Daphnia dominance and zooplankton community structure in fishless ponds

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Predation by fish has commonly been viewed as a primary driver of spatial and seasonal variation in Daphnia dominance and the size structure of zooplankton communities. Yet, previous research suggests that large Daphnia do not always dominate in the absence of predation. As alternatives to the planktivory model, numerous mechanisms have been put forth, including the effect of resource competition and its interaction with resource quantity and quality and abiotic factors (e.g. temperature). Here results are presented of a field survey of 18 fishless, permanent ponds in southwest Michigan in which spatiotemporal variation in Daphnia pulex abundance and several potential determinants of this variation are explored. Results revealed a large amount of variation in D. pulex incidence and relative biomass, with some ponds exhibiting seasonal losses, some having few or no Daphnia, and some being dominated by D. pulex for the entire sample period. Redundancy analysis of zooplankton composition and pond environmental variables (biotic and abiotic) showed no relationship between D. pulex biomass and measures of Chaoborus abundance, algal resource production, or algal resource quality (including seston C:N:P). Instead, pH and temperature (both of which covaried) showed the strongest relationship with D. pulex biomass.

INTRODUCTION

A topic of long standing interest in aquatic ecology is the determinant of variable dominance by large bodied *Daphnia* species. Historically, size-selective predation by fish has been regarded as a primary driver of spatial variation in the size structure of zooplankton assemblages and the relative abundance of large *Daphnia* species (Gliwicz and Pijanowska, 1989)—a notion dating back to the pioneering studies of Hrbacek *et al.* (Hrbacek *et al.*, 1961) and Brooks and Dodson (Brooks and Dodson, 1965). In addition to variation among lakes, numerous investigations have also revealed a consistent temporal component to *Daphnia* dominance within systems. Lakes within temperate regions commonly undergo seasonal succession, being dominated by large-bodied *Daphnia* species early in the growing season following the thawing of ice cover and spring mixing. This early season peak is commonly followed by dominance by small-bodied Cladocera (e.g. *Ceriodaphnia* and *Diaphanosoma*) or small copepods (Sommer *et al.*, 1986; Gliwicz and Pijanowska, 1989). Though several factors are thought to drive this pattern, fish predation has frequently been cited as a primary determinant [e.g. (Gliwicz and Pijanowska, 1989)].

There is ample evidence that fish predation can significantly alter the size structure of zooplankton communities and patterns of *Daphnia* dominance both among water bodies and seasonally within systems (Brooks and Dodson, 1965; Hall *et al.*, 1976; Gliwicz and Pijanowska, 1989; Carpenter and Kitchell, 1993; Mittelbach *et al.*, 1995). However, the majority of existing investigations have focused on lake systems. A small but notable body of research centered on shallow, fishless ponds suggests that dominance by large-bodied *Daphnia* need not be invariably linked to the presence of fish; small-bodied taxa can, at times, dominate zooplankton communities even in the absence of these planktivores (Hall *et al.*, 1970; Lynch, 1978; Smith and Cooper, 1982; Steiner, 2003; Steiner and Roy, 2003). These studies imply that the factors determining *Daphnia* relative abundance in these systems may be complex, reaching beyond a simple top-down framework.

Several alternative mechanisms can be invoked that may explain variable *Daphnia* dominance in fishless

ponds. First, predators other than fish are present in fishless systems (e.g. *Chaoborus*, Notonectids, and salamanders). Thus, top-down effects on size structure are still possible. Alternatively, resource-based effects and competitive hierarchies among zooplankton need not be static, temporally or spatially. Historically, larger zooplankton and large-bodied *Daphnia* have been viewed as competitive dominants (Brooks and Dodson, 1965; Hall *et al.*, 1976). Yet, a number of investigations (including laboratory, field, and model-based explorations) have shown that competitive outcomes and dominance between small-bodied zooplankton and large *Daphnia* species can be highly variable and dependent on aspects of algal resources (Neill, 1975a; Lynch, 1978; Smith and Cooper, 1982; Tillmann and Lampert, 1984; Romanovsky and Feniova, 1985; Bengtsson, 1987; Tessier and Goulden, 1987). *Daphnia* population performance and numerical dominance may be favored at high levels of resource abundance, whereas small-bodied taxa may maintain higher population growth rates and dominate communities at low resource levels (Romanovsky and Feniova, 1985).

In addition to quantity, resource quality may have additional impacts, either positive or negative, on *Daphnia* populations. *Daphnia* can access a broader size spectrum and larger size classes of algae compared with many small-bodied zooplankton (Burns, 1968; Neill, 1975b) and thus may be favored when larger-sized resources predominate. Conversely, large *Daphnia* are known to be inhibited by filamentous cyanobacteria and *Microcystis* due to greater susceptibility to feeding interference by these taxa (Gliwicz and Seidlar, 1980; Richman and Dodson, 1983; Gliwicz and Lampert, 1990). Thus, a preponderance of these large algal forms could promote dominance by small zooplankton. More recently, a large body of research has accumulated, focusing on algal stoichiometry (i.e. C:N:P content) as an important aspect of resource quality. *Daphnia* generally have higher phosphorus requirements compared with many small-bodied taxa (most small-bodied Cladocera and copepods) and may be favored when algal C:P and N:P ratios are low (Sterner and Hessen, 1994; Urabe *et al.*, 1997; Steiner, 2003).

Finally, abiotic factors (e.g. pH, temperature, and dissolved oxygen concentrations) have the potential to affect community structure through direct effects on species membership, selecting species with differential, physiologically-based tolerances. However, abiotic factors may also interact with biotic conditions. For instance, temperature could enhance the negative effects of exploitative resource competition, potentially altering competitive hierarchies. *Daphnia* are believed to be especially prone to high temperatures (Lynch, 1978; Moore and Folt, 1993).

Studies of zooplankton seasonal dynamics in fishless ponds have been largely relegated to studies of single systems; broader surveys, encompassing both spatial and temporal variation, are still lacking. In this paper data are presented from a survey of 18 fishless ponds in southern Michigan. In addition to tracking seasonal changes in zooplankton composition, several limnological variables (both biotic and abiotic) were also measured with the intention of exploring potential drivers of variation in *Daphnia* abundance.

METHOD

All ponds were within a 100 km radius around the W. K. Kellogg Biological Station (Hickory Corners, Michigan, USA), were fishless, and contained water year-round in the one to two years prior to the study (personal observation). Systems were chosen based on proximity to public roads and included a variety of gross physiognomies (including small forested ponds with tree canopies, larger wetlands with dense lily pad cover, and more open water systems). Maximum depth encountered was ∼1.6 m. Pond surface areas (measured in August 1997 or July 1998) ranged between 34 and 10 558 m^2 (Table I) (J. Chase, Missouri, personal communication). Note, however, that depth and surface areas varied greatly within several of the ponds during the year of the survey due to drought conditions.

Ponds were sampled monthly in 1998, beginning in late April and ending in late August. In most cases, zooplankton were collected with integrated tube samplers that extended to pond bottoms, with the exception of ponds less than ∼0.5 m in depth (which were sampled with a 2 L hand pitcher). Tube samplers varied in length (according to need) and were constructed of hard plastic tubing with an inner diameter of ∼7 cm. Sampling was conducted at mid-day. Samples were collected at several points, at even intervals, along a qualitative transect spanning from ∼1 m in from the pond edge to the center of each pond. At each sample point along the transect, the water column was sampled and the water poured through a 60 μm sieve to retain zooplankton; this was then repeated and a sample of equal volume poured through a separate 60 μm sieve. Thus, two replicate zooplankton samples were taken, each integrating spatial variation in the pond. Total sample volumes varied among ponds and ranged between 12 and 54 L per replicate. Larger sample volumes obtained in a subset of the study ponds spanning a range of productivities revealed that sample volumes of 10–24 L were adequate for detecting the majority (>80%) of zooplankton taxa. Since this study is concerned only with dominant zooplankton taxa, failure to detect rare taxa should not greatly affect the present results.

Zooplankton were preserved in acid Lugol's solution and later identified to the genus or species level, excepting

copepods, which were classed as calanoid or cyclopoid. Rotifers were identified to the genus or species level with the exception of members of the Notommatidae and Proalidae, which were identified to the family level, and the Bdelloidea, which were identified to the level of order. Protozoa and copepod nauplii were not enumerated. In each sample, fifty randomly chosen individuals of each taxon were also measured to obtain dry mass estimates using length-mass regressions (McCauley, 1984). *Chaoborus* were enumerated from zooplankton samples and a subset measured to obtain dry mass estimates using length–mass regressions. Low water levels late in the season made zooplankton sampling unfeasible in six ponds during the August sample period.

Pond water (1.5 L total) was collected at each sample point along the transect using the same samplers used to collect zooplankton, pooled, and immediately placed on ice, in the dark, for later analysis of chlorophyll *a* (Chl *a*), total phosphorus (TP), and seston C:N:P. Half of the water collected for chlorophyll was filtered onto Gelman A/E glass fiber filters (Gelman Sciences, Ann. Arbor, MI, USA) for measurement of total Chl *a* as a measure of algal biomass. The other half was first filtered through a 35 μm mesh and then filtered onto A/E filters to measure the 'edible' size fraction. Chl *a* was extracted in 95% ethanol and measured using narrow band fluorometry (Welschmeyer, 1994). Several traits may affect algal edibility, however, size was chosen as a key trait since it is known to be an important feeding constraint and it is easily measured. Thirty-five microns was chosen as an upper size limit for 'highly edible' versus 'grazer-resistant' algae based on known size preferences of *Daphnia* and small-bodied Cladocera (Sterner, 1989). Note, however, that edibility may be poorly estimated for copepods, overestimated for the remaining small-bodied zooplankton assemblage, and underestimated for *Daphnia* (Sterner, 1989). Water volumes filtered for analysis of each Chl *a* fraction varied, depending on pond productivity, but ranged between 10 and 200 mL.

Water samples for analysis of carbon, nitrogen, and phosphorus content of the edible size fraction of the seston were first filtered through a 35 μm mesh to remove zooplankton and large algae. This water was then divided in two and filtered onto two separate, precombusted A/E glass fiber filters. One filter was immediately frozen for later analysis of particulate phosphorus (see below). The other filter was first fumed with concentrated HCl to remove carbon contributions from $CaCO_3$ and then frozen for later analysis of carbon and nitrogen content using a Carlo-Erba CHN analyzer (Carlo Erba Strumentazione, Milan, Italy). As with Chl *a* analyses, water volumes filtered for C:N:P analysis varied with pond productivity but fell between 10 and 200 mL. Water samples (250 mL) for TP measurement were frozen for later analysis. TP and particulate phosphorus were analyzed using the ammonium molybdate method, following persulfate digestion (Wetzel and Likens, 1991).

Four to five days following biotic sampling, abiotic measures were taken. Temperature, pH and dissolved oxygen concentrations were measured in the field, midday, using a Horiba U-10 multi-probe (Horiba Ltd., Kyoto, Japan). Measures were taken at mid-depth at 3–5 points along qualitative transects and then averaged. Due to low water levels and an overabundance of sediments in the water column, abiotic measures were not taken in four ponds in late July. For the same reason, abiotic measures could not be obtained in eight ponds during the late August sample period.

For analyses, measures from each sample period and pond were treated as separate data points. Except for two sample dates in two ponds, in which *Daphnia ambigua* and *Daphnia dubia* were observed, *D. pulex* was the only *Daphnia* species encountered in the survey. When present, *D. ambigua* and *D. dubia* only comprised a minor fraction of zooplankton biomass (<5%) and were thus excluded from analyses (their inclusion does not alter results).

Hereafter, *D. pulex* is referred to as *Daphnia*. Zooplankton assemblages were first characterized by placing taxa into four categories: *Daphnia*, copepods (calanoid plus cyclopoid), rotifers (all taxa combined), and small-bodied Cladocera (all taxa combined). Relationships between the $\log_{10} (x+1)$ transformed biomasses of these zooplankton groups and potential explanatory variables were analyzed using redundancy analysis (RDA), a form of direct gradient analysis (Legendre and Legendre, 1998). A constant was added to zooplankton biomass measures due to zero values. A total of ten environmental measures were entered as explanatory variables in the RDA. These included $\log_{10}$ *Chaoborus* biomass, $\log_{10}$ TP, $\log_{10}$ total Chl *a*, $\log_{10}$ <35 μm Chl *a*, $\log_{10}$ >35 μm Chl *a*, pH, temperature, oxygen concentration, and <35 μm seston C:P and N:P (atomic ratios). RDA was performed using the program RDACCA, distributed free of charge from the web site http://www.fas.umontreal.ca/BIOL/legendre/. All other analyses were performed using Systat Version 8.0.

RESULTS

Table I summarizes means and ranges for several of the variables measured in the ponds. A total of 79 zooplankton taxa were encountered in the survey. When averaging responses of the major zooplankton groupings from all ponds, *Daphnia* dominated early in the growing

Table I: Means and ranges of limnological variables measured in the study ponds over the survey period

Pond	Latitude	Longitude	Surface area (m^2)	Temp (°C)	Dissolved oxygen (mg L^{-1})	pH	Total phosphorus (µg L^{-1})	Total Chl *a* (µg L^{-1})
Lux13	42°28.79′N	85°27.22′W	449	22 (17.0–28.0)	8.8 (4.9–11.0)	7.6 (6.8–7.9)	55.8 (30.7–80.0)	10.7 (4.4–28.6)
Lux14	42°28.53′N	85°27.69′W	570	20.9 (16.0–27.5)	9.1 (7.7–10.6)	6.4 (5.6–7.4)	95.8 (77.0–135.2)	29.3 (10.0–56.6)
4H	42°23.56′N	85°22.82′W	960	20.7 (15.0–26.8)	13.2 (9.5–19.3)	8.8 (8.1–9.5)	152.1 (70.6–272.3)	125.0 (1.6–471.4)
P15	42°24.54′N	85°23.51′W	707	21.5 (15.0–25.8)	12.9 (7.0–24.2)	7.6 (7.5–7.6)	14.1 (11.3–18.4)	2.8 (0.7–4.9)
P14	42°24.54′N	85°23.51′W	707	21.4 (15.0–25.4)	12.8 (5.2–31.1)	7.6 (7.4–7.9)	17.1 (13.7–18.8)	3.3 (2.1–4.5)
BMR	42°39.21′N	85°25.15′W	340	18.4 (11.5–25.2)	4.5 (3.5–5.2)	6.3 (6.2–6.4)	102.4 (69.6–130.7)	30.6 (9.8–46.8)
Lux12	42°28.53′N	85°27.69′W	260	24.2 (15.0–33.2)	18.6 (7.2–31.4)	6.0 (4.9–6.9)	389.7 (247.5–555.7)	207.6 (69.3–572.0)
Lux19	42°28.76′N	85°27.43′W	34	17.4 (15.0–20.0)	0.4 (0.2–1.0)	5.9 (5.6–6.2)	229.9 (106.4–335.8)	69.8 (3.6–112.8)
Upt3	42°40.06′N	85°27.32′W	4337	17.2 (11.0–21.9)	1.4 (0.3–3.3)	5.9 (5.7–6.2)	135.3 (78.4–225.1)	77.5 (7.7–155.3)
Lux11	42°28.37′N	85°27.70′W	439	19.6 (16.0–26.0)	9.7 (8.6–10.5)	7.0 (5.9–8.9)	88.8 (35.7–200.9)	75.1 (10.7–254.3)
Shaw5	42°36.00′N	85°23.59′W	2534	18.4 (13.0–23.7)	4.1 (3.4–5.7)	5.5 (5.3–5.8)	51.5 (29.5–86.9)	40.4 (8.5–78.1)
Upt2	42°40.07′N	85°27.05′W	320	16.4 (10.0–20.5)	1.3 (0.16–4.3)	5.6 (5.3–6.0)	150.2 (72.2–285.4)	37.1 (13.0–59.8)
Upt1	42°40.06′N	85°27.32′W	662	14.8 (10.0–18.0)	6.7 (0.4–17.0)	6.5 (6.4–6.6)	156.6 (54.1–339.2)	45.7 (7.0–142.6)
Shaw4	42°36.00′N	85°23.59′W	4208	19.4 (15.0–24.0)	4.6 (0.3–9.0)	5.4 (5.3–5.4)	136.8 (32.7–370.7)	54.1 (5.1–239.7)
OL1	42°35.94′N	85°24.67′W	10558	19.4 (14.0–24.7)	2.4 (2.0–2.9)	6.2 (6.1–6.3)	112.1 (72.0–154.0)	18.3 (2.6–30.9)
P12	42°24.54′N	85°23.51′W	707	20.3 (15.0–23.0)	4.9 (1.9–9.7)	7.3 (7.2–7.7)	18.8 (12.9–25.7)	3 (1.6–6.5)
Lux16	42°28.43′N	85°27.82′W	400	18.3 (13.5–22.6)	9.6 (7.0–15.0)	6.6 (6.2–7.0)	208.3 (101.0–293.0)	82.1 (41.1–115.6)
Shaw3	42°35.97′N	85°25.50′W	1094	18.9 (13.5–26.0)	6.6 (0.7–15.0)	5.5 (5.0–5.8)	272.3 (179.6–412.6)	14.8 (3.2–38.2)

(continued)

Table I: Continued

Pond	<35 µm Chl a (µg L⁻¹)	>35 µm Chl a (µg L⁻¹)	Zooplankton dry weight (µg L⁻¹)	*Daphnia pulex* % relative biomass	*Chaoborus* dry weight (µg L⁻¹)	Seston C:P (atomic)	Seston N:P (atomic)
Lux13	6.2 (2.5–17.6)	4.5 (1.2–11.0)	1936.5 (97.8–3901.7)	0.00	0.008 (0–0.04)	382 (323.1–474.8)	38.5 (32.1–43.7)
Lux14	8.7 (4.2–19.6)	20.6 (4.1–39.2)	752.6 (225.8–1778.4)	0.15 (0–0.33)	3.1 (0–14.6)	281.2 (234.7–373.3)	27.9 (21.6–44.1)
4H	85.1 (1.74–346.9)	40 (0–124.6)	177.4 (9.5–513.6)	0.72 (0–3.60)	57.2 (13.7–170.0)	235.4 (173.1–317.2)	27.4 (14.9–46.0)
P15	1.5 (0.8–2.8)	1.3 (0–3.2)	54.6 (12.4–84.9)	2.64 (0–10.36)	49.1 (4.5–135.2)	425.9 (289.8–497.2)	38.2 (27.1–53.3)
P14	1.7 (1.3–2.7)	1.7 (0.8–2.4)	62.9 (26.6–140.7)	4.51 (0–16.52)	43.0 (8.7–132.5)	422.1 (256.4–525.0)	56.6 (22.7–143.0)
BMR	14.2 (7.8–27.2)	16.3 (2.0–32.1)	151.6 (74.2–238.5)	30.09 (0–89.19)	38.0 (0–82.0)	295.4 (183.7–430.4)	30 (18.5–38.9)
Lux12	175.7 (59.3–545.2)	31.9 (5.6–93.3)	145.0 (12.6–314.9)	30.99 (0–72.41)	171.1 (19.9–411.4)	198.9 (171.9–222.6)	16.5 (13.1–19.2)
Lux19	53.7 (1.9–88.5)	16.1 (1.7–25.2)	329.2 (57.6–1013.1)	36.01 (0–95.10)	168.0 (0–575.7)	171.9 (124.6–205.3)	25.4 (16.9–38.7)
Upt3	43.1 (3.8–111.5)	34.4 (1.0–106.1)	79.7 (32.2–181.7)	36.32 (13.75–62.00)	203.7 (0.6–380.3)	335.7 (124.8–596.7)	58.7 (15.7–153.5)
Lux11	64 (5.0–232.9)	11.1 (5.0–21.4)	45.3 (3.6–159.1)	38.82 (0–74.39)	75.7 (8.9–229.1)	338.3 (266.6–443.1)	33.8 (27.9–46.5)
Shaw5	10 (3.3–18.5)	30.4 (5.2–59.6)	30.7 (18.6–52.1)	40.45 (20.29–73.32)	36.3 (14.8–62.9)	379.2 (265.4–564.6)	44.6 (18.1–103.8)
Upt2	25.2 (8.1–36.6)	11.9 (4.9–23.2)	240.8 (7.8–769.7)	40.71 (0–93.69)	160.5 (14.7–454.4)	227 (143.1–342.2)	27.2 (15.3–39.3)
Upt1	18.1 (3.7–45.7)	27.6 (0–96.9)	629.0 (14.3–1374.7)	48.79 (1.74–84.76)	78.2 (0.12–303.4)	215.3 (116.8–337.4)	28.2 (12.4–52.1)
Shaw4	12.7 (1.7–51.6)	41.3 (2.7–188.1)	67.9 (29.2–130.9)	52.26 (1.02–80.67)	16.2 (2.2–47.3)	397.4 (238.1–586.6)	44.3 (24.3–91.0)
OL1	7.7 (1.9–13.6)	10.5 (0.7–17.5)	390.8 (16.2–1021.1)	65.78 (0–97.94)	91.6 (0–198.0)	290.3 (220.5–397.0)	27.1 (22.6–36.8)
P12	1.9 (0.7–4.2)	1.1 (0.7–2.3)	171.4 (89.3–1262.2)	69.88 (42.43–98.13)	71.5 (25.2–193.2)	435.2 (284.2–548.7)	50 (21.7–105.8)
Lux16	41.7 (21.0–81.6)	40.4 (15.5–71.8)	48.3 (11.4–86.5)	71.81 (31.11–94.13)	115.2 (8.3–250.1)	236.1 (121.0–347.1)	24.4 (11.3–51.0)
Shaw3	8.7 (1.3–20.8)	6.2 (1.9–17.5)	1012.1 (70.9–2868.3)	80.92 (52.83–99.37)	119.9 (7.4–266.4)	418.6 (268.8–639.7)	39.9 (26.3–60.3)

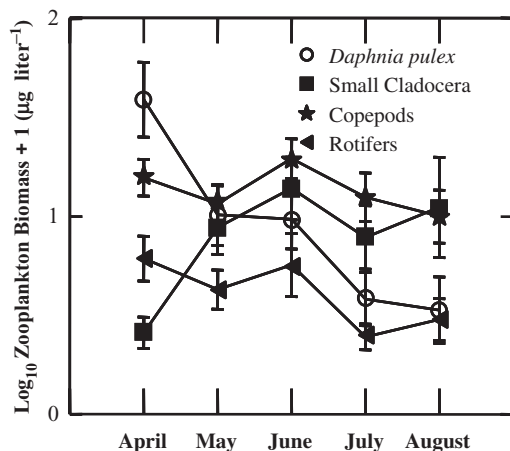Surface area was estimated in August 1997 or July 1998. Ponds are ordered as in Figure 2.

Fig. 1. Seasonal patterns of zooplankton biomass averaged across all 18 study ponds. Shown are responses for *Daphnia pulex*, rotifers (all taxa combined), small-bodied Cladocera (all taxa combined), and copepods (all taxa combined, excluding nauplii). Standard error bars are displayed.

season and then declined mid-season (Figure 1). In contrast, small-bodied Cladocera biomass increased later in the survey period (Figure 1). A weak negative correlation between *Daphnia* and small-bodied Cladocera biomass was detected ($r = -0.26$, $P = 0.019$). Small Cladocera were dominated by *Ceriodaphnia* spp., *Diaphanosoma brachyurum*, *Chydorus sphaericus*, *Scapholeberis* spp., *Alona* spp. and *Pleuroxus* spp. Total copepod biomass was relatively stable across the sample period when averaging across systems, while rotifers showed a decline in biomass during the last two sample dates (Figure 1). *Daphnia* biomass was only weakly correlated with copepod biomass ($r = -0.19$, $P = 0.085$); no relationship was detected with rotifer biomass ($r = 0.059$, $P = 0.59$).

Patterns averaged across systems mask the large degree of among pond variation in zooplankton seasonal dynamics (Figure 2). For example, in several systems, *Daphnia* comprised a minor fraction of total zooplankton biomass, even early in the growing season (e.g. Figure 2A–D). Conversely, some ponds failed to exhibit strong successional patterns, with *Daphnia* comprising a major component of the zooplankton assemblage for the duration of the study period (Figure 2P–R). Relative biomass of the major small zooplankton groupings also varied greatly both temporally (within ponds) and spatially (among the ponds).

Though fish were absent, several planktivores inhabited the study ponds—primarily species of Notonectids, Dytiscids, Chaoborids, Pleids and salamanders, though relative abundances varied greatly among systems (personal observation). Of these, *Chaoborus* was the only taxon that attained sufficient densities in plankton samples to be accurately enumerated. A significant relationship

between $\log_{10}$ *Daphnia* biomass and $\log_{10}$ *Chaoborus* biomass was not detected ($P = 0.44$), nor was a relationship detected with rotifer ($P = 0.74$) or copepod biomass ($P = 0.28$). A negative but very weak relationship between $\log_{10}$ small Cladocera biomass and $\log_{10}$ *Chaoborus* biomass was detected ($r_2 = 0.066$, $P = 0.020$).

Redundancy analysis allowed examination of the relationship between pond environmental measures and variation in zooplankton community structure across all samples. The first four canonical axes generated by the RDA accounted for 16.6, 12.5, 5.7 and 1.1% of the variation in zooplankton composition. The analysis was focused on the first two axes as the third and fourth axes explained a minor proportion of variation. *Daphnia* biomass correlated negatively and small Cladocera biomass correlated positively with the first canonical axis (Table II, Figure 3). Hence, this axis captured variation in *Daphnia* biomass and its negative relationship with small-bodied Cladocera biomass. Copepods correlated positively and small Cladocera correlated negatively with RDA axis 2 (Table II, Figure 3). Temperature and pH were strongly and positively related to axis 1 (Table II). Thus, *Daphnia* biomass decreased and small-bodied Cladocera increased with increasing pH and temperature (Figure 3). RDA axis 2 correlated with measures of algal productivity and nutrient limitation; algal production (total, <35 μm and >35 μm Chl *a*) was positively associated with RDA axis 2 while seston C:P was negatively correlated with axis 2 (Table II, Figure 3). Thus, copepods were associated with higher algal production while small-bodied Cladocera biomass was negatively associated with RDA axis 2 (Figure 3). RDA results were similar when using percent relative biomass of *Daphnia*, small-bodied Cladocera, copepods, and rotifers as dependent variables.

By utilizing all samples from the survey, the RDA encompassed both spatial (among pond) and temporal (within pond) variation in zooplankton composition and environmental variables. Figure 4 shows how RDA axis 1 scores were distributed in relation to both time of sample and pond identity. RDA 1 scores became more positive later in the growing season (Figure 4A), consistent with the general seasonal decline in *Daphnia* biomass (Figure 1). However, RDA scores varied greatly among ponds, growing more negative in ponds that were, on average, dominated by *Daphnia* (Figure 4B). Temperature and pH showed contrasting patterns in spatial and temporal variation. pH showed a weak trend with time of year, with variability among systems declining later in the sample period (Figure 5A). However, pH varied most strongly among ponds, with *Daphnia*-dominated systems being associated with lower median values of pH (Figure 5B). In contrast to pH, temperature varied most strongly with time of year, increasing later in the sample period (Figure 6A). However,
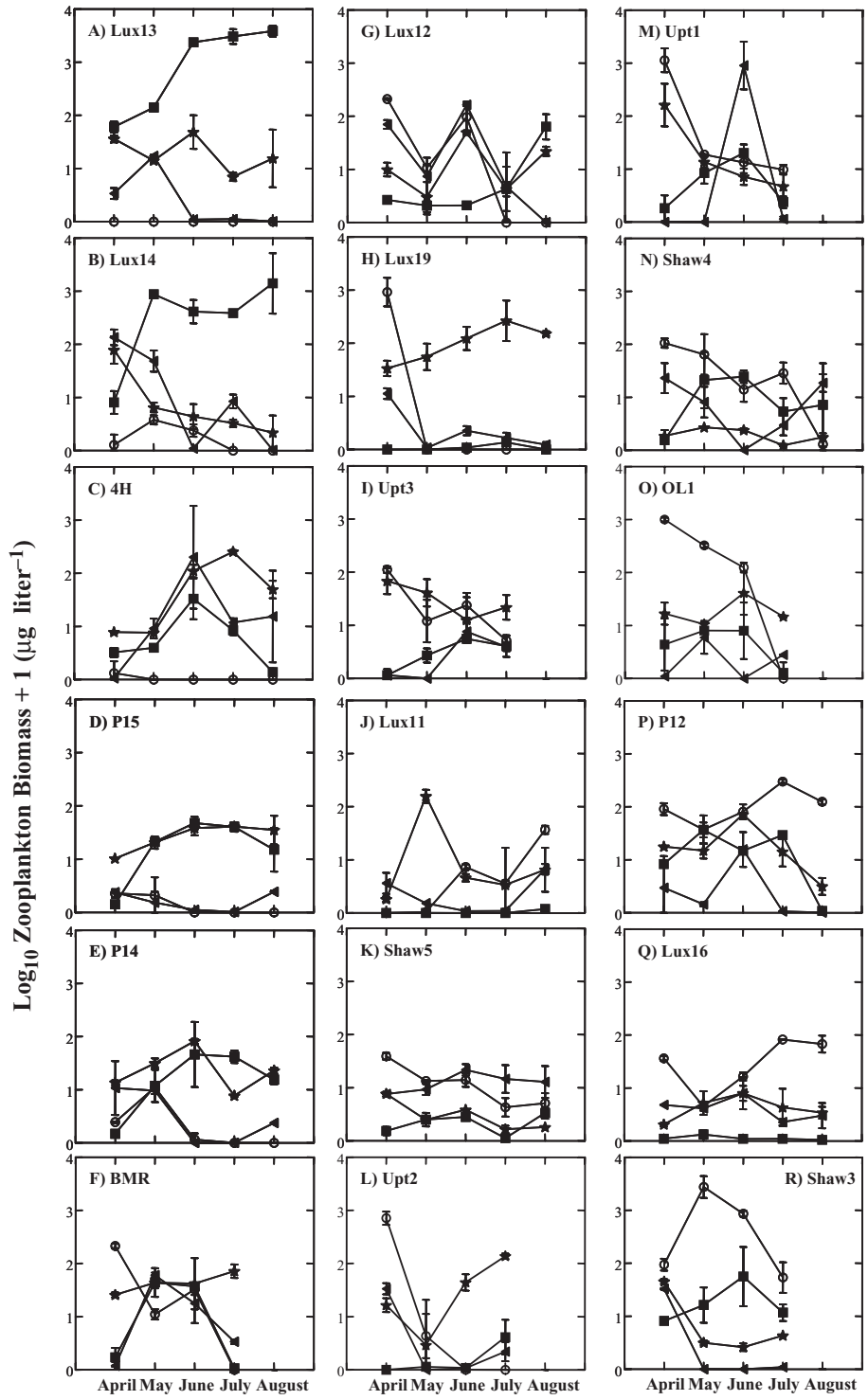
Fig. 2. Biomass responses of *Daphnia pulex*, rotifers, small-bodied Cladocera, and copepods in all 18 fishless ponds (**A**–**R**). Symbols as in Figure 1. Ponds are ordered from low to high mean relative biomass of *Daphnia pulex*, based on monthly measures averaged over the sampling period. Data points are the means of two replicate samples (±1 SE).

Table II: Results of the RDA of zooplankton biomass (response variables) and pond environmental measures (explanatory variables)

	Axis 1	Axis 2	Axis 3	Axis 4
Response variables				
Log_{10} *Daphnia*	**−0.541**	−0.272	0.024	0.062
Log_{10} small Cladocera	**0.414**	**−0.476**	−0.023	0.059
Log_{10} copepod	0.163	**0.354**	**0.351**	0.211
Log_{10} rotifer	0.002	0.218	**−0.473**	0.124
Explanatory variables				
Log_{10} TP	−0.216	0.230	−0.295	0.338
Log_{10} total Chl *a*	0.017	**0.558**	**−0.478**	−0.006
Log_{10} <35 μm Chl *a*	0.006	**0.655**	−0.283	−0.005
Log_{10} >35 μm Chl *a*	0.066	**0.417**	**−0.661**	−0.089
Log_{10} Chaoborus	−0.280	0.312	0.084	0.098
pH	**0.657**	0.217	0.184	0.275
Temperature	**0.779**	−0.246	−0.063	−0.165
Oxygen concentration	0.279	0.052	**−0.527**	−0.027
Seston C:P	−0.097	**−0.396**	0.134	**−0.532**
Seston N:P	0.021	−0.132	0.260	0.055

Shown are correlations with the ordination axes (fitted site scores). Variables that were significantly correlated with each axis are shown in bold ($P < 0.05$, Bonferroni adjusted).

Fig. 4. Box plots of RDA 1 scores. (**A**) Variation in scores through time. (**B**) Spatial (among pond) variation in RDA 1 scores. Ponds are ordered as in Figure 2 from ponds with low mean relative biomass of *Daphnia* to systems that were, on average, dominated by *Daphnia*.

temperature also varied among systems; ponds in which *Daphnia* were consistently a minor component of the zooplankton community (e.g. Lux13, Lux14, 4H and P15) tended to have higher median temperatures (Figure 6B).

DISCUSSION

When averaging among all ponds, results supported the general model of early season *Daphnia* dominance and late season dominance by small-bodied taxa. Yet, more striking was the large amount of spatial variation in *Daphnia* seasonal abundance revealed by the survey; *Daphnia* dominance is not assured in these systems, even early in the growing season. This is a surprising finding when considering the substantial amount of research that has emphasized fish predation as a primary regulator of large *Daphnia* populations. It is clear that variability in *Daphnia* abundance and changes in zooplankton community size structure need not be invariably linked to fish predation, a

Fig. 3. Canonical ordination (RDA) of zooplankton biomass and environmental variables. Response variables (solid symbols) were log_{10} biomass of *Daphnia pulex* (D. pulex), Small-bodied Cladocera (Sm. clad), copepods (Cop), and rotifers (Rot). Explanatory environmental variables (open symbols) were log_{10} *Chaoborus* biomass (Chaob), log_{10} total phosphorus (TP), log_{10} total chlorophyll *a* (Tchl), log_{10} < 35 μm chlorophyll *a* (<35 chl), log_{10} > 35 μm chlorophyll *a* (>35 chl), pH, temperature (Temp), oxygen concentration (Oxy), and <35 μm seston C:P and N:P. Shown are correlations between variables and each RDA axis.
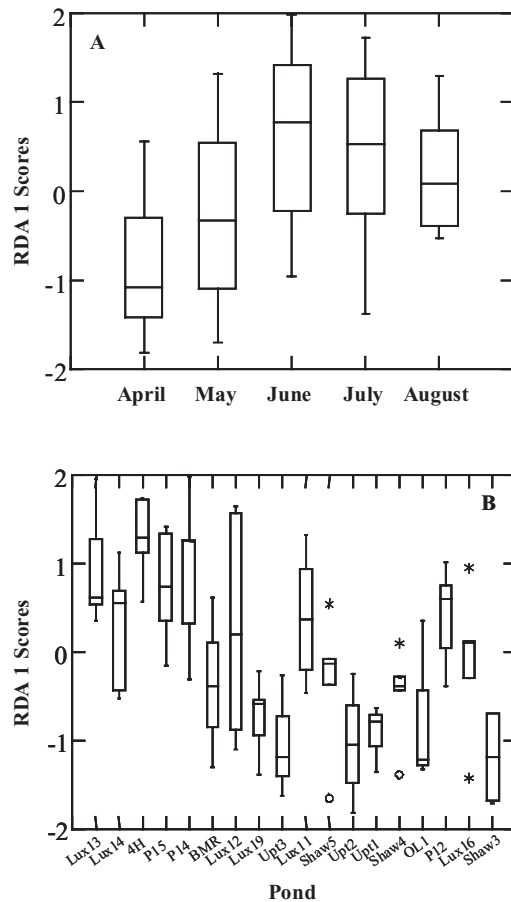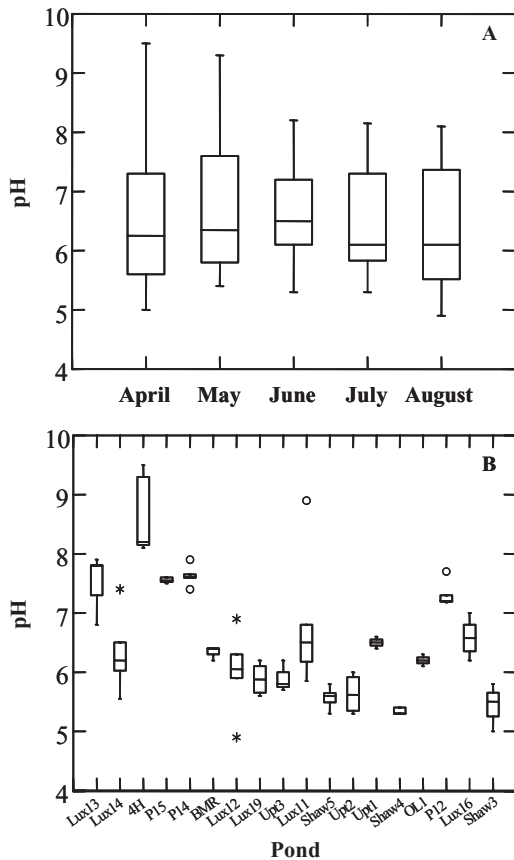
Fig. 5. Box plots of pond pH. (**A**) Variation in pH through time. (**B**) Variation in pH among ponds. Ponds are ordered as in Figure 2.
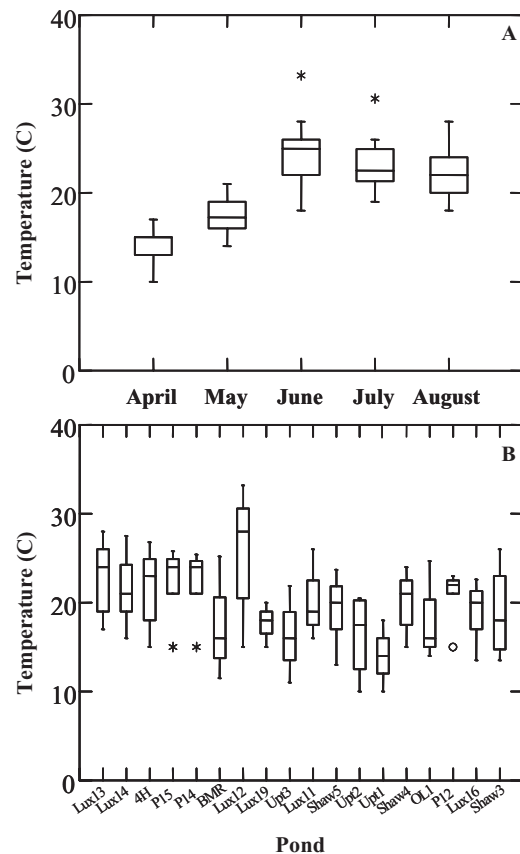

Fig. 6. Box plots of pond temperature. (**A**) Variation in temperature through time. (**B**) Variation in temperature among ponds. Ponds are ordered as in Figure 2.

finding that complements previous pond studies that have drawn similar conclusions (Hall *et al.*, 1970; Lynch, 1978; Steiner, 2003; Steiner and Roy, 2003).

Though fish were absent, several other predators were present in the study ponds. The most prominent in samples of the water column were species of the phantom midge larvae, *Chaoborus*. The ability of this planktivore to control large-bodied *Daphnia* populations is uncertain; though some studies have found significant negative effects (Mackay *et al.*, 1990), many have revealed weak or inconsistent impacts on large *Daphnia* species (Lynch, 1979; Neill, 1981; Steiner, 2003). Results of the RDA and correlations from the field survey suggest that *Chaoborus* may not be an effective determinant of *Daphnia* abundance or zooplankton community structure. However, because other planktivorous taxa were not enumerated, the role that alternate predators play in generating observed patterns remains unknown. Previous research indicates that *Notonecta* and salamanders (e.g. *Ambystoma*) can effectively control large *Daphnia* populations (Murdoch *et al.*, 1984; Morin, 1987; Arner *et al.*, 1998). Yet, several studies

suggest that *Daphnia* declines in fishless ponds need not be linked to these predators; *Daphnia* perform poorly even when all predators are excluded (Lynch, 1978; Smith and Cooper, 1982; Morin, 1987; Steiner, 2003; Steiner and Roy, 2003). Though the relative importance of planktivory remains unclear, these studies indicate that abiotic factors and/or biotic factors other than predation may drive variable *Daphnia* dominance in fishless systems.

As an alternative to the planktivory framework, interspecific competition has been previously cited as a potential driver of *Daphnia* midsummer declines (DeMott, 1989). A negative relationship between *Daphnia* and small-bodied Cladocera biomass (Figure 3) is consistent with the existence of exploitative resource competition. For competition to drive spatiotemporal variation in *Daphnia* abundance, however, competitive effects must be variable in space and time. Multiple factors have been hypothesized to mediate the strength and outcome of competition between large *Daphnia* and small-bodied taxa (Bengtsson, 1987; DeMott, 1989). For example, several studies have pointed to productivity

and algal resource concentration as important influences on zooplankton competitive outcomes [e.g. (Tillmann and Lampert, 1984; Romanovsky and Feniova, 1985; Bengtsson, 1987)]. Algal resource quality, including C:N:P content and the inhibitory effects of large algae, has also been frequently cited (Gliwicz and Seidlar, 1980; Richman and Dodson, 1983; Sterner and Hessen, 1994; Gliwicz and Lampert, 1990; Urabe *et al.*, 1997; Steiner, 2003). However, patterns exposed in the present investigation provided little support for the importance of algal stoichiometry. Moreover, system productivity and algal-resource abundance (including concentrations of edible and inedible algae) appeared to have little influence on *Daphnia* biomass. Instead, negative covariation between *Daphnia* and small-bodied competitors appeared to be linked primarily to abiotic factors. *Daphnia* biomass increased, and small-bodied Cladocera biomass decreased, with decreasing levels of pH and temperature.

Previous studies have suggested that temperature may effect changes in zooplankton dominance and size structure (Bengtsson, 1987; Moore and Folt, 1993). Large *Daphnia* are thought to be favored by low temperatures, facilitating their dominance early in the growing season. Increasing temperatures may differentially favor small-bodied taxa, permitting competitive reversals and shifts in relative abundance (Bengtsson, 1987; Moore and Folt, 1993). In a recent experiment utilizing several of the ponds in this survey, the strength of competitive effects of small zooplankton on *Daphnia pulex* was found to vary most strongly with algal C:P content (Steiner, 2003); a finding that appears to contradict the present results. However, this study also noted that temperature was correlated with seston C:P; high C:P ratios were associated with higher temperatures (Steiner, 2003). Though C:P may have influenced competition effects in Steiner (Steiner, 2003), these survey data suggest that temperature may have been a more important driver of variable competition intensity.

Results indicate that pond pH may have also influenced patterns of *Daphnia* abundance. The role of pH as a driver of zooplankton community structure has been explored, largely within the context of lake acidification. Many available studies suggest that high pH actually favors *Daphnia* relative to other taxa (Barmuta *et al.*, 1990; Berzins and Bertilsson, 1990; Hornstrom *et al.*, 1993; Beklioglu and Moss, 1995). This runs counter to results of this survey in which high pH was associated with a greater abundance of small-bodied Cladocera. However, *Daphnia pulex* may be unique among its congenerics; in a study of fishless, acidic bog-lakes, Arnott and Vanni (Arnott and Vanni, 1993) showed that *D. pulex* is favored by low pH. In these systems, increasing pH facilitated the invasion of small-

bodied taxa, a finding entirely consistent with the natural relationships exposed in the present investigation.

The majority of empirical studies of the determinants of zooplankton community structure have centered on biotic mechanisms—namely the impact of planktivory, resource competition, resource quantity, and resource quality (DeMott, 1989; Gliwicz and Pijanowska, 1989). Though these factors may have influenced patterns in some ponds and time periods in the present study, observed variation in zooplankton community organization was most strongly related to abiotic factors. This does not negate the potential influence of biotic processes; abiotic conditions may have interacted with competition effects, planktivory, or resource-based effects. Hence, an interesting direction for future research is stronger experimental quantification of such abiotic–biotic interactions. Indeed, the small amount of variation accounted for in my analyses indicates that much remains unexplained in these ponds. Regardless, my results may have important implications given the considerable evidence that large-bodied *Daphnia* can have strong effects on the structure, stability, and functioning of planktonic ecosystems (Mazumder, 1994; Schindler *et al.*, 1997; Cottingham and Schindler, 2000; Steiner, 2002). Human-induced environmental impacts and global change include effects on both the temperature and pH of aquatic systems. Consequently, understanding and predicting how environmental impacts will alter the structure and functioning of aquatic systems may critically depend on understanding how such factors will affect key species such as large-bodied *Daphnia*. The overriding influence of temperature and pH exposed in this study suggests that such impacts in shallow ponds and wetlands could be substantial.

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