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PRIMARY RESEARCH PAPER

Crustacean zooplankton community structure in temporary and permanent grassland ponds

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Abstract 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. We studied the effects of pond drying and fish absence on crustacean zooplankton across a gradient of pond sizes in a Texas grassland. We determined the species compositions and size distributions of crustacean zooplankton in 20 temporary and 18 permanent ponds in April after March rains had refilled the ponds. The surface areas of temporary and permanent ponds ranged from <0.01 to 0.21 ha and 0.04 to 13.8 ha, respectively, and temporary ponds were significantly smaller, on average, than permanent ponds. Fish were absent from all temporary ponds and present in all permanent ponds. We detected a difference in the zooplankton species assemblages of the temporary and permanent ponds. Out of 14 total zooplankton taxa that occurred in eight or more ponds, seven taxa were significantly more prevalent in temporary ponds and four taxa were significantly more prevalent in permanent ponds. The sizes of zooplankton in the temporary fishless ponds were greater than those in the permanent ponds with fish present. We concluded that pond size mediated susceptibility to pond drying, and pond drying determined the presence and absence of fish and their secondary trophic-level effect on zooplankton community structure.

Keywords Crustacean zooplankton · Temporary and permanent ponds · Pond size

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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). Organism body size and species composition of communities along this gradient are determined by both physical factors, such as pond drying, and biotic factors, such as predation (Wellborn et al., 1996). Pond studies conducted across environmental gradients can enhance our understanding of patterns in species traits and species assemblages (Wellborn et al., 1996; De Meester et al., 2005).

Wellborn et al. (1996) offered a schematic model of how species assemblages of lentic communities might be affected by pond drying and fish predators. According to their model, lentic systems would range from relatively small, temporary habitats with large-bodied invertebrates to larger permanent habits with predatory fish and small-bodied invertebrates. 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 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.

Zooplankton inhabit all sizes of lentic systems and have a wide range of phenotypes that allow them to live in temporary and permanent ponds. 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. Permanent ponds have fish that can have secondary effects through their predatory effects on large zooplankton. Thus temporary and permanent pond habitats potentially contain alternative zooplankton community types with different species assemblages (Wellborn et al., 1996).

Although studies have examined differences in zooplankton in natural water bodies with temporary to permanent hydroperiods (Cole, 1966; Brucet et al., 2005; Seminara et al., 2008; Tavernini, 2008), Wellborn et al.'s (1996) hypotheses have not been tested for zooplankton across a size gradient of small man-made water bodies by comparing zooplankton communities in fishless temporary ponds and permanent ponds with fish. Millions of small (<1 ha), artificial water bodies have been constructed across the U.S., with the greatest density of these impoundments from Kansas south to Texas (Smith et al., 2002). Our study is a unique study of the zooplankton of these man-made systems that dominate the central part of the US. In this article, we test Wellborn et al.'s (1996) hypotheses using data from a field study of the zooplankton assemblages of temporary and permanent ponds in the Lyndon B. Johnson (LBJ) Grassland, Texas. Specifically, we test three hypotheses: (1) Pond size is a determinant of whether the pond is temporary and fishless versus permanent with fish, (2) Crustacean zooplankton species assemblages are different in temporary versus permanent ponds, and (3) The body lengths of crustacean zooplankton differ between temporary fishless ponds and permanent fish ponds.

Methods

The LBJ National Grassland is located in Wise County in north-central Texas, approximately 80 km northwest of the Dallas-Ft. Worth area and consists of 8,220 ha of hardwood forests and prairie in numerous non-contiguous units (Fig. 1) (USDA, 1999). Before the U.S. government purchased the grassland in the 1930s, the area mostly consisted of abandoned farms with severe soil erosion problems. The grassland is managed by the USDA-Forest Service, which built hundreds of water retention levees and ponds to reduce soil erosion between 1958 and 1995. The ponds range from <0.1 to 13.7 ha and include both temporary and permanent ponds. An extended period of extreme drought in winter 2005–2006 (U.S. Drought Monitor Archives (http://www.drought.unl.edu/dm/archive.html)) ensured that most temporary ponds dried and provided the opportunity to compare the zooplankton communities of temporary and permanent ponds across a range of sizes once the ponds refilled.

In January and February of 2006, we located numerous ponds that had dried or that still retained water. From these ponds, we identified 20 that had dried and had not contained fish as evidenced by the lack of fish remains. These are termed temporary ponds. We do not have information about the hydroperiods of the temporary ponds. We further identified 18 ponds that had not dried and contained fish which are termed permanent ponds. In order to prevent possible pseudoreplication (Hurlbert, 1984) due to pond locations, we selected temporary and permanent ponds that were distributed across the grassland (Fig. 1). Pond surface areas at full capacity were determined by on-site measurements and aerial photography for smaller and larger ponds in June 2007.

Fish communities of ponds were categorized as either present or absent. Large permanent lakes have been stocked with gamefish and maintain established fish communities while smaller permanent ponds contain fish from unknown origins. We confirmed that smaller permanent lakes had fish by observing

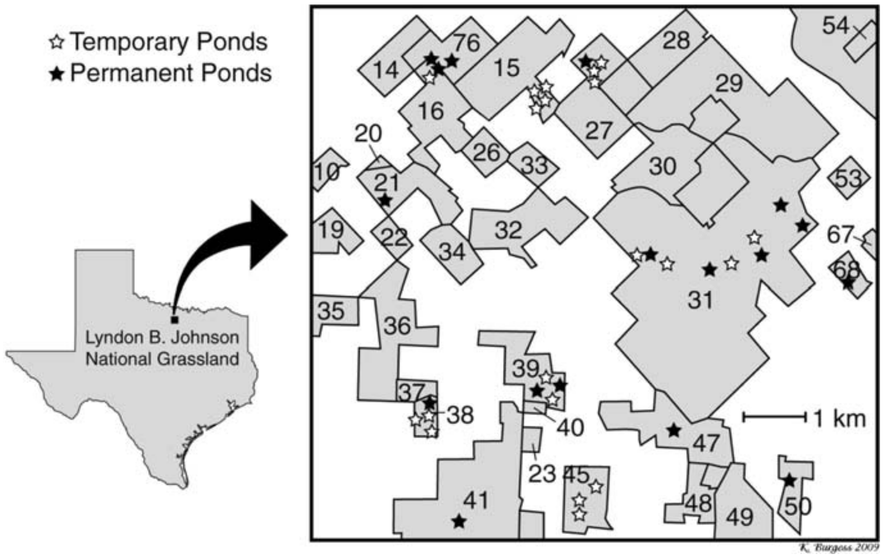

Fig. 1 Map of the LBJ National Grassland northwest of Dallas/Fort Worth, TX. The gray-shaded, numbered areas are units of the grassland, and the white-shaded areas are privately-owned land. Temporary and permanent ponds are indicated with white and black stars, respectively

fish from the shoreline or seining. Fish captured by seining were immediately released unharmed into the ponds**.** Fish absence in temporary ponds were confirmed by shoreline observations and observations during zooplankton sampling.

Temporary ponds were inundated and water levels increased in permanent ponds during the rains in March 2006. In order to determine zooplankton species composition, two composited horizontal tows with an 80-μm mesh conical plankton net were taken from each pond during the months of March (14–15) and April (5–7). Zooplankton samples were preserved in 75% undenatured ethanol. Because the copepods were not mature enough for species identification in the March sample, only the April sample was used for this study. Crustacean zooplankton were identified to the species level using taxonomic keys (Edmondson, 1959; Balcer et al., 1984; Hudson et al., 1998; Thorp & Covich, 2001). Each sample was examined two to three times by two different individuals to identify all species.

For each of the ponds, zooplankton body lengths were measured for a randomly-selected subsample of 25 individuals using a Zeiss dissecting microscope at 5X magnification with a digital camera (Axio Vision). Thus, there were 500 length measurements from the set of temporary ponds and 450 measurements from the set of permanent ponds. Using an equal number of measures from each pond allows the data to be combined to form a composite test of differences in size distributions. 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.

Because trophic state can impact zooplankton communities (Dodson, 1992; Jeppesen et al., 2000; Thackeray, 2007), we collected water samples for analysis of total phosphorus (TP) and total nitrogen (TN), by submerging a 250-ml Nalgene bottle under the surface of each pond 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).

Data analyses were performed using the Statistical Analysis System (SAS; Cody & Smith, 2006). Where departures from the assumptions of normality or homogeneity of variance occurred, data were analyzed using either nonparametric tests or transformations to logarithms.

Results

Temporary and permanent ponds differed in surface area (Table 1, Fig. 2). Temporary ponds ranged from

<0.01 to 0.21 ha in size while permanent ponds ranged from 0.04 to 13.8 ha (Fig. 2). Temporary ponds had a significantly smaller mean surface area than permanent ponds (Analysis of Variance of areas transformed to logarithms; $F = 17.1$; df = 1, 36; $P = 0.0002$; Zar, 1999). Nine of the 18 permanent ponds occurred within the size range of the temporary ponds and 13 of the 20 temporary ponds occurred within the size range of the permanent ponds.

Temporary and permanent ponds differed in concentrations of TN but not in the concentrations of TP (Table 1). Concentrations of TP and TN ranged from 22 to 265 mg/l and 552 to 2316 µg/l, respectively, which would classify the ponds as eutrophic (Wetzel, 2001) (Table 1). Mean TP concentrations in temporary ponds and permanent ponds did not differ significantly (Analysis of Variance on data transformed by logarithms; all $F = 0.58$; df = 1, 36; $P = 0.450$), but mean TN concentrations were significantly less (Analysis of Variance on data transformed by logarithms; all $F = 6.11$; df = 1, 36; $P = 0.018$) in temporary ponds than in permanent ponds. During the severe drought, we observed that cattle relied on the permanent ponds for water and the increased livestock densities in the pond watersheds may have contributed to increased nitrogen in the permanent ponds.

Table 1 Suface area, total nitrogen (TN) and total phosphorus (TP) of 20 temporary and 18 permanent ponds

Parameter	Temporary ponds		Permanent ponds	
	Mean	SD	Mean	SD
Area (ha)	0.08	0.06	2.12	3.78
TN (µg/l)	973	410	1247	404
TP (µg/l)	72	57	59	34

Shoreline observations and seining of the small permanent ponds revealed variable fish assemblages comprised of golden shiners (*Notemigonus crysoleucas*), bullheads (*Ictalurus* spp.), mosquitofish (*Gambusia affinis*), green sunfish (*Lepomis cyanellus*), bluegill (*L. macrochirus*), and largemouth bass (*Micropterus salmoides*). Previous surveys of larger permanent ponds which had been stocked with gamefish found fish species assemblages including largemouth bass, bluegill, green sunfish, redear sunfish (*L. microlophus*), warmouth (*L. gulosus*), gizzard shad (*Dorosoma cepedianum*), common carp (*Cyprinus carpio*), golden shiner, black bullhead, yellow bullhead (*I. natalis*), white crappie (*Pomoxis annularis*), and channel catfish (*Ictalurus punctatus*) (personal communication Dave Peterson, USDA).

We found 28 taxa of crustacean zooplankton in the 38 ponds (Drenner, 2008). Zooplankton taxa occurred in 1 to 19 of the 38 ponds and most taxa occurred in six or more ponds. The number of taxa per pond ranged from 2 to 10. The median taxa per pond were

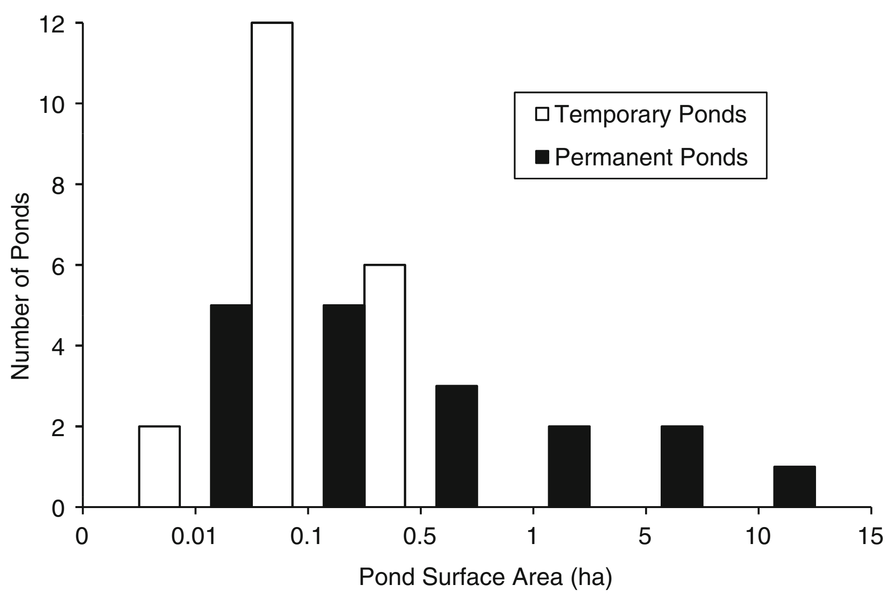

Fig. 2 Size frequency distributions of temporary and permanent ponds

seven and six for temporary and permanent ponds, respectively, with no statistically significant difference between pond types (Siegel–Tukey test of medians $\chi^2 = 0.004$; df = 1; $P = 0.9507$; Richter & Higgins, 2006). The number of taxa per pond was not correlated with pond area either within or across pond types (Spearman Rank Correlation Coefficient; $-0.10 < r_s < 0.23$; all $P > 0.30$; Zar, 1999).

There were 14 commonly occurring taxa that were observed in eight or more ponds, and the distribution of these taxa between pond types differed significantly (Likelihood Ratio Chi-Square = 100.6, df = 13, $P < 0.001$; Richter & Higgins, 2006) from that expected for a random distribution of occurrences relative to the frequency of each type of pond. Some taxa were more frequently observed in temporary ponds, while others were more frequently observed in permanent ponds. In order to evaluate whether these distribution patterns for individual taxa differed significantly from a random expectation, the probabilities of the observed distributions for each taxa among temporary and permanent ponds were computed using the hypergeometric distribution (Zar, 1999). For example, the hypergeometric probability that all 10 of the occurrences of *Bosmina longirostris* would occur in the 18 permanent ponds and none in the 20 temporary ponds is <0.001. Other taxa that were significantly more prevalent in permanent ponds included *Skistodiaptamus pallidus* ($P < 0.001$), *Tropocyclops prasimus* ($P = 0.013$) and *D. ambigua* ($P = 0.018$). Taxa that were significantly more prevalent in temporary ponds included *Simocephalus vetulus* ($P = 0.029$), *Microcyclops rubellus* ($P = 0.014$), *Daphnia laevis* ($P = 0.009$), *Acanthocyclops vernalis* ($P = 0.003$), *Ceriodaphnia* ($P = 0.001$), *Agliodiaptomus clavipes* ($P < 0.001$) and *Streptocephalus texanus* ($P < 0.001$). There were only three taxa whose frequencies of occurrence in the two pond types did not differ significantly from a random expectation. These included *Chydorus brevilabris* ($P = 0.255$), *Diaphanosoma* ($P = 0.259$) and *Alona quadrangularis* ($P = 0.208$). Thus, a majority (11 of 14) of the commonly occurring taxa were more prevalent in one type of pond (Fig. 3).

The mean sizes of zooplankton from all temporary and permanent ponds were 1.034 mm (SD = 1.399; $n = 500$) and 0.345 mm (SD = 0.260; $n = 450$), respectively. Most of the 450 zooplankton that were measured from permanent ponds had lengths <0.26 mm whereas most of the 500 zooplankton from temporary ponds had lengths >0.51 mm. More than 25% of the zooplankton from temporary ponds had lengths >1.0 mm, but fewer than 5% of zooplankton from permanent ponds had lengths >1.0 mm. The size frequency distributions of lengths in 500 individuals from temporary and 450 individuals from permanent ponds were significantly different (Kolmogorov–Smirnov Test, D = 0.403; $P = 0.0001$; Richter & Higgins, 2006) (Fig. 4).

We also examined the effects of pond type and size on the minimum and maximum sizes of zooplankton. The minimum lengths of zooplankton from temporary ponds were significantly greater than the minimum lengths from permanent ponds (Fig. 5A; Analysis of Variance on data transformed to logarithms; $F = 10.1$; df = 1, 36; $P < 0.001$; Zar, 1999). The maximum length of zooplankton from temporary ponds were also significantly greater than those from permanent ponds (Fig. 5B; ANOVA on data transformed to logarithms; $F = 32.4$; df = 1, 36; $P < 0.001$). The minimum and maximum zooplankton lengths in temporary and permanent ponds were not correlated with pond size (all $|r_s| < 0.38$; all $P > 0.10$).

Discussion

In our study, temporary ponds had significantly smaller surface areas than permanent ponds. The five smallest ponds were temporary and the nine largest ponds were permanent, but there was not a distinct size boundary between the two types for the other 24 ponds. Instead there was a broad overlap in sizes of temporary and permanent ponds which indicates other factors such as pond depth, soil permeability, potential goundwater sources, and the ratio of watershed area to pond area may also be important determinants of pond drying.

According to a species area curve for crustacean zooplankton in North American lakes (Dodson, 1992), four to nine species of crustacean zooplankton would be expected in ponds within the range of surface areas of our study. In our study, the number of crustacean zooplankton taxa per pond ranged from 2 to 10. The number of zooplankton taxa per pond was not correlated with pond area either within or across pond types. This lack of correlation between the number of

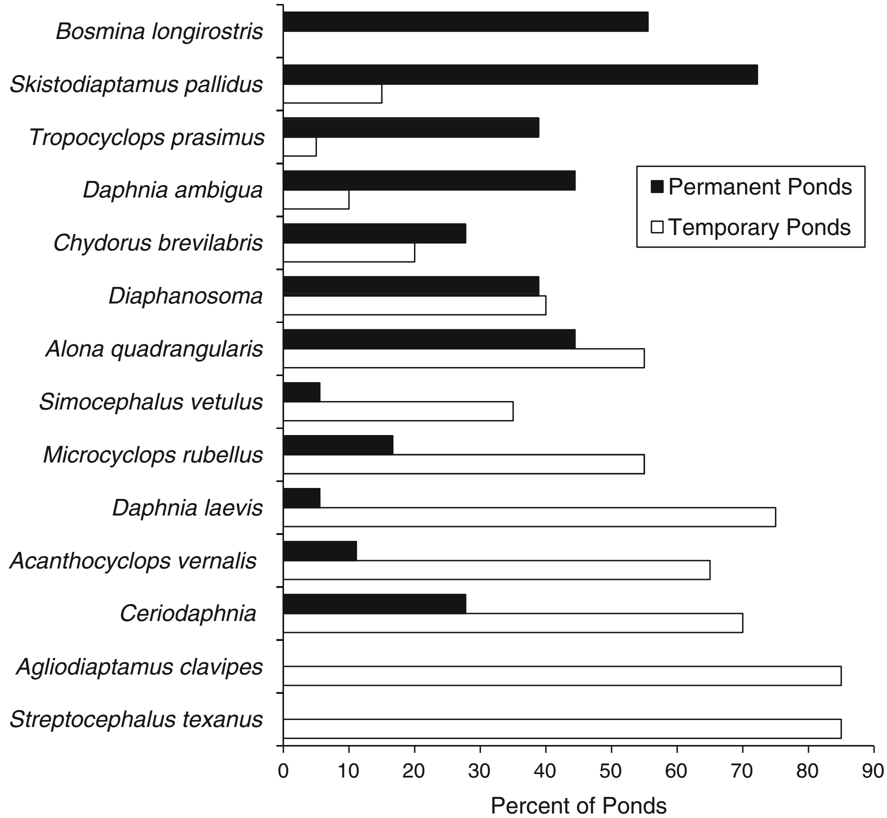

Fig. 3 Percent occurrence of the most commonly occurring zooplankton taxa in temporary and permanent ponds

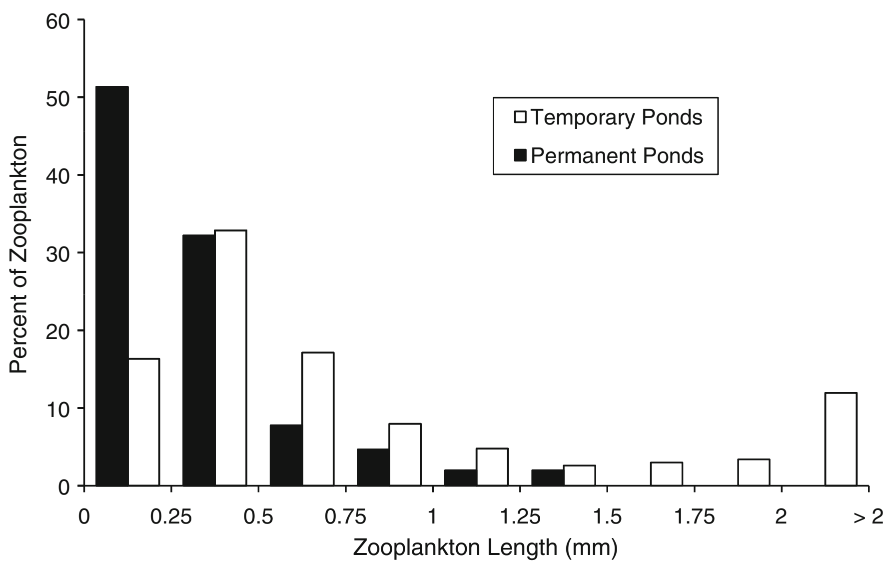

Fig. 4 Size frequency distributions of zooplankton in the temporary and permanent ponds

zooplankton taxa and pond size probably reflects the relatively narrow range of pond sizes in our study. Also our study is based on a single sampling time period and temporal variation in crustacean communities was not addressed by our study. This may have resulted in underestimating species numbers,

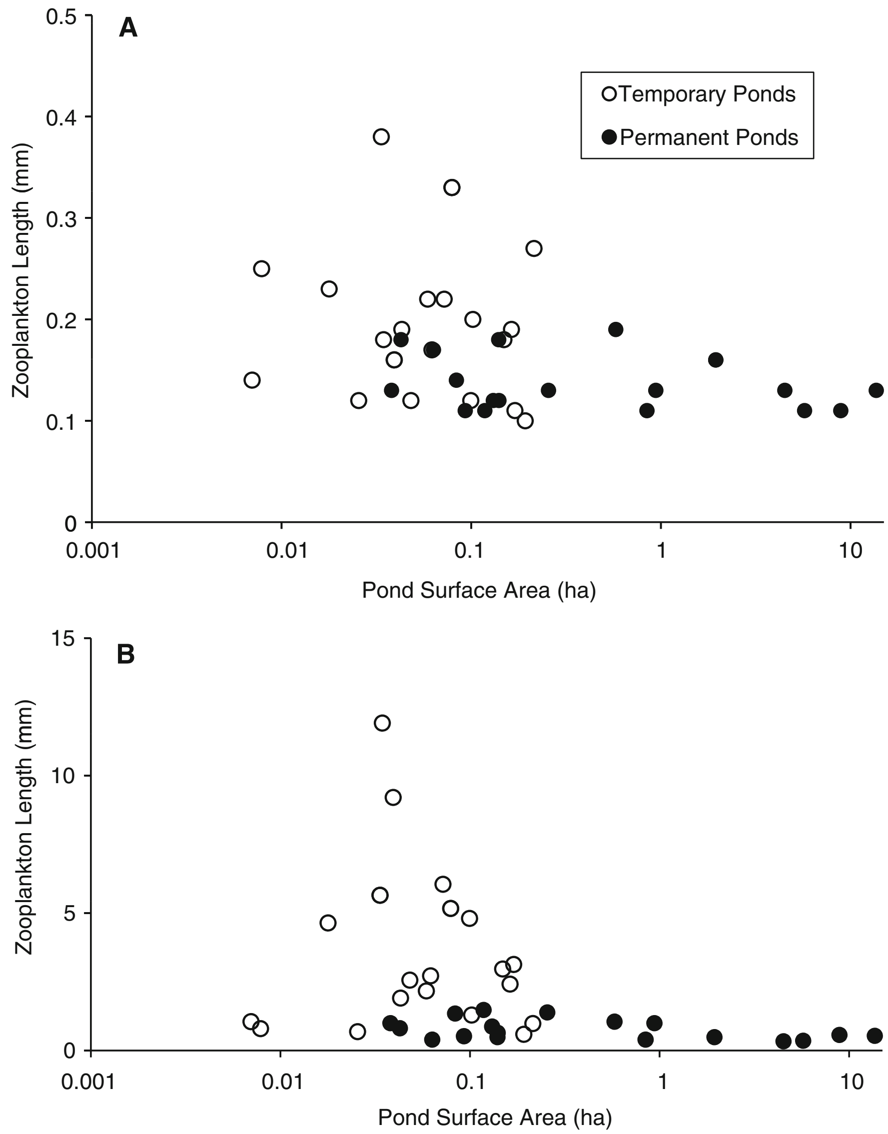

Fig. 5 Minimum and maximum sizes of zooplankton are shown in panels(**A**) and (**B**), respectively

especially in larger permanent ponds that might experience seasonal succession (Hutchinson, 1967).

Pond permanence affected the sizes of zooplankton. The mean, maximum, and minimum sizes of zooplankton were larger in temporary ponds than permanent ponds. Temporary ponds had larger zooplankton than permanent ponds because fish, which were present in the permanent ponds, feed as size-selective predators on large zooplankton (O'Brien, 1979; Lazzaro, 1987) and eliminate zooplankton species that cannot survive to a large adult size necessary for successful reproduction (Brooks & Dodson, 1965). Minimum zooplankton size may have been larger in the temporary ponds because, in the absence of fish, larger invertebrate predators selectively feed on the smaller zooplankton prey (Pastorok, 1981; Dodson, 1984), shifting the zooplankton community to larger species that are not as vulnerable to invertebrate predation (Dodson, 2005).

Pond permanence also affected the zooplankton community structure. The temporary and permanent ponds contained different communities, with the majority of species having an affinity for either temporary or permanent ponds. Only three of the 14 commonly occurring species were found in similar frequencies in temporary and permanent ponds.

The results of our study were, in general, consistent with the model of Wellborn et al. (1996) that recognized pond drying and fish as key ecological factors that shape freshwater communities. They predicted that lentic systems would range from relatively small, temporary habitats with large-bodied invertebrates to larger permanent habits with predatory fish and small-bodied invertebrates. On the grassland, ponds below 0.04 ha had dried, intermediate-sized ponds from 0.04 to 0.21 ha included both temporary and permanent ponds, and ponds larger than 0.25 ha were permanent. Temporary ponds had no fish and large-bodied zooplankton while permanent ponds had fish and small-bodied zooplankton assemblages.

Although we can conclude that the zooplankton community composition is different in the two types of ponds, we do not know whether it is due to the presence/absence of fish or due to pond permanence/impermanence because these variables are not independent in our study. Pond experiments where fish are added to the temporary ponds, or removed from the permanent ponds could help tease apart these confounding effects. One explanation for the different zooplankton assemblages in permanent ponds may be the differences in fish community structure. In order to examine this further, entire fish assemblages could be manipulated.

Biodiversity conservation at the landscape level has been shown to be dependent on maintenance of a diversity of water body types of different sizes, permanence and flow patterns (Williams et al., 2004; De Bie et al., 2008). Although small water bodies such as ponds can be the most common type of freshwater habitat (Smith et al., 2002; De Bie et al., 2008), small ecosystems have only recently been recognized as important habitats that maintain unique species assemblages that contribute to biodiversity (Collinson et al., 1995; Oertli et al., 2002; Scheffer et al., 2006; De Bie et al., 2008). Therefore, a region with a mixture of pond sizes will have higher biodiversity than an area with only one size of pond. In our study, temporary ponds had a significantly smaller mean surface area than permanent ponds but temporary and permanent ponds had about the same number of zooplankton species. We conclude that both temporary and permanent ponds appear to play important roles in maintaining total zooplankton species richness of the grassland, an area in Texas with few natural lakes. Small man-made water bodies are expected to increase 1–3% per year in the U.S. as more impoundments are constructed (Smith et al., 2002). Future increases in the number of small man-made water bodies in the U.S. (Smith et al., 2002) will increase the zooplankton species richness of landscapes that otherwise had few lakes.

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