POPULATION ECOLOGY

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Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates

Abstract Despite the importance of dispersal to ecology, accurate estimates of dispersal rates are often difficult to obtain, especially for organisms that rely on passive dispersal of propagules to colonize new sites. To investigate potential dispersal vectors and relative colonization rates of zooplankton, we conducted a field experiment in which we restricted potential dispersal vectors (insects, birds, amphibians) from transporting zooplankton to mesocosms. Twenty-six non-insect invertebrate taxa invaded our array during 2 years. Colonization rates of organisms varied considerably, with some species appearing several weeks after the experiment began and others appearing after a year. We observed no difference in colonization rates among treatments, suggesting that species were transported to our experiment primarily by wind or rain, rather than by animal vectors. The absence of an additional 13 zooplankton species common in ponds immediately adjacent to the array either occurred because of dispersal limitation or an inability to invade the existing communities. Ecologists generally assume that all zooplankton are rapidly dispersed hence the potential for dispersal limitation is generally ignored. Our results suggest that zooplankton vary in their dispersal and colonization ability. Hence, increased attention should be focused on the potential role of dispersal limitation and its importance for understanding the structure and function of aquatic communities.

Keywords Migration · Community structure · Rotifers · Cladocera · Copepods

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Introduction

Most organisms live in spatially and temporally varying environments where dispersal can play a key role in altering relative fitness and influencing ecological and evolutionary dynamics (Gadgil 1971; Levin et al. 1984; McPeek and Holt 1992; Ricklefs and Schluter 1993). Although dispersal abilities vary among species, studies of freshwater planktonic communities generally ignore this potential variation and assume that dispersal and colonization by all zooplankton species must be "rapid and frequent" (Brooks and Dodson 1965; Pennak 1989; Lampert and Sommer 1997). This belief is based largely on the fact that freshwater zooplankton are small, produce desiccation-tolerant resting stages and often reproduce parthenogenetically. Despite the potential importance of the assumption of "rapid and frequent" colonization for interpreting the results of many studies, this idea has rarely been examined experimentally and there are few quantitative data documenting the spatial or temporal scale on which colonization occurs.

Anecdotal evidence documenting overland transport of zooplankton by vectors such as wind, rain, insects and vertebrates has been accumulating for over a century (Darwin 1859; McAtee 1917; Lansbury 1955; Maguire 1959; Proctor 1964; Proctor and Malone 1965; Swanson 1984; Bohonak and Whiteman 1999). Experimental studies provide conflicting evidence about the dispersal rates and the role of dispersal in structuring zooplankton assemblages. Maguire (1963) found a decrease in colonization with distance from source in one experiment but not another. Experiments in artificial systems (experimental ponds, wading pools) suggest that dispersal limitation is likely important in structuring zooplankton assemblages (Jenkins 1995; Jenkins and Buikema 1998; Jenkins and Underwood 1998; Holland and Jenkins 1998), while experiments in natural fishless ponds and larger lakes conclude that dispersal limitation plays a minor role (Lukaszewski et al. 1999; Shurin 2000). Similarly, indirect estimates of colonization rates provided by population genetic data indicate that some aquatic organ-
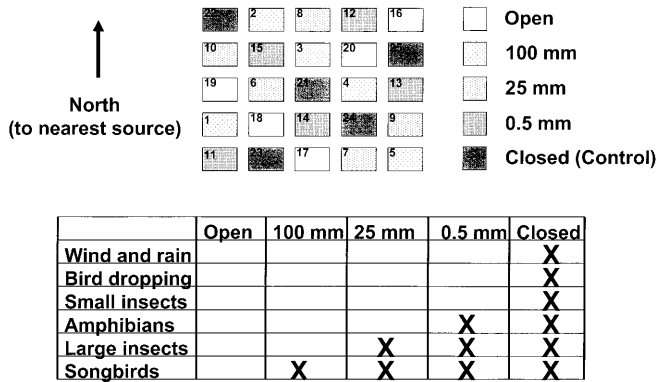
Fig. 1 Schematic of Latin square design and hypothesized dispersal vectors. An *X* in a column indicates treatments from which we meant to exclude that dispersal vector. Identification numbers are indicated for each mesocosm. Mesocosms were <1 m from their nearest neighbor and the nearest source (cattle tanks) were <10 m from the array

isms disperse and colonize readily, while others do not (Crease et al. 1997; Boileau and Hebert 1991; Bohonak 1998). Shurin et al. (2000) in a literature review that examined zooplankton assemblages in 2,832 lakes over a variety of spatial scales suggested that dispersal limitation might become important over large distances.

Understanding the rates and the mechanisms by which zooplankton move between habitats has important consequences for understanding how zooplankton assemblages recover from natural and anthropogenic disturbance, and for interpreting the outcomes of experimental manipulations of aquatic systems. To evaluate rates of colonization by zooplankton, and to determine the vectors responsible for their dispersal, we conducted a 2-year field experiment in mesocosms. Using nylon netting we manipulated colonization by restricting access to the mesocosms by potential dispersal vectors (wind and rain, insects, amphibians, and small birds, see Fig. 1). We hypothesized that if zooplankton were primarily dispersed in the wind and the rain, then we would observe no effect of treatment (mesh size) on species richness per mesocosm or on time to colonization (TTC) for each species. However, if certain animals (i.e., insects, amphibians and small birds) were the primary dispersal vectors, then we would observe an increase in the colonization rate of zooplankton in the treatments that allowed access by these animals.

Materials and methods

We used nylon netting and plastic sheeting to manipulate access to 151.4-l Rubbermaid RoughTote mesocosms (91×50×43 cm). A wooden frame was built to support a netting or plastic cover for each enclosure and was sealed to the top of the enclosure with silicone. For the netted treatments or closed control, a cover was constructed with one of the types of netting or a piece of plastic and was screwed to the frame. We partially buried each mesocosm to moderate temperature and facilitate access by amphibians. The array was in a 7×7-m fenced area within the Experimental Pond Fa-

cility of the Illinois Natural History Survey (Champaign, Ill.). The pond site contained 21 ponds and numerous cattle tanks within 10–200 m of the experiment.

Four treatments and one closed control were chosen to progressively exclude potential dispersal vectors from the mesocosms (Fig. 1). All putative vectors could and did enter the open treatments, whereas the netting restricted any vector larger than the aperture size from entering that treatment. Systat 7.0 was used to generate a fully randomized 5×5 Latin square in which to arrange the following treatments: (1) open (no netting or plastic), (2) 100-mm netting, (3) 25-mm netting, (4) 0.5-mm netting, (5) closed (covered with plastic-contamination control) (Fig. 1). We employed the randomized Latin square design to reduce potential effects of proximity to the experimental ponds (north-south gradient) and potential effects along the east-west gradient.

The experiment began on 5 May 1998 and concluded on 26 May 2000. Prior to the start of the experiment, each tank was rinsed with EtOH and filled with 130 l of filtered (1 μm) city water. Each tank was then treated with Amquel water conditioner to remove NH_3 and chloramines. Five Tetra Luft aquarium air pumps (one per row) were used to aerate the tanks through individual air stones.

Samples were collected 32 times over 2 years. Sampling was weekly May–August 1998, but became less frequent after colonization curves appeared to plateau. We used pail pumps (15 mm aperture; pump rate 4 l/min; Consolidated Plastics Company) to stir the water and to collect approximately 2 l from each mesocosm. When necessary, we added filtered (1 μm) city water to maintain water levels. To minimize contamination, each mesocosm had its own pump and sampling containers. The open, 25-mm netting, and 100-mm netting treatments were sampled through the mesh whereas the cover was unscrewed and removed briefly while we sampled the 0.5-mm netting treatment and the closed controls. Ice-cover often precluded sampling in the winter, but the mesocosms did not freeze solid. Prior to preservation in 95% EtOH, the pH of each sample was measured and the live sample was scanned for taxa that would be difficult to identify once preserved (e.g., bdelloid rotifers, annelids). Temperatures were recorded for selected mesocosms initially with maximum-minimum thermometers and subsequently with Stowaway (Onset) thermal data loggers.

At week 14, a severe thunderstorm partially removed the plastic sheeting on all five closed controls and contaminated these mesocosms. We did not replace this plastic, but continued to monitor the contaminated controls as if they were an additional treatment. In addition, mesocosms 11 and 22 cracked prior to the termination of the experiment. Mesocosm 22 (closed) was sampled until week 45, and Mesocosm 11 (0.5 mm) was sampled until week 68. These mesocosms were excluded from the analysis of final colonization at week 107.

The regional species pool was assessed by sampling all ponds and cattle tanks within the Experimental Ponds Facility on five dates (September 1998, November 1998, August 1999, April 2000, July 2000). We towed an 80-μm zooplankton net through each pond and cattle tank, and preserved the combined sample in 95% EtOH. Each sample was scanned and all taxa present were identified and recorded.

Statistical analyses were performed using SYSTAT 9.0 or Data Desk 5.0. We used Latin square ANOVA (Data Desk 5.0) to compare the average TTC for each taxon. TTC in each mesocosm was calculated as the midpoint between the first sampling date on which a taxon was detected and the previous sampling date. If a particular taxon was not recorded from all 25 mesocosms, a value of 107 weeks (end of the experiment) was assigned to the mesocosms where it was not found.

To measure similarities in the final community composition between mesocosms, taxon presence/absence data were analyzed by generating a matrix of Jaccard dichotomy coefficients for each pair-wise comparison of mesocosms (Systat 9.0). The Jaccard coefficients (C_J) were calculated as:

$$C_J = j/(a+b-j) \tag{1}$$

where j is the total number of taxa in common between two mesocosms and a and b are the number of taxa in each mesocosm. The Jaccard matrix was used because it reports similarity of taxa found and does not consider the mutual absence of species as an indicator of similarity.

Results

Water temperatures in the mesocosms fluctuated with season and ranged from a low of 0°C (ice-cover) to a high of 38°C. The pH of the replicates also varied with season, but typically ranged between 7.5 and 10.9.

At least 40 micro-invertebrate taxa were present at the Experimental Pond Facility, but only 26 colonized the experiment (Table 1). Individual mesocosms were colonized by 11–21 taxa. There was no significant effect of treatment on final colonization (Latin square ANOVA: $F_{4,10}=1.02$, $P=0.44$; Fig. 2). Although there was no difference in cumulative colonization along the north-south gradient (Latin square ANOVA: $F_{4,10}=2.0$, $P=0.17$), there was a significant effect of position along the east-west gradient (Latin square ANOVA: $F_{4,10}=11.5$, $P=0.0009$). On average, 18.7 ± 1.2 ($\pm$SE) taxa colonized the western-most mesocosms, whereas only 13.0 ± 0.3 taxa colonized the eastern-most mesocosms (Fig. 3).

Over the first 21 weeks of the experiment, new taxa colonized all replicates (Fig. 2). Early colonization was primarily by rotifers, which reproduce parthenogenetically. However, the sexually reproducing cyclopoid copepods *Eucyclops agilis* and *Paracyclops fimbriatus poppei* also arrived early (Table 1). Most cladoceran taxa, which are able to reproduce parthenogenetically, were not recorded until spring 1999. Calanoid copepods, despite being present at the pond site, were not recorded from any of the mesocosms.

We observed similar colonization rates across all mesocosms, including the "closed" controls, which were rapidly colonized by bdelloid rotifers, flatworms, *Cephalodella*, and the annelid *Aeolosoma* (Table 1). Initial slopes (weeks 1–21) of the individual colonization curves were not influenced by treatment, or position in the array (Latin square ANOVA: treatment $F_{4,12}=0.56$, $P=0.70$; row $F_{4,12}=1.3$, $P=0.34$; column $F_{4,12}=1.03$, $P=0.43$). The colonization rate in each treatment declined sharply from August to September 1998, although new species continued to be added until July 1999 (Fig. 2). Local taxonomic richness was typically less than eight taxa per mesocosm (Fig. 4).

Treatment influenced average TTC for three of the 26 taxa, but two of those taxa (bdelloid rotifers and flatworms) were the early colonists of the closed controls, and likely represent contamination from the water source. Therefore, *Eucyclops agilis* was the only colonist in which treatment significantly altered TTC (Latin square ANOVA: $F_{4,12}=4.21$, $P=0.03$). However, this effect was largely influenced by the increased time needed to invade the closed controls (i.e., they did not invade these enclosures until after they had opened). An analysis of TTC which excluded the closed replicates revealed
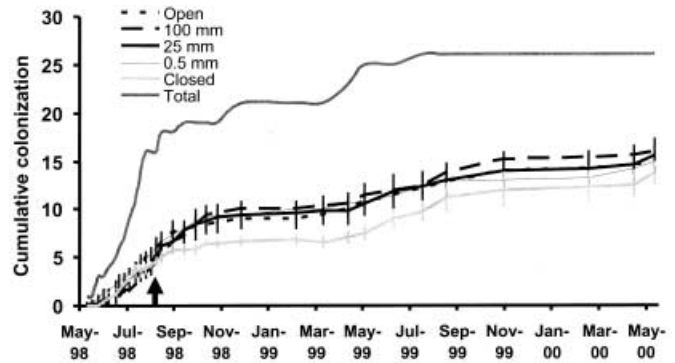
Fig. 2 Mean cumulative colonization (number of taxa) ±1 SE for the five treatments as well as the experiment-wide colonization. The *arrow* at week 14 indicates the point at which the closed controls became open to the environment (see text for details)
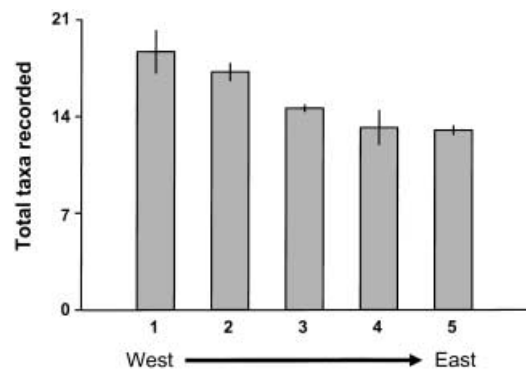
Fig. 3 Effect of position in the array along the west-east gradient on final colonization. *Error bars* are 1 SE
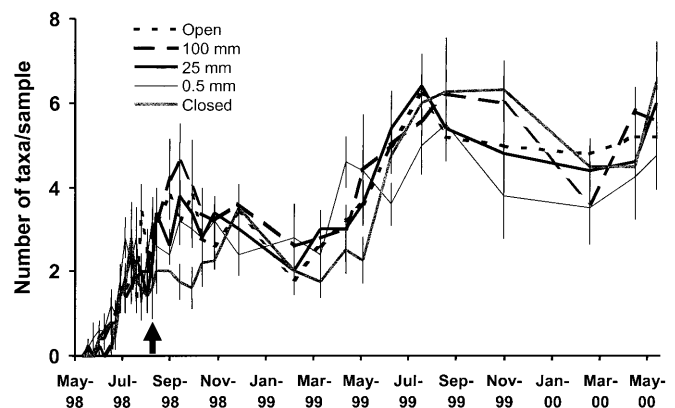
Fig. 4 Average number of taxa per treatment on each of the 32 sampling dates. These estimates for local taxonomic richness indicate both the seasonal dynamics of some species and the interaction between new colonists and the apparent extinction of some early colonists. *Error bars* are 1 SE. The *arrow* at week 14 indicates the point at which the closed controls became open to the environment (see text for details). *Jul* July, *Sep* September, *Nov* November, *Jan* January, *Mar* March

no significant difference among the other four treatments (ANOVA: $F_{3,16}=1.5$, $P=0.25$). Excluding the closed controls did not result in a significant effect of mesh size on any of the other taxa (all $P>0.05$).

Table 1 Week (midpoint of sampling interval) that each taxon was first recorded in each of the 25 mesocosms. Mesocosms 11 and 22 cracked prior to the end of the experiment and therefore did not experience colonization for the full 107 weeks. The following taxa were recorded from the experimental pond site, but not from any of the mesocosms: rotifers – Lecane sp. 3, Polyarthra, Asplanchna, Brachionus calyciflorus; copepods – Mesocyclops edax, Acanthocyclops vernalis, Diaptomus sp., Skistodiaptomus pallidus; cladocera – Daphnia ambigua, Daphnia dentifera, Simocephalus, Diaphanosoma, Ceriodaphnia lacustris, Moina. Treatments (mesh sizes) are indicated on the Table; see also Fig. 1

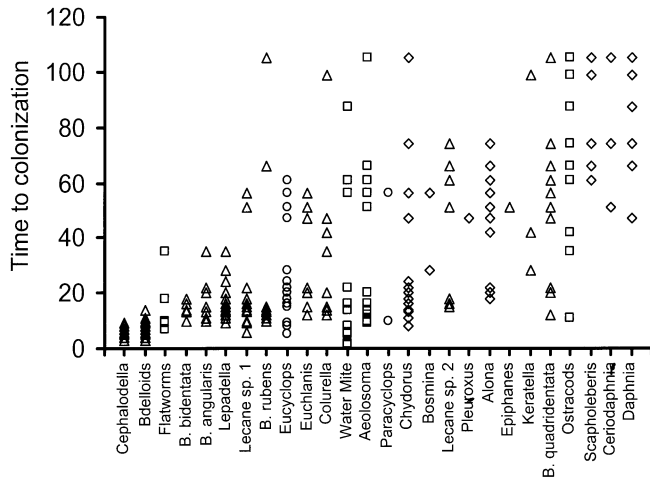| Treatment (aperture)	100 mm					25 mm					0.5 mm					Open					Control				
Mesocosm no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Rotifers																									
Cephalodella	7	4	6	8	8	6	9	4	8	4	7	3	6	8	4	7	9	5	7	6	7	6	7	8	8
Bdelloid spp.	11	10	11	7	7	9	8	6	9	14	4	3	4	5	6	11	10	4	10	4	5	4	6	4	5
Lecane sp. 1	13	13	14	51	16	14	15	18	18	16	16	9	16	16	6	56	14	15	14	16	15	16	10	16	22
Lepadella	11	14	15	14	24	9	28	24	20	15	15	15	16	18	18	12	18	28	9	12	14	35	15	13	16
Brachionus angularis	20										11														
Brachionus bidentata	14	13	18			15	13	16		14		14	14		13			13	10						
Brachionus rubens			14	14	66	12		15	15	10	11	11		56	12	11					14		51		
Euchlanis		12				22				15	20	35	20	20	47	20		12	12	12		22			105
Colurella		20	20	99	20	15				42	42	105	105	61		47	66	14	12						47
B. quadridentata	51	66	20	22	22	56	74	74	105	66				61	61	15	51	12	16	66	74		56	56	66
Lecane sp. 2	18	74	16	66			66			18	61									16			16	105	66
Keratella					28					42					99										
Epiphanes		51																							
Copepods																									
Eucyclops agilis	51	8	20	22	28	20	15	9	20	24	47	18	56	56	20	22	61	16	8	5	51	22	51	56	56
Paracyclops fimbriatus poppei	10			56																					
Cladocera																									
Chydorus sphaericus	74	16	11	74	22	18	105	8	51	56		13	24		14	16	47	20	24	56	66		74		
Alona affinis	42	20	61	18	22	56	51	51		56		47	51	61	22	51	42	74	74	47			61		66
Bosmina longirostris						56											28						28		
Pleuroxus																	47								
Daphnia pulex	47	87	87	74		74		87		99		99			99		99	74	74		105		66	99	
Ceriodaphnia reticulata		74	74	105					105								51		74						
Scapholeberis mucronata		66		74		105			99	66					105			61	74		105		74		
Other																									
Water mite	16	56	2		56	56	56	61	5	2	1	22	10	87	2			8	14	6	61		56	61	8
Flatworms	35						61	10		18		9	66		7						9		10		9
Aeolosoma	16	105	14	61		51		12		20	10		66	9	10	56			66	61	10	13	9	12	10
Ostracods	11	74	66	66	66	74		105	61	74	35			99	61		42	61	87	99	105		66	87	
Total colonists	17	18	15	17	13	18	11	15	13	21	12	14	14	14	18	12	15	15	18	13	14	7	17	11	13

Fig. 5 Time to colonization (weeks) into each mesocosm for each of the 26 colonists. Taxa are listed in order of average time to colonization. ◇ Cladocera, ○ copepods, △ rotifers, ■ all other taxa; see also Table 1
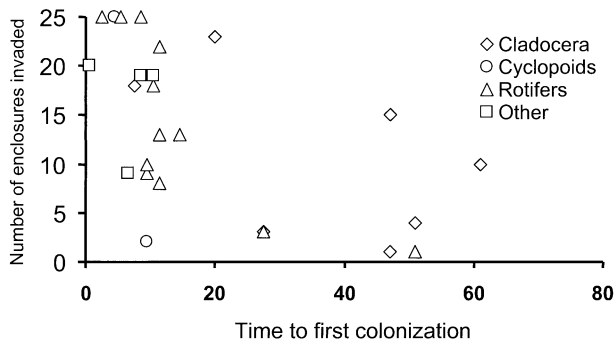

Fig. 6 Negative correlation between the week each taxon was first found in the array, and the number of mesocosms that were invaded over the 2 years. The *Other* category includes annelids, flatworms, water mites, and Ostracods. Data for each taxon can be found in Table 1

Fig. 7 Relationship between overlap in species composition with distance between individual mesocosms (**A**), and difference in opening size (**B**). Overlap in species composition was calculated as a Jaccard's dichotomy coefficient for all possible pair-wise comparisons. Inter-mesocosm distance was measured as distance between the centers of each mesocosm. Difference in opening size was calculated using the minimum opening size that allowed access into each of the treatment groups (open=440 mm, 100 mm, 25 mm, 0.5 mm; closed=270 mm size of opening after plastic was torn)

There was considerable variation in the number of replicates invaded by each of the 26 taxa (Table 1, Fig. 5). There was also a significant negative correlation between the week a particular taxon first invaded the array and the total number of mesocosms invaded over the duration of the experiment (r^2=0.35, P=0.002; Fig. 6). This negative relationship is influenced by the seven taxa that invaded after week 21. Prior to week 21, there is no relationship between week invaded and number of mesocosms colonized (r^2=0.08, P=0.24).

Jaccard measures of similarity were plotted against physical distance between the mesocosms (Fig. 7A) and the absolute difference in minimum opening size (Fig. 7B). Regression analysis indicated that similarity between mesocosms was negatively correlated with distance between the centers of the mesocosms, but little of the variance in similarity was explained by this relationship (r^2=0.09, P<0.0001). Difference in opening size (i.e., treatment) also explained little of the variance

and was not significantly correlated with similarity (r^2=0.001, P=0.53).

We recorded all of our chosen dispersal vectors in the experimental array, including members of all major subfamilies of chironomids (Chironominae, Orthocladinae and Tanypodinae), larval odonates (*Tramea* and *Pantella*), dyticid larvae, *Chaoborus*, caddisflies, mosquitoes, and Baetid mayflies. Frogs (*Rana* and *Acris*) were often found during late summer in the open and 100-mm replicates. We frequently observed small birds and their droppings in and around the array. Terrestrial insects were also found dead in the mesocosms.

Discussion

We originally hypothesized that if wind and rain were the primary dispersal vectors, then we would observe no difference in either total colonization of zooplankton, or TTC for individual taxa in the mesocosms. However, if particular animal vectors were the dominant mode of transportation, then the more open treatments (25-mm aperture, 100-mm aperture, and completely open) would be colonized faster and by more taxa. Given that we

found no effect of mesh size on total colonization or TTC for each taxon, the most likely conclusion is that dispersal into our experimental array was primarily the result of wind and rain. The finding that similarity between assemblages is better explained by the distance between them than by difference in accessibility to animal dispersal vectors further supports this conclusion.

Anecdotal evidence does exist for zooplankton being transported by insects, birds, amphibians and mammals (Lansbury 1955; Maguire 1959; Proctor 1964; Proctor and Malone 1965; Bohonak and Whiteman 1999). We observed many of these animals in our array but their presence in the more open treatments (25-mm aperture, 100-mm aperture, completely open) did not appear to influence colonization rates. This lack of increase may be the result of some dispersal vectors (e.g., ducks, large mammals) being excluded from the site. Although frogs were found in and around many of the mesocosms, each mesocosm was only partially buried and thus movement in and out by amphibians may have been restricted. Had we facilitated visitation by these groups, we may have increased the overall colonization rate.

Our mesocosms were not sampled destructively during the course of the experiment. Hence, for all but the first colonists of each mesocosm, our colonization measurements represent a combination of the ability to arrive at the site, invade the resident community and persist until collection. While our design precludes making some conclusions about the dispersal vectors of these other taxa, it does provide some insight into the role of dispersal in structuring planktonic communities. For those species that failed to colonize, they either could not reach the array, or they could not establish a reproducing population once they had arrived. Failure to establish could either be the result of biotic interactions or because the abiotic conditions of the experimental mesocosms were unsuitable. When we seeded enclosures with potential colonists we found that taxa such as *Diaphanosoma*, *Mesocyclops edax*, *Acanthocyclops vernalis* and *Daphnia ambigua* could survive in the enclosures (unpublished data), suggesting that these taxa were excluded from the assemblages either by dispersal limitation or local biotic interactions.

Local biotic interactions undoubtedly influenced assemblage structure in our experiment. The plateau in the experiment-wide colonization rate in July 1999 is reflected by a plateau in the taxonomic richness of the individual mesocosms. This saturation of local sites was also reported by Jenkins and Buikema (1998) who observed an increase in species richness in newly created ponds over the first 6 months, after which local richness remained fairly constant. It is likely that some species present in the regional species pool that had not colonized by July 1999 were not recorded because they could not invade the local communities. These interactions likely vary among seasons. Had we begun our experiment at a different time of year, we might have observed differences in the trajectories of our communities.

Local processes likely played a role in shaping our experimental communities; however, we have evidence suggesting that a low rate of dispersal limited the distribution of some taxa. We found considerable variation in the amount of time taxa needed to establish in the array. If all species had high dispersal rates, we would expect that all mesocosms would be quickly saturated with propagules and many of the 40 locally occurring species would have colonized during the early weeks of the experiment, long before priority effects began excluding taxa. The relative importance of dispersal limitation in determining a species distribution, however, depends not only on the absolute dispersal and establishment rate, but also on the probability of extinction from the local site. Many zooplankton populations establish long-lived diapausing egg banks (De Stasio 1989; Hairston et al. 1995; Cáceres 1998) which lower the risk of local extinction. Theoretical and empirical data predict trade-offs between dormancy and dispersal, since dormancy is essentially dispersal in time (Venable and Lawlor 1980; Levin et al. 1984; Hairston and Cáceres 1996). Using this logic, species such as cyclopoid copepods that are generally not known for prolonged dormancy should therefore be good spatial dispersers, while taxa such as *Daphnia* and *Diaptomus* whose eggs can remain dormant for centuries should have lower relative dispersal ability (Hairston et al. 1995; Hairston and Cáceres 1996; Cáceres 1998). Following this prediction, we found the cyclopoid *Eucyclops agilis* to be one of the first colonists, whereas cladocerans required weeks or months to invade and the diaptomid copepods never colonized the array.

To understand the relative impact of any ecological process in structuring communities, it is essential to understand the spatial and temporal scale relevant for the particular question being addressed (Addicott et al. 1987). It is clear that zooplankton are not uniformly "good" dispersers on short time scales but rather range between high and low vagility (this study, but also see Stemberger 1995; Jenkins 1995; Jenkins and Buikema 1998). Our study also highlights the fact that traits such as resistant dormant eggs and parthenogenesis, which are often thought of as increasing dispersal and colonization ability, are not necessarily good predictors of colonization success, at least on the time scale of 2 years. While it may be true that many species are not dispersal limited on the scale of a few kilometers in the time since the last glaciation, shorter distances and smaller time scales are likely also important. It is becoming more frequent that lakes and ponds are manipulated, either intentionally (e.g., biomanipulation, experimental acidification) or unintentionally (pollution, exotic species' introduction, etc.). Considering how dispersal limitation and priority effects interact to modify community assemblage in the short term may allow ecologists to better predict recovery rates of zooplankton assemblages following such perturbations.

References

Addicott JF, Aho JM, Antolin MF, Padilla DK, Richardson JS, Soluk DA (1987) Ecological neighborhoods: scaling environmental patterns. Oikos 49:340–346

Bohonak AJ (1998) Genetic population structure of the fairy shrimp *Branchinecta coloradensis* (Anostraca) in the Rocky Mountains of Colorado. Can J Zool 76:2049–2057

Bohonak AJ, Whiteman HH (1999) Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): effects of hydroperiod and salamanders. Limnol Oceanogr 44:487–493

Boileau MG, Hebert PDN (1991) Genetic consequences of passive dispersal in pond-dwelling copepods. Evolution 45:721–733

Brooks JL, Dodson SI (1965) Predation, body size, and composition of the plankton. Science 150:28–35

Cáceres CE (1998) Interspecific variation in the abundance, production and emergence of *Daphnia* diapausing eggs. Ecology 79:1699–1710

Crease TJ, Lee S-K, Yu S-L, Spitze K, Lehman N, Lynch M (1997) Allozyme and mtDNA variation in populations of the *Daphnia pulex* complex from both sides of the Rocky Mountains. Heredity 79:242–251

Darwin C (1859) The origin of species. McKay

De Stasio BT Jr (1989) The seed bank of a freshwater crustacean: copepodology for the plant ecologist. Ecology 70:1377–1389

Gadgil M (1971) Dispersal: population consequences and evolution. Ecology 52:253–261

Hairston NG Jr, Cáceres CE (1996) Distribution of crustacean diapause: micro- and macroevolutionary pattern and process. Hydrobiologia 320:27–44

Hairston NG Jr, Van Brunt RA, Kearns CM, Engstrom DR (1995) Age and survivorship of diapausing eggs in a sediment egg bank. Ecology 76:1706–1711

Holland TA, Jenkins DG (1998) Comparison of processes regulating zooplankton assemblages in new freshwater ponds. Hydrobiologia 387/388:207–214

Jenkins DG (1995) Dispersal-limited zooplankton distribution and community composition in new ponds. Hydrobiologia 313/314:15–20

Jenkins DG, Buikema AL Jr (1998) Do similar communities develop in similar sites? A test with zooplankton structure and function. Ecol Monogr 63:421–443

Jenkins DG, Underwood MO (1998) Zooplankton may not disperse readily in wind, rain or waterfowl. Hydrobiologia 387/388:15–21

Lampert W, Sommer U (1997) Limnoecology: the ecology of lakes and streams. Oxford University Press, Oxford

Lansbury I (1955) Some notes on invertebrates other than insecta found attached to water-bugs (Hemipt.-Heteroptera). Entomologist 88:139–140

Levin S, Cohen D, Hastings A (1984) Dispersal strategies in patchy environments. J Popul Biol 26:165–191

Lukaszewski Y, Arnott SE, Frost TM (1999) Regional versus local processes in determining zooplankton community composition of Little Rock Lake, Wisconsin, USA. J Plankton Res 21:991–1003

Maguire B Jr (1959) Passive overland transport of small aquatic organisms. Ecology 40:312

Maguire B Jr (1963) The passive dispersal of small aquatic organism and their colonization of isolated bodies of water. Ecol Monogr 33:161–185

McAtee WL (1917) Showers of organic matter. Mon Weather Rev 45:217–224

McPeek MA, Holt RD (1992) The evolution of dispersal in spatially and temporally varying environments. Am Nat 140:1010–1027

Pennak RW (1989) Fresh-water invertebrates of the United States, 3rd edn. Wiley, Chichester

Proctor VW (1964) Viability of crustacean eggs recovered from ducks. Ecology 45:656–658

Proctor VW, Malone CR (1965) Further evidence of the passive dispersal of small aquatic organisms via the intestinal tract of birds. Ecology 46:728–729

Ricklefs RE, Schluter D (eds) (1993) Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Ill.

Shurin JB (2000) Dispersal limitation, invasion resistance and the structure of pond zooplankton communities. Ecology 81:3074–3087

Shurin JB, Havel JE, Leibold MA, Pinel-Alloul B (2000) Local and regional zooplankton species richness: a scale-independent test for saturation. Ecology 81:3062–3074

Stemberger RS (1995) Pleistocene refuge areas and postglacial dispersal of copepods of the northeastern United States. Can J Fish Aquat Sci 52:2197–2210

Swanson GA (1984) Dissemination of amphipods by waterfowl. J Wildl Manage 48:988–991

Venable DL, Lawlor L (1980) Delayed germination and dispersal in desert annuals: escape in space and time. Oecologia 46:272–282