



Comparison of processes regulating zooplankton assemblages in new freshwater pools

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Abstract

We compared the relative importance of colonization history to other known regulators of freshwater zooplankton assemblages (i.e. disturbance and nutrient enrichment) during this six-month study of initial colonization in artificial freshwater pools. We experimentally manipulated 16 small (1.5 m diameter) pools for permanence (permanent vs. temporary) and resource availability (\pm nitrogen & phosphorus). Nitrogen and phosphorus were added to high resource level pools in concentrations typical of eutrophic waters, while low resource level pools did not receive added nutrients. Permanent pools were maintained with added tap water and temporary pools dried out naturally for one month.

Zooplankton colonization was limited to only 10 rotifers (species of *Brachionus*, *Cephalodella*, *Lecane*, *Lepadella*, *Rotaria*, and *Trichocerca*) and 2 crustaceans. Treatments significantly affected physical-chemical variables, colonization curves (species richness through time), and mean cumulative species number. Results indicate that local conditions (habitat permanence and resource availability) had the greatest effect on zooplankton species richness. However, low species diversity and little treatment effect on species relative abundance patterns suggest that colonization history (dispersal) was also important. Therefore, colonization history and local conditions were jointly responsible for structuring zooplankton assemblages in this study. Colonization history may have lasting effects on zooplankton composition in older, natural systems as well, but may be overlooked at some scales of measurement.

Introduction

Successful colonization of isolated bodies of water is the combined result of an organism arriving and then persisting within a particular body of water. Regional processes of dispersal that determine colonization history increase species richness by supplying communities with new species and new individuals of existing species. On the other hand, local processes (biotic interactions) and environmental conditions tend to increase mortality, thereby decreasing species richness (Ricklefs, 1987). Although regional and local processes are expected to affect community composition (Ricklefs, 1987), the relative roles of each have been examined in only a few systems (Underwood et al., 1983; Roughgarden et al., 1987; Tilman, 1997).

This study was designed to evaluate the relative roles of regional (colonization history) and local processes (disturbance and resource availability) during

initial colonization of freshwater pools. We experimentally manipulated local processes and used strong treatments (drying and high nitrogen and phosphorus levels) with the rationale that if colonization was important despite strong treatments, it may also be important given less extreme local processes. In addition, we reasoned that colonization should be most important to community composition during initial colonization: if colonization history (dispersal) was unimportant initially, its influence in established communities would likely be unimportant as well.

Materials and methods

The experiment was performed on the campus of the University of Illinois at Springfield. Sixteen plastic wading pools (1.5 m diameter and 0.3 m deep) were manipulated for permanence and resource availability,

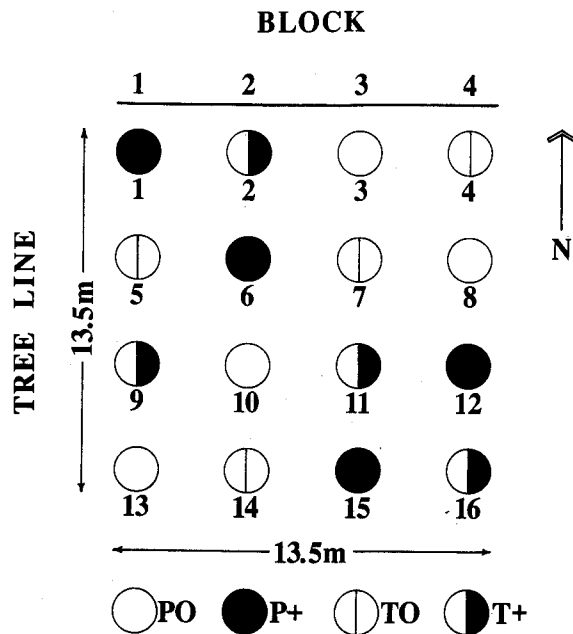


Figure 1. Diagram of experimental randomized block design. P = permanent pools, T = temporary pools, (+) = with N & P, (0) = without N & P.

thus establishing different habitat conditions. Tap water was added as necessary to one half of the pools (permanent habitat), while the other half of the pools dried out naturally (temporary habitat). High resource availability was established by adding nitrogen (as NH_3Cl) and phosphorus (as P_2O_5) in concentrations typical of eutrophic waters. Minimum nitrogen (N) and phosphorus (P) concentrations in nutrient enriched pools were 2.4 mg l^{-1} and 0.08 mg l^{-1} , respectively (Wetzel, 1983). Furthermore, in an attempt to limit growth of cyanobacteria, N and P were manipulated to obtain TN:TP ratios of 30:1 (Smith, 1983). Low resource level pools, on the other hand, did not receive added nutrients.

In all, there were 4 treatment combinations: permanent / +NP, permanent / ONP, temporary / +NP, and temporary / ONP (hereafter referred to as P+, P0, T+, and T0, respectively). All treatment combinations were replicated 4 times. To account for a possible tree-line effect, the pools were arranged in a randomized block design (Figure 1). The blocks were aligned with the tree line so that successive blocks were progressively farther away from the tree line. One of each treatment combination was randomly assigned to each block.

The experiment ran for 25 weeks, from 25 May 1995 through 17 November 1995. Pools were sampled in random order on the same day every week and at approximately the same time each day. All equipment used for sampling was cleaned with alcohol and rinsed with distilled water between pool samples. Water temperature, dissolved oxygen (DO), and pH were measured in each pool weekly using appropriate meters. A 500 ml water sample (125 ml from each quadrant) was also collected for the following chemical analyses: chlorophyll *a*, total nitrogen (TN), total phosphorus (TP), soluble-reactive phosphate (SRP), total alkalinity, conductivity, and total hardness. All analytical procedures were performed according to APHA (1989).

In addition, a 2-l water sample (500 ml from each quadrant) was collected from each pool for zooplankton analysis. The pooled water sample was concentrated onto 35- μm mesh plankton netting, rinsed into a 20 ml scintillation vial, and preserved with 4% buffered sugar-formalin (Haney & Hall, 1973; Steedman, 1976). Approximately 10% of the preserved volume was examined microscopically in Sedgwick-Rafter chambers for species identification and relative abundance. Zooplankton relative abundance scores were based on the number of organisms observed in the entire Sedgwick-Rafter chamber at 100 \times magnification. Scores ranged between 1 and 5 (1 = rare, 5 = abundant). The following keys were used for zooplankton species identification: Harring & Myers (1924, 1926), Brooks (1966), Edmondson (1966), Yeatman (1966), and Stemberger (1979).

Treatment effects on zooplankton colonization curves and physical-chemical variables were assessed using a two-way, repeated measures ANOVA for a randomized block design (SAS, 1985). Two-tailed *t*-tests were used to compare mean cumulative number of zooplankton species among treatments (Borland, 1991). Canonical discriminant analysis (SAS, 1985) was used to explore zooplankton relative abundance and physical-chemical variable patterns through time. For purposes of the statistical analyses, data were entered as zeros when temporary pools were dry (weeks 15 through 21). Following the experiment, leaf litter was collected from each pool, dried, and weighed. Leaf litter biomass results were analyzed using a two-way ANOVA for a randomized block design and were used to evaluate the effect of leaf fall on treatments.

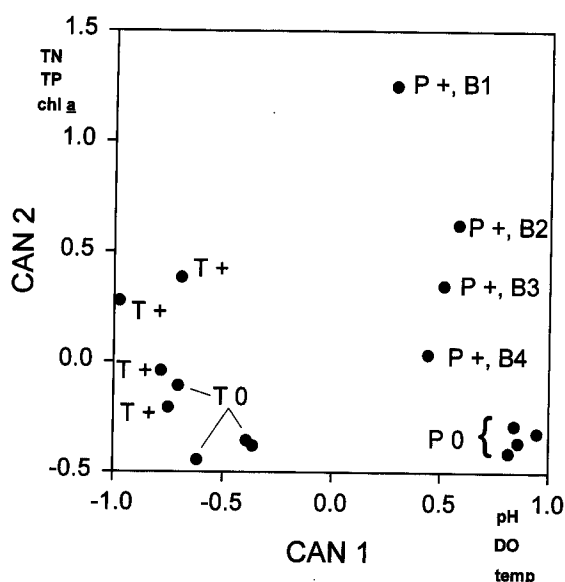


Figure 2. Canonical discriminant analysis of physical-chemical variables. CAN 1 and CAN 2 = 48% and 21%, respectively, of total data set variation. Overall canonical variate, $p = 0.0001$. Variables listed on an axis were strongly correlated with that canonical variate. Note separation of permanent (P) and temporary (T) pools on CAN 1, +NP (+) and ONP (0) pools on CAN 2, and the block effect (B) as a gradient on CAN 2.

Results

Physical-chemical variables

As expected, treatment differences were found for most physical-chemical variables. Temporary pools dried completely by 27 September (week 18) and remained dry until 25 October. Drying had the most pronounced effect on physical-chemical variables, but effects due to nutrient enrichment and block were also evident (Figure 2). Significantly ($p = 0.0003$) more leaves fell into the pools in blocks closest to the tree line (Figure 1). This result explained the significant block effect ($p < 0.05$) on important variables such as N, P, and chlorophyll *a* (Figure 2). Time significantly affected all variables ($p < 0.001$).

Drying significantly affected ($p < 0.05$; Table 1) water temperature, pH, dissolved oxygen (DO), total nitrogen (TN) and total phosphorus (TP). Higher water temperature and lower DO concentrations were obvious consequences of lower water volumes in temporary pools (Table 2). Although drying affected both TN and TP, the effect was most evident following leaf fall, especially for phosphorus. Leaf fall also affected DO concentrations, presumably due to the increased respiration accompanying leaf decomposition.

As intended, nutrient enrichment resulted in significantly greater ($p < 0.01$; Table 1) concentrations of TN, TP, and chlorophyll *a* and a higher TN:TP ratio ($p = 0.0001$) compared to non-enriched treatments (Table 2). Also as intended, mean TN:TP ratios in nutrient-enriched pools were greater than 30:1 (mean = 32), while TN:TP ratios in non-enriched pools averaged 15. Cyanobacteria were never observed in any pool. Therefore, greater phytoplankton abundance (chlorophyll *a*) suggests that nutrient enrichment increased the resource quantity available for colonizing zooplankton species. The apparent absence of cyanobacteria also suggests that resource quality was adequate, although phytoplankton composition was not specifically manipulated for edibility given the uncontrolled zooplankton assemblages developing during this natural colonization study.

Zooplankton species richness and abundance

Colonization was limited to only 10 rotifer species, 1 cladoceran, and 1 cyclopoid copepod (Table 3). Colonization patterns were evaluated at three scales of measurement: (1) overall mean cumulative species richness per treatment, (2) species richness through time (colonization curves), and (3) zooplankton relative abundance through time.

A comparison of cumulative species richness among treatments (Table 3) shows a significant reduction ($p < 0.01$) in species richness in temporary treatments compared to permanent ones, although species richness was low in all treatments. Cumulative species richness was not significantly affected by nutrient enrichment.

Similarly, drying had the greatest effect on colonization curves (Figure 3), or species richness through time. There was a significantly greater number of species ($p < 0.05$) present in permanent pools compared to temporary ones. However, in contrast to results of cumulative species richness, colonization curves were also significantly affected ($p < 0.05$) by nutrient enrichment, most notably in permanent pools. Differences in colonization curves were apparent by approximately week 12, when temporary pools began to dry (Figure 3). Species richness gradually decreased in temporary pools during the drying period, while in permanent pools, species richness continued to increase (Figure 3). In general, the most successful colonizers in temporary pools arrived prior to week 10 (Table 4).

Table 1. P-value results from repeated measures ANOVA of physical-chemical variables. Time significantly affected all variables ($p < 0.001$)

Variable	Treatment			
	Block (df = 3)	Permanence (df = 1)	Nutrient Enrichment (df = 1)	Permanence X Nutrient Interaction (df = 1)
Temperature	0.03	0.0001	0.26	0.62
pH	0.11	0.0001	0.0001	0.009
Dissolved oxygen	0.03	0.02	0.82	0.12
Total nitrogen	0.001	0.04	0.0001	0.85
Total phosphorus	0.0001	0.0001	0.01	0.97
TN:TP	0.0001	0.62	0.0001	0.003
Chlorophyll <i>a</i>	0.033	0.17	0.002	0.93

Table 2. Mean level (\pm SD) of physical-chemical variables per treatment: P = permanent, T = temporary, (+) = +NP, (0) = ONP

Variable	Treatment			
	P0	P+	T0	T+
Temperature °C	20.5 (6.5)	20.8 (6.6)	23.0 (6.9)	22.4 (7.6)
pH	8.1 (0.74)	7.9 (0.9)	7.8 (0.8)	7.1 (1.2)
Dissolved oxygen mg l ⁻¹	8.08 (3.1)	8.33 (3.0)	7.70 (3.0)	6.97 (3.4)
Total nitrogen mg l ⁻¹	2.6 (2.1)	5.9 (3.5)	2.0 (2.1)	5.6 (4.1)
Total phosphorus mg l ⁻¹	0.21 (0.26)	0.37 (0.48)	0.45 (1.0)	0.69 (1.2)
TN:TP	17.2 (14.6)	27.4 (16.0)	10.8 (11.8)	36.9 (33.2)
Chlorophyll <i>a</i> µg l ⁻¹	26.7 (23.3)	83.8 (108)	29.6 (22.3)	95.2 (219.6)

Table 3. Colonization summary by pool. (X) Indicates species presence at any time during the study period. Pools are grouped by treatment: P+ = Perm / +NP, P0 = Perm / ONP, T+ = Temp / +NP, T0 = Temp / ONP

Species	Treatment														No. pools per species		
	P+		P0				T+				T0						
Pool no.:-	1	6	12	15	3	8	10	13	2	9	11	16	4	5	7	14	
<i>Rotaria</i> sp. Scopoli	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	16
<i>Cephalodella gracilis</i> (Ehrenberg)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	16
<i>Lepadella patella</i> (Müller)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	14
<i>Cephalodella catellina</i> (Müller)	X	X		X	X	X	X	X	X	X	X	X	X		X	X	14
<i>Brachionus bidentata</i> Anderson	X		X	X	X	X	X	X						X			8
<i>Colurella obtusa</i> (Gosse)	X	X	X	X	X	X	X	X									8
<i>Eucyclops agilis</i> (Koch)	X	X	X		X	X	X		X								7
<i>Lecane closterocerca</i> Schmarda			X	X	X	X	X	X									6
<i>Brachionus angularis</i> Gosse			X	X	X												3
<i>Illoricata rotifer</i>	X						X										2
<i>Trichocerca porcellus</i> (Gosse)	X																1
<i>Alona costata</i> Sars	X																1
Cumulative species richness per pool	10	6	8	8	9	8	9	7	5	3	4	4	5	3	4	3	

Table 4. Number of pools that a single species was recorded in for the specified week

Species	Week												
	1	3	5	7	9	11	13	15	17	19	21	23	25
<i>Lepadella patella</i> (Müller)	1						1	3	7	7	8	12	8
<i>Rotaria</i> sp. Scopoli		2	6	7	10	14	15	11	14	9	8	9	8
<i>Cephalodella gracilis</i> (Ehrenberg)			1	8	9	8	10	9	7	3	4	4	1
<i>Cephalodella catellina</i> (Müller)			3	12	5	1	3						
<i>Eucyclops agilis</i> (Koch)				2	1		1	1	2	2	4	3	5
<i>Trichocerca porcellus</i> (Gosse)				1	1								
<i>Brachionus bidentata</i> Anderson							1	2	6	5	3	2	
<i>Colurella obtusa</i> (Gosse)							2	3	5	4	6	5	2
Illoricate rotifer							1			1	1	1	
<i>Lecane closterocerca</i> Schmarda								1	1	5	4	5	3
<i>Alona costata</i> Sars									1	1	1	1	1
<i>Brachionus angularis</i> Gosse									1	1	1		

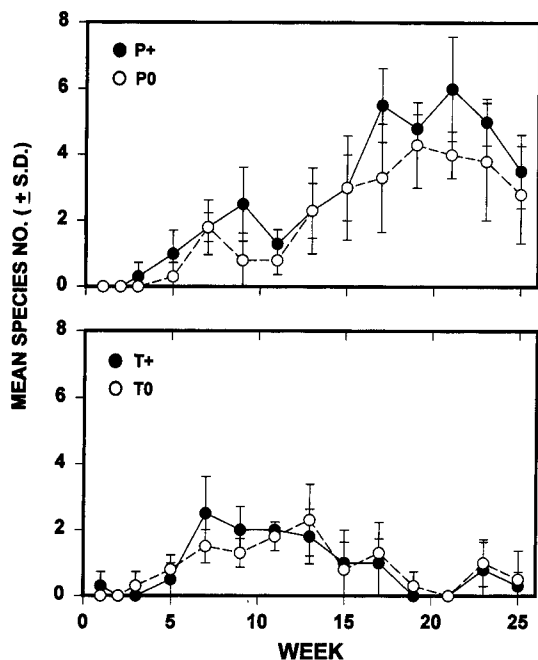


Figure 3. Colonization curves, showing number of species per treatment through time. P+ = Perm/+NP, P0 = Perm/ONP, T+ = Temp/+NP, T0 = Temp/ONP.

Despite marked differences in physical-chemical characteristics and species richness among treatments, zooplankton relative abundance patterns (Figure 4) were generally unaffected by treatment, with two exceptions. Pool #1 had the greatest number of species throughout the study period (Table 3) and Pool #6

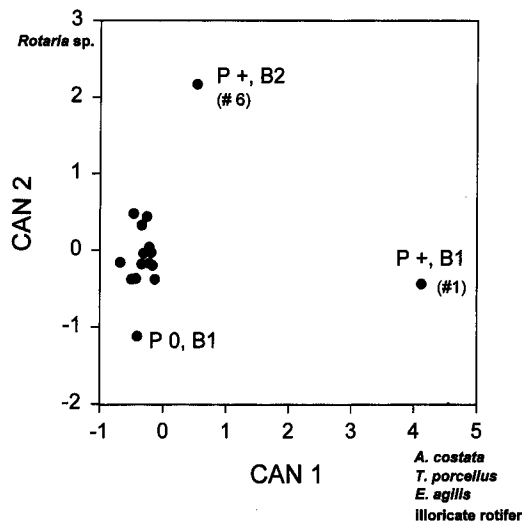


Figure 4. Canonical discriminant analysis of zooplankton relative abundance through time. CAN 1 and CAN 2 = 49% and 19%, respectively, of total data set variation. Overall canonical variate, $p = 0.0001$. Variables listed on an axis were strongly correlated with that canonical variate. Symbols are the same as in Figure 2.

differed, not so much in species composition, but in colonization timing and persistence of species present.

In summary, cumulative species richness and colonization curves (species richness through time) were negatively affected by drying. Nutrient enrichment had no effect on cumulative species richness per treatment, but did positively affect colonization curves. However, colonization history (dispersal) was important to community assembly, indicated by limited species richness (only 12 species in all pools) and confounded

treatment effects on zooplankton relative abundance patterns.

Discussion

The effect of disturbance on community structure is dependent on the severity and frequency of the disturbance (Sousa, 1984). Loss of habitat represents a severe disturbance. In temporary environments, species survival depends on the ability of established species to adapt to a dry environment (Wiggins et al., 1980). Species assemblages in temporary habitats are limited and dependent on life history strategies (Wiggins et al., 1980) and habitat duration (Schneider & Frost, 1996), and species richness tends to increase with increasing hydroperiod (Schneider & Frost, 1996).

As expected, both mean cumulative species richness and species richness through time (colonization curves) were negatively affected by drying. We also found that community composition was limited by the timing of species arrival in temporary pools. Half of all species observed arrived in the first 7 weeks, prior to the temporary pools drying. In general, the early-arrivals were more successful colonizers in temporary pools than the species arriving after the pools began to dry. Of the late-arrivals (Table 4), only *Brachionus bidentata* Anderson was able to establish viable populations in temporary pools. The fact that species richness continued to increase in permanent pools after week 10 indicates that viable zooplankton propagules were available, but were limited in the temporary pools by severe habitat conditions.

Although resource availability generally tends to increase recruitment to an area (Hobbs, 1989), the effect of nutrient enrichment on phytoplankton and zooplankton species richness and abundance is not easy to predict (Hall et al., 1970; O'Brien & DeNoyelles, 1974; Lynch & Shapiro, 1981). In the present study, nutrient enrichment appeared to increase the availability of high-quality resources for colonizing zooplankton species based on increased levels of chlorophyll *a* in the absence of cyanobacteria. Increased resources positively affected species richness through time, but did not affect cumulative species richness. Although two species, *Trichocerca porcellus* (Gosse) and *Alona costata* Sars, both present in a single P+ pool (Table 3), may have contributed to increased species richness in permanent enriched pools, overall species composition varied little with nutrient enrichment (Table 3).

In contrast, species persistence varied considerably among species and treatment (Table 4). Several species, notably *Eucyclops agilis* (Koch), *Colurella obtusa* (Gosse), and *B. bidentata*, demonstrated greater persistence in nutrient enriched pools compared to non-enriched ones. Therefore, in this study, nutrient enrichment increased species richness in permanent pools due to increased persistence of some species, rather than to a greater diversity of low-persistence species.

Species relative abundance patterns through time reflect an undetermined combination of seasonal timing and colonization history. However, if observed species were uniformly present via colonization (dispersal), then all species present should have undergone seasonal successions at similar timings, but at amplitudes determined by treatments. In other words, treatment differences should have been most evident (unconfounded by colonization) if local conditions were primarily responsible for species abundance patterns. Since abundance patterns generally did not reflect treatment differences, colonization history seemed to be a confounding factor in species relative abundance through time.

The zooplankton species observed in this study consisted almost entirely of rotifer species common to this geographic region (Harring & Myers, 1924; 1926; Brooks, 1966; Edmondson, 1966; Yeatman, 1966; Stemberger, 1979). Considering the proximity of the study location to a permanent body of water (1 km), it may be surprising that a greater number of species were not able to colonize the pools: relatively few other groups were observed during the study period (species of Chironomidae, Odonata, Coleoptera, Culicidae, Notonectidae). Also worth noting, is the absence of species typical of temporary waters (Wiggins et al., 1980; Williams, 1987), such as the larger cladoceran species and species of Anostraca, Ostacoda, and Conchostraca.

However, the low species diversity in this study is consistent with results in intertidal (Underwood et al., 1983; Roughgarden et al., 1987) and terrestrial environments (Tilman, 1997) where species recruitment was limited by long-distance passive dispersal of larvae or seeds. Recruitment of zooplankton to new pools depends on similar processes. For many zooplankton species, resting and anhydrobiotic stages not only allow for species survival during unfavorable periods (Pennak, 1989; Wallace & Snell, 1991), but they also provide the means by which species are passively dispersed via wind, rain, aquatic insects or migratory

waterfowl (Maguire, 1959, 1963; Proctor & Malone, 1965; Lampert & Sommer, 1997). While the belief that many zooplankton species have cosmopolitan distributions is based on the supposed ease of dispersal of resting and anhydrobiotic stages (Pennak, 1989; Pejler, 1995), in actuality, dispersal mechanisms and efficiency of dispersal for many zooplankton species remain largely unknown.

While this experiment was not designed to evaluate dispersal mechanisms, the low species diversity and type of species present in this study seem to indicate that cosmopolitan distributions are slowly developed, and dispersal is neither uniform nor easily predicted. While some zooplankton may be cosmopolitan, others are not (Frey, 1986; Wallace & Snell, 1991) and some species are more readily dispersed than others (Boileau & Hebert, 1991; Jenkins, 1995).

We have attempted to show that during initial colonization in this study, zooplankton species assemblages were regulated by a combination of local conditions and colonization history. Local conditions affected species richness and persistence, but colonization history was a constraint on species richness and a confounding variable for relative abundance patterns through time.

Although this study was limited to colonization in new pools, the importance of colonization history has been demonstrated in other established, natural environments (Underwood et al., 1983; Tilman, 1997). Additional studies comparing local processes and colonization history are needed for a better understanding of the relative importance of the processes regulating community structure in natural, freshwater environments.

Acknowledgments

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