

## Dispersal-limited zooplankton distribution and community composition in new ponds

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### Abstract

Twelve new experimental ponds were constructed identically, filled simultaneously, had similar physical and chemical properties, and were maintained with minimal manipulation. Colonizing zooplankton communities were sampled bi-weekly for one year. Rotifers dominated zooplankton communities in densities, biomass, and species number (47 of 61 observed species were rotifers). Only 14 species were observed in all 12 ponds; 9 were rotifers. Twenty-nine species (26 rotifers) were recorded in  $\leq 6$  ponds. Species with high vagility exhibited greater viability. Ponds differed in zooplankton community composition throughout the year, due to differences in both vagility and viability among colonizing species.

### Introduction

Local processes affecting zooplankton viability are widely studied (e.g., Gilbert, 1985; Kerfoot & Sih, 1987; Vanni, 1987), but relatively little attention has been applied to regional processes of zooplankton vagility (Ricklefs, 1987). Recent efforts with metapopulation models (e.g., Gilpin & Hanski, 1991) and in marine intertidal systems (e.g., Roughgarden *et al.*, 1987; Underwood *et al.*, 1983) have renewed focus on dispersal processes in general. Zooplankton (especially rotifer) dispersal is commonly assumed to occur readily, and is not thought to limit local species distributions (e.g., Krebs, 1978; Pennak, 1978). The purpose of this study was to test this assumption, using results of a 1-year study of colonization of 12 new ponds.

### Materials and methods

Twelve ponds (405 m<sup>2</sup> surface area, 2.1 m maximum depth) were excavated between June and November 1987 near Blackstone, Virginia, USA (Fig. 1). Each pond was bermed at the top to prevent surface runoff into ponds. Ponds were sealed with 15 cm of com-

packed clay and lined with 15 cm topsoil from the site. All twelve ponds were filled simultaneously with chlorinated tap water in late January 1988. Well water was supplied to ponds individually during the study to maintain water levels. Pond water was never interchanged among ponds. No fish were stocked in the ponds and fish were not observed in any pond during the study.

Zooplankton were sampled biweekly for one year (5 February 1988–10 February 1989). Ponds were sampled in random order to ensure no spatial patterns developed due to repeated, inadvertent transfer of organisms during sampling. Each pond was sampled at the center (2.1 m depth) and at 2 of the 4 sides (1.1 m depth), chosen by coin toss.

Microcrustaceans and insects (*Chaoborus*) were collected with an 80- $\mu$ m mesh Wisconsin-style plankton net and preserved in 4% buffered formalin containing 5 g l<sup>-1</sup> sugar (Haney & Hall, 1973; Steedman, 1976). The net was gently placed on the pond bottom for about 2 min before hauling to obtain representative samples of the entire water column. Two vertical hauls were collected at each station. The net was washed with 70% ethanol between ponds.

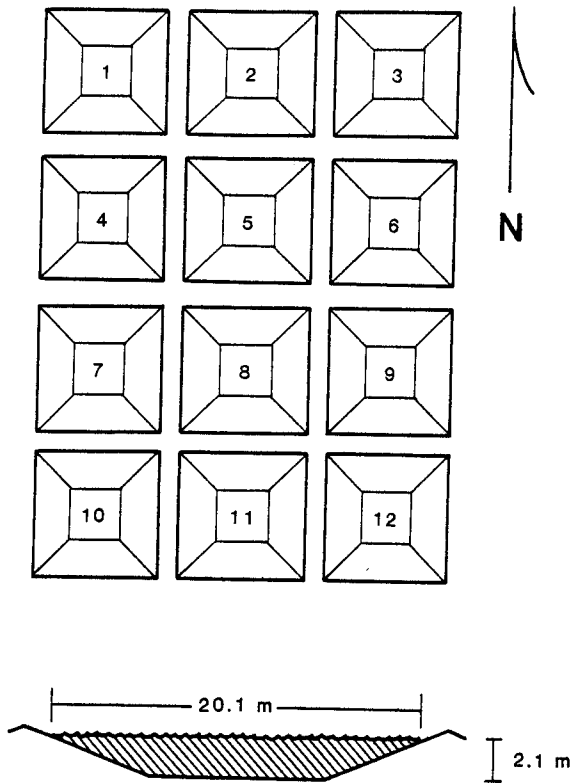


Fig. 1. Schematic view of experimental ponds. All slopes = 2.5:1.

Rotifers were collected with a transparent, acrylic tube (1.8 m long, 5 cm i.d.) similar to that used by Ganf & Blazka (1974). Five samples were collected at each station (1.8 m depth at center, 0.9 m depth at side stations). All collected water (approx. 35 l) was pooled and mixed, then 4.0 l was subsampled, concentrated on 35- $\mu$ m mesh plankton netting, and preserved as above. All zooplankton were identified (using Edmondson, 1959; Ruttner-Kolisko, 1974, and Stemberger, 1979 for rotifers) and counted at 40 $\times$  or greater. Densities were expressed as organisms  $l^{-1}$ . At least 3 subsamples or entire samples were counted, depending on zooplankton density.

Environmental variables measured in the field included temperature, pH, dissolved oxygen (DO), and Secchi depth. Variables measured in the laboratory on field-prepared samples included chlorophyll *a*, total hardness, total alkalinity, conductivity, ammonia-nitrogen ( $NH_3-N$ ), nitrate-nitrogen ( $NO_3-N$ ), nitrite-nitrogen ( $NO_2-N$ ), and soluble-reactive phosphate (SRP). Analytical techniques followed APHA (1985).

Data were processed to compute a Vagility Score (VA) and a Viability Score (VI) for each recorded species. Each score was composed of two, additive components:  $VA = P + P1$ , and  $VI = OL + ROMD$ , where  $P$  = proportion of ponds colonized during the study period,  $P1$  = proportion of ponds colonized during the month (4 weeks) after first observation of that species,  $OL$  = overall longevity, or proportion of sample events species was observed in at least 1 pond, and  $ROMD$  = Relative Overall Maximum Density, or  $[\ln(\text{maximum recorded species density} + 1)] / [\ln(\text{maximum recorded density among all species} + 1)]$ .  $P1$  was used to indicate invasion intensity.  $OL$  was calculated for each species (rather than longevity per pond) to focus on species' characteristics rather than pond conditions.  $ROMD$  was calculated with a species' maximum among all ponds for the same purpose. Each species' maximum density was scored relative to the maximum density observed among all species during the study: 6546 organisms  $l^{-1}$  (*Keratella cochlearis* Gosse). Each component could range up to 1.000; vagility scores could range from 0.166–2.000, and viability scores could range from 0.038–2.000. Regressions were calculated by least squares analysis.

## Results

### Environmental variables

Ponds were generally similar in measured physical-chemical variables and exhibited typical seasonal cycles for temperature and dissolved oxygen: no stratification was observed (Jenkins, 1990). Ponds contained soft water: total alkalinity stabilized at approximately 45  $mg\ l^{-1}$  as  $CaCO_3$  and hardness held steady at approximately 75  $mg\ l^{-1}$  as  $CaCO_3$ . Mean pH increased slightly during the study from 6.8 to 7.6 and mean conductivity decreased (230–175  $\mu S\ m^{-1}$ ). After initial modest levels of  $NH_3-N$  and  $NO_3-N$  (approx. 0.08 and 1.25  $mg\ l^{-1}$  respectively), dissolved inorganic nitrogen levels were very low. SRP levels were generally low (<0.05  $mg\ l^{-1}$ ) throughout the study. Chlorophyll *a* levels slowly increased to average values of 3–4  $mg\ m^{-3}$  in spring, declined in summer, and returned to previous levels again in autumn. Secchi depths were about 1 m until summer, when chlorophyll *a* levels declined, and Secchi depths increased to about 2 m. Secchi depths decreased again in autumn, varying between 1–2 m.

### Zooplankton assemblages

Rotifers dominated zooplankton assemblages in species recorded (47 of the 61 observed species), densities, and biomass (Jenkins, 1990). Eleven microcrustacean and 3 *Chaoborus* species were observed. Only 14 of 61 zooplankton species were observed in all 12 ponds, and 9 of those 14 species were rotifers: *Anuraeopsis fissa* (Gosse), *Brachionus urceolaris* Müller, *Conochilus dossuarius* (Koste), *Hexarthra mira* (Hudson), *Keratella americana* (Carlin), *K. cochlearis*, *Keratella crassa* Ahlstrom, *Lecane flexilis* (Gosse), and *Polyarthra vulgaris* Carlin.

### Vagility score components

A bimodal distribution was observed in the number of ponds colonized during the year (*P*: Fig. 2a), indicating a general tendency to either low or high colonization ability among zooplankton species. Rotifers were primarily responsible for this bimodal distribution due to their dominance of observed species.

Relatively few species colonized multiple ponds rapidly (*P*<sub>1</sub>: Fig. 2b). Again, rotifers dominated this overall pattern. Comparison of Figs 2a and 2b indicates that relatively few species colonizing most (>6) ponds did so within a month. In fact, a weak negative correlation existed between *P* and *P*<sub>1</sub> scores ( $R^2=0.14$ ,  $p=0.002$ ).

### Viability score components

Zooplankton predominantly exhibited low *OL* values (Fig. 2c). Rotifers especially had low *OL* values relative to microcrustacean and *Chaoborus* species. Microcrustacean species tended to have intermediate *OL* values, with wide variation among species.

With a few exceptions (e.g., *A. fissa*, *K. americana*, *K. cochlearis*, *P. vulgaris*), most species had low *ROMD* values (Fig. 2d). Ponds were oligotrophic in the first year and generally did not support large zooplankton densities. All *Chaoborus* species exhibited low *ROMD* scores, but rotifer and microcrustacean *ROMD* scores were distributed roughly similarly.

A significant, positive correlation existed between *OL* and *ROMD* ( $R^2=0.36$ ,  $p<0.001$ ), indicating that species present longer were more likely to exhibit larger maximum population sizes.

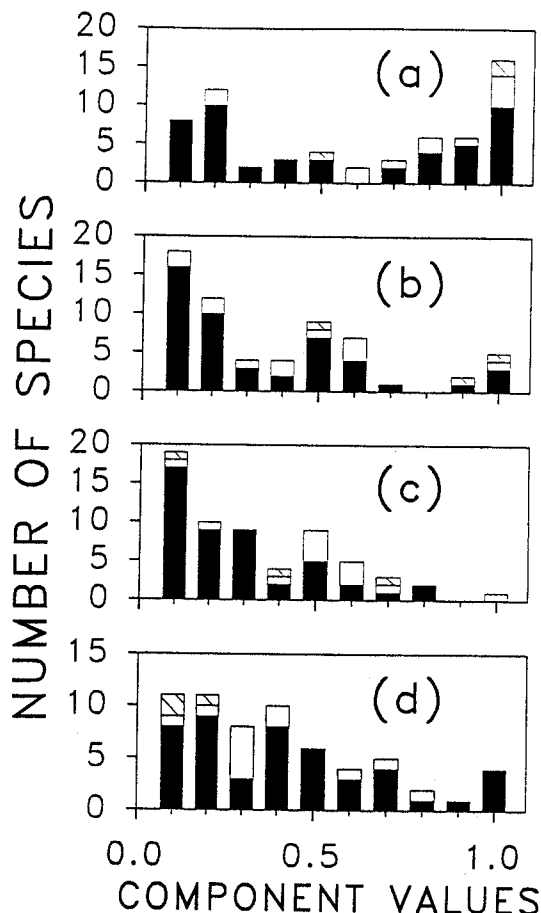


Fig. 2. Vagility and Viability Score Component distributions among taxa. (a) *P*, (b) *P*<sub>1</sub>, (c) *OL*, and (d) *ROMD*. See text for explanations of terms. Filled bars = rotifers, open bars = microcrustaceans, striped bars = *Chaoborus*.

### Vagility and viability scores

Combined VA and VI Scores for all species are shown in Fig. 3. Thirty-one of the 61 recorded species (51%) had VA < 1; of those species, 26 (84%) were rotifers. Of the 30 species with VA ≥ 1, 21 (70%) were rotifers. By contrast, only 4 of the 12 (33%) crustacean species exhibited VA < 1.

All species with low vagility (VA < 1) also exhibited low viability (VI < 1); no low-vagility species were scored as having high viability (Fig. 3). The only species to exhibit high viability (VI ≥ 1) were 10 species that also exhibited high vagility (VA ≥ 1) including the rotifers *A. fissa*, *C. dossuarius*, *Filinia terminalis* (Plate), *H. mira*, *K. cochlearis*, *K. americana*, *L. flexilis*, and *P. vulgaris*. *Bosmina longirostris* (Müller) and

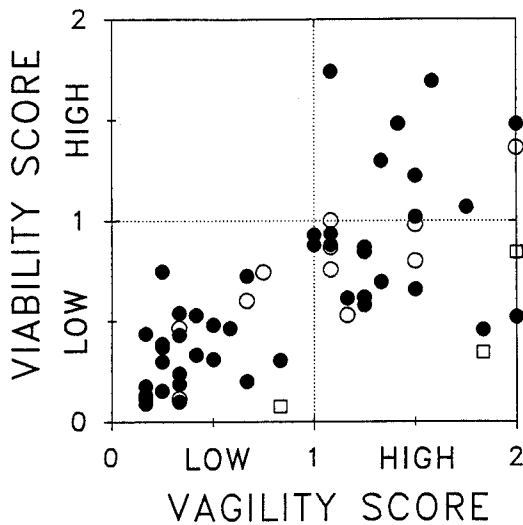


Fig. 3. Relationship between Vagility and Viability Scores. Each symbol represents one species. Filled circles = rotifers, open circles = microcrustaceans, open squares = *Chaoborus*. See text for explanations of scores. Regression equation is  $VI = 0.181 + (0.512)VA$ ;  $R^2 = 0.48$ ,  $p < 0.001$ .

*Tropocyclops prasinus* (Fischer) also exhibited VI and VA scores  $\geq 1$ .

The remaining 20 species with high vagility exhibited lower ( $VA < 1$ ) viability. Species among this group with VI scores  $> 0.9$  were *B. urceolaris*, *Lecane lunaris* (Segers), and *Eucyclops agilis* (Koch). A few species had high VA scores but relatively low VI scores, including *K. crassa*, *Lecane quadridentata* (Segers), and *Chaoborus americanus* (Johannsen).

VA and VI scores were significantly correlated ( $R^2 = 0.48$ ,  $p < 0.001$ ). Species that colonized most ponds within a brief time interval tended to exhibit greater densities and longevity. Conversely, species that slowly colonized few ponds tended to exhibit lesser densities and longevity.

## Discussion

Results of this study indicate zooplankton species differ in both vagility and viability, and that vagile species were more likely to develop viable populations. Common species with large, persistent populations should produce more propagules (resting eggs, ephippia, diapausing individuals, cysts), providing numerous large source pools and a greater likelihood of dispersal to favorable sites. Conversely, specialized species present

in relatively low densities and in few habitat patches may provide a small source pool of propagules, thereby limiting vagility (Brown, 1984). If so, metapopulations of common, dominant zooplankton species (high VA and VI scores) should be more genetically homogeneous than metapopulations of scarce species, due to more frequent dispersal events among ponds.

Given the apparent link between vagility and viability, it is interesting that so many species dispersed poorly (low VA scores) and developed small, ephemeral populations (low VI scores). In addition, many other taxa were conspicuous in their absence throughout the year-long study (e.g., *Synchaeta*, *Asplanchna*, *Ceriodaphnia* and other cladocerans, and calanoid copepods). Environmental conditions could have prevented some colonists from developing detectable or sizable populations upon arrival, especially species requiring hard water and/or eutrophy. Relatively subtle physical and chemical differences are often considered responsible for differences in zooplankton community species lists among lakes and ponds (e.g., Schmid-Araya, 1993). However, this argument does not explain why some species colonized only a few of the identically-constructed and environmentally-similar ponds. Dispersal apparently played a role in limiting zooplankton community composition, in much the same way that settlement can limit composition of marine intertidal communities (Roughgarden *et al.*, 1987; Underwood *et al.*, 1983). Dispersal may be an overlooked factor regulating zooplankton community composition in other systems.

Species evolved in stable habitats may be selected for low vagility (Krebs, 1978). However, many freshwater habitats are seasonally variable and ephemeral in evolutionary time (Wetzel, 1979). Many zooplankton species reduce temporary risks of local extinction via dormancy (DeStasio, 1989; Marcus *et al.*, 1994). Zooplankton propagules 'designed' for dormancy on site may be coadapted to survive overland dispersal. However, passive dispersal is stochastic and may operate at low delivery rates, especially if a propagule source pool is small and sites are isolated. Results of this study indicate that zooplankton species vary in vagility: it is possible that zooplankton propagules are selected for traits that enhance their dispersal efficacy, as are some seeds (Fenner, 1985).

Colonization is a continuous process that occurs in new and old aquatic systems. Results of this study indicate intervals  $\geq 1$  year may be necessary for dispersal to new habitats for many zooplankton species, and that local and metapopulation dynamics operate

at about the same time scales (Hanski, 1982). Therefore, metapopulation dynamics (i.e., dispersal among ponds) may play a role in seasonal successions and other local dynamics of some zooplankton communities.

The bimodal  $P$  distribution (Fig. 2a) is predicted by the core-satellite hypothesis, primarily as a result of a strong rescue effect (Hanski, 1982). The rescue effect maintains rare (satellite) species by: immigration from outside, existence of superior habitat in some patches, and migration among patches, especially from large or better patches (Hanski & Gyllenberg, 1993). Because ponds were identical in size and similar in habitat quality, species with low  $P$  likely existed due to immigration from distant ponds or lakes. Species with high  $P$  likely existed due to immigration, suitable habitat in most or all ponds, and cross-migration among ponds.

Finally, species that dispersed well and quickly established large, persistent populations were not necessarily 'fugitive' species (Krebs, 1978), in that most are considered common in many aquatic systems (Edmondson, 1959; Pennak, 1978).

In summary, zooplankton communities in 12 new, similar ponds varied in composition due to both vagility and viability of colonizing species. Rotifers dominated, but were not distributed evenly among ponds. Vagile species were more likely to develop viable populations, but many species were rare and sparsely distributed among ponds. The relative importance of dispersal to zooplankton community composition in established ponds and lakes is probably secondary, but remains untested.

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