

CRUSTACEAN ZOOPLANKTON COMMUNITY STRUCTURE IN TEMPORARY
AND PERMANENT PONDS IN A TEXAS GRASSLAND

by

STEPHEN MATTHEW DRENNER

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Texas Christian University
Fort Worth, Texas

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INTRODUCTION

The size gradient of lentic systems has been recognized as a critical axis along which aquatic communities are organized (Wellborn et al., 1996). The species composition of communities along this gradient is determined by both physical factors, such as pond drying, and biotic factors, such as predation (Wellborn et al., 1996). Here we present a study of the effects of pond drying and fish presence on crustacean zooplankton assemblages across a gradient of pond sizes in a Texas grassland following an exceptional drought.

Droughts represent an extreme of the hydrological continuum, and are important ecological disturbances (Lake, 2000). Drought has subtle effects on large and deep lentic systems, lowering water levels, exposing shorelines of lakes and displacing littoral zone communities. Drought has more acute effects on small and shallow lentic systems, resulting in basin drying and temporary elimination of the aquatic fauna. Crustacean zooplankton including branchiopods and copepods survive pond drying as diapausing stages in the sediments (Dodson, 2005), and recolonize lentic systems after the systems are filled by rainfall.

Pond drying can also have secondary trophic-level effects by eliminating fish and their predation effects on zooplankton community structure. Planktivorous fish feed as size-selective predators on large zooplankton (O'Brien, 1979) and eliminate zooplankton species that cannot survive to a large adult size necessary for successful reproduction (Brooks & Dodson, 1965). In the absence of planktivorous fish, invertebrate planktivores feed as size-selective predators on small zooplankton (Pastorok, 1981; Dodson, 1984),

shifting the zooplankton community to larger species that are not as vulnerable to invertebrate predation (Dodson, 2005).

Wellborn et al. (1996) offered a schematic model of how species assemblages of lentic communities might be affected by pond drying. According to their model, lentic systems would range from relatively small temporary habitats with rapidly developing large prey and invertebrate predators to larger permanent habits with predatory fish and small prey. Species living in temporary ponds are those with phenotypes adapted to the ephemeral nature of this environment. Species that live in temporary ponds may be absent from permanent ponds because predators such as planktivorous fish selectively consume and eliminate them. Species that live in permanent ponds may be absent from temporary ponds because they cannot cope with the physical stress of pond drying. Thus temporary and permanent pond habitats potentially contain alternative community types with different species assemblages (Wellborn et al. 1996).

Chase (2007) offered a related conceptual model of how species assemblages of lentic systems might be affected by drought and pond drying. He hypothesized that drought alters the species assemblage of aquatic systems by acting as a harsh environmental filter that restricts species presence, reduces the number of species and the variability of species assemblages. In permanent systems that do not go dry, the species assemblage is highly variable due to stochastic factors such as dispersal. In temporary systems that dry, the species assemblage is less variable and limited to those species that can survive the harsh conditions. Chase (2007) predicted that communities in lentic systems that dry will have greater similarity than permanent systems.

In this paper, I examine the community assemblage models of Wellborn et al. (1996) and Chase (2007) using data from a field study of the zooplankton assemblages of temporary and permanent ponds in the Lyndon B. Johnson (LBJ) Grasslands, Texas. Specifically I test four hypotheses: 1) Crustacean zooplankton species assemblages are different in temporary versus permanent ponds; 2) The number of species of crustacean zooplankton occurring in temporary ponds are less than permanent ponds; 3) The zooplankton community similarity is greater in temporary ponds than permanent ponds; and 4) the body lengths of zooplankton are greater in temporary ponds than permanent ponds.

METHODS

The LBJ National Grasslands is located in Wise County in north-central Texas, approximately 80 km northwest of the Dallas-Ft. Worth area. The LBJ Grasslands consists of 8,220 ha of hardwood forests and grasslands in numerous non-contiguous units (Fig. 1) (USDA, 1999). Before the U.S. government purchased the grasslands in the 1930's, the area consisted of mostly abandoned farms that were suffering from severe soil erosion due to poor agricultural practices. Since 1955 the grasslands have been managed by the USDA-Forest Service, and private livestock owners are allowed to use the grasslands for livestock grazing.

The grasslands contain hundreds of man-made ponds and lakes ranging in size from less than one hectare to 13.65 ha. Although no information is available about the dates of construction of most of the ponds, their dams are colonized by trees indicating

that the ponds were probably several decades old. Thus it is likely that the ponds have experienced several droughts and drying disturbance episodes in their history.

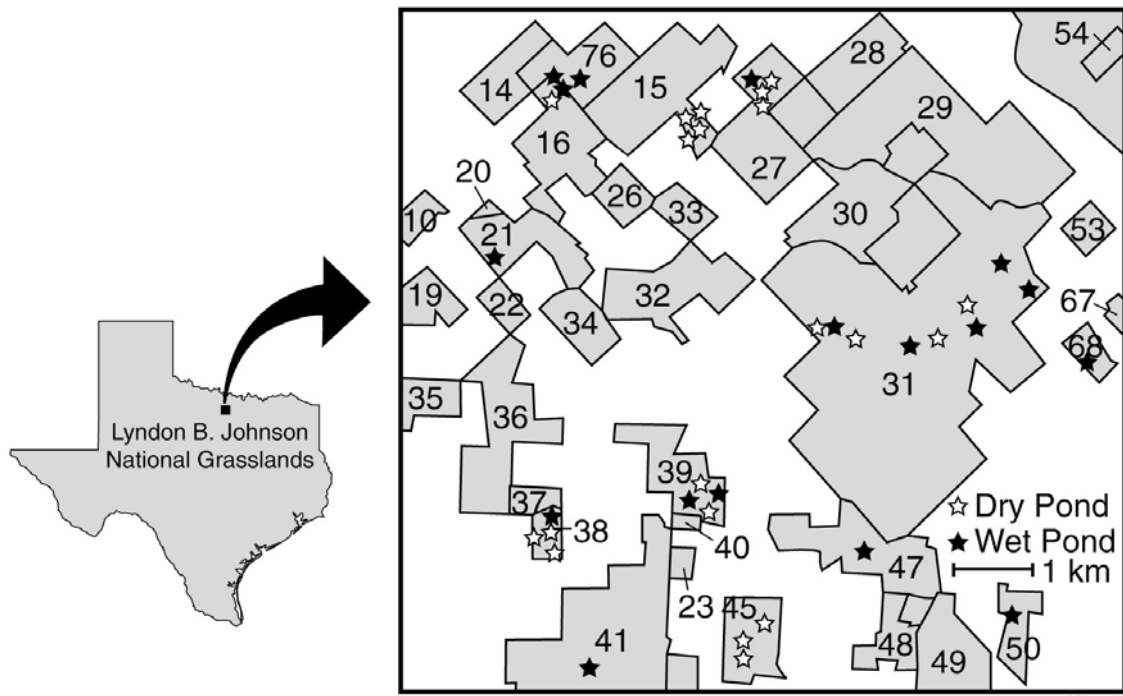


Fig. 1-- Map of the LBJ National Grasslands northwest of Dallas/Fort Worth, TX. The gray-shaded, numbered areas are units of the grassland, and the white-shaded areas are privately-owned land. The stars indicate the locations of the ponds. Pond names are derived from the number of the unit on which they are located and either the name of the pond or an arbitrary letter assigned for identification.

The ponds of the grassland were affected by a severe drought in 2005. According to the National Weather Service, 2005 was the 5th driest year on record for the Dallas-Fort Worth area (<http://web2.airmail.net/danb1/drought.htm>), which is southeast of the grasslands. In January 2006, the grasslands were in a region classified by the National Oceanic and Atmospheric Administration as experiencing an “exceptional drought”. The drought caused many of the smaller ponds to dry, while larger ponds still retained water and fish. Although some small ponds may dry in most years, this severe drought provided the opportunity to assess drought and drying effects on a broad size spectrum of grassland ponds.

In January and February of 2006, I located 20 dry ponds and 18 water-containing ponds for our study. Patalas (1990) found that >90% of the species present in a region were generally found by sampling 20 lakes. I classified ponds as either temporary (i.e. those that had gone dry, and presumably go dry periodically) or permanent (i.e. those that still retained water, and presumably retain water constantly). Surface areas of the ponds were obtained using Google Earth or on-site measurements. The sampled ponds ranged in surface area from 0.01 to 13.65 ha.

Ponds filled with water from rains in March 2006, and water and zooplankton samples were collected in April 2006. To analyze for concentrations of total phosphorus (TP) and total nitrogen (TN), water samples were collected by submerging a 250-ml Nalgene bottle under the surface about 1 m offshore. Water samples were digested using a modified persulfate autoclave digestion method (Koroleff, 1983). Digested samples were analyzed for TP using an Astoria segmented flow analyzer (Astoria Pacific Inc., Clackamas, OR) and TN using a Westco Smartchem (Westco Scientific Instrument, Inc., Brookfield, CT).

Two composited horizontal tows with an 80- μ m mesh conical plankton net were taken from each pond on one sampling date during the month of April. Zooplankton samples were preserved in 50% undenatured ethanol. After each pond was sampled, the plankton net was submerged in a solution of bleach to avoid introduction of zooplankton to ponds. For each of the 38 sampled ponds, crustacean zooplankton were identified to the species level using taxonomic keys (Edmondson, 1959; Balcer et al., 1984; Hudson et al., 1998; Thorp & Covich, 2001), dissecting and compound microscopes. Each sample was examined two to three times by two different individuals to identify all species.

The crustacean zooplankton species compositions of communities in ponds were compared using Jaccard's similarity measure for presence/absence data (Magurran 1988) which expresses similarity from 0, indicating no species held in common between the two ponds, to 1, indicating the same species composition in the two ponds. Jaccard's similarities were computed for every combination of ponds using EstimateS 8.0 software (<http://viceroy.eeb.uconn.edu/estimates>). The similarity measures for pairs of ponds were separated into groups of 1) comparisons between temporary ponds, 2) comparisons between permanent ponds, and 3) comparisons of temporary ponds with permanent ponds. Non-parametric statistical analyses were used to test the null hypothesis of equal frequency distributions of similarity measures among these groups. A Wilcoxon Ranked Sums test implemented in the NPAR1WAY procedure of SAS (Richter & Higgins, 2006) was used to test for any significant differences ($P < 0.05$) among the three groups followed by pair-wise Kolmogorov-Smirnov comparisons among the groups to determine which of these differed. The pair-wise tests were evaluated for significance at the $P < 0.05$ level by using $P < 0.0167$ to control Type 1 error rates (Richter & Higgins, 2006).

For each of the 38 pond samples, zooplankton body length was measured using a Zeiss dissecting microscope at 5X magnification with a digital camera (Axio Vision). I measured the length of 25 randomly-selected individuals from each zooplankton sample for a total of 950 individual zooplankton measurements. Cladocerans were measured from the top of the head to the posterior end of the carapace, excluding tail spine. Copepods were measured from the top of the head to the posterior end of the caudal ramus, excluding caudal setae. The size distribution of zooplankton in temporary and permanent ponds were compared by first combining all the 25 measures in each pond into

a set of 450 measures of length in temporary ponds and a set of 502 measures for permanent ponds. The frequency distribution of these two sets was compared using Smirnov's test (Conover, 1971) which tests the null hypothesis of equal distributions versus the alternative hypothesis that the distributions differ in at least some range of the data.

Fish communities of ponds were categorized as either present or absent. All temporary ponds were presumed to be fishless after being filled by spring rains. Large permanent lakes have been stocked with gamefish and maintain established fish communities while smaller permanent ponds contain fish from unknown origins. I confirmed that smaller permanent lakes had fish by observing fish from the shoreline or seining. Fish captured by seining were immediately released unharmed into the ponds. In the small permanent ponds, I found variable fish assemblages comprised of golden shiners (*Notemigonus crysoleucas*), bullheads (*Ictalurus* spp.), mosquitofish (*Gambusia affinis*), green sunfish (*Lepomis cyanellus*), bluegill (*Lepomis macrochirus*), and largemouth bass (*Micropterus salmoides*).

RESULTS

Temporary ponds differed in surface area but not nutrient concentrations from permanent ponds. Temporary ponds had a significantly smaller mean surface area of 0.081 ha (SD \pm 0.064) while permanent ponds had a mean surface area of 2.12 ha (SD \pm 3.783) (t-test of means assuming unequal variances = 2.29; df = 17; P < 0.05). Concentrations of TP and TN ranged from 31-307 and 670-2130 μ g/L, respectively, which would classify the ponds as eutrophic (Wetzel, 2001). Mean concentrations of TP

in temporary ponds and permanent ponds was $73.3 \mu\text{g/L}$ ($\text{SD} \pm 56.0$) and $57.7 \mu\text{g/L}$ ($\text{SD} \pm 34.1$) respectively and were not significantly different (t-test of means assuming unequal variances = 1.05; $\text{df} = 32$; $P > 0.05$). Mean concentrations of TN in temporary and permanent ponds was $1001.4 \mu\text{g/L}$ ($\text{SD} \pm 413.2$) and $1215.3 \mu\text{g/L}$ ($\text{SD} \pm 420.4$) respectively and were not significantly different (t-test of means assuming unequal variances = 1.57; $\text{df} = 35$; $P > 0.05$).

I found 28 taxa of crustacean zooplankton in the 38 ponds (Table 1). The total number of crustacean zooplankton taxa per pond ranged from 2 to 11, and was not correlated with pond surface area ($r^2 = 0.01$) because of the relatively narrow range of pond sizes in our study. According to a species area curve for crustacean zooplankton in North American lakes (Dodson, 1992), 4 to 9 species of crustacean zooplankton would be expected in ponds with the range of surface areas I sampled at the grasslands.

Pond type did not affect zooplankton species richness at the local level, but did affect species number at the regional level. Crustacean zooplankton species assemblages in temporary and permanent ponds were variable with mean numbers of crustacean zooplankton taxa per pond of 7.1 ($\text{SD} \pm 1.9$) and 5.8 ($\text{SD} \pm 2.4$), respectively. At the regional level, 17 crustacean zooplankton species were observed in at least one of the temporary ponds, and 24 species were observed in at least one of the permanent ponds. This equates to a 29 % reduction of species in the temporary ponds compared to the permanent ponds.

I detected a difference in the zooplankton species assemblages of the temporary and permanent ponds. Although zooplankton taxa occurred in both fish and fishless

| Pond | Permanence | Pond Surface Area (ha) | Average zooplankton size (mm) | Daphnia laevis | Daphnia ambigua | Daphnia pulex | Scapholeberis | Macrothrix | Chydorus brevilabris | Camptocercus | Pleuroxix | Chydorid species A | Alona quadrangulans | Alona monocantha | Ceriodaphnia | Bosmina longirostris | Simocephalus vetulus | Diaphanosoma | Agliodiptamus clavipes | Skistodiptamus pallidus | Leptodiptamus siciloides | Acanthocyclops vernalis | Microcyclops rubellus | Tropocyclops prasinus mexicanus | Eucyclops agilis | Eucyclops elegans | Diacyclops thomasi | Paracyclops chiltoni | Mesocyclops americanus | Macrocyclus albidus | Streptocephalus texanus | Number crustacean zooplankton | | |
|-------------|------------|------------------------|-------------------------------|----------------|-----------------|---------------|---------------|------------|----------------------|--------------|-----------|--------------------|---------------------|------------------|--------------|----------------------|----------------------|--------------|------------------------|-------------------------|--------------------------|-------------------------|-----------------------|---------------------------------|------------------|-------------------|--------------------|----------------------|------------------------|---------------------|-------------------------|-------------------------------|----|---|
| P15A | 0 | 0.0336 | 3.533 | 1 | | | | | 1 | | | | 1 | | | | | | 1 | | 1 | | 1 | | | | | | | | 11 | | | |
| P15B | 0 | 0.0070 | 0.441 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | 8 | | |
| P15C | 0 | 0.0589 | 1.233 | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | 6 | | |
| P15D | 0 | 0.1019 | 0.657 | 1 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | 5 | | |
| P16C | 0 | 0.0995 | 0.546 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 7 | | |
| P27A | 0 | 0.1698 | 0.552 | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 8 | | |
| P27B | 0 | 0.0255 | 0.218 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 8 | | |
| P27C | 0 | 0.1924 | 0.233 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 7 | | |
| P31B | 0 | 0.2144 | 0.477 | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 7 | | |
| P31D | 0 | 0.1488 | 1.001 | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 10 | | |
| P31F | 0 | 0.0790 | 1.407 | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 8 | | |
| P31H | 0 | 0.0481 | 0.839 | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 8 | | |
| P38B | 0 | 0.0601 | 0.784 | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | 3 | | |
| P38C | 0 | 0.0477 | 0.619 | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 6 | | |
| P38E | 0 | 0.0720 | 1.526 | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 10 | | |
| P39A | 0 | 0.0345 | 1.298 | 1 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 5 | | |
| P39C | 0 | 0.0079 | 0.473 | 1 | | | | | 1 | | | | 1 | | | | | | | | | | | | | | | | | | | 5 | | |
| P45A | 0 | 0.1628 | 1.118 | 1 | 1 | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 7 | | |
| P45AA | 0 | 0.0178 | 2.555 | | 1 | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 6 | | |
| P45B | 0 | 0.0393 | 1.214 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 7 | |
| P15AA | 1 | 0.0632 | 0.288 | | | | 1 | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | 8 | | |
| P16A | 1 | 0.0396 | 0.393 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 3 | |
| P16B | 1 | 0.0835 | 0.721 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | 2 | |
| P21 Rhodes | 1 | 4.5010 | 0.2044 | | | | | | 1 | | | | 1 | | | 1 | | | | | | | | | | | | | | | | 8 | | |
| P27D | 1 | 0.0426 | 0.322 | | | | | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | | 5 | |
| P31 a LCtwd | 1 | 0.8443 | 0.254 | | 1 | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | 8 | |
| P31 Ctwd | 1 | 8.8812 | 0.229 | | | | | | | 1 | 1 | 1 | | | | | | | | | | | | | | | | | | | | | 8 | |
| P31C | 1 | 0.1395 | 0.321 | | | 1 | | | 1 | | | | 1 | | | | | | | | | | | | | | | | | | | | 6 | |
| P31E | 1 | 0.1307 | 0.408 | | 1 | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | 5 | |
| P31G | 1 | 0.0914 | 0.224 | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | 6 | |
| P38D | 1 | 0.5783 | 0.567 | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | 3 | |
| P39B | 1 | 0.1179 | 0.588 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 7 | |
| P39D | 1 | 0.1284 | 0.216 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 |
| P41 Clear | 1 | 5.7209 | 0.204 | | | | | | 1 | | 1 | | 1 | 1 | | 1 | | | | | | | | | | | | | | | | | 10 | |
| P47 BlkCk | 1 | 13.6543 | 0.208 | | 1 | | | | | | | | 1 | | | 1 | | | | | | | | | | | | | | | | | 5 | |
| P50 Bic | 1 | 1.9470 | 0.286 | | 1 | | | | | | | | 1 | | | 1 | | | | | | | | | | | | | | | | | 5 | |
| P68 Dan | 1 | 0.9400 | 0.349 | | | 1 | | | | | | 1 | 1 | | | 1 | | | | | | | | | | | | | | | | | 9 | |
| P76B | 1 | 0.2555 | 0.422 | | 1 | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | 5 | |

Table 1--Pond name, permanence, surface area, average zooplankton size, and presence of zooplankton taxa.

ponds, some taxa were more prevalent in temporary versus permanent ponds (Fig. 2). Species that were more prevalent in temporary ponds versus permanent ponds were *Daphnia laevis*, *Ceriodaphnia dubia*, *Acanthocyclops vernalis*, and *Microcyclops rubellus*. Species that were more prevalent in permanent versus temporary ponds were *Skistodiaptamus pallidus* and *Daphnia ambigua*. Two of the larger zooplankton taxa, *S. texanus* and *Agliodiaptomus clavipes*, were found exclusively in temporary ponds while the small *Bosmina longirostris* was only found in permanent ponds.

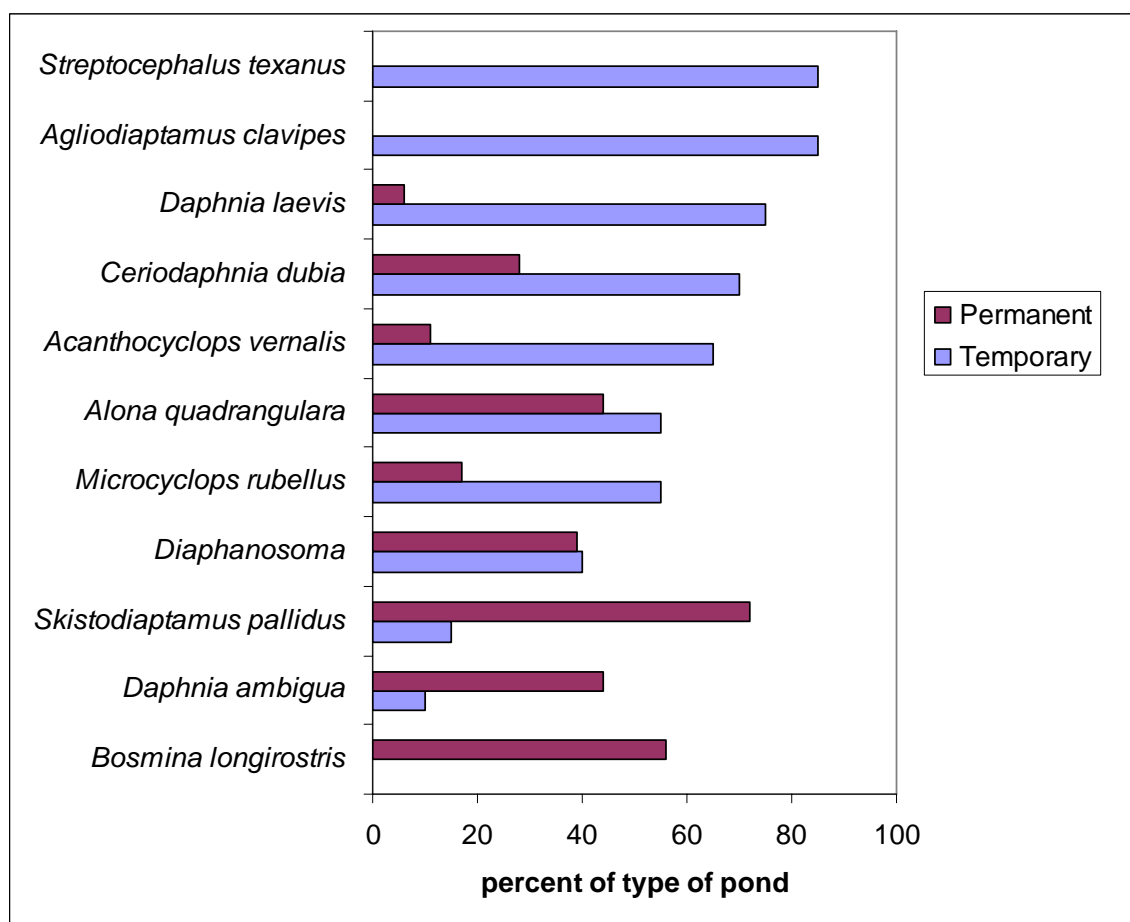


Fig. 2-- Percent occurrence of the most commonly occurring zooplankton taxa in temporary and permanent ponds.

Jaccard similarity measures ranged from 0 to 1 with median measures of 0.400, 0.160, and 0.110, respectively, for comparisons between temporary ponds, comparisons

between permanent ponds, and comparisons between temporary and permanent ponds (Fig. 3). The frequency distributions of similarity measures differed among these groups (Wilcoxon Ranked Sums $\chi^2 = 240$; $df = 2$; $P < 0.001$), and Kolmogorov-Smirnov tests indicated: 1) significantly greater measures between temporary ponds than between temporary and permanent ponds ($D = 0.600$; $P < 0.01$); and 2) significantly greater measures between permanent ponds than between temporary and permanent ponds ($D = 0.189$; $P < 0.01$). There was also greater similarities between temporary ponds than between permanent ponds ($D = 0.502$; $P < 0.010$).

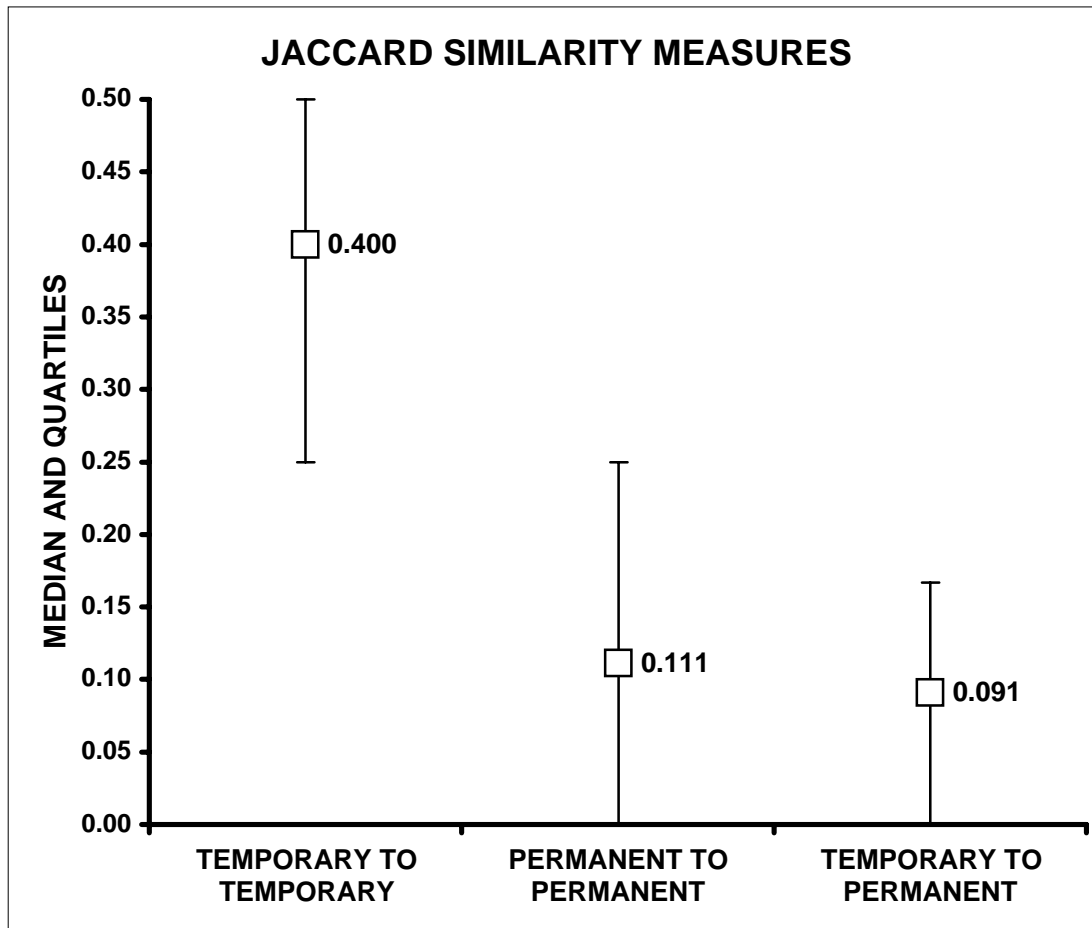


Fig. 3-- Jaccard similarity measures for comparisons between temporary ponds, comparisons between permanent ponds and comparisons between temporary and permanent ponds.

Zooplankton size ranged from 0.1 mm (copepod nauplii) to greater than 4.0 mm (*S. texanus*). The mean sizes of zooplankton in temporary and permanent ponds were 1.034 mm (SD \pm 1.399) and 0.345 mm (SD \pm 0.260), respectively. Size frequency distributions in temporary and permanent ponds were significantly different (Smirnov, $P < 0.0001$) (Fig. 4).

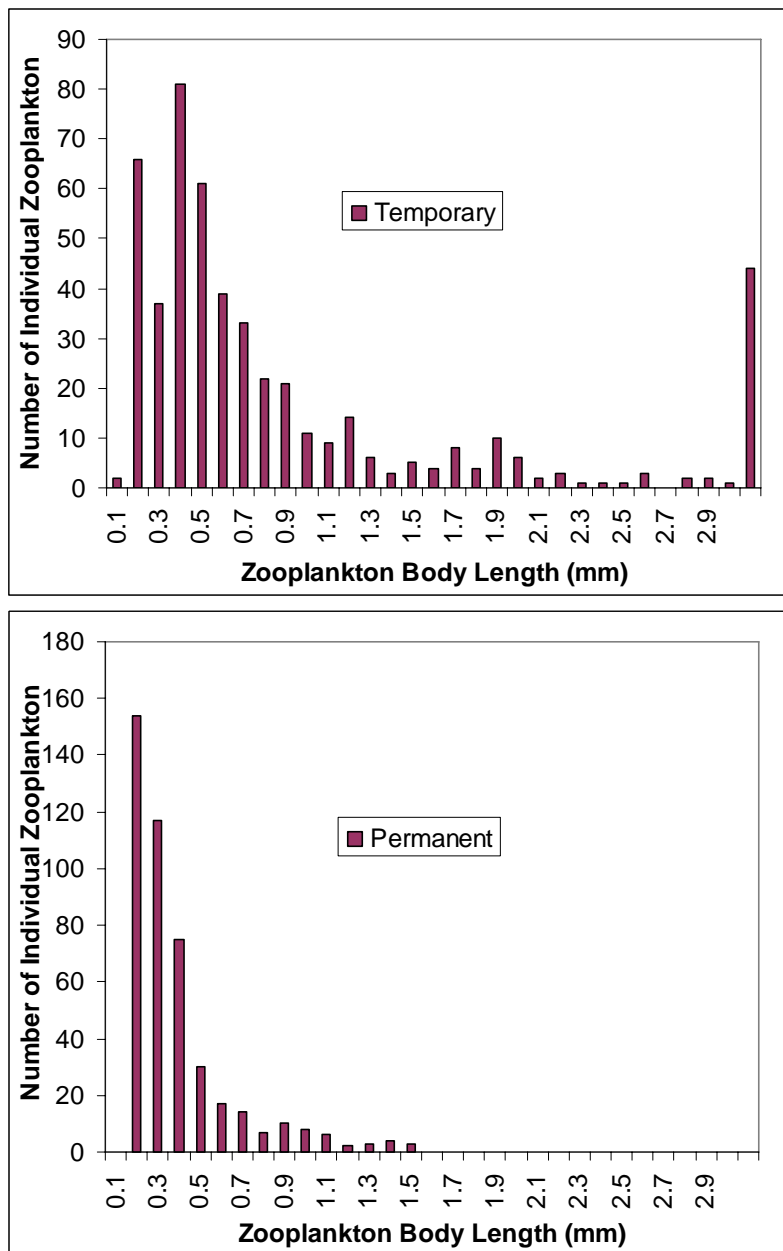


Fig. 4-- Size frequency distributions of zooplankton in the temporary and permanent ponds.

DISCUSSION

The results of my study are consistent with the schematic model of Wellborn et al. (1996) of the mechanisms creating community structure across size gradients of lentic systems. Wellborn et al.'s (1996) model recognized pond drying and fish as key abiotic and biotic factors, respectively that interact to shape freshwater communities. I found that pond size was the primary factor determining the effects of the extreme drought on zooplankton community structure of the grassland. Larger ponds retained water and fish while smaller ponds dried and became devoid of fish. The elimination of fish resulted in secondary trophic-level effects that affected the species composition and size distributions of the crustacean zooplankton assemblage.

The zooplankton communities in temporary and permanent ponds were consistent with the predictions of Chase (2007). Chase (2007) examined the effects of drought on community assemblages in an experiment with fishless mesocosms that were environmentally similar except for a simulated drought and drying. Chase (2007) found that the mesocosms that experienced drought and dried had a species reduction of 45% of species at the regional level, including macrophytes and invertebrates. In the mesocosms that experienced drying, community structure was less variable and community similarity was greater. I found a 29% reduction in zooplankton species in the temporary versus permanent ponds. I also found that the temporary ponds affected by drought had higher community similarity than permanent ponds.

Ecologists have hypothesized that drought and pond drying may have an effect on species biodiversity at a regional level (Chase, 2007). Specifically pond drying results in alternative community assemblages with different species compositions. Chase (2007)

concluded that even if local species diversity is able to recover following a drought, regional diversity may be compromised. In my study, I found two alternative species assemblages in temporary and permanent ponds. While the temporary ponds had fewer species of crustacean zooplankton, they contained two zooplankton species, *S. texanus* and *A. clavipes*, that I did not detect in the permanent ponds. One zooplankton species, *B. longirostris*, was only found in permanent ponds. Although the drying of ponds during a drought may reduce the number of species at the local level, it maintains alternative community types and thereby increases biodiversity of crustacean zooplankton at the regional level.

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VITA

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| Personal Background | Stephen Matthew Drenner Fort Worth, Texas Son of Dr. Ray W. Drenner and Pamela Drenner |
| Education | Diploma, Trinity Valley High School, Fort Worth, Texas, 2002 Bachelor of Arts, Biology, Texas Christian University, 2006 |
| Awards | Dean's Honor List and TCU Scholar in Spring 2005 and Spring 2006 Best Biology Undergraduate Research Poster in the 2006 College of Science and Engineering Student Research Symposium |
| Experience | Research Assistant, Texas Christian University, Teaching Assistant, Texas Christian University, 2006-2008 |
| Presentations | M.M. Chumchal, M.C. Slattery, R.W. Drenner, S.M. Drenner and L. Newland. 2007. How Will New Coal Burning Power Plants in Texas Affect Mercury Contamination in Fish? Oral Presentation. Texas Chapter of the American Fisheries Society Annual Meeting, Lake Jackson, Texas. Drenner, S.M., Stone, M., Drenner, R., Newland, L., and Chumchal ¹ , M., Biology Department, Texas Christian University, Fort Worth, TX and ¹ University of Oklahoma, Norman, OK. 2007. Mercury Concentrations in Largemouth Bass from Six North Texas Reservoirs. Poster Presentation. Texas Chapter of the American Fisheries Society Annual Meeting, Lake Jackson, Texas. |
| Professional Memberships | Texas Chapter of the American Fisheries Society |

ABSTRACT

CRUSTACEAN ZOOPLANKTON COMMUNITY STRUCTURE IN TEMPORARY AND PERMANENT PONDS IN A TEXAS GRASSLAND

by Stephen Matthew Drenner, M.S., 2008
Department of Environmental Science
Texas Christian University

Thesis Advisor: Ray W. Drenner, Professor of Biology and Chair of the Department

Lentic community structure varies across a size gradient of ponds and lakes with physical factors, such as pond drying, and biotic factors, such as fish predation, determining the species assemblage. To test these concepts, I studied the effects of pond drying and consequent fish loss on crustacean zooplankton across a gradient of pond sizes in a Texas grassland following an exceptional drought where smaller ponds dried and lost their fish communities. After rains filled ponds in March, crustacean zooplankton were sampled in 20 temporary and 18 permanent ponds in April. Compared to permanent ponds, temporary ponds had fewer zooplankton species, more similar community assemblages and larger individual zooplankton. Thus, pond size mediated whether ponds dried during a drought, and drying determined the presence and absence of fish and its secondary trophic-level effects on zooplankton community structure.