specific differences in surface patterns between *A. amargosus* and *A. relictus* eggs (Perrilat W., unpublished manuscript, Southern Oregon University Dept. of Biology), providing further support for the separation of these two species.

Important aspect of naucorid reproductive biology that remain unresolved are length of time to hatching, and selection of oviposition substrates. Although our microhabitat sampling was not specifically designed to address these questions, during sample processing we did record the number of eggs observed. Nine eggs were recovered from gravel-pebble substrates, six from cobble substrates, and twenty one from submersed vegetation. No eggs were recovered from coarse sand or boulder surfaces. Along with our results on distribution among microhabitats of nymph and adult life stages (see below), these observations suggest that providing a diversity of microhabitats for oviposition will be important in restoring and maintaining naucorid populations. Further, these observations suggest that fine substrates (e.g., like those that currently dominate large stretches of most spring outflows) are unsuitable oviposition sites. Further research is required to confirm these observations and reveal details of this important aspect of naucorid life history.

### Habitat Preferences

#### *Experimental Results*

Results of the field experiment clearly show that flow and substrate are key habitat variables determining naucorid distribution and abundance (Fig. 9). Two-way ANOVA revealed strong, and highly significant, effects of substrate size ( $p=0,0001$ ,  $df$  1,20) and flow velocity ( $p=0.0024$ ,  $df$  1,20), but not the flow-substrate interaction ( $p=0.046$ ,  $df$  1,20), on the number of naucorids colonizing substrate baskets. Naucorid abundance was

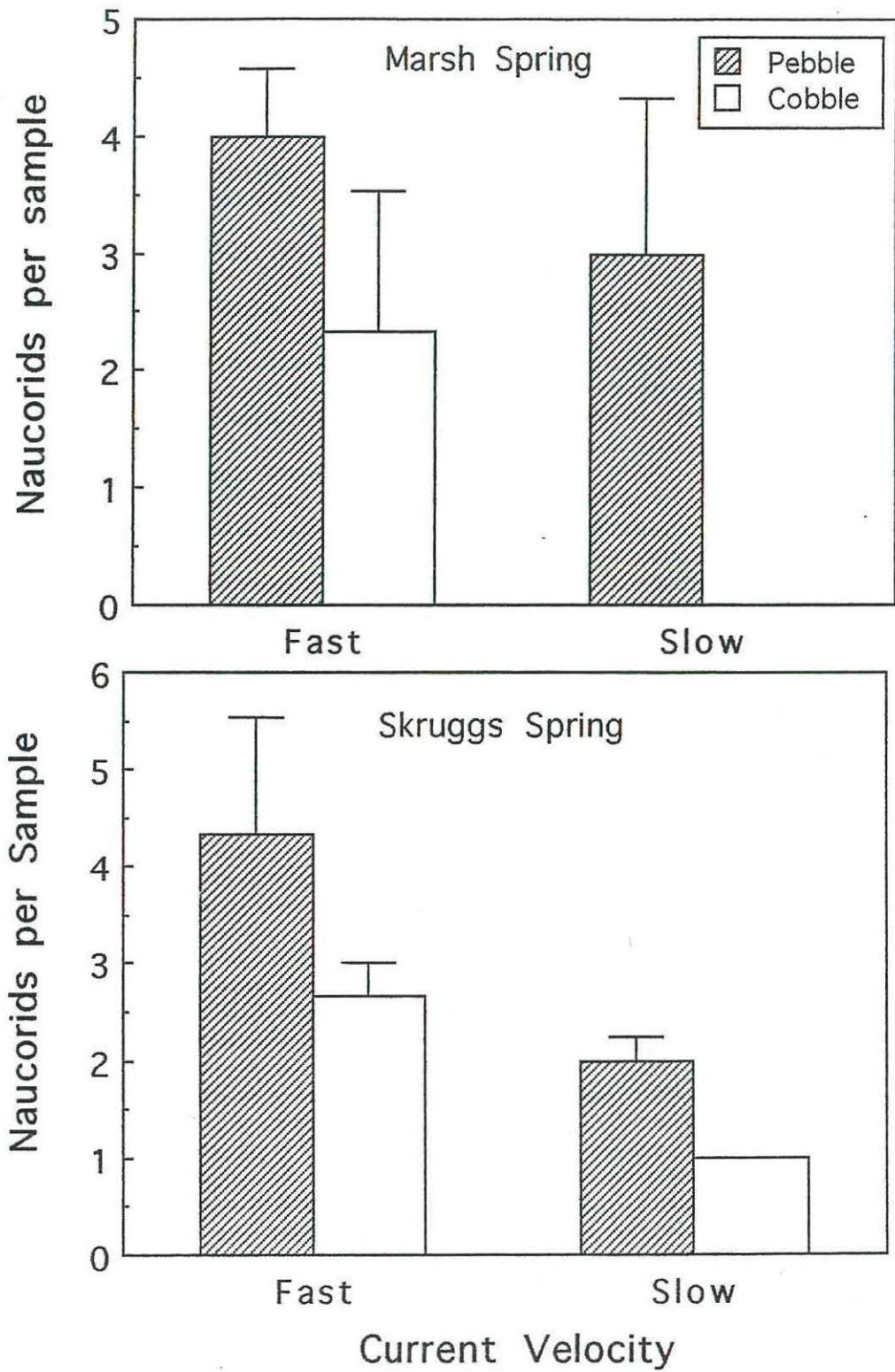


Figure 9. Effects of substrate size and flow velocity on *Ambrysus relictus* abundance within Marsh and Skruggs springs. Values are means  $\pm$  1SE (n=3)

highest on pebble substrates in high current velocities and lowest on cobble in low current velocities. In general, pebble substrates provide more heterogeneous microhabitats, with considerably more surface area and interstitial space, than do cobble substrates (Minshall 1984; Parker 1984). Total macroinvertebrate abundances were also significantly higher within pebble substrates at high flows (Fig. 10). There was considerable variation, however, among responses of the most common taxa (Fig. 11) between the two spring systems. Of these common taxa, *Hyalella* sp., an important prey species, was strongly influenced by substrate and flow, with its greatest abundance also in pebble substrate at faster current velocities (Fig. 11).

In addition to direct effects of substrate size and flow velocity, there were likely indirect effects of fine sediment deposition which contributed to differences in naucorid, and associated invertebrate, densities. Considerably more fine sediment was deposited in baskets at slower current velocities, and greater proportions of substrate surface and interstitial space were reduced by deposited sediments in cobble than pebble substrates. An additional line of evidence that fine sediments have a negative effect on naucorid abundance comes from our population monitoring results. Naucorid densities were consistently higher in samplers at upstream sites in both Marsh and Skruggs springs (Fig. 12). These sites had higher current velocities, coarser streambed sediments, and less fine sediment accumulated within the samplers.

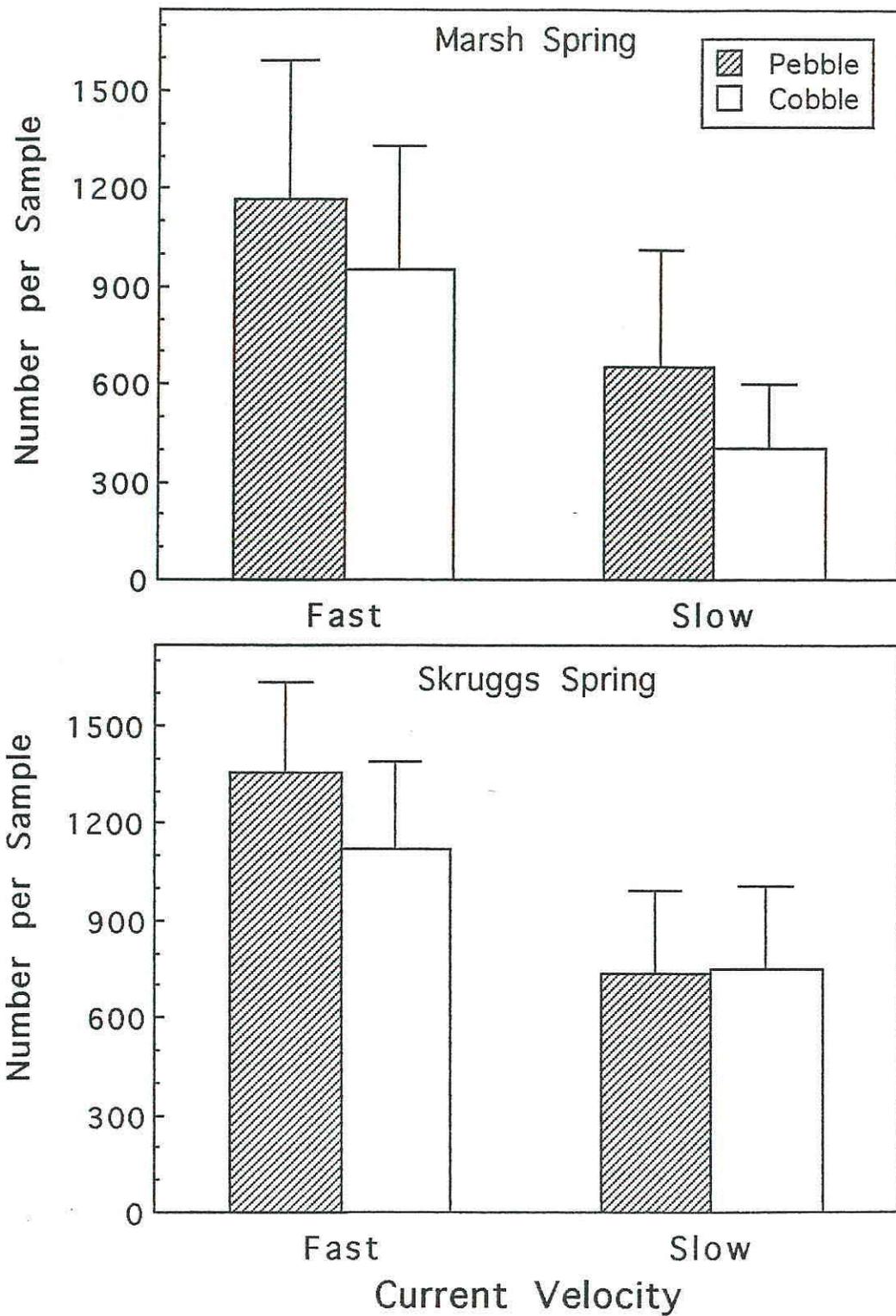


Figure 10. Effects of substrate size and current velocity on total macorinvertebrate abundances within Marsh and Skruggs Springs. Values are means  $\pm$  1SE (n=3)

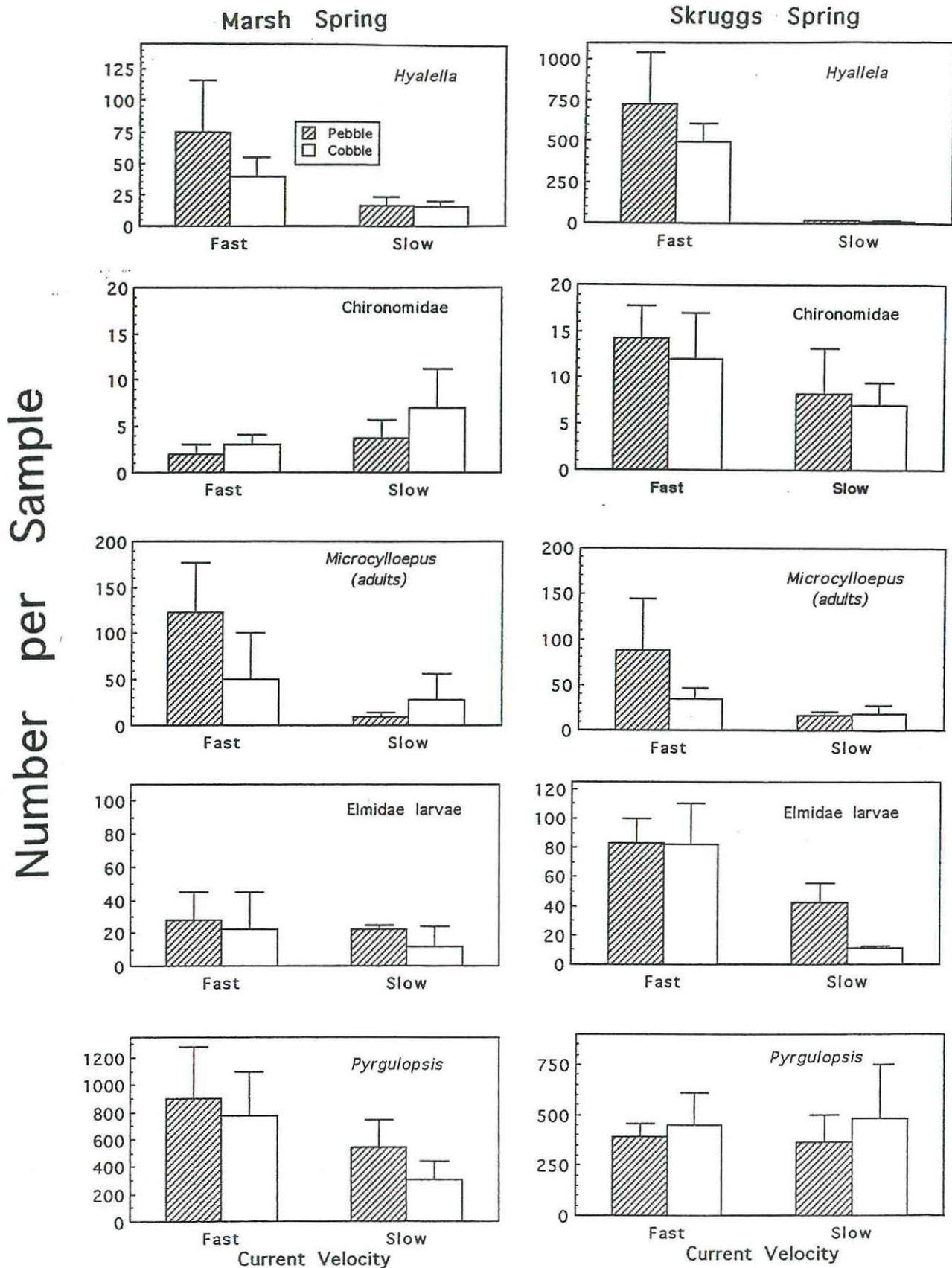


Figure 11. Effects of substrate size and current velocity on 5 most common benthic invertebrate taxa in Marsh and Skruggs springs.

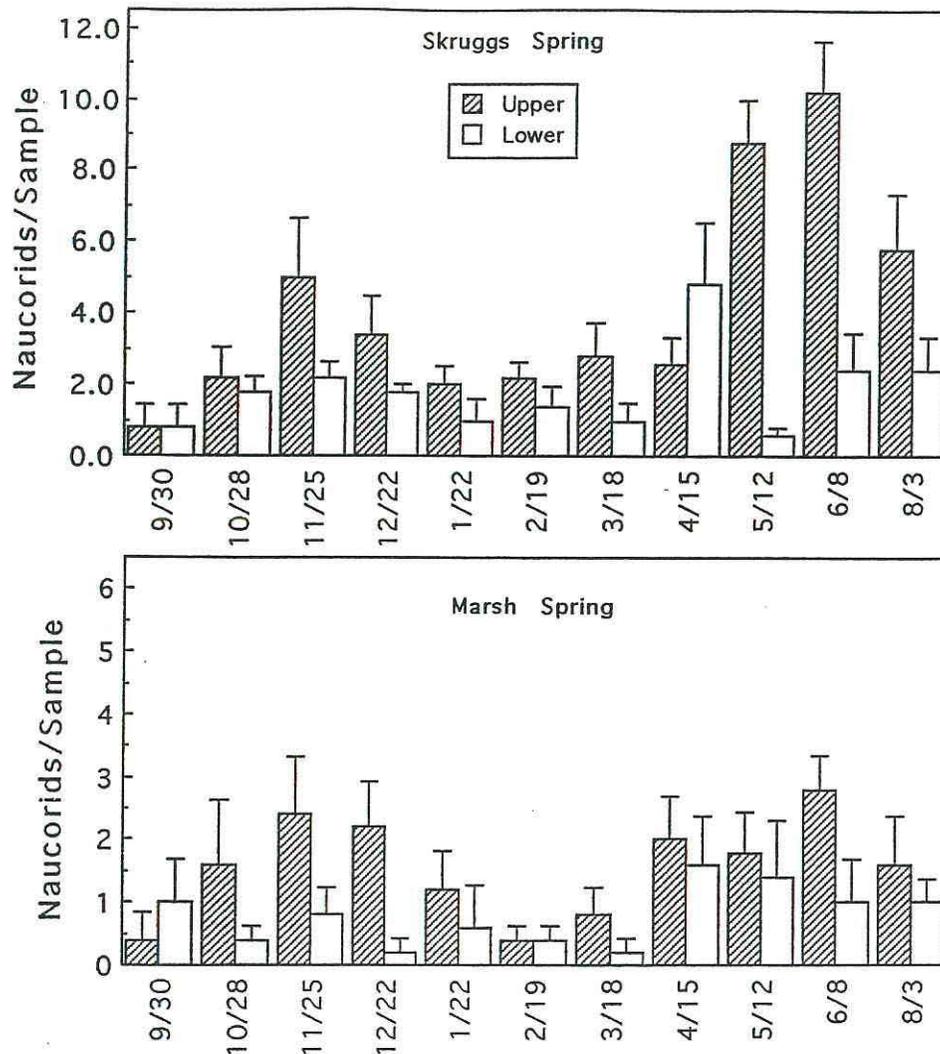


Figure 12. Naucorid abundance at upstream and downstream sites in Skruggs and Marsh springs, showing effects of fine sediments on distribution. Values are means  $\pm$  1SE (n=5).

Sites and Willig (1991) and Herrmann et al. (1993) also demonstrated that substrate and flow are important in determining the distribution and abundance of naucorids. In contrast, however, their results showed a general preference for cobble over pebble and gravel substrates for three sympatric species

(including one *Ambrysus* species) within a large river system. A key difference between *Ambrysus* species from Ash Meadows and other naucorids is body size. *Ambrysus* species within the Amargosa River drainage (*A. funebris* from Death Valley and *A. amargosus* and *A. relictus* from Ash Meadows), are considerably smaller than other North American naucorids (e.g. Menke 1979; Usinger 1954) and inhabit much smaller and more constant stream environments. Their apparent preference for smaller, more complex substrates and higher flows is likely related to these factors, and the distribution of their preferred prey.

In addition to the pattern revealed by the experimental results, there were significant differences in abundance among microhabitats within the Kings Pool outflow (Fig. 12). Most striking was the absence of naucorids from the coarse sand microhabitat, and nearly equal total abundances within gravel-pebble and submersed vegetation. An important distinction among microhabitats is the difference in distributions of nymphs and adults. Within the mineral substrates, adult naucorids outnumber nymphs, but the reverse is true for submersed vegetation. These results support experimental results, showing that total naucorid density is higher in pebble versus cobble substrates, but further show that naucorids inhabit a wide range of microhabitats, including submersed vegetation, and there are important differences in habitat use by different life stages.

These results have important implications for restoration efforts within these spring channels. Currently, very little habitat consisting of complex, gravel-pebble size substrates

exists within most springs, and aquatic vegetation is sparse. Introduction of these types of substrate materials to spring channels (as was done in the Refugium Spring channel) may provide short-term improvements in habitat, but they will likely become buried by fine sediments over time. Therefore, the best long-term solution will to reestablish historical flow patterns so that larger substrate materials are naturally deposited in spring channels from adjacent washes, and fine sediments are scoured away during flash floods.

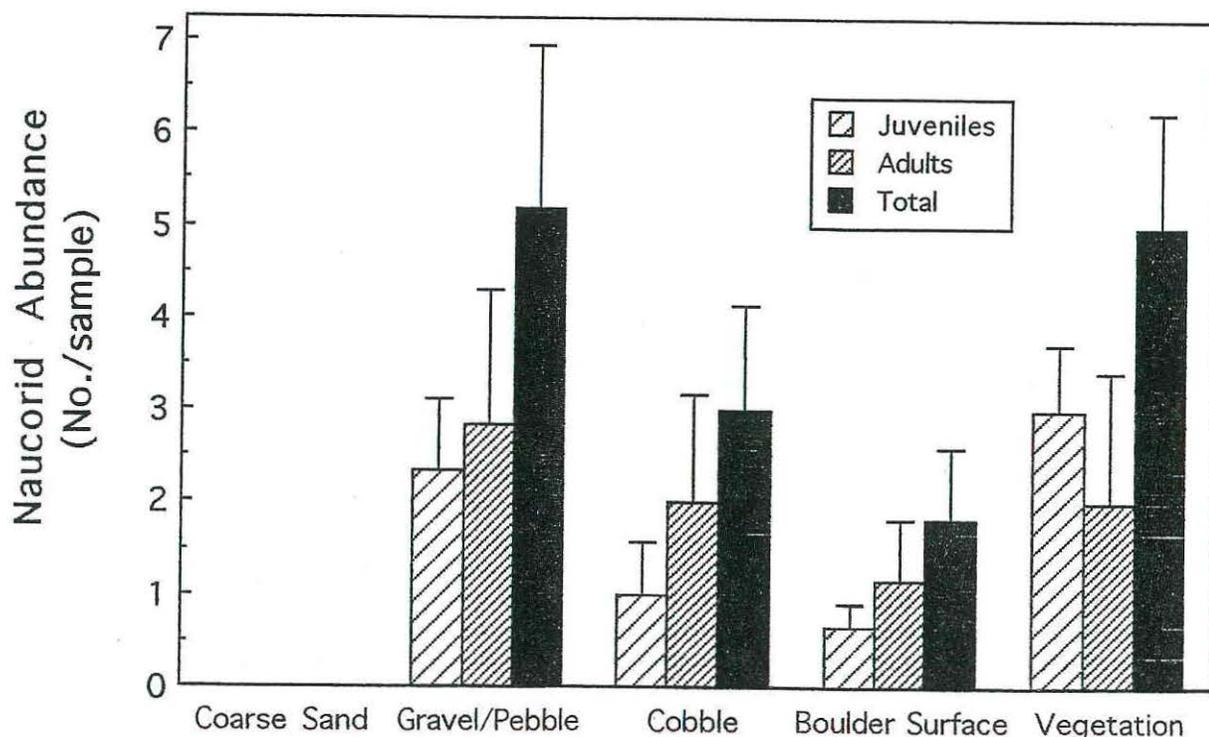


Figure 13. Abundance of *Ambrysus amargosus* within and among substrate patches along the Kings Pool outflow, illustrating differences in total naucorid abundance among microhabitats and differences in microhabitat use by nymphs and adults. Values are means  $\pm$  1SE (n=6, except vegetation n=3).

### Diet, Prey Selection, and Feeding Behavior

Both sets of feeding trials revealed consistent, and predictable, patterns in naucorid prey preferences. Among common prey available in all spring systems, *Hyaletella*, elmidae larvae, and baetid mayfly nymphs were eaten, whereas elmid beetle adults, snails (both native *Pyrgulopsis* and introduced *Melanoides*), and flatworms were not (Tables 6 and 7). In addition, *Helicopsyche*

Table 6. Results of feeding trials testing prey preference by *A. relictus* offered equal densities of 5 common prey taxa. Values are percentages of prey remaining in containers with and without (Control) *Ambrysus*, and are expressed as means ( $\pm 1$  SE). with ranges in number of prey remaining listed below. \*\* =  $P < 0.01$ ; \* =  $0.01 < P < 0.05$ ; NS = no significant difference.

Prey Taxon	Prey/ replicate	Percent Remaining		T-test
		<i>Ambrysus</i>	Control	
<i>Hyaletella</i>	30	49.7 (0.10) (12-18)	98.3 (0.07) (28-31)	**
<i>Microcylloepus</i>	30	100.0 (0.00)	100.0 (0.00)	NS
<i>Stenelmis</i>	30	100.0 (0.00)	100.0 (0.00)	NS
Elmidae larvae	30	81.4 (0.10) (21-27)	98.3 (0.02) (29-30)	*
<i>Pyrgulopsis</i>	30	98.0 (0.06) (27-30)	98.3 (0.02) (29-30)	NS

larvae were susceptible to naucorid predation, suggesting that caddisfly larvae, in general, may be included in naucorid diets, but their very low abundances in most springs (Tables 1-3) probably results in their making a relatively small contribution. Likewise, the generally low natural abundances of many of the other taxa consumed in the feeding trials (mayfly nymphs and elmids larvae) may limit their contributions to naucorid diets. Of the prey consumed, *Hyalella* is typically the most abundant species in all the spring systems sampled (Tables 1-3), and is therefore likely to be the most important prey for populations of both naucorid species.

The species not consumed all possess some form of defense against naucorid predation. The hard shells of spring snails and *Melanoides*, and thick exoskeletons of adult elmids beetles provide effective armor through which naucorid mouth parts can not penetrate. In addition, hydrobiid snails possess a rigid operculum which prevents entry through the shell opening. In contrast, all of the species, or life stages consumed are relatively soft-bodied, and thus are more easily penetrated by the naucorids piercing mouth parts. Among these prey, elmids larvae have the most rigid exoskeleton, and were also fed on at a lower frequency than were amphipods, mayfly nymphs or caddisfly larvae (Table 7). These results suggest that other soft-bodied taxa, such as Chironomidae larvae, oligochaetes, and early instar odonates, may also be consumed by naucorids, but, again, their relatively low densities may restrict their overall contribution to naucorid diets.

Table 7. Results of feeding trials testing susceptibility to predation by *A. amargosus* of common invertebrate prey. Values are percent of prey remaining in containers with and without (Control) *Ambrysus*, and are expressed as means ( $\pm 1SE$ ) with range in number of prey remaining listed below. \*\* =  $P < 0.01$ ; \* =  $0.01 < P < 0.05$ ; NS = no significant difference.

Prey Taxon	Prey/ replicate	Percent Remaining		T-test
		<i>Ambrysus</i>	Control	
<i>Hyalella</i>	10	46.0 (8.50) (2-6)	93.3 (8.10) (8-10)	**
<i>Baetis</i>	10	38.0 (10.90) (1-7)	83.3 (4.10) (8- 9)	**
<i>Helicopsyche</i>	6	70.8 (9.18) (3-5)	100.0 (0.00)	**
<i>Stenelmis</i>	6	100.0 (0.00)	--	--
<i>Microcylloepus</i>	8	100.0 (0.00)	100.0 (0.00)	NS
Elmidae larvae	10	80.0 (5.00) (7-9)	100.0 (0.00)	*
Turbellaria	10	36.0 (5.25) (2-9)	33.3 (4.10) (3-4)	NS
<i>Pyrgulopsis</i>	10	98.0 (2.25) (9-10)	96.7 (4.10) (9-10)	NS
<i>Melanoides</i>	10	100.0 (0.00)	100.0 (0.00)	NS

Direct observation of foraging naucorids, during feeding trials and on natural substrates, showed that they are ambush predators that use a saltatory search pattern (O'Brien et al. 1990). All eleven individuals observed followed the same general pattern of actively searching within a relatively small area (estimated to be 2.5 - 16.0 cm<sup>2</sup>), followed by short periods of inactivity (3 seconds - 2.5 minutes) which were followed by either a return to searching within the same or an adjacent area or large-scale movement (> 10 cm in feeding trial containers and 25 cm to > 1 m on natural substrates) to a new area. Most movements while foraging within a confined area were made by rapidly crawling over the substrate surface. Large scale movements involved both crawling and swimming. The majority of their activity was restricted to the sides, bottoms, or within interstitial spaces between, substrate particles, or within crevices on boulder surfaces. During the period of observation during feeding trials, 51 direct encounters with potential prey were observed, and during observation on natural substrates 13 direct encounters were observed. Twenty seven of 51 and 8 of 13 were encounters with spring snails. None of these direct encounters resulted in the naucorid attacking, or trying to consume the snail. Eleven encounters were with adult elmid beetles (10 *Microcylloepus* and 1 *Stenelmis*) in feeding trials and only one of these encounters resulted in the naucorid grasping the beetle, which was quickly released without being consumed. The remaining encounters in both environments were between naucorids and *Hyalella*. Of the 13 encounters within the feeding trials, 10

resulted in the naucorid pursuing the *Hyalabella* and in 4 of these cases the *Hyalabella* was grasped and consumed. Of the five encounters with *Hyalabella* in the natural environment, all five appeared to result in the naucorid pursuing the prey, but only once was a capture observed. Although not extensive, these observations further support the conclusion that *Hyalabella* is the primary prey of both naucorid species. They also suggest that access to interstitial spaces among substrate particles is important in naucorid foraging behavior and predation efficiency. Restoring and maintaining suitable benthic habitats for both naucorids and their primary prey will be important for the long-term persistence of these populations.

#### CONCLUSIONS

Results of this study provide a number of valuable insights into the biology of Ash Meadows naucorids, including their life histories, feeding ecology, population dynamics, habitat preferences. Most naucorid populations remain at very low abundances due to restricted habitat area and poor conditions within those areas. It is clear from our experimental results, and microhabitat sampling, that naucorids require a diversity of microhabitats with a preference for areas with gravel-pebble substrate and moderate to high current velocity. Densities of associated macroinvertebrate populations, including key prey taxa, were also higher within these areas. There is an abundant

literature on the effects of the same variables on benthic communities in temperate forest and montane streams, and it has been widely shown that patches of intermediate (i.e. pebble) substrate support higher invertebrates densities and diversities in general (reviewed by Minshall 1984). That our results follow a similar pattern is not surprising. What is disturbing, however, is that this type of habitat is not common in most spring systems in Ash Meadows. Restoration of spring habitats should thus focus on reestablishing zones of relatively high flow and with a diverse mixtures of intermediate-size substrate particles. Introduction of substrate into areas within existing channels may be a short term solution to maintaining populations. However, these patches will likely become buried or embedded. A strategy of reconnecting spring outflows to natural drainage networks, so sediments are routed to them during periods of intense surface runoff, may provide be the best long term approach to restoring these systems

The rapid growth and high density of the Kings Pool population suggests that restoration of spring habitats will have relatively rapid, positive effects on naucorid populations. Long-term monitoring of restored channels will determine trajectories of these recovering populations, and the artificial substrate samplers developed in this study would provide an appropriate monitoring tool.