

MICROCRUSTACEAN COMMUNITY ASSEMBLAGES
IN EPHEMERAL WETLANDS AMONG
THE TERRESTRIAL ECOREGIONS
OF OKLAHOMA

By

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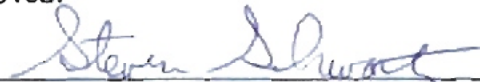
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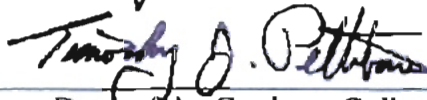
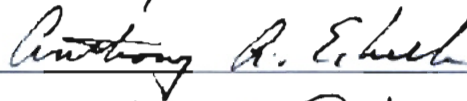
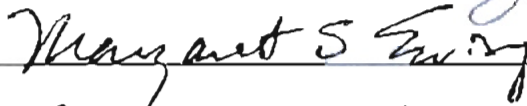
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MICROCRUSTACEAN COMMUNITY ASSEMBLAGES
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OF OKLAHOMA

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Working with ephemeral wetlands in the Great Plains, a truly endangered habitat exhilarated me beyond my wildest dreams. As I waded through these muddy wetlands, I received intriguing looks from onlookers and felt privileged to have the opportunity to research these habitats. The countless hours spent in searching for these pools also gave me a greater appreciation for the Oklahoma landscape. Further, collecting microcrustaceans, some of the most interesting and highly ignored animals, enforced my conviction that this project was an important one to pursue.

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CHAPTER I

MICROCRUSTACEAN COMMUNITY ASSEMBLAGES
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Abstract.- Isolated ephemeral wetlands are ubiquitous in all but the most arid landscapes. Although they provide habitat for many unique invertebrates, our knowledge of species distributions is weak. Recognition of spatial patterns of biotic and abiotic variables is an important facet of revealing differences in communities. The ecoregion concept predicts that areas of similar abiotic characteristics will have similar biotic communities. Given the intimacy of the terrestrial landscape with these shallow (<1 m) habitats, I tested the hypothesis that microcrustacean assemblages can be used to delineate terrestrial ecoregions. I sampled 146 ephemeral wetlands across the 11 level III ecoregions of Oklahoma and determined the species composition for each habitat. Over 40 % of all species were found fewer than three times, resulting in low community similarities within and between ecoregions. These results led to ambiguous delineation of ecoregions, likely attributable to the isolated nature of the habitat.

Introduction

The composition of communities is the result of abiotic and biotic controls (Borcard et al. 1992) including interactions of competition, predation, and mutualism (Krebs 1994). Assembly rules also affect the determination of community assemblages

(Comer and Simberloff 1979, Drake 1991, Stone et al. 1996). The role of mechanistic controls, such as dispersal events and patch occurrences, are not yet understood, but there are indicators that they may be critically important to communities that contain species that disperse slowly. Recognition of spatial patterns of biotic and abiotic variables among communities is an important facet of recent ecological studies (Borcard et al. 1992, Spencer et al. 1999) as data reveal striking differences in community structure in seemingly similar habitats. The association between community processes and landscape variation has only recently been assessed (King et al. 1996, Moorhead et al. 1998, Feminella 2000, Frisch 2002).

Communities often exist in irregular patchworks of disjunct habitats (Kareiva 1986, Kirkman et al. 1999). Ephemeral wetland communities that are isolated within the terrestrial landscape are excellent examples. Widespread across geographically distinct regions, these habitats can be used as models for ecologists to investigate how landscape attributes affect community assemblages. Improved knowledge of the spatial arrangement or connectivity of wetlands is essential in the development of conservation strategies and prioritization of local wetland complexes (Kirkman et al. 1999)

Ephemeral wetlands are among the most abundant and variable of all aquatic habitats; they are both endangered and inadequately studied (Simovich 1998, Schwartz and Jenkins 2000, Jenkins et al. 2003). The technical designation for these small, isolated, habitats is "seasonally ponded isolated wetlands" (SPIW's) (Kirkman et al. 1999). Ephemeral wetlands can exist wherever impermeable soils and seasonal precipitation combine to form pools during wet seasons (Holland and Jain 1981). They are located on every continent, yet the contribution of ephemeral wetlands to regional

biodiversity usually is overlooked by the scientific community (Williams 1987, Kirkman et al. 1999). These habitats are shallow and intermittent, and as a result, fishing, recreational, and agricultural uses are limited (Schwartz and Jenkins 2000). Ephemeral wetlands vary in form and size, and include playa lakes, vernal pools, buffalo wallows, Carolina bays, and prairie potholes. The naturally patchy distribution of these habitats across the landscape creates an ideal natural system in which to study spatial attributes of community structure.

In fragmented habitats, many species exist as metapopulations, that exhibit localized extirpation in some patches, and regional persistence via dispersal into or from nearby patches (Nee and May 1992, Semlitsch and Bodie 1998). The combination of similar populations in a region results in metacommunities (Hanski 1997). The destruction of ephemeral wetlands will potentially reduce the connectedness among remaining species populations (Semlitsch and Bodie 1998). The effect on community composition of invertebrate inhabitants will likely be adverse.

The invertebrate fauna of ephemeral wetlands exhibit high endemism (King et al. 1996), and often contains a mixture of opportunistic and resident species. Evolutionarily, the physical nature of ephemeral pools encourages speciation (Belk and Cole 1974, King et al. 1996). As a result these species often exhibit unique characteristics of either physiology or life history, which makes them successful in temporary waters (Belk and Cole 1974, Williams 1987). For many taxa, the rate of local extinction (extirpation) may be relatively high, a reflection of the fragmented nature of the habitat and the geographic isolation of populations (Holland and Jain 1981)

Regional patterns of landscape elements including chemical, biological and physical attributes that shape biological communities have been recognized by geographers and ecologists for many years (Herbertson 1905, Clements 1916). Recently the ecoregion concept was developed based on the assumption that contiguous landforms with similar, geology, soils and climate are likely to possess similar communities (Omernik 1987, 1995). The fundamental assumptions of this concept are: natural variation within the same region is predictable where environmental features are similar; allocation of natural variation into specific, homogenous ecoregions allows responses at one location to be compared to reference sites in the same ecoregion (Omernik and Bailey 1997, Hughes and Larson 1988, Feminella 2000). The relative importance of landscape attributes varies regionally (Wiken 1986, Omernik 1987, 1995). Ecoregion titles such as Eastern Deciduous Forest, Rocky Mountains, Great Plains and the Great Basin suggest natural regional differences (Abell et al. 2000).

Omernik's (1987, 1995) classification identifies North American ecoregions at two levels: level II is a coarse level that subdivides North America into 32 classes, and level III more finely subdivides the continent into 78 classes. Recognition of the spatial arrangement of natural variation helps determine variability among regions and spurs development of quantitative regional goals of habitat protection (Hughes and Larson 1988).

Aquatic ecoregions have also been established on the basis of drainage basins that form lotic systems (Abell et al. 2000). Lotic systems (flowing water) and lentic systems (standing water) can be incorporated into both terrestrial and aquatic ecoregions (Abell et al. 2000). Ephemeral wetlands are tightly associated with prominent terrestrial features,

generating dynamic wetland characteristics (e.g., pH, turbidity). To confound the issue, wetland systems may be connected via springs, surface flow, and sub-surface connection.

Relatively few broad scale assessments of ecoregions explicitly examine their ability to account for biotic variation (e.g., Whittier et al. 1988, Hughes et al. 1990, Tate and Heiny 1995). Empirical examinations of the appropriate taxonomic level to assess ecoregion sensitivity for aquatic biota are even rarer (Feminella 2000). If a more refined regional designation of ecoregions is used, then monitoring efficiency, data interpretation, and detection of unique communities provides a more logical framework than political boundaries. These facilitate detection of sensitive indigenous communities that may be under increased landscape pressures such as agricultural practices (Omernik and Griffith 1991).

Oklahoma is divided into 11 terrestrial eco-regions based on the Level III classification scheme (Wiken 1986, Omernik 1987, 1995, Figure 1). Oklahoma's heterogeneous landscape provides an ideal opportunity to assess the utility of ecoregions to explain the fauna in ephemeral wetlands. In this paper, I present a survey of microcrustaceans in ephemeral wetlands among terrestrial ecoregions of the state. This contributes toward an understanding of the distributions of invertebrate assemblages and communities in naturally patchy habitats. Although microcrustaceans in Oklahoma have been previously documented in some locations (Mackin 1930, 1935, 1938, Kingsbury 1965, Linder 1952, Wilson 1941, Robertson 1972, Taylor et al. 1987), many counties have no documentation of microcrustaceans.

In this paper I address questions regarding the relationship between the ephemeral wetlands of Oklahoma and the terrestrial ecoregion concept:

1. To what degree is the ephemeral wetland fauna of each ecoregion unique?
2. Can Oklahoma terrestrial ecoregions be delineated using microcrustacean fauna from ephemeral wetlands?
3. To what degree are microcrustacean assemblages correlated with habitat characteristics?

Methods

Sampling and data collection

From March 2001 through October 2002 I collected zooplankton from 146 ephemeral wetlands across the 11 terrestrial ecoregions of Oklahoma from (see Figure 2). Aquatic ecoregions were not used as a sampling framework for sampling ephemeral wetlands as they are an artifact of the terrestrial landscape (Ricketts et al. 1999) and delineated by terrestrial rather than aquatic ecoregions. Both connected and isolated wetland types can be found in Oklahoma. Careful consideration was taken to avoid connected wetlands because water flow between wetlands allows microcrustacean communities to have higher similarities.

Approximately ten wetlands were sampled per ecoregion with sites separated by at least 1 km to minimize the probability that habitats were connected and maximize variability. Thirty additional habitats were sampled in the Central Great Plains ecoregion to determine the efficacy of my sampling scheme via rarefaction techniques (Colwell 2000, Gotelli and Colwell 2001).

Wetlands were identified and located with the use of Oklahoma quadrangular maps (Oklahoma Atlas & Gazetteer, Yarmouth, Maine, USA), computerized topographical maps (Map Source®, GARMIN Corporation, Olathe, Kansas, USA) and

by a search of land adjacent to rural roads. Each wetland was characterized by latitude, longitude and elevation (GARMIN GPS III+ navigator; GARMIN Corporation, Olathe, Kansas, USA).

Each selected habitat was characterized by six parameters. A calibrated dipnet handle held vertically from the substratum to the water surface was used measure maximum depth. Vegetation cover (%) was estimated as cumulative percent cover inside and surrounding the wetland. Area of the wetland was estimated by eye. Water samples were collected during entry into the habitat to minimize disturbance of the sediment. Water parameters which included temperature (C°), pH, and conductivity (mS/cm) were measured in the field with a Yellow Springs Instrument (Yellow Springs, Ohio, USA) Model 63 field meter.

Microcrustaceans were collected with a dipnet (25-cm x 45-cm; 153- μ m netting). I attempted to sample all species present within each wetland by taking multiple sweeps through all microhabitats. Cheal et al. (1993) determined that plankton sweep nets were the most effective sampling method for estimates of species richness and discrimination of microcrustacean communities. Although quantitative samples are difficult to acquire due to the patchy distribution of individuals and the shallowness of habitats, efforts were made to equalize sampling efforts among habitats. All equipment was rinsed with de-ionized water between habitats to prevent accidental transfer of species between habitats.

Sample processing and curation

In the field, woody debris, tadpoles, and salamanders were removed from the samples prior to transportation or preservation. Samples with branchiopods (anostracans and conchostracans) were sorted and preserved directly after sampling to ensure retention

of morphological features. All zooplankton samples were transported on ice in 500-mL polyethylene bottles to Oklahoma State University. In the laboratory, aquatic insects, vegetation and pebbles were removed from the samples. Zooplankton samples were rinsed with de-ionized water, drained, and preserved with 100% absolute ethanol yielding a final alcohol concentration of approximately 75%.

Species identifications

Each sample was examined and sorted in the laboratory at 8.4x- 108x magnification with an Olympus SZX12 dissecting microscope. All morphologically unique individuals were separated for subsequent taxonomic evaluation. Individuals were placed on a slide with a drop of glycerin for identification using an Olympus BX50 compound microscope. I found 816 morphologically unique individuals from the 146 habitats.

Anostracans were identified to species according to Edmondson (1959), Belk (1975), Pennak (1989), and Maeda-Martinez et al. (1995); cladocerans were identified according to Herrick (1881), Frey (1961), Hann (1981), Dumont and Pensaert (1983), Pennak (1989), and Hebert (1995); conchostracans were identified according to Edmondson (1959) and Pennak (1989); copepods were identified according to Yeatman (1944), Edmondson (1959), Robertson (1970, 1972), Smith and Fernando (1978), Pennak (1989) and Einsle (1996); ostracods were identified according to DeLorme (1967), Pennak (1989), and Edmondson (1959). The authors performed all taxonomic identifications. Reference specimens were sorted into vials, labeled, and placed in the Oklahoma State University Zoology museum.

Data Analyses

Analysis of species composition was based on species presence or absence.

Results of analyses from such data are highly conservative (Balmer 2002) but the determination of relative species abundances was beyond the scope of this project due to time constraints. Actual or relative abundance data may be unfeasible for large-scale research projects so that presence / absence lists are better than nonexistent lists (Balmer 2002).

Rarefaction and species accumulation curves

Rarefaction techniques aid in comparison of species richness among ecoregions, (Coleman 1981, Coleman et al. 1982). Rarefaction curves are formed by randomizing the pooled species richness based on a greater sampling effort (e.g., the Central Great Plains ecoregion) (Gotelli and Colwell 2001).

With the use of a rarefaction or Coleman curve (Coleman 1981) in the software package EstimateS (Version 6.0) I determined the efficacy of estimating species richness from the 10 wetlands sampled in each ecoregion compared to the 42 wetlands sampled in the Central Great Plains ecoregion (Colwell 2000). For the sample-based curves, I set the patchiness parameter in EstimateS to 1.0 to emphasize the effect of ephemeral wetland spatial aggregation.

Similarity analysis

The Bray-Curtis similarity metric was used to determine similarities of microcrustacean communities within and among terrestrial ecoregions. Bray-Curtis similarity ranges from 0 (no similarity) to 100 (identical species assemblages) (Clarke and Warwick 2001). An analysis of similarities (ANOSIM) was used to quantitatively compare microcrustacean assemblages within and among ecoregions (Clarke and

Warwick 2001). The ANOSIM procedure computes all possible pairwise comparisons of Bray-Curtis similarity values and ranks paired habitats (wetlands or ecoregions) from least to most similar. Analysis of similarities also generates a test statistic (Global R) computed by comparing average ranks within groups to those among groups. R is recalculated for each of 10,000 data randomizations to provide a distribution of R statistic test values. Comparison of the Global R value to the derived distribution of test values is made to determine the percentages of permutations giving an R-value greater than or equal to the Global R. The Global R generated by ANOSIM is also useful to compare the degree of separation between ecoregions (Clarke and Warwick 2001). R values > 0.75 are categorized as well separated regions, R values $< 0.75 > 0.50$ represent communities that overlap yet are clearly different, and R < 0.25 describe communities that are indistinguishable (Clarke and Warwick 2001). R-values less than the Global R, suggest significant differences between assemblages.

Similarity values among sites were used to generate dendrograms describing ecoregion distinction via the cluster method in Primer-E (Primer Ltd). To determine the alpha level for each pairwise comparison in ANOSIM, the output significance level characterized as a % was divided by 100 for proper interpretation at the $p = 0.05$ significance level (Clarke and Warwick 2001). A Bonferroni correction factor for multiple comparisons was not necessary because sample sizes representing assemblages within ecoregions were adequate.

Generation of similarity values among and between ecoregions allowed me to test the hypothesis that invertebrate assemblages in wetlands within an ecoregion are more similar than those between ecoregions. Bray-Curtis similarity values were also used in

MEANSIM (Version 6, Van Sickle 1997) to calculate a measure of the classification strength of ecoregions. The classification strength (CS) is calculated by subtracting the mean similarity between-classes (\bar{E}) from the overall mean similarity within-classes (\bar{I}), ($CS = \bar{I} - \bar{E}$). A high CS (> 5.0) value implies that within-ecoregion similarity is much greater than between-ecoregion similarities. This index retains the original units of Bray-Curtis similarity (%). To determine if classifications are statistically different from random placement of sites into classes, MEANSIM calculates the CS from 10,000 randomizations, and then compares what proportion of permuted classifications have values less than the observed values (Van Sickle 1997).

In addition, I used a unit-less index of classification strength (M) computed as \bar{E} / \bar{I} . Classifications with highly distinct ecoregions have values near 0. Values near 1 indicate relatively weak classifications (Van Sickle 1997). The CS of an individual ecoregion (I_i) can also be measured as \bar{E} / I_i , in which values are primarily used to determine branch lengths in the dendrogram.

Environmental data analysis

Correlations between species richness and physico-chemical data were performed from the 146 sites and all six environmental variables (altitude, pH, percent cover, conductivity, depth, and temperature) and designation to one of 11 ecoregions.

Results

Distribution of species

Wetlands were sampled in 30 of the 77 Oklahoma counties (Appendix A). Most of these have no historical documentation of microcrustaceans. Studies have been conducted on select taxa (Mackin 1930, 1935, 1938, Robertson 1970, 1972) the

assessment of ephemeral wetland microcrustacean communities in Oklahoma is nonexistent

Only one genus of calanoid copepod was collected, but it included seven species (Table 1). Of these, one species (*Diaptomus novamexicanus*) is a new record for the state. This and the other calanoids species I collected occur elsewhere in the Great Plains or in neighboring states.

The cyclopoid copepods were represented by 16 species in 7 genera all in the family Cyclopidae (Table 1). The cyclopoid *Acanthocyclops vernalis* was the most commonly found species throughout the state (Table 1). Other cyclopoids, such as *Acanthocyclops crassicaudis* and *Cyclops bicusbidatus*, were rare. Four species of harpacticoid copepods were identified. The most common harpacticoid was *Attheyella illinoisensis*, collected primarily in western Oklahoma.

Cladocerans in the survey comprised six families, 21 genera and approximately 40 species (Table 1). The most commonly found cladocerans were *Ceriodaphnia reticulata*, *Simocephalus serrulatus*, *Pseudochydorus globosus*, and *Scapholebris kingi* (Table 1).

Taylor et al. (1987) most recently documented the branchiopods of Oklahoma. Ten of the 18 previously documented species of branchiopods were collected in the present survey. The anostracans were represented by two families comprising four species. The conchostracans, represented by the orders Laevicaudata and Spinicaudata, included four families and five species. Although notostracans were not found in this survey, they were collected in subsequent sampling.

Patterns of species richness

I determined that there were 92 microcrustacean species among the 816 morphologically unique individuals I identified (Appendix B). The mean species richness per wetland for all 146 habitats was 5.58 (Figure 3) with significant differences between ecoregions as determined by analysis of variance (ANOVA) ($p < 0.02$, S.E. = 0.22, $N = 146$; Figure 3). Species richness ranged from 1 to 15 and 52.7 % (77) of the wetlands contained 4 to 7 species (Figure 4). The mean number of microcrustacean species per ecoregion was 26 with a maximum of 61 species recorded from the Central Great Plains (Figure 5), probably as a result of the greater sampling effort in that ecoregion. The proportion of unique species found in only one ecoregion also increased with sampling effort (Figure 6).

Over 34% (32 of 93) of the species were found in only one wetland with an additional 7% (7) found in only two wetlands (Figure 7). Common species were rare with only one species (*Acanthocyclops vernalis*) found in 66% (97) of the wetlands. The next most prevalent taxa (*Cypridopsis* sp. and *Eucyclops agilis*) both occurred in 42% of the habitats.

The rarefaction curve based on the Central Great Plains ecoregion indicated that all but the Central Oklahoma Plains ecoregion had species richness lower than anticipated (Figure 8). Species richness was approximately 19 to 38% lower than predicted by analysis. Depending on the number of wetlands sampled per ecoregion, total species richness ranged from 17 to 31, where 27 to 38 species would be expected.

The sample based species accumulation curves derived from a total of five western, centrally and easterly-located ecoregions were used to extrapolate the number of

species expected if 200 additional wetlands in each ecoregion had been sampled (see Table 2 for regression equations). In ecoregions with < 30 species, species richness would potentially double (Table 3). In the Central Great Plains ecoregion where 42 wetlands were sampled, only an additional 20 species would accrue if 200 more wetlands were sampled (Table 3).

Figures 8 and 9 represent two sample based accumulation curves based on collections from all eleven ecoregions sampled. The accumulation curve with jagged edges (Figure 9) represents the accumulation of new individuals as additional wetlands were sampled, and Figure 10 represents the permuted curve (random ordering) of individuals collected from samples. These curves show how sample based protocols aggregate individuals within each sample.

Wetland water chemistry, physical attributes and species richness

The pH for all wetlands ranged from 5.10 – 10.16 (Appendix C; Table 4) with a mean of 7.51 and significant differences ($F = 1.901$, $p < 0.05$) among mean pH values across ecoregions. Conductivity ranged from 3.3-1511 mS/cm (Appendix C), also significantly different among ecoregions ($F = 1.901$, $p < 0.05$). Depending on time of day and season, water temperatures are highly variable in ephemeral wetlands and these values differed significantly among ecoregions ($F = 1.902$, $p < 0.05$). Percent vegetation cover for wetlands across all ecoregions ranged from completely open (0%) to completely shaded (100%). Although cover is highly variable regionally and seasonally, at the time of collection there were significant differences between ecoregions ($F = 1.901$, $p < 0.004$). Water depth ranged from 5 to 300 cm. However, some wetlands were not adequately measured because of difficulties in sampling habitats deeper than 1 meter

(Appendix C). Wetland water depths between ecoregions were not significantly different ($F = 1.901$, $p = 0.163$). Wetland altitude varied from west to east with elevations from 1351 meters in the far west to only 146 meters on the eastern edge of the state (Appendix C). Wetland elevation was significantly greater in the western part of the state ($F = 1.901$, $p < 0.05$). Wetland size ranged from 1 to 10,000 m^2 (Appendix C) and was highly variable among ecoregions. However, western ecoregions (Southwestern Tablelands and Western High Plains) had significantly larger mean wetland size (Table 4).

The six physico-chemical variables were poor correlates of species richness. Regression analysis revealed that no single variable (pH, conductivity, temperature, depth, altitude and surface area) was correlated with species richness (Table 5).

Similarity of species assemblages

The global ANOSIM test among ecoregions revealed significant differences in species assemblages ($R = 0.114$, $p < 0.001$). The low R-value suggests considerable assemblage overlap, but differences among ecoregions are large enough to be significant. However, the dendrogram based on similarity indices revealed no clear correlation between ecoregions and their geographic location; i.e., major nodes of species assemblages for wetlands do not coincide with the terrestrial ecoregions of Oklahoma (Figure 11). This result explains why the pair-wise Bray-Curtis similarity values were relatively low even though statistical significance was observed. Ecoregions distinction based on soil, geology, precipitation and land-use characteristics are relatively weak proxies for microcrustacean assemblages.

ANOSIM revealed a broad pattern of ecoregion distinctions (Table 6). Approximately 24 of 55 (43 %) pairwise comparisons were significant, a demonstration

of faunal distinction between ecoregions (Table 6). Of the 24 significant comparisons, 16% represented differences between northwestern and southeastern ecoregions, 33% between northeastern and southeastern ecoregions, and 45 % between northwestern and northeastern ecoregions.

Within-ecoregion assemblage similarity was variable. Similarity between geographically close wetlands (within the same ecoregion) should be relatively high, with the assumption that nearby wetlands share physical conditions (i.e., soils, geology, precipitation) and therefore species. Wetlands with unique species, or species rare in the data set, have low similarity values. Wetlands within the Flint Hills (the smallest ecoregion) had the highest Bray-Curtis similarity value (41.671) and those within the Western High Plains had the lowest (19.144; Table 7). The Western High Plains had the second highest number of unique species; the Central Great Plains ecoregion had the largest sample size and also the highest number of unique species.

A dendrogram based on similarities among ecoregions (after summing species occurrences across all wetlands within each ecoregion) reveals ecoregions cluster into three clusters. The most distinct cluster consists of the northern and western located ecoregions (WHP, SWT, FH and CIP) (Figure 12). Eastern ecoregions also cluster together to form a large cluster with a relatively high mean similarity. This result is strictly for visual distinction as no statistical tests can be used to evaluate the results due to software constraints.

The MEANSIM (Van Sickle 1997) analysis revealed differences of within-ecoregion similarity. The mean within ecoregion similarity (\bar{I} = 25.10) was significantly higher than the between-ecoregion similarity (\bar{E}) (18.36, $p < 0.0001$) yielding a

classification strength (CS) of 6.7%. This low ratio indicates ecoregions have weak classification strength for invertebrate assemblages even though the ratio is highly significant. The unit-less ratio of M was equal to 0.734 ($p < 0.0001$). With respect to within-ecoregion classification, some ecoregions had little structure, resulting in short dendrogram branches (Figure 13). All mean within- and between-ecoregion values are listed in Table 8. Ecoregions such as the Boston Mountains, Central Great Plains, Ozark Mountains had very short branches whereas the Western High Plains, Ouachita Mountains and Flints Hills have long branches, suggesting distinct species assemblages in the latter group. The Central Great Plains ecoregion has a very short branch, suggesting the mean within-ecoregion similarity is not different from the mean similarity. This does not support the indication from ANOSIM that unique species are often encountered in this ecoregion.

Discussion

This research represents the first statewide survey of aquatic microcrustaceans in Oklahoma. This documentation of ephemeral wetland invertebrate fauna of the Great Plains is of critical importance in a region where a majority of wetlands have been destroyed (Jenkins et al. 2003). Seventy three percent of the 93 microcrustacean species I detected were not previously recorded from Oklahoma. The majority of previously documented species are branchiopods (Spinicaudata, Laevicaudata and Anostraca) and copepods (Calanoida). The range extensions reported are primarily due to the lack of previous sampling efforts.

Two of the three most common species in Oklahoma wetlands (*Acanthocyclops vernalis* and *Eucyclops agilis*) either have extensive geographic distributions or they are

pioneer species in newly filled wetlands (Fryer 1985, King et al. 1996, Holland and Jenkins 1998). Many species of ephemeral wetland microcrustaceans are widespread in the Great Plains (e.g., *Cyzicus moorsei*, *Diaptomus clavipes* and *Eubranchipus oregonus*), but have not been documented in Oklahoma. Rare species (those occurring in three or fewer habitats) were common. Rare zooplankton species are frequently reported in ephemeral wetland surveys (King et al. 1996, Mahoney et al. 1990) and among Canadian lakes (Patalas 1990), probably as a result of low vagility of the species, loss of habitat and inadequate knowledge of species distributions.

Estimating species richness

The Central Great Plains ecoregion had the highest species richness, reflecting the greater number of samples and aerial extent of this ecoregion, which encompasses nearly two-thirds of the state. In Wisconsin, Dodson and Lillie (2001) found lower species richness (3.88) in wetlands in agricultural settings than in those undisturbed wetlands (7.21). These results are in contrast to the vernal pools of California, where wetlands average up to 31.8 microcrustacean species (King et al. 1996). The low species richness in Oklahoma and Wisconsin ephemeral wetlands merit further study and is suggestive of common process at work in these likely very different habitats. Factors such as energy flow and trophic dynamics that might be responsible for species richness certainly merit further study.

Wetland disturbance from agricultural practices decreases or alters microcrustacean communities (Dodson and Lillie 2001, Beaver et al. 1999), a factor that might affect Oklahoma wetlands where a high percentage of land is used for agricultural, or livestock practices. The alteration of small wetlands into stock ponds through

excavation extends wetland hydroperiod, which encourages proliferation of predaceous insects (Clausnitzer and Huddleston 2002) and thus eliminates easily preyed upon species. The potential for agricultural based wetland disturbance is high in Oklahoma, and is likely to have negative effects on large-scale community assemblages in both space and time.

Differences in mean wetland species richness among ecoregions was marginally significant ($p = 0.02$), indicating that wetland species diversity is not equivalent across the state. The greatest mean species richness per wetland occurred in the Central Oklahoma Plains (7.4 species), while the least speciose wetlands were in the Southwestern Tablelands (4.2 species). The physico-chemical parameters I measured (conductivity, pH, temperature) were weak correlates of species richness among and between ecoregions.

Species richness is an elusive quantity to measure (May 1988, Gotelli and Colwell 2001). Estimating species richness using ecoregions with low sample sizes ($n = 11 - 12$) and non-asymptotic species accumulation curves may not accurately estimate species richness (Gotelli and Colwell 2001). For the ecoregions represented by 11- 42 wetlands (Table 3), an estimated 42 - 71% species in the ecoregions were collected. By contrast, Patalas (1990) found that 20 lakes per region were sufficient to provide 90% of species in Canadian lakes, a result that emphasizes the differences between permanent and ephemeral aquatic systems.

In the Central Great Plains where sampling intensity was nearly four times greater than other ecoregions, species richness was only two times greater than that of other ecoregions. Extrapolation based on the accumulation curve derived from the Central

Great Plains ecoregion predicts 66 species in 60 wetlands, a small increase from the 62 species I found in 42 wetlands. Extrapolating to 200 wetlands predicts that an estimated 85 species will be accumulated. Although not asymptotic, using the CGP accumulation curve to extrapolate species richness can be useful with the important conclusion that many species remain to be collected. Conversely, the statewide sample based accumulation curve (that appears asymptotic) suggests that additional sampling will yield few additional species. An extrapolation based on the statewide regression equation predicts 95.71 species if 200 wetlands were sampled (Figure 10), an addition of only 3 species. The dichotomy between local and regional estimates of species diversity warrants further investigation to understand the limitations of species extrapolations with sample sets and different landscape scales.

A method used to compare similar habitats in which sampling effort has not been equivalent is a Coleman rarefaction curve (Krebs 1994, Gotelli and Colwell 2001). I interpolated the expected number of species (species richness) in other ecoregions of smaller sample sizes based on the Coleman rarefaction curve generated from the Central Great Plains ecoregions. Nearly all Oklahoma ecoregions have lower than expected species richness (Figure 8). For example, in the Boston Mountains ecoregion, 38 species are expected to be accumulated, yet only 21 species were found. Because ephemeral wetlands may function dissimilarly between ecoregions, we should not expect the same number of species. Agricultural manipulation has a significant effect on species richness through turbidity, sedimentation, herbicide, and pesticide runoff (Lahr 1997, Dodson and Lillie 2001, Gleason et al. 2003). Wetlands in agricultural watersheds have fewer species per wetland and fewer species overall than undisturbed wetlands (Dodson and Lillie

2001) as species richness can be adversely affected by water chemistry (pH, conductivity). No evidence was observed to support this hypothesis although many of the wetlands sampled in this survey were in agricultural settings. However, specific anthropogenic stressors were not investigated and individual species limitations need further investigation to understand interactions among species and specific wetland parameters.

Another explanation for the low species richness detected in Oklahoma wetlands is that the sampling scheme may have inadvertently selected for species tolerant to relatively high water temperatures. Eastern Oklahoma receives approximately twice the precipitation than the western half of the state (55 cm in west central and 114 cm in east central; Oklahoma Climatological Survey 1998), so that wetlands in the eastern Oklahoma wetlands are likely to have extended hydroperiods. I took advantage of this pattern to initiate sampling in western Oklahoma in early spring and subsequent sampling in eastern and southeast Oklahoma in late spring when water temperatures were consequently 10°C warmer than wetlands earlier sampled in western Oklahoma. Physico-chemical parameters such as temperature and pH can control the occurrence of species in small isolated wetlands (Horne 1967, Belk 1975, Williams 1987), ultimately limiting species richness.

Each wetland was sampled only once due to time constraints. Some seasonal species may not have been present at the time of collection because seasonal and annual variation in faunal assemblages is common within wetlands (Horne 1971, Wiggins et al. 1980, Williams 1987, Schneider and Frost 1996). The result is that species richness was probably underestimated uniformly across all ecoregions. However, broad scale surveys

adequate for comparison of biodiversity across many wetlands in most areas are non-existent and time and manpower considerations preclude repeated sampling.

Why is there such low species similarity across the ecoregions of Oklahoma?

Community similarity values were consistently low across Oklahoma's ecoregions. The mean similarity of wetlands across all ecoregions was 26%, and ranged from 19% to 41%, an indication of the dissimilarity between communities in each ecoregion. There are at least three explanations to explain this result; low rates of dispersal, effects of disturbance, and abiotic factors.

Microcrustaceans are passive dispersers via egg or cyst stages that persist in the environment for several years until conditions become favorable. Dispersal of microcrustaceans is low even for cysts and eggs that are viable for extended periods of time in hospitable conditions (Belk and Cole 1974, Williams 1987, Hairston and Cáceres 1996). For any organism to increase its range it has to disperse to a new habitat, withstand potentially unfavorable conditions during its passage, and establish viable populations upon its arrival (King et al. 1996). Passively dispersing microcrustaceans are subject to secular migration (Brown & Lomolino 1998) in which migration occurs slowly over many generations, with generous opportunities for adaptation and gradual dispersal across broad regions. Once a species establishes a population in a wetland, nearby wetlands may act as stepping-stones for further dispersal. However, the low rate of dispersal among microcrustaceans isolates taxa and enhances their uniqueness among individual wetlands. Stochastic dispersal that is slow and rare may hinder the classification of ecoregions using wetland species similarities.

Secondly, disturbance of the landscape may alter wetland invertebrate communities in favor of broadly distributed weedy species, e.g., *Acanthocyclops vernalis* and *Eucyclops agilis*, (Fryer 1985, Lukaszewski et al. 1999). With much of the landscape altered in the past 100 years due to agricultural practices (Hoagland 2000) the degree to which Oklahoma wetlands are disturbed is unknown.

Thirdly, wetland distinctiveness due to past and present abiotic factors may have many consequences on community assemblages. Factors favorable for a dispersing propagule may hinder or support a given species in a given wetland. Annual variability of hydroperiod and seasonal fluctuations of temperature operate to add more stochasticity to freshwater crustacean assemblages. Yet other abiotic variables (depth, suspended solids, elevation) as well as geographic location influence the structure of crustacean assemblages. Such assemblages vary among pools of the same habitat type and among pools at the same site, confounding the ability to recognize factors causing assemblage composition (King et al. 1996).

Habitat duration (hydroperiod) can mediate shifts in abiotic and biotic processes determining assemblage composition (Wiggins et al. 1980, Schneider and Frost 1996). Abiotic variables had the greatest influence on relatively young communities in mesocosm experiments (Holland and Jenkins 1998, Cáceres and Soluk 2002) with competition and predation more important in habitats with extended hydroperiods (Moorehead et al. 1998). Crustaceans dominate the species richness of wetlands with short hydroperiods. As the hydroperiod becomes longer a trophic shift to insects occurs (Jeffries 1994, Moorhead et al. 1998). Moreover, the abundance of predatory insects increases in later stages of wetland inundation, which influences crustacean assemblages

in wetlands (Schneider and Frost 1996, Moorhead et al. 1998). Similar richness and diversity of all invertebrates through time suggests that colonization is an important factor that affects the structure of invertebrate assemblages in early wetland succession (Moorehead et al. 1998).

Can the wetland invertebrate fauna of Oklahoma be delineated by terrestrial ecoregions?

The eleven terrestrial ecoregions of Oklahoma could not be delineated on the basis of ephemeral wetland invertebrate assemblages. The hypothesis that terrestrial ecoregions represent a useful framework by which to characterize the natural variation of ephemeral wetland biota (Hughes and Larsen 1988) is not supported in contrast to the work of Feminella (2000). There are three distinct patterns among the pair-wise comparisons (Table 6); Northwestern ecoregions were distinct from southeastern ecoregions, northeastern were distinct from southeastern ecoregions, and northwestern ecoregions were distinct from northeastern ecoregions. The Global R and M statistic was significant among wetlands across the Oklahoma landscape using both ANOSIM and MEANSIM, respectively. This result suggests that the invertebrate fauna of isolated wetlands is structured similarly within ecoregions. However, other analyses contradict this conclusion. The dendrogram of wetlands similarities (Figure 11) reveals that wetlands clustered independently of ecoregion assignment. The dendrogram also revealed long branch lengths, indicative of high community distinctiveness due in part to rare species in nearly all wetlands which weaken assemblage similarities within each ecoregion.

The Western High Plains and Central Great Plains had the lowest mean similarity values (19.1 % and 19.2%, respectively; Table 7). Although the Central Great Plains had

the greatest number of unique species it may not be the most biologically distinct ecoregion in Oklahoma. Rather, the Western High Plains ecoregion was the most distinct ecoregion based on the number of significant pair-wise comparisons and distinctiveness in the cluster analysis (Table 6; Figure 12). These results clearly point to the difficulty classifying the most distinct ecoregion based on community dissimilarity versus unique species with varying sample sizes. In the Central Great Plains, the increased sampling effort resulted in more unique species, an indication that even within an ecoregion the species assemblages are not particularly similar and that cosmopolitan species are rare, contrary to other current hypotheses (e.g., Shurin 2000, Dodson and Lillie 2001). These results indicate that more intense sampling in a given area (ecoregion) is important to understand community structure (Feminella 2000).

The analysis of MEANSIM revealed an overall classification strength of 6.7%, indicative of a significant, yet weak classification, similar to the results of VanSickle and Hughes (2000) who used stream fishes to delineate ecoregions. This low CS value is also verified by the unit less ratio (M) being relatively close to 1 (0.734). The dendrogram depicts few ecoregions with relatively short branches (OUM, AV), likely because these regions have low wetland species richness, increasing the probability of within ecoregion similarity. Overall, dendrogram patterns were not easily discernable, which supports the weak indices of classification strengths.

My results support the conclusions of other studies that found microcrustaceans to be poor, inactive dispersers (Mahoney et al. 1990, Jenkins and Underwood 1998, King et al. 1996, Cáceres and Soluk 2002). Poor dispersal among microcrustaceans, even to nearby wetlands, restricts wetlands from developing similar assemblages within an

ecoregion, unlike results found with macroinvertebrate communities in riparian systems (Rabeni and Doisy 2000).

I found that more intensive sampling in an ecoregion enhanced the distinctiveness of the Central Great Plains ecoregion. This result is confounded for two reasons. First, this ecoregion has the greatest area of the Oklahoma ecoregions. Island biogeography theory (MacArthur and Wilson 1963) predicts more species in larger areas (the species area relationship) because of the greater potential for habitat diversity. There was a relatively weak correlation between species richness and ecoregion area ($\log(y) = 0.2224(\log x) + 0.5373$, $R^2 = 0.4456$). However, the z-value of 0.2224 was slightly lower than the suggested minimum value of 0.26 for continental islands (Leitner and Rosenzweig 1997) and thus supporting a weak effect of area on species richness.

The possibility of ecoregion delineation based on crustaceans may never be clear. Certainly resolution and separation of ecoregions by the fauna of isolated ephemeral wetlands could be enhanced with greater sample size and strategically timed sampling regimes. Contradictory results regarding the use of aquatic invertebrates to delineate the terrestrial landscape have been reported. Some workers suggest that ecoregions should be used to resolve natural landscape heterogeneity, specifically for aquatic biota protection. (Hughes and Larsen 1988, Feminella 2000, Van Sickle and Hughes 2000, Battle and Golladay 2001). The terrestrial ecoregions of Oklahoma are distinct but they are poorly delineated by aquatic microcrustaceans. The results of my study are similar to studies that found regional differences in community assemblages that occurred in spite of, rather than because of differences in water pH or conductivity (Rundle and Ramsey 1997, Hawkins and Vinson 2000, Waite et al. 2000, Marchant et al. 2000). This is

demonstrated clearly by differences in community assemblages in wetlands of similar pH and other factors (conductivity and area) in different regions. Baseline parameters that characterize wetlands were certainly not the most explanatory variables of biological differences between ecoregions in the present study.

Other factors that distinguish an ecoregion may indeed serve as proxies for wetland communities. Topographic relief, littoral vegetation, precipitation, and hydroperiod may be strong determinants of community structure. Overall, inadequate ecoregion delineation with the use of microcrustacean communities underscores the importance of the individual wetland to biodiversity.

Conservation

Oklahoma ephemeral wetlands harbor unique crustacean assemblages that remain unattributable to specific ecoregions. Low predictability of species occurrence based on ecoregions highlights the importance of careful planning in efforts to conserve biodiversity in ephemeral wetlands. Nearly 50 % of all species occurred three or fewer times in this survey and 33 % of these occurred only once.

In the past century, a great deal of the Oklahoma landscape has been modified by human activity. Agricultural and livestock operations have led to intense wetland drainage in the Great Plains (Hoagland 1999, Jenkins et al. 2003). With approximately 70% of Oklahoma wetlands lost (Redelfs 1980, unpublished thesis), the recognition of the importance of small isolated ephemeral wetlands is critical. The lack of appreciation of these habitats contributes to their demise and having both a wet and dry cycles complicates their delineation and slows their protection by federal and state agencies.

Although the idea of wetland conservation has gained momentum in the United States (Simovich 1998, Hoagland 2000, Calhoun et al. 2003), national losses continue at a rate of 58,500 acres per year, a decrease 80% from the previous ten years (Dahl 2000). Yet, in Dahl's (2000) report on the status of United States wetlands, ephemeral wetlands were not recognized as true wetlands, leaving the loss of these wetlands unknown and their importance unrecognized. Hoagland (2000) highlighted the lack of existing data for Oklahoma wetland vegetation and the same applies to the aquatic invertebrate fauna. This survey serves as a first step in supplying the data that will be needed for the protection of these valuable and unique habitats.

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Table 1.- Classified microcrustacean species and the number of wetlands each was found.

Order	Family	Species	# of sites	
Cladocera	Chydoridae	<i>Alona barbata</i>	2	
		<i>Alona guttata</i>	3	
		<i>Alona rectangula</i>	1	
		<i>Alona rustica</i>	19	
		<i>Alonella dadayi</i>	1	
		<i>Biapertura affinis</i>	1	
		<i>Camptocercus oklaomensis</i>	15	
		Chydoridae A unknown	1	
		<i>Pleuroxus denticulatus</i>	18	
		<i>Pleuroxus striatus</i>	2	
		<i>Pseudochydorus globosus</i>	34	
		<i>Dunhevedia crassa</i>	1	
		<i>Kurzia latissima</i>	1	
		<i>Leydigia acanthocercoides</i>	13	
		<i>Leydigia leydigi</i>	5	
		<i>Leydigia quadrangularis</i>	1	
		Daphnidae	<i>Daphnia ambigua</i>	18
			<i>Daphnia exilis</i>	2
			<i>Daphnia laevis</i>	3
			<i>Daphnia obtusa</i>	10
	<i>Daphnia parvula</i>		4	
	<i>Daphnia prolata</i>		7	
	<i>Daphnia pulex</i>		12	
	<i>Daphnia pulicaria</i>		1	
	<i>Daphnia pileata</i>		2	
	<i>Daphnia unknown</i>		1	
	Bosminidae	<i>Scapholeberis kingi</i>	22	
		<i>Simocephalus expinosus</i>	13	
		<i>Simocephalus serrulatus</i>	31	
	Moinidae	<i>Ceriodaphnia quadrangula</i>	6	
		<i>Ceriodaphnia reticulata</i>	31	
		<i>Ceriodaphnia rigaudi</i>	4	
		<i>Bosmina longirostris</i>	17	
		<i>Eubosmina hagmanni</i>	6	
	Moinidae	<i>Moina macrocopa</i>	17	
		<i>Moina micrura</i>	7	
		<i>Moina wierzejskii</i>	6	

Order	Family	Species	# of sites	
Copepoda	Sididae	<i>Diaphanosoma brachyurum</i>	10	
		<i>Latonopsis fasciculata</i>	1	
		<i>Sida crystallina</i>	1	
	Macrothricidae	<i>Ilyocryptus spinifer</i>	3	
		<i>Macrothrix hirsuticornis</i>	1	
		<i>Macrothrix laticornis</i>	2	
	Canthocamptidae	<i>Attheyella illinoisensis</i>	9	
		<i>Canthocamptus assimilis</i>	1	
		<i>Canthocamptus robertcokeri</i>	4	
		Unk Harpacticoda	1	
		Cyclopidae	<i>Acanthocyclops crassicaudis</i>	1
			<i>Acanthocyclops vernulis</i>	97
			<i>Cryptocyclops bicolor</i>	11
			<i>Cyclops bicusbidatus thomasi</i>	1
			<i>Cyclops exilis</i>	4
			<i>Cyclops haueri</i>	1
			<i>Cyclops navus</i>	8
			<i>Cyclops Spp4</i>	1
			<i>Cyclops Spp5</i>	1
			<i>Eucyclops agilis</i>	42
			<i>Macrocyclops alibidus</i>	14
			<i>Mesocyclops edax</i>	5
			<i>Mesocyclops hyalinus</i>	1
			<i>Mesocyclops tenuis</i>	12
			<i>Mesocyclops leukarti</i>	1
	<i>Microcyclops varicans rubellus</i>	4		
	Diaptomidae	<i>Diaptomus clavipes</i>	28	
<i>Diaptomus novamexicanus</i>		2		
<i>Diaptomus pallidus</i>		32		
<i>Diaptomus reighardi</i>		3		
<i>Diaptomus saltillinus</i>		3		
<i>Diaptomus sanguineus</i>		1		
<i>Diaptomus siciloides</i>		22		
Ostracoda	Candoniidae	<i>Candona</i>	4	
	Cyclocyprididae	<i>Cyclocypris</i>	28	
		<i>Physocypris</i>	9	
	Cypridopsidae	<i>Cypridopsis</i>	43	
		<i>Potamocypris</i>	1	

Order	Family	Species	# of sites
	Cyprididae	<i>Eucypris virens</i>	1
		<i>Chlamydotheca arcuata</i>	1
		<i>Chlamydotheca flexilis</i>	3
		<i>Cyprinotus incongruens</i>	1
		<i>Cypris</i>	18
	Limnocythidae	<i>Limnocythere</i>	7
Anostraca	Chirocephalidae	<i>Eubbranchipus oregonus</i>	4
	Streptocephalidae	<i>Streptocephalus dorotheae</i>	3
		<i>Streptocephalus seali</i>	6
		<i>Streptocephalus texanus</i>	3
Laevicaudata	Lynceidae	<i>Lynceus brevifrons</i>	1
Spinicaudata	Caenestheriidae	<i>Caenestherieila helfragei</i>	2
		<i>Eocyclus concavus</i>	1
	Limnadiidae	<i>Eulimnadia texana</i>	1
	Leptestheriidae	<i>Leptestheria compleximanus</i>	1
		Unknown Conchostraca A	1
		Unknown Conchostraca B	1

Table 2.- Regression equations and R² values from the sample-based species accumulation curves from five selected Oklahoma ecoregions

Ecoregions	Equation	R²
WHP	$y = 9.8525\text{Ln}(x) + 1.3689$	0.9584
CGP	$y = 16.43\text{Ln}(x) - 1.179$	0.9885
FH	$y = 7.5033\text{Ln}(x) + 3.2032$	0.9566
BM	$y = 6.9279\text{Ln}(x) + 3.5976$	0.9939
OZM	$y = 7.3031\text{Ln}(x) + 6.7254$	0.9989
State	$y = 21.067\text{Ln}(x) - 15.9$	0.9778

Table 3.- Extrapolation of species richness using the regression equations from the sample- based species accumulation curves of the five selected ecoregions

Ecoregion	# of species	Wetlands Sampled	Additional wetlands sampled within an ecoregion		
			60	146	200
WHP	28	12	41.71	50.46	53.57
CGP	61	42	66.79	80.71	85.87
FH	23	11	33.92	40.59	42.95
BM	21	12	31.96	38.12	43.9
OZM	24	11	36.62	43.01	45.41
State	93	146	70.35	89.08	95.71

Table 4.- Mean physico-chemical values for wetlands sampled among ecoregions. Area (m²) of wetland, altitude (ft) where wetland was located, % cover describes the amount of vegetation covering water, conductivity (mS/cm), depth (cm) sediment surface to surface of water, pH (acidity/alkalinity) of water, temperature (C°).

	Area	Altitude	% cover	Condu- ctivity	Depth	pH	Temper- ature
WHP	1729.92	3272.58	6.67	369.03	33.83	8.1	18.69
SWT	904.2	2692.6	1	204.52	31.65	8.3	16.55
CGP	460.01	1229.5	27.5	393.93	75.24	7.7	23.82
FH	139.95	1113.45	0	342.79	56.36	7.63	16.76
COP	1560	1040.1	11.5	115.32	72	7.72	27.95
CIP	33.3	850.7	19.5	220.93	34	7.83	19.94
OZM	582.18	1048.55	38.64	86.38	92.73	7.25	27.96
BM	217.25	1022	16.67	90.37	67.92	7.02	18.92
AV	243.18	690.36	21.36	139.56	38.64	6.61	25.01
OUM	107.4	843.3	38.5	80.04	25.5	6.78	30.28
SCP	201	581.29	24.29	74.07	89.29	7.01	29.21

Table 5.- Species richness was not correlated with physico-chemical variables. Low R^2 values indicates this result.

	Equation	R^2
Species richness vs. pH	$y = 0.1991x + 4.0934$	$R^2 = 0.0046$
Species richness vs. conductivity	$y = 0.0012x + 5.29$	$R^2 = 0.0135$
Species richness vs. C^0	$y = 0.1376x + 2.4128$	$R^2 = 0.0876$
Species richness vs. depth	$y = 0.0097x + 5.0137$	$R^2 = 0.0634$
Species richness vs. altitude	$y = -0.0005x + 6.2563$	$R^2 = 0.0242$
Species richness vs. area	$y = 7E-06x + 5.5851$	$R^2 = 0.0001$
Species richness vs. % cover	$y = 0.0116x + 5.3527$	$R^2 = 0.0157$

Table 6.- Bray Curtis Global R permutation statistic for ANOSIM values among pairwise comparisons for ecoregions. Asterisks indicate significant differences between ecoregion species assemblages at the $\alpha = 0.05$ level. R values greater than or equal 0.25 were designated as distinguishable communities.

Ecoregions	R Statistic	Significance level (%)	Number > observed
CGP, SWT	-0.046	68.8	688
CGP, CIP	0.101	10.6	105
CGP, FH	-0.112	94.7	947
CGP, WHP	0.168	2.1	20
CGP, OZM	0.217	0.3	2
CGP, COP	0.067	18.5	184
CGP, SCP	0.089	16.3	162
CGP, OUM	-0.109	93.7	937
CGP, AV	0.071	18.6	185
CGP, BM	0.09	10.4	103
SWT, CIP	0.184	1.4	13
* SWT, FH	0.274	0.1	0
SWT, WHP	0.03	28.3	282
* SWT, OZM	0.552	0.1	0
SWT, COP	0.238	1.8	17
* SWT, SCP	0.339	0.4	3
SWT, OUM	0.22	1.3	12
* SWT, AV	0.266	0.3	2
SWT, BM	0.164	2.3	22
CIP, FH	0.104	4.3	42
* CIP, WHP	0.28	0.2	1
* CIP, OZM	0.489	0.2	1
* CIP, COP	0.393	0.1	0
* CIP, SCP	0.287	0.7	6
* CIP, OUM	0.405	0.1	0
* CIP, AV	0.361	0.1	0
* CIP, BM	0.268	0.4	3
* FH, WHP	0.324	0.1	0
* FH, OZM	0.571	0.1	0
* FH, COP	0.436	0.1	0
* FH, SCP	0.518	0.1	0
* FH, OUM	0.464	0.1	0

* FH, AV	0.285	0.1	0
* FH, BM	0.31	0.2	1
* WHP, OZM	0.491	0.1	0
* WHP, COP	0.158	2.5	24
* WHP, SCP	0.269	0.4	3
WHP, OUM	0.241	0.3	2
* WHP, AV	0.294	0.3	2
WHP, BM	0.146	1.5	14
* OZM, COP	0.246	0.1	0
* OZM, SCP	0.261	0.7	6
* OZM, OUM	0.289	0.2	1
OZM, AV	0.241	0.1	0
OZM, BM	0.189	1.6	15
COP, SCP	-0.04	62	620
COP, OUM	0.126	6.1	60
COP, AV	0.035	25.1	250
COP, BM	0.069	15.8	157
SCP, OUM	0.101	15.7	156
SCP, AV	0.079	20.1	200
SCP, BM	0.028	32.6	325
OUM, AV	0.066	16.2	161
OUM, BM	-0.005	47.3	472
AV, BM	0.104	7.1	70

Table 7.- Mean Bray-Curtis community similarity values from each ecoregion and the number of wetlands sampled in each ecoregion.

Ecoregions	Number of Wetlands	Mean Bray-Curtis Similarity
Western High Plains	12	19.114
Southwestern Tablelands	10	27.975
Central Great Plains	42	19.235
Flint Hills	11	41.671
Central Oklahoma Plains	10	25.127
Central Irregular Plains	10	23.303
Ozark Mountains	11	30.818
Boston Mountains	12	20.944
Arkansas Valley	11	20.029
Ouachita Mountains	10	35.419
South Central Plains	7	24.57

Table 8.- MEANSIM results for the classification of each ecoregion, values derived from MEANSIM algorithm. See Figure 11 for illustration

Ecoregion	I_i	\bar{E} / I_i	$I_i - \bar{E}$
WHP	13.57	1.355	-4.83
SWT	20.75	0.886	2.35
CGP	18.196	1.011	-0.202
FH	23.028	0.799	4.628
COF	20.437	0.9	2.037
CIP	15.775	1.166	-2.625
OZM	18.087	1.017	-0.312
BM	18.515	0.993	0.115
AV	21.799	0.844	3.399
OUM	24.798	0.741	6.398
SCP	19.788	0.929	1.388

Figure 1 - Level III Terrestrial Ecoregions of Oklahoma. (WHP = Western High Plains; SWT = Southwestern Tablelands; CGP = Central Great Plains; FH = Flint Hills; COP = Central Oklahoma Plains; SCP = South Central Plains; OUM = Ouachita Mountains; AV = Arkansas Valley; BM = Boston Mountains; OZM = Ozark Mountains; CIP = Central Irregular Plains). Map adapted from Omernik 1995.

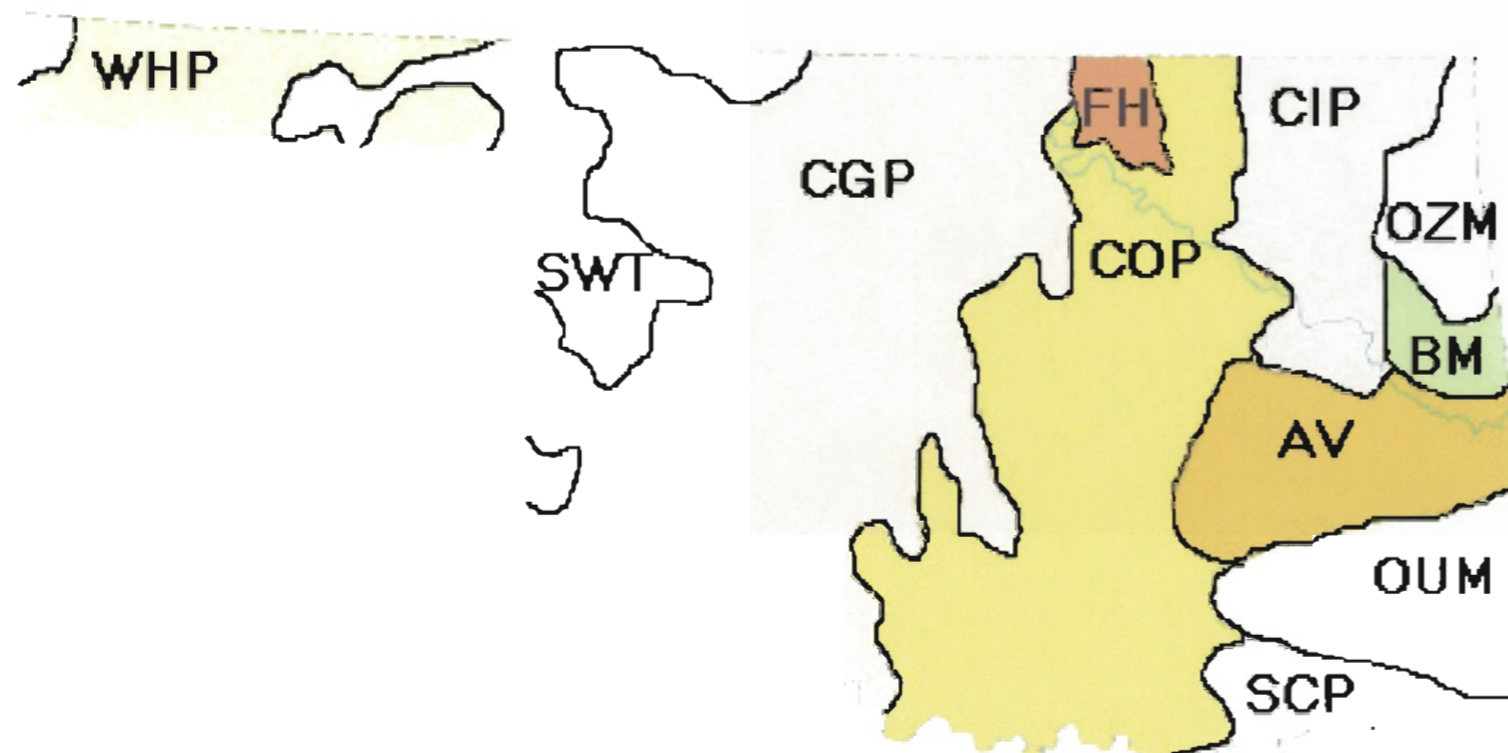


Figure 2 - Dots represent the approximate positions of the 146 sampled wetlands within the 11 terrestrial ecoregions of Oklahoma. Map adapted from Omernik 1995.

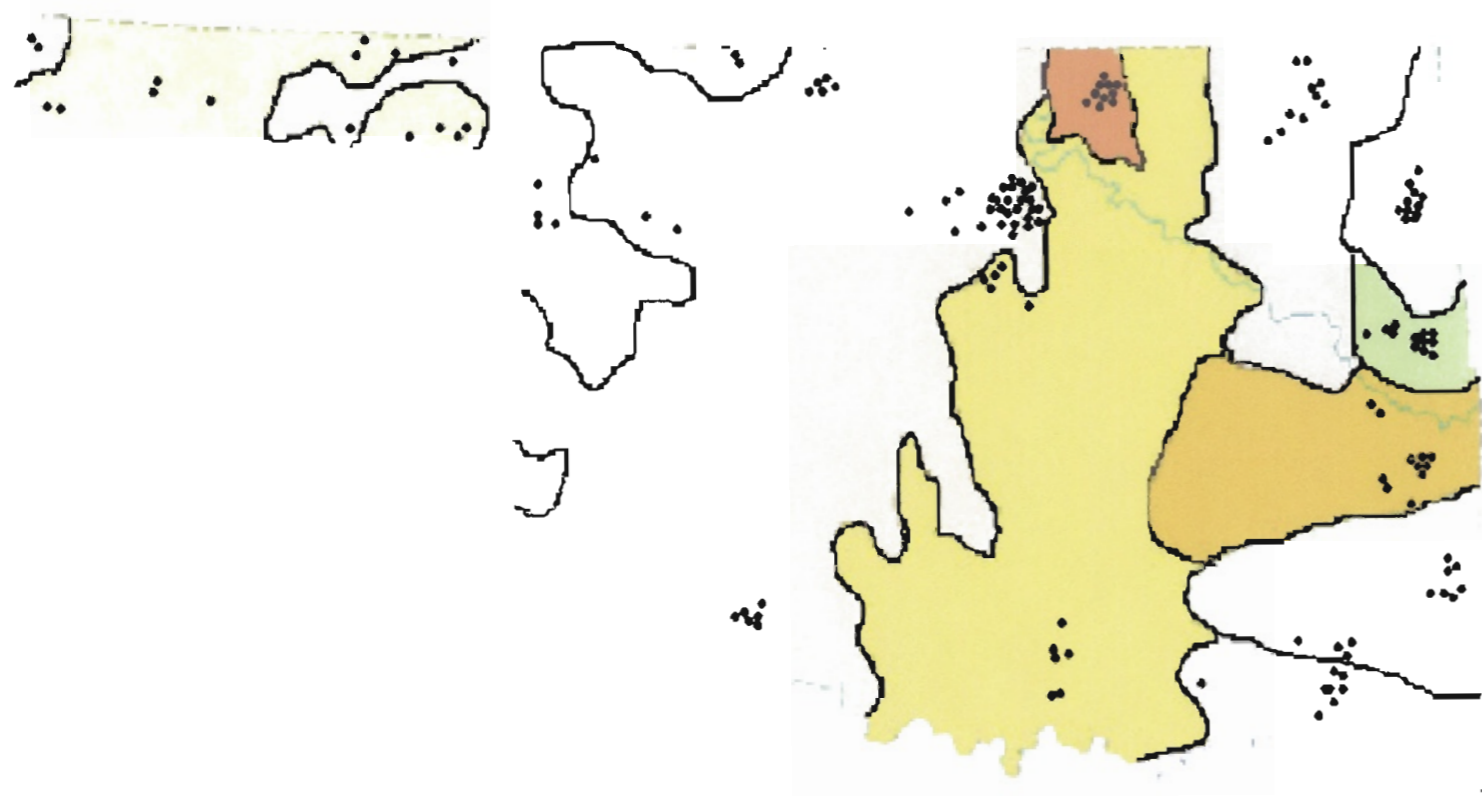


Figure 3.-The frequency of mean species richness among wetlands of Oklahoma ecoregions. Results of Analysis of Variance (ANOVA) found significant differences between wetland species richness in ecoregions ($p < 0.02$, $s.e = 0.22$, $N=146$).

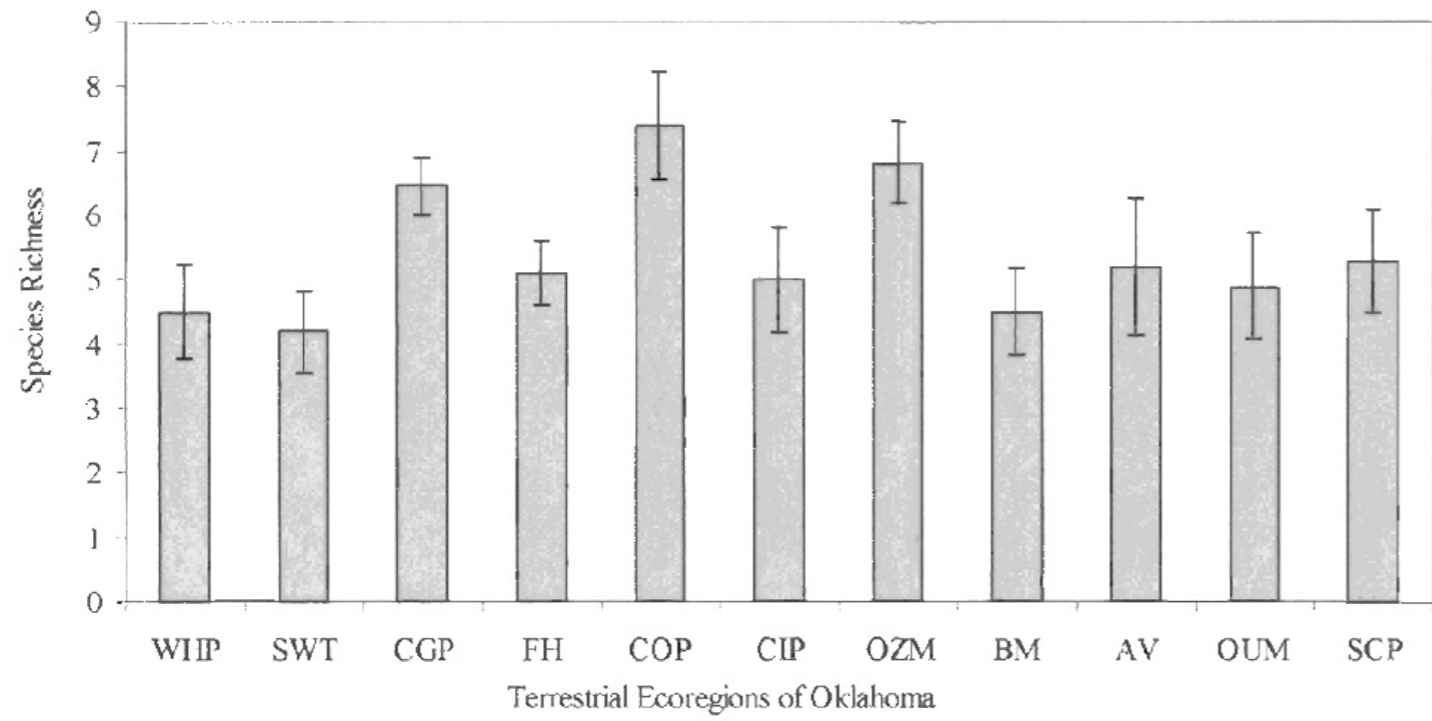


Figure 4.-The distribution of wetland species richness versus number of wetlands.

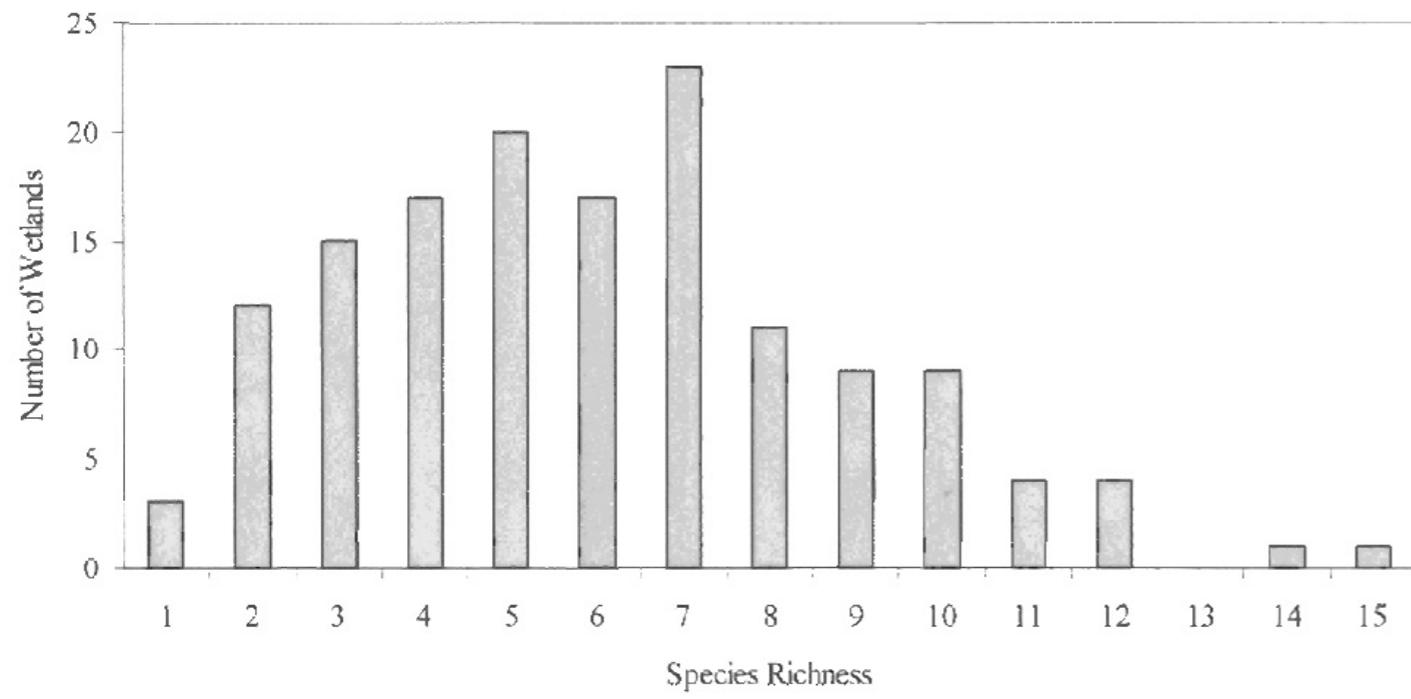


Figure 5.-Histogram representing the total species richness identified and number of wetlands sampled in the corresponding ecoregion

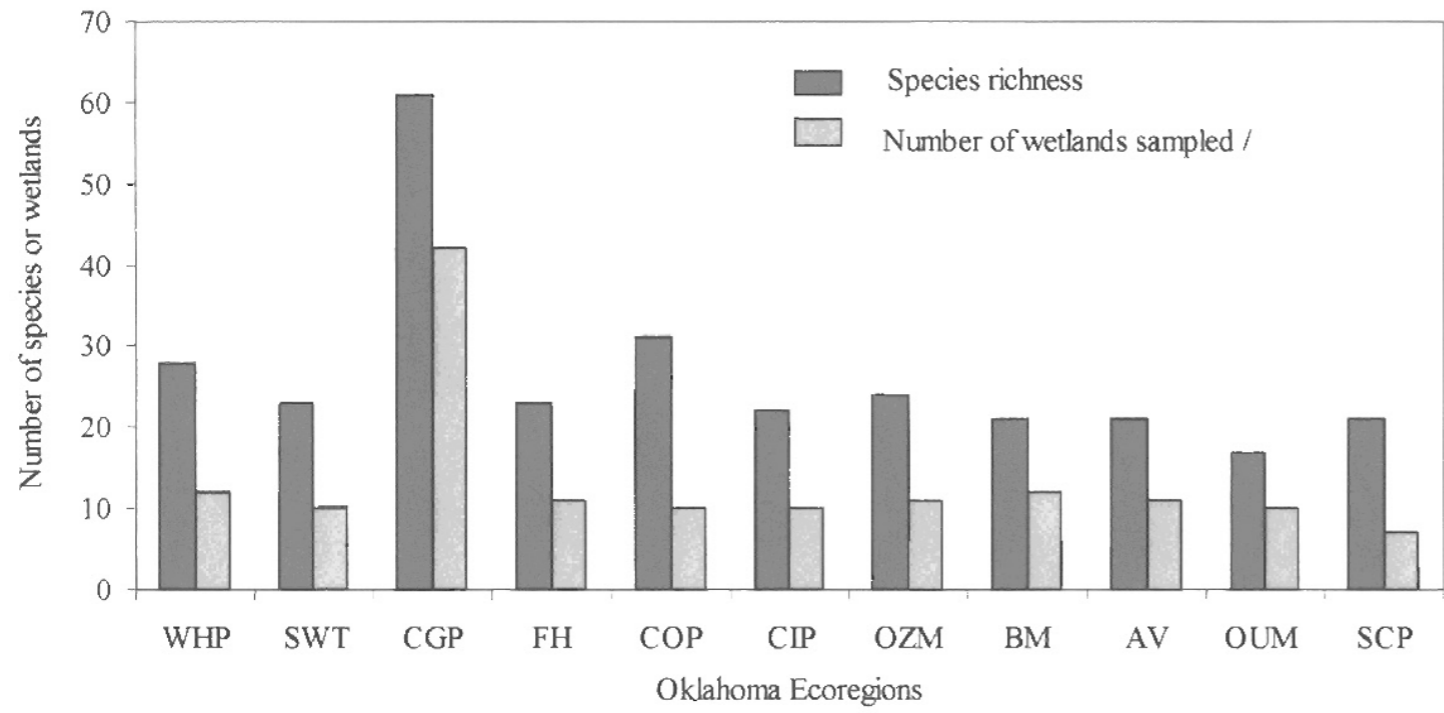


Figure 6.-Histogram depicting mean ecoregion crustacean species richness and the number of unique species (species only found once) in corresponding ecoregion

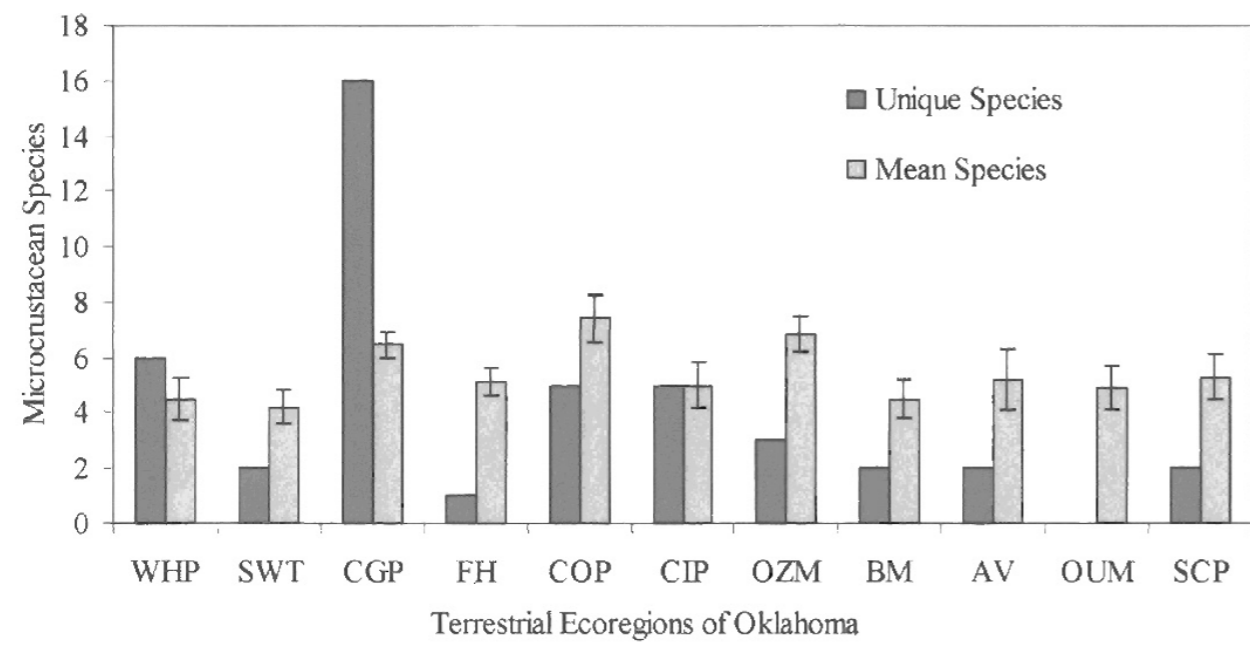


Figure 7.-The frequency of species occurrences among 146 sampled wetlands across the state. Over 34% were found in only one wetland with an additional 7% (7) found in only two wetlands. The most common species (*Acanthocyclops vernalis*) found in as many as 66% (97) of 146 wetlands and the next most prevalent taxa (*Cypridopsis* sp. and *Eucyclops agilis*) each occurring in 42% of the wetlands

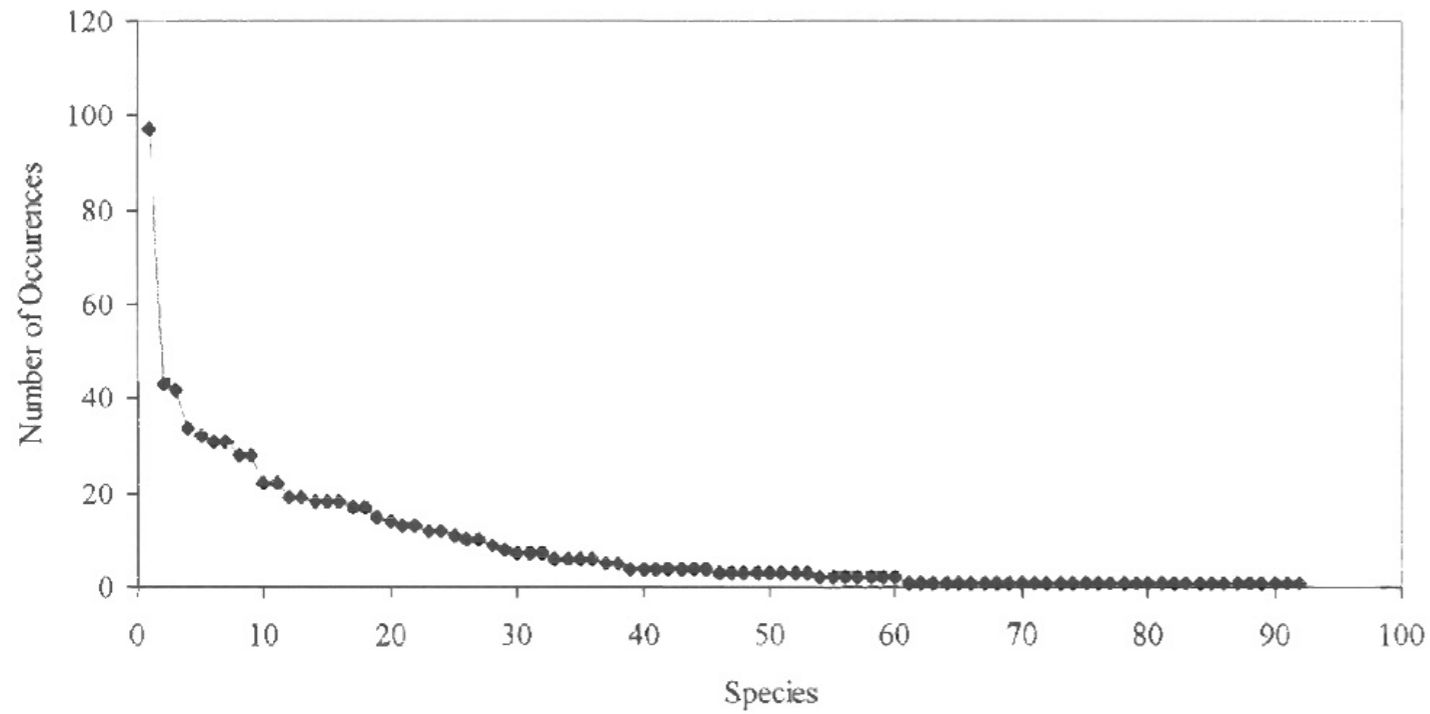


Figure 8.-Sample based Coleman rarefaction analysis derived from the Central Great Plains ecoregion representing the mean of all pooled individuals with 500 iterations. Ecoregions located below the curve have lower than anticipated species richness. The curve was computed using *EstimateS*, error bars represent the standard deviation

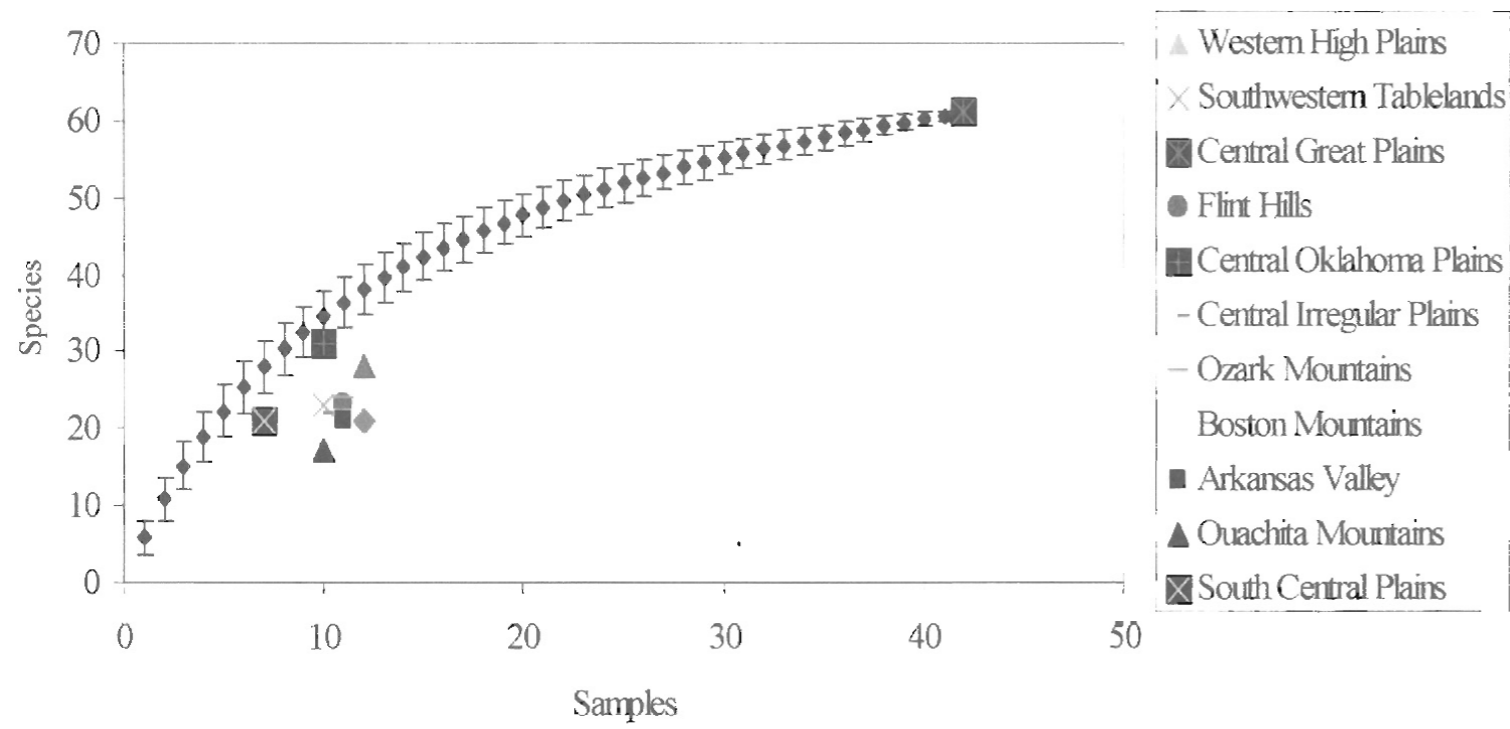


Figure 9.-Sample based species accumulation curve of non-permuted data from each newly acquired wetland in the survey. Each diamond represents a newly encountered species.

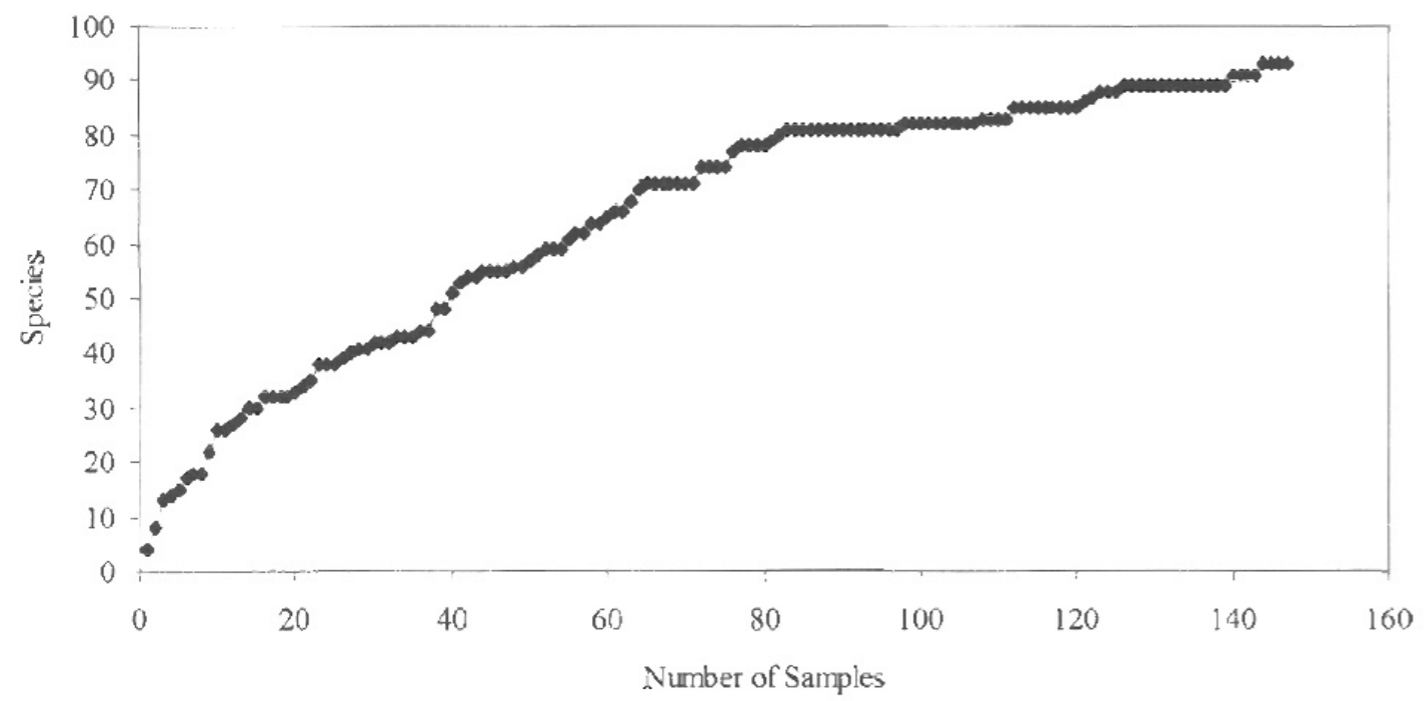


Figure 10.-Sample based species accumulation curve (randomized with 1000 iterations) for each newly acquired species in the survey. Each diamond represents a newly encountered species

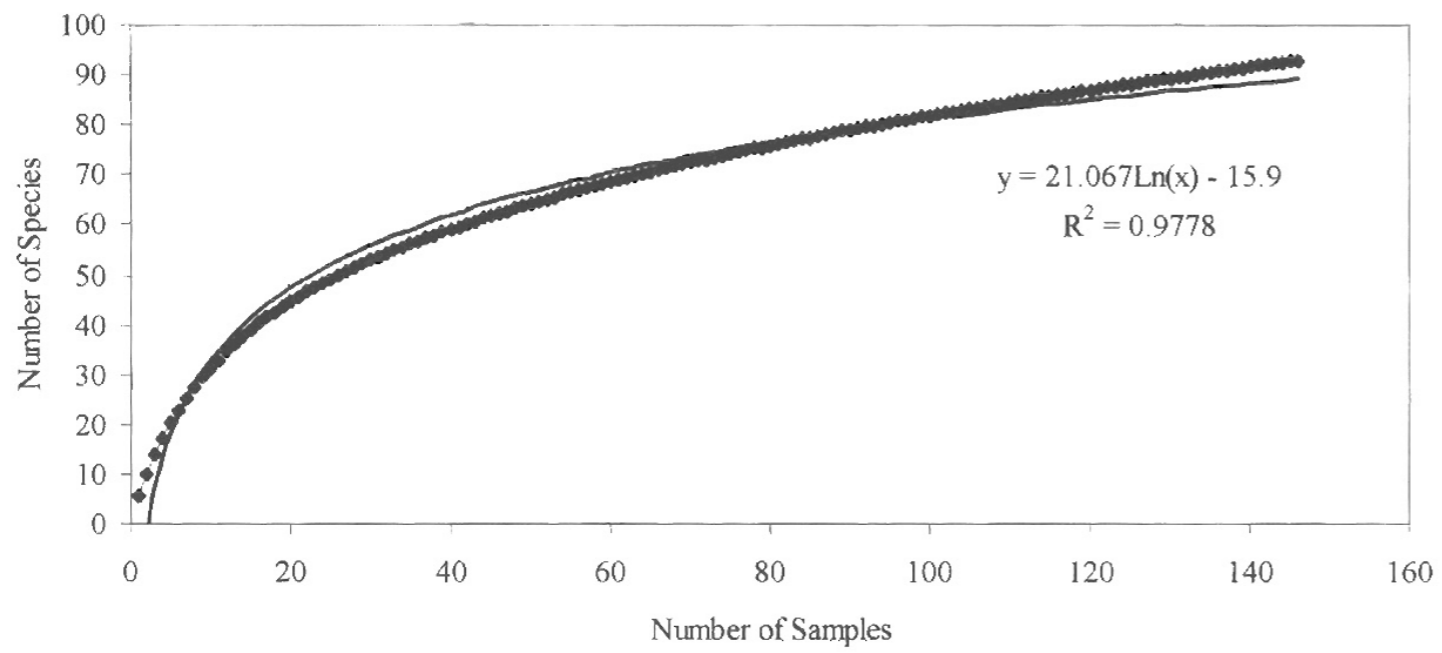


Figure 11.-ANOSIM cluster analysis using the Bray-Curtis index of similarity for invertebrate species assemblage in each wetland. 100 = maximum similarity, and 0 = no similarity between clusters. Although significant, the clustering of wetlands do not correspond to ecoregions ($p < 0.001$; 10,000 iterations). Wetlands names are transcribed to ecoregion names



Figure 12.-Summary dendrogram using Bray-Curtis similarities for wetland invertebrate communities among Oklahoma ecoregions. Species were pooled according ecoregion (*a priori*) to derive this dendrogram. Brackets represent clustering of similar ecoregions (e.g., plains, mountainous, and northern ecoregions).

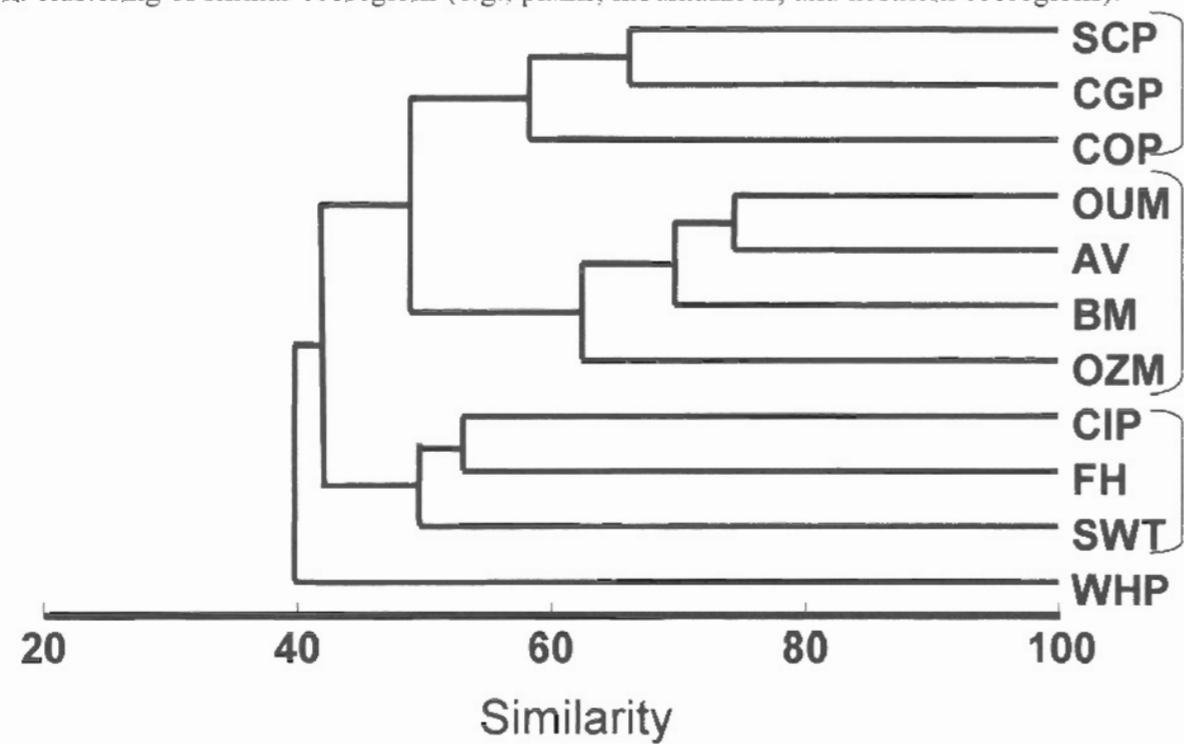
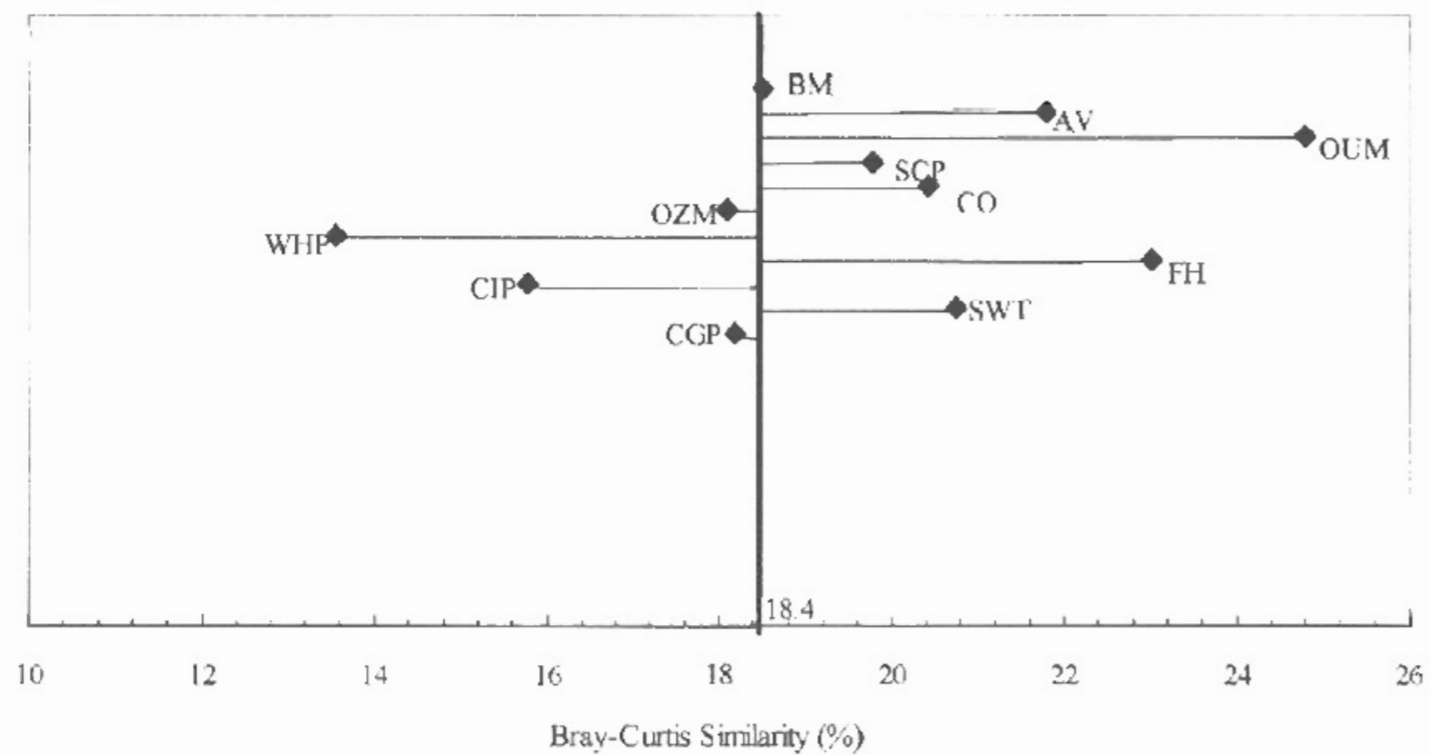


Figure 13 -Mean Similarity analysis using presence and absence data for Oklahoma Ecoregion classification on invertebrate fauna for 146 ephemeral wetlands. Analysis significant at $\alpha = 0.001$ level. Each diamond represents an ecoregion. The vertical solid line represents the overall mean between ecoregion similarity (18.36), and each branch end is mean with-in class similarity (I_i) for that class



CHAPTER II

MICROCRUSTACEAN SPECIES RICHNESS IN
EPIHEMERAL WETLANDS: LANDSCAPE
INFLUENCES AND ISLAND
BIOGEOGRAPHY

Abstract.- Isolated ephemeral wetlands are ubiquitous and provide habitats for many unique invertebrates. By definition these habitats are highly fragmented in space and time and without connection across the landscape so that inhabitants exist in metacommunities. Although their distribution is global our knowledge of local and regional patterns of species distribution and richness is weak. Given the intimacy between the terrestrial landscape and these shallow (<1 m) habitats, I questioned if linear distances between wetlands within different terrestrial ecoregions can be used to predict community assemblage similarity of microcrustaceans. In the spring of 2001 and fall of 2002, 22 ephemeral wetlands were sampled within the Western High Plains and Southwestern Plains ecoregions of Oklahoma. In addition, 30 wetlands were sampled in Payne and Noble counties to assess species-area relationships by use of island biogeography models. I found weak, although significant ($p = 0.005$), correlations between geographic proximity and species assemblage similarity. This suggests that the distance between habitats is not a strong determinant of community assemblage. An analysis of the nested species-area relationships within two north central Oklahoma counties suggests that ephemeral wetlands act as islands. A z-value of 0.334 for the

wetlands in this confined region is similar to that of archipelagos. The results of my study support the hypothesis that dispersal by zooplankton is limited and stochastic and that ephemeral wetlands harbor unique species that disperse slowly to nearby habitats. Based on the common occurrences of relatively rare species, I offer suggestions for future research and conservation needs for ephemeral wetlands of Oklahoma.

Introduction

Species exist as metapopulations in fragmented habitats, with extirpation in some patches and regional persistence via dispersal into or from nearby patches (Nee and May 1992, Semlitsch and Bodie 1998). The combination of these metapopulations forms a metacommunity (Hanski 1997). The relationships among patchiness, competition, predation and limited dispersal may lead to high regional diversity (Levin and Paine 1974). In temporally patchy habitats, communities may be similar because interactions such as competition, parasitism, and predation are truncated, which promotes coexistent species and leads to taxonomically similar communities (Hutchinson 1967, Weatherby et al. 1998, Harrison and Bruna 1999, Wang et al. 2002).

Isolated wetlands in the terrestrial landscape are good models of fragmented habitats. Widespread across geographically distinct regions, ephemeral wetlands can be used as models to investigate spatial arrangements of community assemblages so that ecologists can better understand how communities and species are affected by fragmentation. Understanding the spatial arrangement or connectivity of wetland complexes may be an essential component for the development of conservation and prioritization strategies (Kirkman et al. 1999).

Once an abundant habitat, ephemeral wetlands are increasingly rare due to anthropogenic actions (Simovich 1998, Schwartz and Jenkins 2000, Jenkins et al. 2003). These small, isolated, habitats are technically termed "seasonally ponded isolated wetlands" (SPIW's; Kirkman et al. 1999). Though located on every continent, their contribution to biodiversity is often overlooked by the scientific community (Williams 1987, Kirkman et al. 1999). Because these habitats are shallow and intermittent, fishing, recreational and agricultural uses are limited (Schwartz and Jenkins 2000). These wetlands vary in form and size, and include playa lakes, vernal pools, buffalo wallows, Carolina bays, and prairie potholes. Ephemeral wetlands have recently been recognized as areas of particular concern for conservation (e.g., Jenkins et al. 2003); as their destruction causes a reduction in connectedness between populations of vertebrate species, particularly amphibians (Semlitsch and Bodie 1998). However, the effect of increased fragmentation on community composition of the numerically dominant invertebrate fauna is unknown.

The invertebrate fauna of ephemeral wetlands exhibit high endemism (King et al. 1996) with a mixture of opportunistic and resident species. Evolutionarily, the physical nature of ephemeral pools encourages speciation (King et al. 1996, Belk and Cole 1974). Processes such as periodic flooding and drying, in conjunction with variable physico-chemical conditions are the stimuli for adaptation to intermittent ecosystems. These species invariably show unique characteristics of either physiology or life history, which allow them to be successful in temporary waters (Williams 1987, Belk and Cole 1974). Rates of speciation and local extinction may be relatively high for many taxa, a reflection

of the fragmented nature of the habitat and the low rates of dispersal resulting from geographic isolation of populations (Holland and Jain 1981).

Regional patterns of chemical, biological and physical variables that shape biological communities have been recognized by geographers and ecologists for many years (Herbertson 1905, Clements 1916) and recently led to the conceptualization of ecoregions as contiguous landforms with similar, geology, soils and climate that explains biological variation (Omernik 1987, 1995). The recognition of spatial patterns of biotic and abiotic variables that affect communities is an important facet of recent ecological studies (Borcard et al. 1992, Spencer et al. 2002). The association between community processes and landscape variation has only recently been assessed (King et al. 1996, Moorhead et al. 1998, Feminella 2000, Frisch 2002). The composition of communities is most likely the result of environmental and biotic factors (Borcard et al. 1992, Krebs 1994), which include, species interactions such as competition, predation, and mutualism. Mechanistic controls, such as dispersal events and patch occurrences have yet to be understood. In addition, the sequence in which species invade habitats (i.e., assembly rules) are known to be important determinants of community assemblages (Conner and Simberloff 1979, Drake 1991, Stone et al. 1996).

The relationship between species richness, time and space is among the most studied in ecology (Ebert and Balko 1987, Palmer and White 1994) and was first synthesized in the theory of island biogeography (MacArthur and Wilson 1963, 1967). Knowledge of how and why species richness varies aids in understanding biological processes that account for species diversity (Palmer and White 1994). Central to the theory of island biogeography is the species area relationship (SPAR; after Rosenzweig

1995), which is used to understand and characterize species richness on islands or other isolated habitats (MacArthur and Wilson 1963, 1967). The theory states that island area and distance from source populations determine species richness through their effects on habitat diversity available for exploitation, which results in predictable extinction and immigration rates (MacArthur and Wilson 1967). The efficacy of the theory is such that it has been used to predict wetland species richness based on habitat area (Ebert and Balko 1987). In addition, the use of mainland landscapes (i.e., fragmented terrestrial regions) to understand species diversity for conservation reserves with the use of SPAR is gaining acceptance (Leitner and Rosenzweig 1997, Lomolino and Weiser 2001). Species area relationships can be used to assess species richness and composition, knowledge of which are important if we are to understand the influences of habitat fragmentation or destruction of wetlands on microcrustaceans.

Oklahoma's heterogeneous landscape provides an ideal opportunity to assess ecoregions to explain the microcrustacean community assemblage and to assess the role of physico-chemical parameters in determining the regional wetland biota. A survey of microcrustaceans in ephemeral wetlands among terrestrial ecoregions represents an important step for comprehension of the distributions of invertebrate assemblages and communities in naturally patchy habitat and broadens knowledge of species distributions that may be instrumental for conservation implementation.

In this paper I address the following questions related to the biodiversity of ephemeral wetlands of Oklahoma.

1. Can patterns of community assemblage in ephemeral wetlands be attributed to measured environmental factors?

2. What are the patterns of species co-occurrence of ephemeral wetland microcrustacean species in Oklahoma?
3. What is the distance-similarity relationship for the Oklahoma wetland fauna?
4. To what extent do ephemeral wetlands have characteristics similar to those determined for islands by use of a nested species area analysis?

Methods

Methods of sampling, sample processing, curation and species identifications for this research project are found in Chapter I.

Data Analyses

Ordination of physico-chemical parameters

Multivariate analysis based on the ordination method, Canonical Correspondence Analysis (CCA) was conducted with CANOCO 4.0 (ter Braak, and Šmilauer 1997). (ter Braak, and Šmilauer 1997). Due to the high frequency of rare species in the data set, I used the down-weighting for rare species option to minimize their affect on the results (Jongman et al. 1995). CCA is a direct gradient analysis technique that ordines species assemblages based on measured environmental variables (Palmer 1993). To assess the strength of relationships between species assemblages and physico-chemical variables (see Chapter I for methods of collection), I used a Monte Carlo permutation procedure in CCA (ter Braak and Šmilauer 1997). Separation of variables such as conductivity, % cover, and pH can determine whether one set of variables explains variation in species composition not explained by other variables.

Species Co-occurrence

I employed the species co-occurrence model in EcoSim V. 7.0 to test whether wetland microcrustacean species are distributed in a non-random pattern (Gotelli and Entsminger 2001). If species co-occur in the same site then their distribution will be described as “non-random” in the landscape. EcoSim’s C-score setting for the co-occurrence index measures the degree to which all species co-occur in a community. The C-score is calculated by counting the number of distinct species arrangements from the matrix columns (Gotelli and McCabe 2002). A C-score value significantly larger than chance if co-occurring species are present or if the community is competitively structured (Gotelli and Entsminger 2001). In EcoSim, I also used the SIM2 algorithm that randomizes the occurrence of each species among sites to model passive colonizers (i.e., zooplankton) (Gotelli 2000, Gotelli and Entsminger 2001).

Distance versus faunal similarity

To determine the degree to which microcrustaceans disperse to nearby wetlands in an ecoregion, I compared the Bray-Curtis similarity metric to similarities of microcrustacean communities within and among terrestrial ecoregions. Bray-Curtis similarity ranges from 0 (no similarity) to 100 (identical assemblages) (Clarke and Warwick 2001).

Distances between each pairwise combination of wetlands within three ecoregions, Western High Plains, Southwestern Tablelands, and Flint Hills (WHP, SWT and FH respectively), were determined using computerized topography maps (Map Source®, GARMIN Corporation, Olathe, Kansas, USA). Inter-wetland distances from three of eleven ecoregions were used because of time constraints in the determination of

all pairwise distances. The WHP and SWT ecoregions were selected because their landscape characteristics are very similar, allowing me to assess the degree of faunal similarity in adjacent ecoregions. Wetlands from the Flint Hills ecoregion were used because it is the smallest Oklahoma ecoregion and it retains a landscape relatively undisturbed by anthropogenic activities. As the distances between habitats become greater it is expected that Bray-Curtis pairwise similarities will decrease with the result that the plot has a negative slope.

Nested species area analysis

To test the degree to which wetlands mimic patterns of island biogeography theory, I used the analysis of nested species area relationships (SPAR; Rosenzweig 1995) devised by Leitner and Rosenzweig (1997). For this analysis I used a set of data collected from wetlands in neighboring counties (Payne and Noble) in north central Oklahoma because I had sampled a high density of wetlands in this relatively small region (1432 km²). I cut properly scaled acetate squares to the mean area of these two counties (716 km²) and termed this the province. I placed the province on a proportionally scaled map of the two counties that incorporated the location of all 30 wetlands within the provinces' boundaries. I then scaled the province down sequentially in steps from 1/2 to 1/128 of the original size of the province, which yielded seven "sampling windows" (after Leitner and Rosenzweig 1997, Collins et al. 2002). With these seven windows I randomly orientated the sampling window 20 centimeters above the province and released it onto the map; species richness was then calculated among all the habitats within the boundaries of each window. I repeated this procedure for each window ten times for a total of 70 trials (10 samples per window).

The relationship between species (S) and area (A) is expressed as the power function $S = cA^z$. To linearize this relationship, I used the log-log model: $\log S = \log b_0 + b_1 (\log (A))$, where b_0 and b_1 (known as C and z -values, respectively) are constants; specifically b_0 is the y -intercept of the line and b_1 is the slope of the line. The z -value represents the slope of the relationship between species and area (e.g., $\log S$ and $\log A$ respectively; Brown and Lomolino 1998) and is often used for comparisons of island systems

Results

Ordination

In the biplot from CCA (Figure 1) the arrows represent measured environmental variables and their length indicates the relative strength (i.e., longer arrows are stronger gradients, (Jongman et al. 1995). Points orthogonal to the arrow indicate species that correlate with that particular variable. The closer a species is to the origin of the arrow the lower the correlation between that species and that variable (Rundle and Ramsey, 1997). Test of significance with the Monte Carlo permutation (999 iterations) resulted in $F = 4.025$ and $p = 0.010$. Eigenvalues for the first axis are 0.198 and 0.177 and the cumulative percent variance explained by these two axes was 59.7 %.

Axis 1 was most strongly associated with altitude, canopy cover, and temperature whereas axis 2 correlated with temperature and conductivity. In essence, axis 1 associated with wetland location and the terrestrial environment, and axis 2 associated with chemical parameters.

Co-occurrence

Evidence of microcrustacean co-occurrences within most ecoregions was not significant with the exception of the Flint Hills ($p > 0.015$, Table 1). With an overall mean distance of 7.8 km between wetlands and a mean Bray-Curtis similarity of 41.13%, there was no correlation between these variables.

Among all 92 species found in this survey, only two species (*Diaptomus siciloides* and *Diaptomus clavipes*) co-occurred as often as 25% (12) of the 50 times one or the other was found.

Distance vs. Community Similarity

A plot of the Bray-Curtis similarity against geographic distances among wetlands in the Western High Plains, Southwestern Tablelands and Flint Hills ecoregions resulted in significant negative correlations. Although statistically significant, the predictive values of these regressions were low, an indication that little of the variance in similarity is explained by the distance between habitats (Table 2). Of the 66 comparisons 29 had similarity values of zero and a mean distance of 93.82-km between all pairwise wetlands in the Western High Plains (Figure 2). For the 45 comparisons in the Southwestern Tablelands five had similarity values of zero and a mean distance of 167-km between all pairwise wetlands (Figure 3).

The regression for distance versus similarity in the Flint Hills ecoregion was significant as well (Table 2) but a poor predictor of community similarity (Figure 4). This was the case even though the mean distance between wetlands was only 7.8 km with a mean Bray-Curtis of 41.13%.

Species area relationships

The nested species-area analysis for isolated wetlands in central Oklahoma yielded a z-value of 0.333, within the range detected from studies of true islands (Figure 5, MacArthur and Wilson 1967). The mean distance between wetlands was 18 km and the mean Bray-Curtis similarity was only 20 %. Species richness was significantly correlated ($p < 0.02$) with the area of the 11 Oklahoma ecoregions (Table 3, Figure 6).

Discussion

The large geographic extent of the study necessitated compromises in the design of the sampling scheme. As large-scale geographic surveys of microcrustaceans in the Great Plains are non-existent, the decision was made to cover a greater area with less intensity rather than a smaller area with greater intensity. It is likely that the data set would have been more complete for each ecoregion by repeated seasonal and annual sampling. However, this extensive survey provides an extensive portrayal of the ephemeral wetlands fauna in Oklahoma. In addition, the large sample size provides for confidence in these conclusions.

Wetlands are crucial habitats, islands in the landscape that hold unique species assemblages. This study determined that microcrustacean assemblages in ephemeral wetlands have a pattern of diversity that is not attributable to terrestrial ecoregions. Overall results of community dissimilarity at different landscape scales support the conclusion that ubiquitous distributions are non-existent among these taxa. The near absence of co-occurrence among species within- and between-ecoregions supports the notion that species neither readily disperse nor establish ubiquitous distributions, a

conclusion that contradicts inferences based on manipulated mesocosms (Lukazewski et al. 1999, Shurin 2000).

Ordination

Correlations between species occurrence and environmental variable derived by CCA indicate that these environmental factors are poor predictors of the distribution of species. A pitfall of CCA is the distinction of species that occupy extremes of environmental gradients and the single (rare) occurrences of those species. Of all collected species, 33% occurred only once and 7% occurred twice so that the reliability of the association of these species with particular gradients may be poor. The three strongest gradients (altitude, temperature and conductivity) that explain species composition suggest that abiotic factors prevail. However, most of the taxa do not correlate with these results. In summary, the results of the CCA warrant further investigation of conditions used to characterize wetlands.

Co-occurrence

Studies that assess dispersal of microcrustaceans conclude that dispersal is very slow (Boileau and Hebert 1988, Drake 1991, Jenkins and Buikema 1998, Cáceres and Soluk 2002,). Species richness peaks in newly filled artificial wetlands after 9 to 24 months (Jenkins and Buikema 1998, Cáceres and Soluk 2002). The sequence in which colonizing species is important as early immigrants prevent later arriving species from establishing successful populations. There is no clear understanding of which species are better at dispersing so priority rules have not been established for isolated ephemeral wetlands.

Although investigators have found that abiotic and biotic factors simultaneously work together to regulate zooplankton species in a given body of water, it has been suggested that abiotic conditions (e.g., those characteristic of ecoregions) may have a greater impact on species richness than biotic conditions (Lukazewski et al. 1999). Experiments by Jenkins and Underwood (1998) and Cáceres and Soluk (2002) addressed aerial dispersal and found relatively few zooplankton disperse to isolated mesocosm wetlands in this fashion. However, in the Flint Hills ecoregion (the smallest of all Oklahoma ecoregions, Table 3), with the shortest inter-pool distances and highest mean Bray-Curtis value, microcrustacean species co-occurred more frequently than in other ecoregions.

The fact that other ecoregions did not follow this pattern is not surprising; the lack of dispersal and coexisting species could be an artifact of habitat fragmentation and lack of a natural vector for cyst/egg dispersal. The Flint Hills ecoregion retains one of the last contiguous tracts of the tall grass prairie that once dominated the Great Plains of North America (Hoagland 2000). In this preserved remnant of contiguous prairie many ephemeral wetlands (both anthropogenic and natural) still exist. Reintroduced bison (*Bos bison*) drink and wallow in these wetlands. As the sediment of these wetlands contains eggs and cysts of microcrustaceans and attaches to the bison, dispersal may be initiated much like the ungulate mediated seed dispersal of grasses (Connell and Slatyer 1977, Collins and Uno 1985).

Geographic distance versus wetland similarity

I found that invertebrate assemblages in ephemeral wetlands of Oklahoma are weakly associated with geographic distance between them. In attempts to explain

variation between zooplankton community composition in the WHP and SWT ecoregions in the Oklahoma panhandle, I computed all the pairwise inter-wetland distances and Bray-Curtis indices. This resulted in 231 comparisons and a significant negative regression that again was a weak function of distance (Table 2). Other studies of microcrustacean assemblage similarity and spatial pattern (with both greater and smaller distances) also found weak relationships (Mahoney et al. 1990, King et al. 1996, Spencer et al. 2002) despite similarity of wetland types. The absence of strong spatial pattern and lack of similar community composition can be attributed to factors such as wetland disturbance, biotic interactions and slow stochastic dispersal events.

SPAR Analysis

Isolated wetlands function as land-locked islands (Figuerola and Green 2002). The tendency for species richness to increase with island area and decrease with isolation has been observed for decades (Brown and Lomolino 1998). Island biogeography theory is based on the idea that extinction and immigration balance the equilibrium of species richness. The frequency and duration of ephemeral wetlands in time is analogous to distance from a source in space (Ebert and Balko 1987). Temporary wetlands, unlike oceanic islands are also islands in time, which periodically disappear and reappear. They are recolonized primarily from the *in situ* 'seed bank' rather than by dispersal from other habitats (King et al. 1996). Species which persist as resting eggs or cysts stages must be able to remain viable through time until a habitat is again inhabitable (Ebert and Balko 1987). Furthermore, ephemeral wetlands, by definition, are periodically disturbed, and therefore are not expected to reach equilibrium due to the dynamic nature of ephemerality (King et al. 1996).

Leitner and Rosenzweig (1997) argue that most nested species area relationships from successively smaller subsets of a continent lead to slopes (z-values) ≈ 0.2 . Oceanic islands typically have z-values ranging from 0.25 to 0.55, and large contiguous landmasses have z-values ranging from 0.1 to 0.2 (Rosenzweig 2001). The z-value of 0.334 I derived for ephemeral wetlands in central Oklahoma is similar to that of Ebert and Balko's (1987) study on microcrustaceans and ephemeral wetlands ($z = 0.355$). These similar results, from two independent studies with different methods of analysis, support the conclusion that ephemeral wetlands act as real islands. Since small isolated islands typically have steeper species-area slopes than larger contiguous landmasses, their higher z-values reflect this difference (Brown and Lomolino 1998). Wetlands in this study have z-values greater than other provincial studies, perhaps as a result of the diversity of wetland types in the Oklahoma region (Great Plains), which directly influence microcrustacean species richness. Although habitat diversity may be the most straightforward explanation for these patterns (Meffe and Carroll 1997), it is likely that the species-area relationship is multicausal, encompassing biotic, abiotic and stochastic factors.

Summary

A critical factor for conservation of biological diversity is biogeographical data on the distribution of focal habitats (Brown and Lomolino 1998). Island biogeography theory has expanded the focus of scientist and conservationist to consider the impact of habitat area and isolation on biodiversity (Meffe and Corroll 1997). This study represents the first large scale collection and analysis of ephemeral wetland microcrustacean fauna

in Oklahoma and the Great Plains. Managers can use the data and analysis presented here to develop conservation plans to maximize the number of species in an area.

Microcrustaceans are dependent on water to develop and reproduce, and do not actively disperse to adjacent wetlands. Passive dispersal capacity is a key trait, which explains patterns of distribution and community composition of non-mobile organisms (Jenkins and Buikema 1998). Although species dispersal is slow, it is crucial to regional diversity as highlighted by the low similarity values among wetlands. The high frequency of rare species results in low co-occurrences among taxa in Oklahoma ephemeral wetlands, and is likely a function of stochastic colonization processes.

The documentation of weak spatial patterns is as significant as documentation of strong spatial pattern (Spencer et al. 2002). In natural communities it is important to establish extent and cause of spatial pattern for two reasons. First, theories of community structure unable to explain spatial pattern fail to portray ecosystem components. Secondly, the existence of spatial pattern can be problematic to hypotheses that address observational and experimental data (Borcard et al. 1992, Spencer et al. 2002). Furthermore, the assessment of the species area relationship and its causes is essential (Meffe and Corroll 1997) particularly for the establishment of baseline knowledge of species diversity among highly endangered habitats such as ephemeral wetlands. The relationship between species richness and area has major practical implications for wetland management, such as location, design and reserve establishment to maintain invertebrate biodiversity. This extensive survey of ephemeral wetland microcrustaceans highlights the importance of the individual wetland to biodiversity, and the importance of habitat diversity for conservation.

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Table 1.- Results of crustacean co-occurrence within ecoregions using ECOSIM. Ten of eleven ecoregions had non-significant values. The exception was the Flint Hills ecoregion ($p > 0.015$). Asterisk indicates the ecoregion with significant patterns of co-occurrence ($\alpha = 0.05$).

Ecoregion	Observed index	Mean of sim. indic	Var of sim. Indic.	P-value (obs. \geq expec.)
WHP	2.00794	2.08713	0.00728	0.8362
SWT	1.5415	1.56436	0.00725	0.6502
CGP	11.88525	12.20359	0.02631	0.9668
*FH	2.12253	1.87406	0.01817	* 0.0158
COP	2.65524	2.63287	0.00943	0.4634
CIP	2.09091	2.38717	0.01851	0.9728
OZM	3.96377	4.01819	0.03367	0.6622
BM	3.58571	3.6041	0.03073	0.5878
AV	2.3	3.14596	0.02885	1
OUM	2.41176	2.93085	0.04265	0.982
SCP	1.53333	1.51861	0.00865	0.499
STATE	47.85297	48.82083	0.14863	0.9922

Table 2.- Results of correlations between inter-wetland distances and Bray-Curtis index of community similarity from three selected ecoregions (Western High Plains and Southwestern Tablelands and Flint Hills). The p-values, equations from trend line and R² values from regression analysis indicate significant correlations between these variables.

Ecoregion	Trendline equation	R²	P-Value	F
WHP	$y = -0.0699x + 21.748$	0.0635	0.041	0.342
SWT	$y = -0.0509x + 34.336$	0.1282	0.015	6.324
FH	$y = -1.8057x + 55.234$	0.127	0.007	7.707
WHP and SWT	$y = -0.0339x + 23.736$	0.0331	0.005	7.842
Province	$y = -0.1359x + 22.525$	0.0077	0.066	3.374

Table 3.- Approximate areas (km²) of Oklahoma terrestrial ecoregions (according to Omernik 1995) and the number of wetlands species sampled in each corresponding ecoregion.

Ecoregion	Ecoregion area (km²)	Species richness
Western High Plains	7825.62	28
Southwestern Tablelands	10306.73	23
Central Great Plains	42898.46	61
Flint Hills	1530	23
Central Oklahoma Plains	30652.12	31
Central Irregular Plains	8950.24	22
Ozark Mountains	3455.38	24
Boston Mountains	2103	21
Arkansas Valley	8854.51	21
Ouachita Mountains	7424.56	17
South Central Plains	4673.67	21

Figure 1.- Canonical correspondence analysis (CCA) biplot for the first two axes. Arrows (vectors) represent measured physio-chemical environmental variables; Species are designated by a solid circle. Length of arrow indicates relative strength of the gradient. Test of significance with the Monte Carlo permutation (999 iterations) resulted in $F = 4.025$ and $p = 0.010$. Eigenvalues for the first axis are 0.198 and 0.177 and the cumulative percent variance explained by these two axes was 59.1 %.

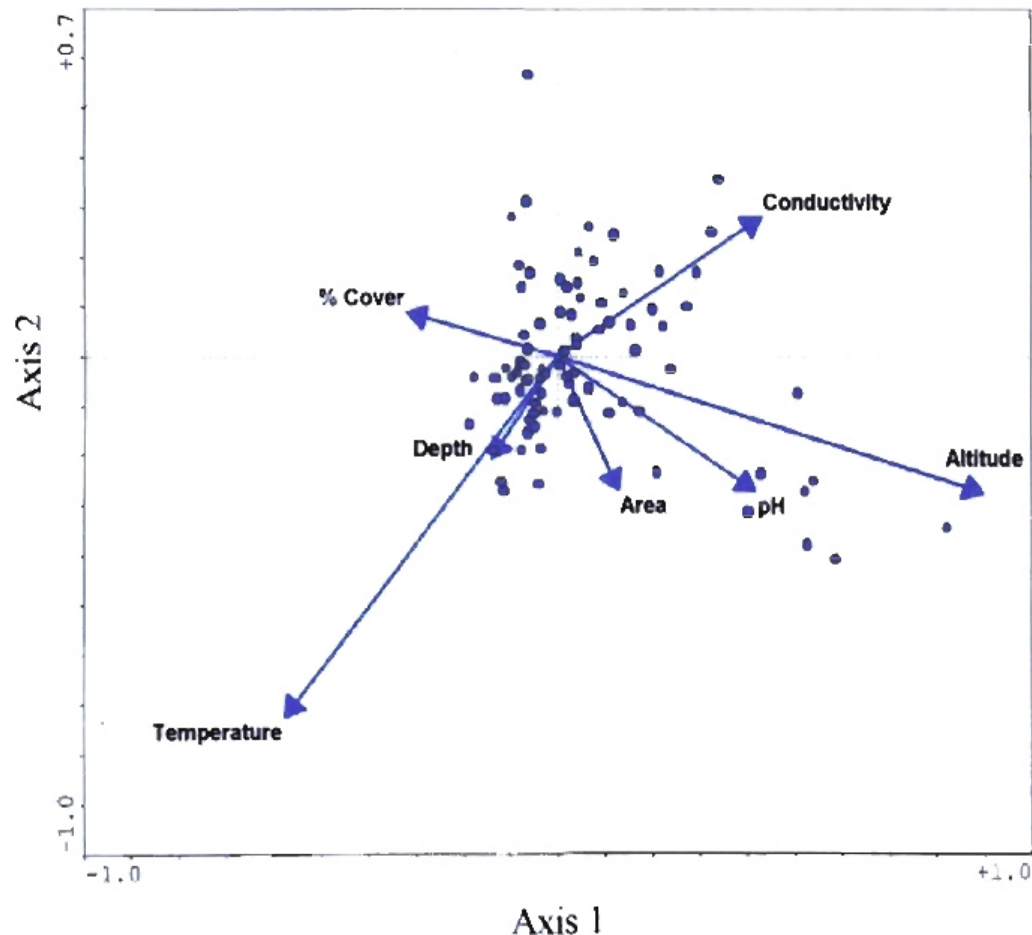


Figure 2.-Relationship between community similarity and distance between wetlands (n = 66 comparisons) in the Western High Plains ecoregion. The mean Bray Curtis similarity and mean distance were 15.19% and 93.82 km respectively.

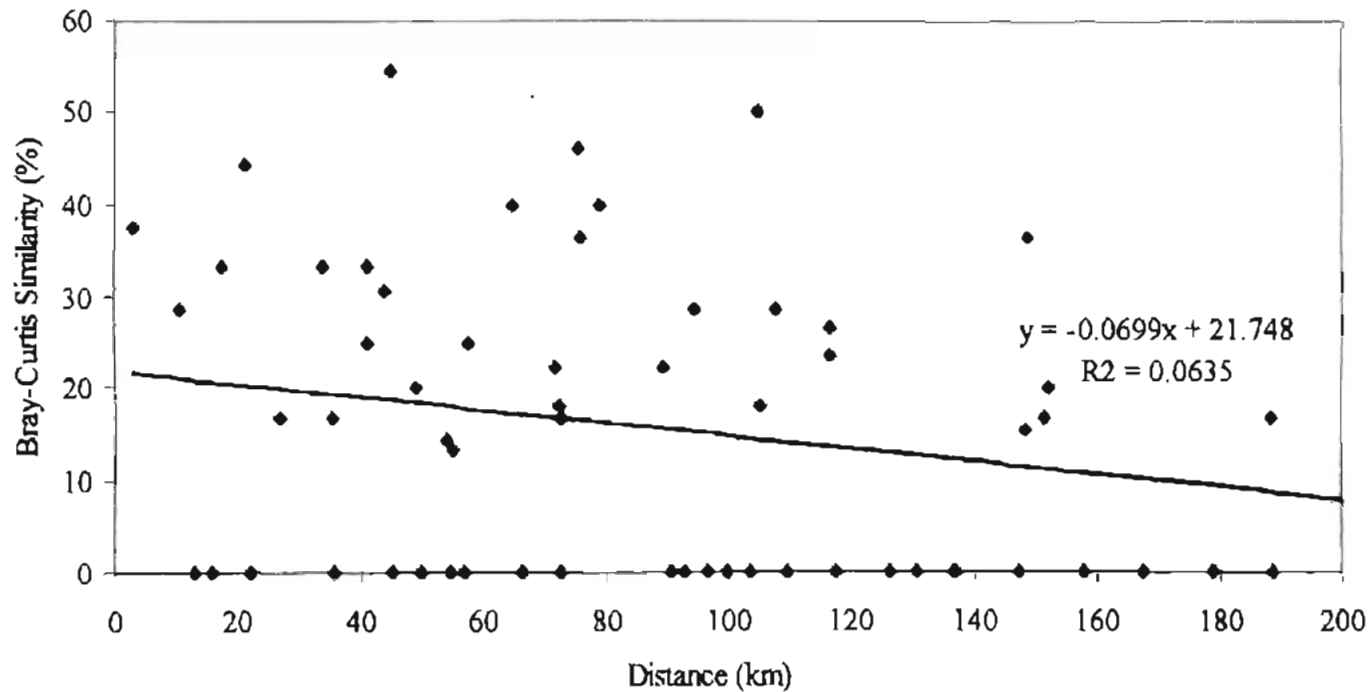


Figure 3.- Relationship between community similarity and distance between wetlands (n = 45 comparisons) in the Southwestern Tablelands ecoregion. The mean Bray Curtis similarity and mean distance were 25.84% and 167 km respectively.

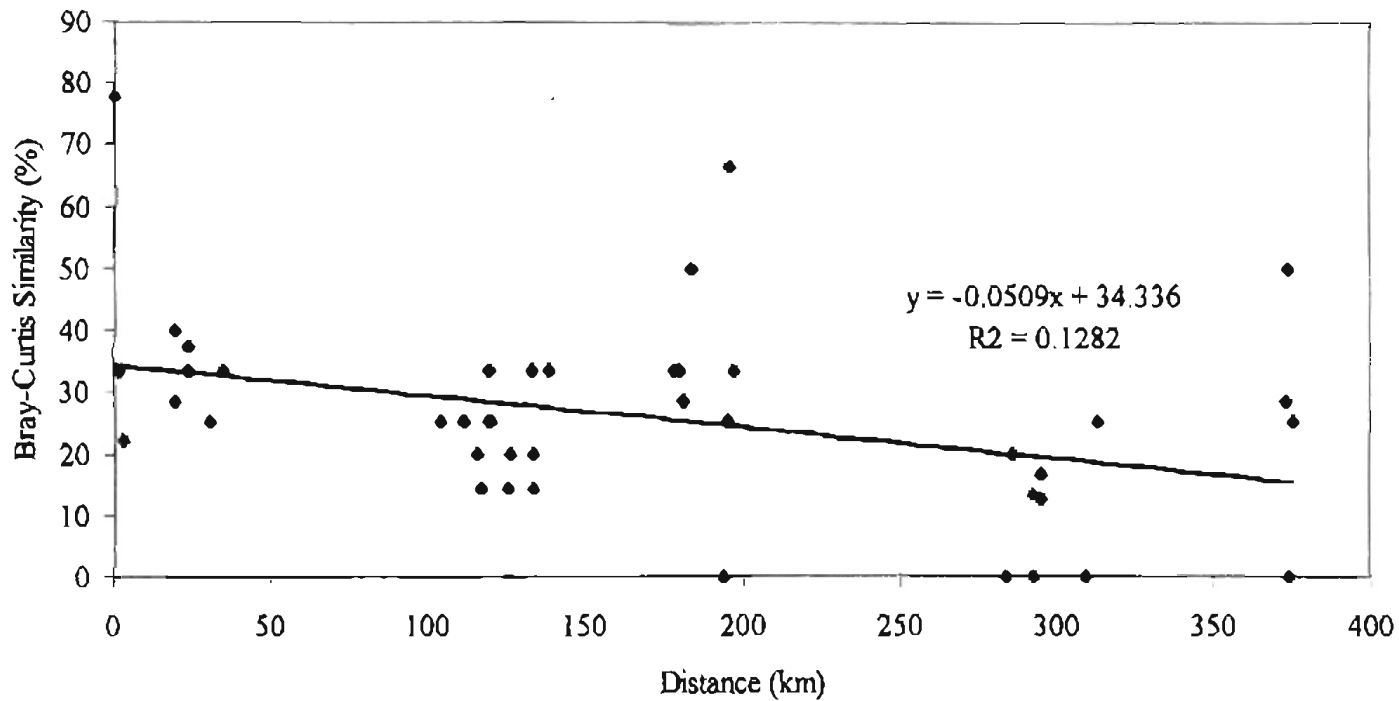


Figure 4.- Relationship between community similarity and distance between wetlands (n = 55 comparisons) in the Flint Hills ecoregion. The mean Bray Curtis similarity and mean distance were 41.13% and 7.8 km respectively.

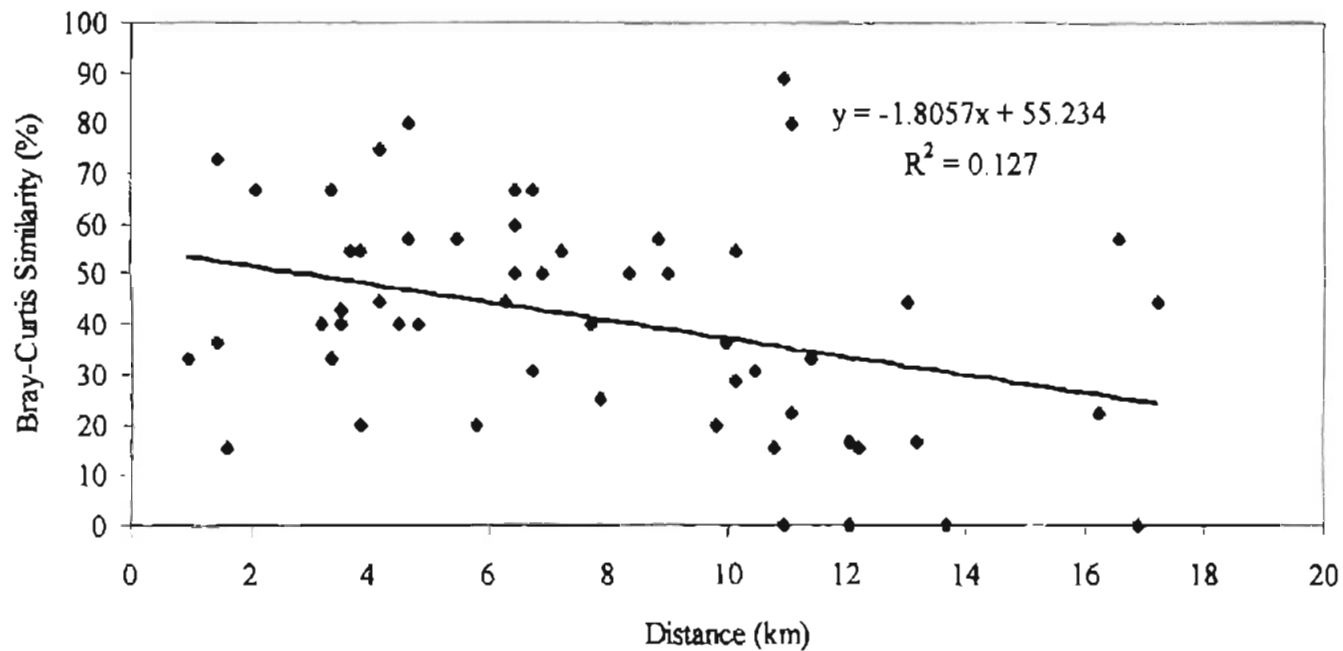


Figure 5.- Nested species-area relationship (SPAR) between microcrustaceans species richness and ephemeral wetlands in the province composed of Payne and Noble Counties, OK. The nested species-area relationship resulted in a z-value 0.333, in range of what other researchers characterize as true islands.

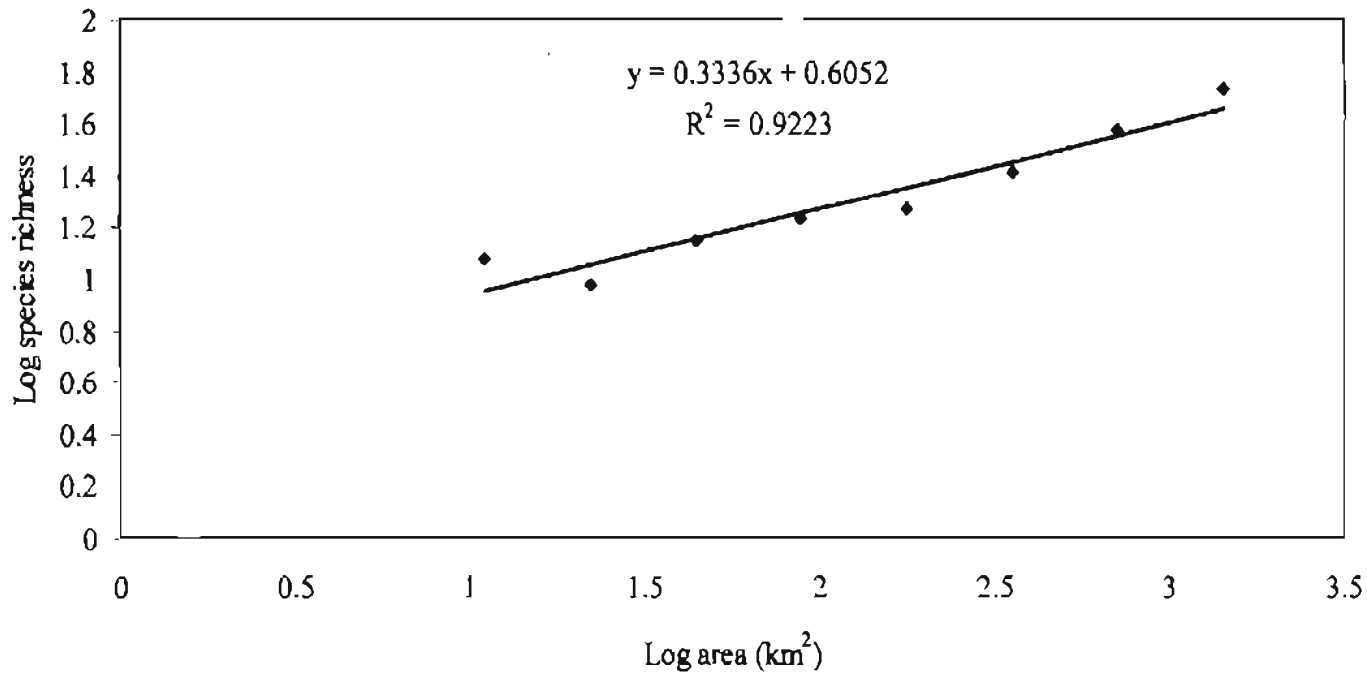
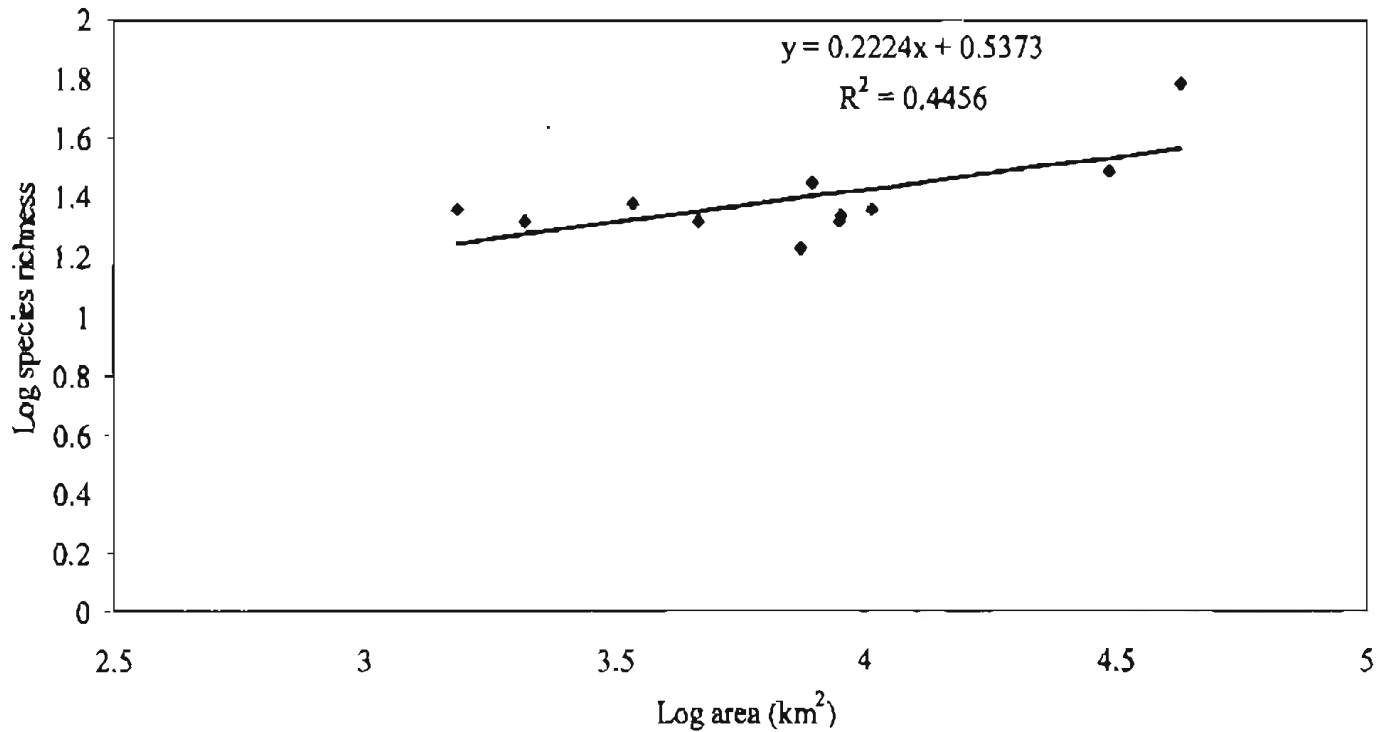


Figure 6.- Correlation between area of Oklahoma ecoregions and species richness of wetland microcrustaceans. The species area relationship was significantly correlated ($p < 0.02$) using ecoregion area versus species richness.
 $y = 0.2224x + 0.5373$ $R^2 = 0.4456$



APPENDIX A

Site number	Wetland name	Latitude	Longitude	County
1	Stillwater 1	N36 01.544	W97 05.202	Payne
2	John Deere	N36 04.191	W97 04.290	Payne
3	EW-53	N36 14.968	W97 06.019	Noble
4	Stephan	N36 13.979	W97 11.401	Noble
5	Fir Road	N36 17.609	W97 29.359	Garfield
6	Cottonwood	N36 16.838	W97 29.205	Garfield
7	Peepers	N36 07.443	W99 07.044	Dewey
8	480	N36 19.240	W99 23.030	Woodward
9	E 510	N36 16.647	W99 46.904	Ellis
10	283 S	N36 03.718	W99 45.458	Ellis
11	283 N	N36 03.835	W99 45.460	Ellis
12	Nomad	N36 04.572	W99 32.310	Ellis
13	Flyby	N36 40.483	W97 53.662	Grant
14	Grouse	N36 40.856	W98 12.414	Alfalfa
15	Old Cedar	N36 40.999	W98 14.269	Alfalfa
16	NWR	N36 47.819	W98 10.924	Alfalfa
17	Sand Piper	N36 48.138	W98 15.128	Alfalfa
18	Road Grader	N36 54.227	W98 41.073	Woods
19	Outlook	N36 54.973	W98 42.169	Woods
20	HWY 10	N36 52.801	W95 30.224	Nowata
21	HWY 10-2	N36 53.258	W95 25.690	Nowata
22	Turkey	N36 46.727	W95 18.342	Craig
23	Rd 170	N36 46.151	W95 18.351	Craig
24	Rd 200	N36 44.158	W95 16.172	Craig
25	Rock	N36 43.699	W95 14.555	Craig
26	N 290	N36 38.927	W95 21.577	Craig
27	E 250	N36 39.338	W95 23.415	Craig
28	E 300	N36 35.853	W95 25.659	Craig
29	N 4240 Rd	N36 35.230	W95 28.298	Rogers
30	Metate	N36 50.745	W96 27.023	Osage
31	Burned	N36 47.640	W96 24.690	Osage
32	Bonita	N36 46.185	W96 23.335	Osage
33	Carcass	N36 48.068	W96 28.694	Osage
34	Sandstone	N36 48.789	W96 26.618	Osage
35	Bison	N36 48.417	W96 25.794	Osage
36	Soggy Bottom	N36 49.822	W96 29.571	Osage
37	Pewter	N36 50.518	W96 26.037	Osage
38	Ramp	N36 48.578	W96 33.869	Osage

39	Hawk	N36 54.074	W96 28.191	Osage
40	Bufo	N34 41.364	W98 43.936	Comanche
41	Rana	N34 41.546	W98 42.986	Comanche
42	Fort Sill	N34 41.139	W98 56.712	Kiowa
43	Wichita Mtn.	N34 41.381	W98 56.649	Kiowa
44	Holy City	N34 44.209	W98 35.220	Comanche
45	Black Jack	N34 41.564	W98 41.985	Comanche
46	Sheppard	N36 54.391	W100 42.049	Beaver
47	Coyote	N36 54.409	W100 49.339	Beaver
48	Yucca	N36 56.833	W101 11.891	Texas
49	Cabbage	N36 52.659	W101 22.218	Texas
50	Clines	N36 44.660	W101 57.756	Texas
51	Watkins	N36 39.206	W101 28.485	Texas
52	Ridge	N36 36.983	W100 51.966	Beaver
53	Shamrock	N36 34.362	W100 26.830	Beaver
54	Ellenburger	N36 29.389	W99 30.066	Woodward
55	Ripley Rd	N36 09.328	W96 54.477	Payne
56	Bethell	N36 11.902	W96 53.395	Payne
57	Red Dog	N36 12.162	W96 53.388	Payne
58	Moth	N36 13.055	W97 10.563	Noble
59	Chesmoore	N36 14.161	W97 08.719	Noble
60	Redland	N36 07.938	W97 10.586	Payne
61	Jesse	N36 26.233	W94 53.909	Delaware
62	Kenwood	N36 18.886	W94 59.326	Delaware
63	Sally	N36 15.831	W94 58.701	Delaware
64	Flint Creek	N36 11.451	W94 55.346	Delaware
65	Yates	N36 10.847	W94 55.572	Delaware
66	Liberty	N36 07.308	W94 56.809	Cherokee
67	Victoria	N36 07.535	W95 00.463	Cherokee
68	Maxine	N36 08.012	W95 00.172	Cherokee
69	Grappler	N36 11.809	W95 01.756	Mayes
70	Kristi	N36 11.809	W95 01.754	Mayes
71	Bryer	N36 15.807	W94 57.153	Delaware
72	Rumen	N36 04.342	W97 11.421	Payne
73	Perkins	N35 59.135	W97 02.496	Payne
74	Fire cracker	N34 47.517	W96 50.632	Pontotoc
75	Darter	N34 47.518	W96 50.588	Pontotoc
76	Stubble	N34 33.643	W96 38.175	Pontotoc
77	Aster	N34 24.949	W96 47.610	Johnston
78	Ranae	N34 15.727	W96 40.541	Johnston
79	Tonya	N34 15.732	W96 40.731	Johnston

80	Hugo	N34 04.765	W95 28.154	Choctaw
81	Bazes'	N34 10.291	W95 24.433	Pushmataha
82	Diego	N34 12.026	W95 19.885	Pushmataha
83	Honobia	N34 32.296	W94 56.301	Pushmataha
84	Clearcut	N34 12.289	W95 13.288	Pushmataha
85	Merida	N34 14.524	W95 12.909	Pushmataha
86	Trail	N34 14.184	W95 13.542	Pushmataha
87	Indiana	N34 15.687	W95 11.738	Pushmataha
88	Buzzard	N34 13.117	W95 13.698	Pushmataha
89	Gallo	N34 11.890	W95 22.314	Pushmataha
90	Steaple	N34 13.776	W95 33.295	Pushmataha
91	Tyson	N34 37.371	W95 14.104	Pushmataha
92	FLW	N34 39.979	W95 02.663	Pushmataha
93	Dumpy	N34 39.100	W94 58.969	Pushmataha
94	Robbers Cave	N34 59.962	W95 20.010	Latimer
95	Quinn	N34 59.728	W95 19.242	Latimer
96	Stigler	N35 23.996	W95 18.591	Muskogee
97	Sparrow	N35 24.362	W95 20.393	Muskogee
98	Grubber	N35 41.567	W95 11.930	Muskogee
99	Ron's	N35 42.337	W95 02.143	Cherokee
100	Miguel	N35 42.297	W95 02.043	Cherokee
101	Rancho	N35 42.566	W95 01.860	Cherokee
102	Gertrude	N35 34.327	W94 46.341	Sequoyah
103	Kubota	N35 34.332	W94 46.453	Sequoyah
104	Shana	N35 41.009	W94 50.804	Cherokee
105	Rosa'	N35 41.039	W94 50.893	Cherokee
106	Acacia	N35 41.424	W94 50.548	Cherokee
107	Bedrock	N35 41.817	W94 49.877	Cherokee
108	Argentina	N35 40.143	W94 49.343	Cherokee
109	Trail Ridge	N35 40.311	W94 49.599	Cherokee
110	Poteau	N35 07.111	W94 46.210	Le Flore
111	Phibrose	N35 06.831	W94 44.927	Le Flore
112	Massey	N35 06.730	W94 47.267	Le Flore
113	Trumpet	N35 07.456	W94 47.140	Le Flore
114	Milo	N35 07.759	W94 49.360	Le Flore
115	Treadway	N35 07.836	W94 51.878	Le Flore
116	Cottonmouth	N34 47.513	W94 52.941	Le Flore
117	Boone	N34 44.134	W94 47.617	Le Flore
118	Alto	N34 43.840	W94 45.895	Le Flore
119	La Huerta	N34 44.050	W94 46.552	Le Flore
120	5135	N36 06.950	W97 20.587	Payne

121	Cemetery	N36 04.348	W97 11.698	Payne
122	Lube	N36 04.205	W97 11.614	Payne
123	Bryan	N36 15.641	W97 16.474	Noble
124	Sherri	N36 15.507	W97 16.357	Noble
125	George	N36 16.600	W97 15.893	Noble
126	Chiva	N36 17.424	W97 14.880	Noble
127	Gangler	N36 18.168	W97 15.447	Noble
128	Bill	N36 18.289	W97 15.889	Noble
129	Sofa	N36 18.638	W97 15.432	Noble
130	Mary	N36 14.435	W97 11.338	Noble
131	Ralph	N36 13.861	W97 11.514	Noble
132	Bucky	N36 14.652	W97 08.840	Noble
133	Passow	N36 12.564	W97 00.534	Payne
134	Kyle	N36 13.046	W97 12.416	Noble
135	Leslie	N36 13.154	W97 13.102	Noble
136	Rodney	N36 18.158	W97 18.271	Noble
137	Hobo Joe	N36 16.506	W97 53.718	Garfield
138	Meadow Lark	N36 45.747	W96 23.119	Osage
139	Finale	N36 30.886	W100 41.117	Beaver
140	Gourd	N36 37.290	W102 33.189	Cimarron
141	Shack	N36 36.410	W100 18.453	Beaver
142	Poncho	N36 30.872	W100 17.153	Beaver
143	Bluestem	N36 35.277	W102 47.206	Cimarron
144	Piston	N36 43.130	W101 57.632	Texas
145	Limes. Mesa	N36 51.867	W102 53.766	Cimarron
146	Redtail	N36 50.304	W102 52.632	Cimarron

APPENDIX B

Western High Plains

Species	COYOTE	YUCCA	CABBAGE	CLINES	WATKINS	SHAMROCK	FINALE	GOURD	SHACK	PONCHO	BLUESTEM	PISTON
<i>Acanthocyclops vernalis</i>	1	1	1	1	1	0	0	0	0	1	0	0
<i>Alona barbulata</i>	0	1	0	0	0	0	0	0	0	0	0	0
<i>Alona rustica</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Candona</i>	0	0	0	1	0	0	0	0	0	0	0	0
<i>Cyclocypris</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Cyclops navus</i>	0	1	1	0	0	1	0	0	0	0	0	0
<i>Cypridopsis</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Cypris</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Daphnia exilis</i>	0	0	0	0	1	0	0	0	0	0	0	1
<i>Daphnia obtusa</i>	1	0	0	0	0	0	0	0	0	0	0	0
<i>Daphnia prolata</i>	0	0	0	1	0	0	0	0	0	0	1	1
<i>Diaphanosoma brachyurum</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Diaptomus clavipes</i>	0	0	0	1	1	0	1	0	1	0	0	1
<i>Diaptomus siciloides</i>	0	0	0	1	0	0	1	0	0	0	1	1
<i>Eocyzicus concavus</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Eubranchipus oregonus</i>	0	1	0	0	0	0	0	0	0	0	0	0
<i>Eucyclops agilis</i>	0	0	1	0	0	0	1	0	0	0	0	0
<i>Leptestheria compleximanus</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Leydigia acanthocercoides</i>	0	0	0	1	0	0	0	0	0	0	0	0
<i>Lynceus brevifrons</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Macrothrix hirsuticornis</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Microcyclops varicans rubellus</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Moina macrocopa</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Moina micrura</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Moina wierzejskii</i>	0	0	0	0	0	0	0	1	0	1	1	1
<i>Simocephalus serrulatus</i>	0	0	1	0	0	0	1	0	0	0	0	0
<i>Streptocephalus dorotheae</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Streptocephalus texanus</i>	0	0	0	0	0	0	0	1	0	0	1	0

Flint Hills

Species	METATE	BURNT	BONITA	CARCASS	SNDSTONE	BISON-1	SOGGYBOTTOM	PEWTER	RAMP	HAWK	MEADOWLARK
<i>Acanthocyclops vernalis</i>	1	1	1	1	1	1	1	1	0	1	1
<i>Attheyella illinoisensis</i>	1	1	0	1	0	1	0	0	0	1	1
<i>Camptocercus oklahomensis</i>	1	0	0	1	1	1	0	1	0	1	0
<i>Canthocampus robertcokeri</i>	0	0	0	0	0	0	1	0	0	0	0
<i>Ceriodaphnia quadrangula</i>	0	1	0	0	0	0	0	0	0	0	0
<i>Ceriodaphnia reticulata</i>	0	0	1	1	1	1	0	1	1	1	0
<i>Cryptocyclops bicolor</i>	0	0	0	0	0	0	0	0	1	0	0
<i>Cyclocypris</i>	0	0	0	0	0	0	0	0	1	0	0
<i>Cyclops exilis</i>	0	0	0	0	0	0	0	0	0	1	0
<i>Cypridopsis</i>	1	1	0	0	1	1	1	0	0	0	1
<i>Cypris</i>	0	0	0	0	1	0	0	1	0	0	0
<i>Daphnia ambigua</i>	0	0	0	0	0	0	0	0	1	0	0
<i>Diaphanosoma brachyurum</i>	0	0	0	0	0	0	0	0	1	0	0
<i>Diaptomus clavipes</i>	0	0	0	1	0	0	0	0	0	0	0
<i>Diaptomus siciloides</i>	0	0	0	1	0	0	0	0	1	0	0
<i>Euhosmina hagmanni</i>	0	0	0	0	0	0	0	0	1	0	0
<i>Eucyclops agilis</i>	0	0	0	1	0	0	0	0	0	0	0
<i>Leydigia quadrangularis</i>	0	0	0	0	0	0	1	0	0	0	0
<i>Limnocythere</i>	1	0	0	0	0	0	0	0	0	0	1
<i>Mesocyclops tenuis</i>	0	0	0	0	1	0	0	0	0	0	0
<i>Physocypria sp.</i>	0	0	0	1	0	0	0	0	0	0	0
<i>Pseudochydorus globosa</i>	0	0	0	0	0	0	0	1	0	0	0
<i>Simocephalus serrulatus</i>	0	0	0	0	0	0	0	1	0	0	0

Central Oklahoma Plains

Species	RUMIN	PERKINS	FIRECRACKER	DARTER	STUBBLE	ASTER	RANEA	TONYA-1	CEMETERY	LUPE
<i>Acanthocyclops vernalis</i>	0	1	0	1	1	1	0	0	1	1
<i>Alona rustica</i>	0	0	1	1	0	0	0	1	0	1
<i>Bosmina longirostris</i>	1	1	0	1	0	0	0	0	0	0
<i>Ceriodaphnia rigaudi</i>	0	0	0	0	0	0	0	0	0	1
<i>Cyclocypris</i>	0	0	0	0	0	1	0	0	0	1
<i>Cypridopsis</i>	1	1	1	0	0	0	1	1	1	0
<i>Daphnia ambigua</i>	0	0	1	1	0	0	1	0	0	0
<i>Daphnia pileata</i>	0	0	0	0	0	0	0	0	1	0
<i>Daphnia prolata</i>	0	0	0	0	1	0	0	0	0	0
<i>Daphnia laevis</i>	1	0	0	0	0	0	0	0	0	0
<i>Diaphanosoma brachyurum</i>	0	0	0	0	0	0	1	0	0	0
<i>Diaptomus clavipes</i>	1	0	1	0	0	1	0	0	1	0
<i>Diaptomus pallidus</i>	0	1	1	1	0	0	1	1	0	0
<i>Diaptomus saltillinus</i>	1	0	0	0	1	0	0	0	0	1
<i>Diaptomus siciloides</i>	0	0	0	0	0	1	0	0	0	0
<i>Eucyclops agilis</i>	1	0	1	0	0	0	1	1	0	0
<i>Eulimnadia texana</i>	0	0	0	0	1	0	0	0	0	0
<i>Latonopsis fasciculata</i>	0	0	0	0	0	1	0	0	0	0
<i>Leydigia leydigi</i>	1	1	0	0	0	0	0	0	0	0
<i>Limnocythere</i>	0	1	0	0	0	0	0	0	0	0
<i>Macrocyclus alibidus</i>	1	0	0	0	0	0	1	0	0	0
<i>Macrothrix laticornis</i>	0	0	0	0	0	0	0	0	0	1
<i>Mesocyclops tenuis</i>	0	0	0	0	0	0	0	0	0	1
<i>Moina macrocopa</i>	0	0	0	0	0	0	0	0	0	1
<i>Moina micrura</i>	0	1	1	0	0	0	0	0	0	0
<i>Moina wierzejskii</i>	0	0	0	0	1	0	0	0	0	0
<i>Pleuroxus denticulatus</i>	1	1	0	0	0	0	1	0	0	0
<i>Pseudochydorus globosus</i>	1	1	0	0	0	0	1	0	0	0
<i>Scapholebris kingi</i>	1	1	0	1	0	0	0	0	0	0
<i>Sida crystallina</i>	1	0	0	0	0	0	0	0	0	0
<i>Simocephalus serrulatus</i>	0	1	0	1	0	0	1	1	0	0
<i>Streptocephalus texanus</i>	0	0	0	0	1	0	0	0	0	0

Central Irregular Plains

Species	HWY 10	HWY10-2	TURKEY	RD 170	RD 200	ROCK	N 290	E 250	E 300	N 4240 RD
<i>Acanthocyclops vernalis</i>	1	0	0	1	1	1	1	0	0	1
<i>Attheyella illinoisensis</i>	0	1	1	0	1	1	0	0	0	0
<i>Camptocercus oklahomensis</i>	0	1	0	0	1	0	1	1	0	0
<i>Canthocampus robertcokeri</i>	0	0	0	0	0	0	1	0	0	0
<i>Ceriodaphnia quadrangula</i>	0	0	0	0	0	0	0	0	1	0
<i>Ceriodaphnia reticulata</i>	0	0	0	1	1	1	1	1	0	0
<i>Chlamydotheca arcuata</i>	0	0	0	1	0	0	0	0	0	0
<i>Chydoridae unknown</i>	0	0	0	0	0	0	0	1	0	0
<i>Conchostraca</i>	1	0	0	0	0	0	0	0	0	0
<i>Cryptocyclops bicolor</i>	0	0	1	0	1	1	1	1	0	0
<i>Cyclops haueri</i>	0	0	0	0	0	0	0	0	1	0
<i>Cypridopsis</i>	0	0	0	0	0	0	1	0	0	0
<i>Cypris</i>	0	0	1	0	1	1	1	1	0	0
<i>Diaptomus clavipes</i>	1	0	0	0	0	0	0	0	0	0
<i>Diaptomus pallidus</i>	0	1	0	0	1	0	0	0	0	0
<i>Eubranchipus oregonus</i>	0	0	0	0	1	0	0	0	0	0
<i>Leydigia acanthocercoides</i>	0	0	0	0	0	1	1	0	0	0
<i>Macrocyclops alibidus</i>	0	0	0	0	0	0	0	0	1	0
<i>Mesocyclops leukarti</i>	0	0	0	1	0	0	0	0	0	0
<i>Mesocyclops tenuis</i>	0	0	0	0	1	1	0	0	0	1
<i>Pseudochydorus globosa</i>	0	1	0	0	1	0	0	0	0	0
<i>Simocephalus expinosus</i>	0	0	0	1	0	0	0	0	0	0

Ozark Mountains

Species	JESSE	KENWOOD	SALLY	FLNTCREK	YATES	LIBERTY	VICTORIA	MAXINE	GRAPPLER	KRISTI	IBRYER
<i>Acanthocyclops vernalis</i>	0	1	1	0	0	1	0	0	1	0	0
<i>Alona rectangulara</i>	0	0	0	0	1	0	0	0	0	0	0
<i>Alona rustica</i>	1	0	0	0	0	0	0	0	0	0	0
<i>Bosmina longirostris</i>	0	0	1	1	0	1	0	1	1	1	1
<i>Ceriodaphnia reticulata</i>	0	0	1	0	1	1	0	0	0	0	1
<i>Cryptocyclops bicolor</i>	0	0	0	0	0	0	0	0	0	0	1
<i>Cyclocypris</i>	0	0	0	0	0	0	1	0	0	1	0
<i>CyclopsSpp4</i>	1	0	0	0	0	0	0	0	0	0	0
<i>Cypridopsis</i>	0	0	0	0	0	1	0	0	1	0	0
<i>Daphnia ambigua</i>	0	0	1	0	0	0	1	0	0	0	0
<i>Diaptomus pallidus</i>	0	0	0	1	1	0	0	1	1	1	0
<i>Diaptomus reighardi</i>	0	0	0	1	0	0	1	0	0	0	0
<i>Eubosmina hagdmani</i>	1	0	0	0	0	0	0	0	0	0	0
<i>Eucyclops agilis</i>	1	1	0	1	1	0	0	1	1	1	0
<i>Leydigia acanthocercoides</i>	0	0	0	1	0	0	0	0	0	0	0
<i>Macrocyclops albidus</i>	0	0	0	0	1	0	1	1	0	0	0
<i>Mesocyclops edax</i>	0	0	1	0	0	0	0	0	0	1	0
<i>Moina micrura</i>	0	0	0	1	0	0	0	0	1	1	0
<i>Physocypria sp.</i>	1	1	1	1	0	0	0	1	0	0	0
<i>Pleuroxus denticulatus</i>	1	0	0	0	1	1	1	1	0	0	0
<i>Pleuroxus striatus</i>	0	0	0	1	0	0	0	0	1	0	0
<i>Pseudochydorus globosa</i>	0	0	0	0	0	1	1	1	1	0	0
<i>Scapholebris kingi</i>	1	0	0	1	0	1	1	1	0	0	0
<i>Simocephalus serrulatus</i>	0	0	1	0	1	0	1	1	1	0	0

Arkansas Valley

Species	ROBBERS	QUINN	STIGLER	SPARROW	POTEAU	PHIBROSE	MASSEY	TRUMPT	MILO	TREADWAY	COTTONMOUTH
<i>Acanthocyclops vernalis</i>	0	0	1	1	1	1	0	0	0	1	1
<i>Alona rustica</i>	0	0	1	0	0	0	1	0	0	1	0
<i>Bosmina longirostris</i>	0	0	0	0	1	0	1	0	1	0	0
<i>Ceriodaphnia reticulata</i>	0	0	0	0	0	0	0	0	1	1	0
<i>Cyclocypris</i>	0	0	0	0	0	1	0	0	0	0	0
<i>Cypridopsis</i>	1	1	1	1	1	0	1	0	1	1	1
<i>Daphnia ambigua</i>	0	0	0	0	1	0	1	0	1	0	0
<i>Daphnia pulex</i>	0	0	0	0	0	0	0	0	0	0	1
<i>Diaphanosoma brachyurum</i>	0	0	0	0	1	0	0	0	1	0	0
<i>Diaptomus pallidus</i>	1	0	1	0	1	0	1	0	0	0	0
<i>Eucyclops agilis</i>	1	1	0	0	1	0	1	0	0	1	0
<i>Ilyocryptus spinifer</i>	0	0	0	0	0	0	1	0	0	0	0
<i>Leydigia acanthocercoides</i>	0	0	0	0	0	0	1	0	0	0	0
<i>Macrothrix laticornis</i>	0	0	0	0	0	0	1	0	0	0	0
<i>Mesocyclops edax</i>	0	0	0	0	1	0	0	0	0	0	0
<i>Mesocyclops tenuis</i>	0	0	0	0	0	0	0	1	1	0	0
<i>Moina macrocopa</i>	0	0	0	0	1	0	1	1	0	0	0
<i>Pleuroxus denticulatus</i>	0	0	1	0	0	0	0	0	0	0	0
<i>Pseudochydorus globosus</i>	1	0	1	0	1	0	0	0	0	0	0
<i>Scapholebris kingi</i>	0	0	1	0	1	0	0	0	1	0	0
<i>Simocephalus serrulatus</i>	1	0	0	0	1	0	0	0	0	0	0

Ouachita Mountains

Species	MERIDA	TRAIL	INDIANA	STEAPLE	TYSON	FLW	DUMPY
<i>Acanthocyclops vernalis</i>	1	1	0	1	1	1	1
<i>Alona rustica</i>	0	1	0	1	0	0	0
<i>Cyclocypris</i>	1	1	0	1	1	1	0
<i>Cyclops navus</i>	0	0	0	0	0	1	0
<i>Cypridopsis</i>	0	0	1	0	0	0	1
<i>Daphnia ambigua</i>	0	0	0	0	0	0	0
<i>Daphnia pulex</i>	0	0	1	0	1	0	0
<i>Diaptomus pallidus</i>	0	1	0	1	1	0	0
<i>Diaptomus reighardi</i>	0	0	0	0	1	0	0
<i>Eucyclops agilis</i>	0	1	1	1	1	0	0
<i>Leydigia acanthocercoides</i>	1	0	0	0	1	0	0
<i>Moina macrocopa</i>	1	0	0	0	1	0	0
<i>Physocypris sp.</i>	0	0	0	0	0	0	1
<i>Pleuroxus denticulatus</i>	0	1	0	0	0	1	0
<i>Pseudochydorus globosus</i>	1	1	1	0	1	0	1
<i>Scapholebris kingi</i>	0	0	0	0	1	0	1
<i>Simocephalus serrulatus</i>	0	0	0	1	0	0	1

South Central Plains

Species	HUGO	BAZES	DIEGO	HONOBE	CLEARCUT	BUZZARD	GALLO
<i>Acanthocyclops vernalis</i>	0	0	0	0	1	0	0
<i>Alona rustica</i>	0	0	0	0	0	0	1
<i>Biapertura affinis</i>	1	0	0	0	0	1	0
<i>Bosmina longirostris</i>	1	0	0	1	0	0	0
<i>Ceriodaphnia reticulata</i>	0	0	0	0	0	0	1
<i>Cyclocypris</i>	0	1	0	1	0	0	0
<i>Cyclops Spp5</i>	1	0	0	0	0	0	0
<i>Cypridopsis</i>	0	0	1	1	1	1	1
<i>Cypris</i>	0	1	0	0	0	0	1
<i>Daphnia ambigua</i>	0	0	1	0	0	0	0
<i>Daphnia laevis</i>	0	0	0	1	0	0	0
<i>Diaphanosoma brachyurum</i>	1	0	0	0	0	0	0
<i>Diaptomus pallidus</i>	1	1	0	0	0	1	1
<i>Diaptomus siciloides</i>	1	1	0	0	0	0	0
<i>Eucyclops agilis</i>	0	0	0	0	0	1	0
<i>Leydigia acanthocercoides</i>	0	0	0	1	0	0	0
<i>Moina macrocopa</i>	1	0	0	0	0	0	0
<i>Pleuroxus denticulatus</i>	0	0	0	1	0	0	0
<i>Pseudochydorus globosus</i>	0	1	0	0	1	0	1
<i>Simocephalus expinosus</i>	1	0	0	0	0	0	0
<i>Simocephalus serrulatus</i>	1	0	0	0	1	1	0

Central Great Plains -1

Species	STILLWATER I	JOHNDEER	EW-53	STEPHEN	FIR ROAD	CTNWOOD	PEEPER	480	FLY BY	GROUSE	OLD CEDAR	NWR	SAND PIPER	BUFO
<i>Acanthocyclops crassicaudis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Acanthocyclops vernalis</i>	1	0	1	1	1	1	1	0	1	1	1	0	1	1
<i>Alona barbulata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alona guttata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alona rustica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Attheyella illinoisensis</i>	0	1	0	0	1	1	0	1	0	0	0	1	0	0
<i>Caenestheriella belfragei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Camptocercus oklahomensis</i>	0	0	1	1	1	1	0	0	0	0	0	0	0	1
<i>Candona</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Canthocampus assimilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Canthocampus robertcokeri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ceriodaphnia quadrangula</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	0
<i>Ceriodaphnia reticulata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Ceriodaphnia rigaudi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chlamydotheca flexilis</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	0
<i>Cryptocyclops bicolor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cyclocypris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cyclops bicuspidatus thomasi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cyclops navus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cypridopsis</i>	1	1	0	0	1	0	0	0	0	0	0	0	0	1
<i>Cyprinotus incongruen</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Cypris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Daphnia ambigua</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Daphnia obtusa</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Daphnia parvula</i>	0	0	0	0	0	0	0	0	0	1	1	1	0	0
<i>Daphnia pileata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Daphnia prolata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Daphnia pulex</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Daphnia pulicaria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Daphnia laevis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Diaphanosoma brachyurum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Diaptomius novamexicanus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Central Great Plains - 3

Species	SHERRI	GEORGE	CHIVA	GENGLER	BILL	SOFA	MARY	RALPH	BUCKY	PASSOW	KYLE	LESLIE	RODNEY	HOBBOJOE
<i>Diaptomus clavipes</i>	0	1	1	1	1	1	0	1	1	0	1	0	0	0
<i>Diaptomus pallidus</i>	1	0	0	0	0	0	0	0	0	0	0	1	1	0
<i>Diaptomus sanguineus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Diaptomus siciloides</i>	0	1	1	0	1	1	1	0	0	1	0	0	0	0
<i>Dunhevedia crassa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eubosmina hagmanni</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Eubranchipus oregonus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eucyclops agilis</i>	0	0	1	0	0	0	0	0	1	0	1	0	1	0
<i>Eucypris virens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ilyocryptus spinifer</i>	0	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Kurzia latissima</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leydigia acanthocercoides</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Leydigia leydigi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Limnocythere</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Mucoreocyclops alibidus</i>	1	0	0	0	0	1	1	0	0	0	0	0	0	0
<i>Mesocyclops edax</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mesocyclops hyalinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mesocyclops tenuis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Microcyclops varicans rubellus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Moina macrocopa</i>	1	1	1	1	0	0	0	0	0	0	0	0	0	1
<i>Physocypria sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pleuroxus denticulatus</i>	0	0	0	0	1	0	1	0	0	0	0	0	1	0
<i>Potamocypris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudochydorus globosa</i>	1	0	0	0	0	0	0	0	0	1	0	0	1	0
<i>Scapholebris kingi</i>	1	0	0	0	0	1	0	0	1	0	0	0	1	0
<i>Simocephalus expinosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Simocephalus serrulatus</i>	1	0	0	0	0	1	0	0	1	0	0	0	1	0
<i>Streptocephalus dorotheae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Streptocephalus seali</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0

APPENDIX C

Site num-ber	Wetland name	pH	Conduc-tivity (mS/cm)	Temper-ature (C°)	Depth (m)	Altitude (m)	Area (m ²)
1	Stillwater 1	7.54	102.3	17.4	30	317.4	50
2	John Deere	6.83	632.0	15.0	40	284.4	450
3	EW-53	7.78	707.0	17.3	40	307.2	216
4	Stephan	6.81	3.3	18.2	500	328.5	225
5	Fir Road	8.18	381.9	18.7	30	362.4	300
6	Cottonwood	8.35	978.0	16.8	15	369.3	60
7	Peepers	7.74	580.0	11.2	100	579.9	4800
8	480	8.50	79.8	16.9	20	648.6	400
9	E 510	7.55	27.8	17.0	30	695.1	2500
10	283 S	9.36	199.2	13.1	100	732.6	600
11	283 N	9.98	63.9	14.4	50	738.6	600
12	Nomad	8.66	102.4	15.4	30	711.9	300
13	Flyby	7.79	1150.0	18.0	10	356.4	125
14	Grouse	7.70	707.0	18.5	50	362.4	625
15	Old Cedar	7.06	103.6	20.9	25	350.4	4
16	NWR	8.00	658.0	24.2	40	352.2	300
17	Sand Piper	7.49	8.6	22.3	30	353.1	300
18	Road Grader	7.02	110.9	21.6	30	455.1	90
19	Outlook	8.11	615.0	21.6	30	437.7	120
20	HWY 10	8.84	83.5	26.4	10	257.7	24
21	HWY 10-2	7.92	407.6	17.5	70	251.1	72
22	Turkey	8.69	128.6	22.1	20	283.2	30
23	Rd 170	7.41	91.3	21.0	20	254.1	48
24	Rd 200	7.76	328.6	20.4	30	242.7	40
25	Rock	8.59	149.4	17.6	40	247.5	12
26	N 290	7.16	348.7	19.6	40	271.2	54
27	E 250	6.92	251.0	18.9	35	238.8	30
28	E 300	7.55	263.7	17.0	60	253.8	3
29	N 4240 Rd	7.41	156.9	18.9	15	252	20
30	Metate	8.01	520.0	20.1	10	311.7	12
31	Burned	7.85	454.2	17.1	60	326.4	10
32	Bonita	7.61	357.1	15.5	5	306.3	0.5
33	Carcass	7.48	227.0	12.6	300	343.5	600
34	Sandstone	7.12	218.5	13.7	30	317.4	75
35	Bison	6.77	488.3	13.9	45	329.4	20
36	Soggy Bottom	7.75	408.1	18.2	10	346.5	36
37	Pewter	7.62	292.3	18.1	20	334.8	36
38	Ramp	8.22	463.8	23.3	60	384.3	700
39	Hawk	7.68	213.2	15.8	45	367.8	8
40	Bufo	6.84	338.7	21.2	60	460.2	240
41	Rana	6.72	142.8	23.5	70	477	108
42	Fort Sill	7.32	408.4	24.8	60	442.8	300
43	Wichita Mtn.	7.36	260.2	23.8	60	456	300

44	Holy City	7.25	87.1	24.7	40	516	80
45	Black Jack	6.60	145.8	26.6	40	470.4	100
46	Sheppard	5.88	125.5	12.7	20	803.4	4000
47	Coyote	5.10	130.3	14.6	30	823.2	10000
48	Yucca	7.46	1511.0	19.2	6	908.7	8
49	Cabbage	6.55	284.3	18.3	25	935.4	320
50	Clines	7.66	270.8	20.4	40	1077.6	625
51	Watkins	8.48	243.2	23.1	35	949.5	750
52	Ridge	9.12	143.9	23.2	10	876.3	16
53	Shamrock	8.08	114.5	22.8	30	833.4	40
54	Ellenburger	7.71	89.8	22.5	80	636.9	2400
55	Ripley Rd	6.75	732.0	24.1	60	285	9
56	Bethell	6.95	610.0	24.3	15	316.5	300
57	Red Dog	7.10	745.0	23.0	100	316.5	16
58	Moth	7.18	496.2	22.5	30	333	225
59	Chesmoore	7.18	684.0	23.2	25	314.4	64
60	Redland	6.61	310.1	22.6	70	274.2	22.5
61	Jesse	7.12	130.9	26.1	100	303.3	500
62	Kenwood	9.46	70.9	31.6	30	236.7	300
63	Sally	7.48	127.1	30.7	100	315.9	2000
64	Flint Creek	7.91	82.3	29.3	150	342	600
65	Yates	6.11	37.6	25.2	200	350.4	200
66	Liberty	7.05	25.0	28.3	50	291	96
67	Victoria	8.37	143.1	30.6	100	328.8	800
68	Maxine	6.37	97.2	26.4	50	328.2	450
69	Grappler	6.96	44.8	27.5	200	326.4	1400
70	Kristi	7.11	138.0	25.7	20	300	28
71	Bryer	5.85	53.3	26.2	20	337.5	30
72	Rumen	8.41	174.7	32.5	30	341.1	375
73	Perkins	8.45	75.1	33.8	100	296.1	625
74	Fire Cracker	7.05	130.6	19.3	40	321	60
75	Darter	6.99	24.8	23.7	100	321	250
76	Stubble	7.41	88.0	27.3	40	348.9	1950
77	Aster	7.23	39.7	27.0	150	344.1	750
78	Ranae	8.30	208.8	30.3	100	231.3	225
79	Tonya	8.46	235.7	28.9	100	228.9	10000
80	Hugo	7.47	81.8	28.3	30	139.5	45
81	Bazes'	6.02	44.7	23.6	45	163.8	150
82	Diego	7.01	76.8	27.8	150	177.3	49
83	Honobia	7.04	51.0	29.4	200	194.7	625
84	Clearcut	7.20	114.8	31.4	20	186.3	35
85	Merida	6.59	40.8	28.8	50	246	15
86	Trail	6.47	40.8	32.5	10	240.6	0.5
87	Indiana	7.19	31.6	31.3	5	179.4	6
88	Buzzard	7.22	42.5	32.2	150	186.9	500
89	Gallo	7.14	106.9	31.8	30	172.2	3

90	Steaple	7.63	59.2	33.0	50	177.9	750
91	Tyson	7.54	243.7	37.1	20	195	200
92	FLW	6.38	177.7	33.7	20	198.6	20
93	Dumpy	5.95	43.3	33.3	50	220.2	18
94	Robbers Cave	7.00	191.4	23.4	50	285.9	12
95	Quinn	6.77	40.9	28.2	20	347.4	16
96	Stigler	5.72	95.0	27.1	30	198.3	600
97	Sparrow	6.43	67.8	27.5	20	195.9	12
98	Grubber	6.58	45.1	10.3	30	184.2	400
99	Ron's	6.74	46.5	20.8	150	285.6	625
100	Miguel	6.25	88.3	21.7	100	288.6	500
101	Rancho	6.67	36.1	21.2	150	296.1	500
102	Gertrude	6.50	62.9	18.6	50	297.3	100
103	Kubota	6.50	40.4	18.6	100	295.8	150
104	Shana	6.94	27.6	20.0	100	296.1	225
105	Rosa	6.94	68.3	20.3	30	302.4	12
106	Acacia	6.37	50.3	16.2	50	297.3	60
107	Bedrock	9.08	184.8	20.6	15	375.9	20
108	Argentina	7.60	134.1	18.7	20	369	12
109	Trail Ridge	8.10	300.0	20.0	20	390.9	3
110	Poteau	7.23	568.0	21.4	50	159	1000
111	Phibrose	6.66	38.1	21.3	20	171.9	9
112	Massey	6.81	57.4	23.9	60	162.3	600
113	Trumpet	6.62	175.1	22.4	40	145.8	10
114	Milo	6.48	99.4	25.6	50	158.1	300
115	Treadway	6.82	161.0	25.7	65	173.7	100
116	Cottonmouth	6.14	41.1	28.6	20	279.9	16
117	Boone	7.54	103.5	26.5	10	344.7	3
118	Alto	6.55	35.0	23.8	20	345	60
119	La Huerta	5.93	24.8	22.8	20	382.5	1.5
120	5135	8.24	1013.0	26.3	35	344.1	24
121	Cemetery	7.48	124.2	27.2	40	341.1	1350
122	Lube	7.43	51.6	29.5	20	346.8	15
123	Bryan	8.63	534.0	33.0	40	339	300
124	Sherri	8.02	847.0	28.2	20	348.9	4
125	George	8.19	727.0	32.4	40	327.9	450
126	Chiva	7.91	333.2	32.5	70	319.2	1500
127	Gangler	8.74	373.8	31.6	70	317.7	875
128	Bill	8.02	337.9	31.4	70	304.5	500
129	Sofa	7.25	89.9	30.5	500	301.2	1000
130	Mary	9.35	60.9	30.7	120	336.6	910
131	Ralph	7.27	98.0	26.7	30	329.7	48
132	Bucky	8.72	70.8	24.9	60	332.4	450
133	Passow	7.90	48.9	28.7	20	318.9	50
134	Kyle	7.81	187.4	27.0	200	312.6	70
135	Leslie	8.64	105.3	26.9	150	317.1	60

136	Rodney	10.16	299.2	25.2	50	333.9	1050
137	Hobo Joe	7.34	277.1	22.3	45	336.9	600
138	Meadow Lark	7.79	128.2	16.1	35	306.3	42
139	Finale	9.28	240.0	18.2	100	872.7	1625
140	Gourd	9.38	245.9	15.3	30	1350.6	75
141	Shack	8.86	610.0	18.6	30	796.8	900
142	Poncho	8.34	154.0	18.2	20	788.4	400
143	Bluestem	9.04	200.4	15.3	30	1350.6	16
144	Piston	9.00	424.0	20.3	30	1094.4	6000
145	Lirnes. Mesa	8.72	416.4	14.5	2	1313.4	800
146	Redtail	8.64	240.2	12.0	15	1313.7	16



VITA

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OF OKLAHOMA**

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