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Zooplankton may not disperse readily in wind, rain, or waterfowl

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Abstract

Zooplankton, and especially rotifers, have long been thought to be readily dispersed by wind, rain and animals (especially waterfowl). Given that premise, local processes (tolerance to abiotic conditions, biotic interactions) have been the main focus of ecological studies. We tested the premise of high dispersal rates by incubating particulates collected with windsocks and rain samplers at two sites over 1 year. The sites were 80 km apart and differed in proximity to water and surrounding terrain. We also incubated fecal material of wild ducks. Pond sediments were identically incubated as a test of incubation method. Only bdelloid rotifers were collected in wind samples, and only four rotifer species were collected in rain samples: *Lecane leontina, Lecane closterocerca, Keratella cochlearis*, and a bdelloid. No metazoans were found in incubated duck feces, yet incubated pond sediments yielded 11 rotifer, one copepod, four cladoceran, and three ostracod species. Our results do not support the premise of readily dispersed zooplankton. If zooplankton dispersal is infrequent and limited to few species, a series of other questions should be addressed on processes regulating zooplankton population dynamics and community composition.

Introduction

Questions of dispersal are central to our perceptions of zooplankton community organization. If sites are saturated with regionally available species, then local processes should regulate community composition (Ricklefs, 1987; Roughgarden, 1989). However, if dispersal processes do not deliver species to a site, local biotic and abiotic processes will act on a subset of potential species and lead to a different community structure: consider the potential differences between a community with a dominant competitor and one without that competitor. The presence or absence of some species may be predictably attributed to local conditions (e.g., Pejler, 1995; Pontin & Langley, 1993), but an alternative hypothesis exists that should be tested before local conditions are assigned general primacy: dispersal processes may also regulate community composition. More explicitly, dispersal could constrain community composition if dispersal is generally limited, as in isolated sites (Jenkins & Buikema, 1998), or dispersal could affect community composition by residual effects of colonization sequence (Robinson & Dickerson, 1987). In reality, both local and regional processes surely determine zooplankton community composition, but most of our understanding of zooplankton communities is based on studies of local processes.

Zooplankton dispersal processes have been underevaluated because it is commonly assumed that zooplankton (especially rotifers) disperse readily, as evidenced by 'cosmopolitan' distributions, dessication-resistant dormant stages, small size, and parthenogenetic reproduction (Brown & Gibson, 1983; Gislen, 1947; Hutchinson, 1967; King, 1980; Lampert & Sommer, 1997; McAtee, 1917; Maguire, 1963; Pejler, 1995; Pennak, 1989; Wetzel, 1983). Widespread distributions of some taxa are testimony to the eventual dispersal of those taxa overland (e.g., Chaplin & Ayre, 1997). However, many zooplankton species do not, in fact, have cosmopolitan distributions (Carter et al., 1980; Frey, 1986; Hebert & Hann, 1986; Hebert & Wilson, 1994; Stemberger, 1995), and gene flow among populations can be limited (Berg & Garton, 1994; Boileau & Hebert, 1991; Thier, 1994; Weider, 1989). Therefore, one should not infer that potential dispersal necessarily translates to actual dispersal and cosmopolitan distributions. In addition, zooplankton species vary in vagility (Jenkins, 1995), indicating that more detailed analyses are needed in place of generalizations.

Zooplankton are potentially dispersed overland via several possible vectors, including vertebrates, insects, wind, and rain (Lowndes, 1930; Maguire, 1959, 1963; Malone, 1965; Proctor, 1964; Proctor & Malone, 1965; Proctor et al., 1967; Schlichting & Milliger, 1969; Sides, 1973; Stewart & Schlichting, 1966). However, most studies of dispersal vectors have been conducted under artificial conditions: the results speak to the potential for dispersal, but leave actual dispersal events largely unstudied.

Maguire (1963) examined the passive dispersal of aquatic microorganisms near ponds. He concluded that wind, rain, insects and vertebrates all play roles in the dispersal of small aquatic organisms, but did not attempt to distinguish the relative importances of each vector in the transport process. In addition, Maguire's local-scale study did not address long-range dispersal; we know of no studies that have empirically assessed long-range zooplankton dispersal frequency by wind and rain or the relative importances of wind and rain dispersal.

It is clear that rotifers and other zooplankton *can* disperse passively overland. However, it is not clear if zooplankton actually disperse at sufficient frequency to saturate a habitat with regionally available species, and thereby elevate the importance of local processes. The assumption that zooplankton disperse readily needs to be evaluated if the relative importances of regional and local processes are to be understood. In addition, zooplankton species do not disperse equally well (Jenkins, 1995), and generalities about zooplankton dispersal may be inadequate for developing an understanding of the role of dispersal dynamics in zooplankton community structure.

The purpose of this study was to examine the importance of wind, rain and waterfowl as zooplankton dispersal vectors. Wind and rain dispersal of zooplankton were evaluated by collecting and incubating airborne particles and rain to identify organisms carried by each vector and the frequency of dispersal events. In addition, water fowl feces were collected and incubated to determine if they contained viable disseminules of zooplankton. Incubation methods were tested with pond sediments.

Materials and methods

Wind and rain samples were collected at two sites, 80 km apart, for over 1 year (October 1994 through December 1995). Samples were collected at various intervals, ranging from biweekly to 4 months, depending on precipitation patterns and season (see Results below for sample dates). Samples were collected continuously, with the exception of wind samples at the UIS site: the windsock was destroyed in a storm in late April 1995 and replaced in July 1995.

Wind samples were collected using nylon windsocks (one per site) lined with 10-μm plankton netting. The windsock mouth (9.5 cm diameter) was shaped like a Wisconsin-style plankton net to reduce backflow and was constructed of stiff plastic to keep it open. The windsock pivoted 360° in the wind atop a 2-m pole.

Rain samplers were designed to collect rain distinct from wind samples. Samplers were modified Buchner funnels; four such samplers were used at each site. The first 100 ml of rain entering a funnel flowed into a small bottle: this volume was sufficient to wash the funnel and remove aerially deposited materials. A floating styrofoam ball sealed the small bottle when it was full, and the rest of the rainwater was diverted through 10-μm Nitex mesh. Collected particles were retained on the 10-μm mesh above water level of the collected rainwater so that any zooplankton propagules would not hatch in the sampler. The mesh was removed and washed with dechlorinated tap water to collect a sample, and rainwater volume was measured in a graduated cylinder. Four rain samplers were placed at each site.

Wind and rainwater samplers were placed at two sites: the University of Illinois at Springfield (UIS) and near Shick Shack Pond (SS). The UIS site was selected to be remote from potential sources of zooplankton propagules, by virtue of its elevation and distance from upwind water bodies. The SS site was near a natural pond, closer to ground level, and was considered more likely to collect propagules than the UIS site. However, the SS sample collectors were more remote from the pond than Maguire's (1963) samplers.

The UIS samplers were placed on the roof of a two-story building, with rain samplers and the windsock approximately 9 and 11 m above ground level, respectively. Land around the UIS site is very flat, and primarily agricultural land use. Samplers were near the west edge of the building, so as to collect particles from the prevailing wind direction (westerly) unaffected by rooftop structures. The UIS samplers were 0.4 km southwest of the campus pond, which was the closest body of water to the sample site. The Campus Pond is relatively young (25 years) with some submerged vegetation at the margins and a muddy bottom. Because prevailing winds were westerly and the Campus Pond was northeast of the samplers, we considered the pond an unlikely source of propagules. The closest water upwind of the samplers (other than roadside ditches) was Lake Springfield, a reservoir approximately 1 km away. No other upwind source of propagules was nearby: any organisms cultured from this site probably travelled some distance in the wind or rain.

Shick Shack Pond (Cass Co.) is approximately 80 km west–northwest of Springfield and one of the Illinois Natural Preserves (Karnes & McFall, 1995). Shick Shack Pond is old (ca 10 000 years) and completely surrounded by shrubs and trees. Surrounding land is hilly and mixed pasture and woods. Samplers were placed on a small hill approximately 150 m northeast of the pond. Rain samplers were placed on the ground and the windsock was 2.5 m above ground. Since the pond was upwind (for prevailing winds), relatively nearby, and samplers were at or near ground level, the pond was a probable source of propagules. In addition, no other water bodies were nearby.

Wind samples were removed from windsocks by transferring collected dry particles to a bottle which had been sterilized by rinsing with 70% alcohol and dechlorinated tap water and exposure to a germicidal UV bulb for 35–60 min. Dechlorinated tap water was used to rinse any remaining material out of the windsock into the bottle.

Rain samples were collected by removing the plankton netting from each apparatus and washing it thoroughly into a sterile bottle using dechlorinated tap water.

Duck feces were collected from mallard ducks at the Washington Park pond (Springfield, IL) in October 1995 and March 1996. The collection procedure was identical on both dates, except that March samples were carefully broken apart and observed under a dissecting scope for ephippia or adult zooplankton: none were observed. Ducks were observed feeding in the water and on shore. Feces were collected within minutes of deposition with a sterile metal spatula. Only the upper three-quarters of a fecal pellet was collected to avoid that part of the feces contaminated by the ground. Feces were placed in sterile bottles transported to the lab. The spatula was rinsed in 70% isopropyl alcohol between each collection.

In the laboratory, fecal material was rinsed with dechlorinated tap water through a 0.45-mm sieve to remove coarse particulate matter. The rinsate was used to culture zooplankton. Rinsed samples were refrigerated for 7 days prior to culturing in an attempt to break dormancy of copepods and cladocerans (Marcus, 1979; Schwartz & Hebert, 1987).

Samples were divided and incubated under one of two conditions: 20°C±2°C with constant fluorescent light (cool white bulbs) or 20°C ±2°C with UV light (Hagiwara, 1995). Samples were observed weekly under a dissecting scope and organisms were preserved with formalin or 70% alcohol. Samples were observed until no organisms were observed for 3 consecutive weeks.

Sediment core samples from Shick Shack Pond and Campus Pond were incubated as a test of incubation technique. Surface sediment was mixed and divided into several parts, diluted with sterile dechlorinated tap water in sterile containers, and incubated as above. Organisms were preserved with formalin or 70% isopropyl alcohol.

Results

Only four species were collected in wind and rain samples: bdelloids, *Lecane leontina*, *Lecane closterocerca* and *Keratella cochlearis* (Table 1). No crustacean species were observed. Bdelloid rotifers were the most common organism found in any of the samples (Table 1). Bdelloids were the only organisms found in the windsocks at both the campus and Shick Shack sites, but sites differed in the frequency of bdelloid occurrence. Bdelloid rotifers were found in only one of 11 (9%) of UIS windsock samples, and in seven of 11 (63.6%) SS windsock samples. Similarly, bdelloid rotifers occurred in 10% of UIS rain samples and 20% of SS rain samples (Table 1). Interestingly, *Keratella cochlearis* ccurred in one rain sample at each site, and on the same sample date. *Lecane closterocerca* and *Lecane leontina* also occurred in one of 40 (2.5%) of SS rain samples.

No metazoans were collected from incubated duck fecal matter (ciliates were present). However, rotifers, copepods, ostracods, and cladocerans were obtained by our incubation of both Campus Pond and Shick Shack Pond sediments (Table 2).

Table 1. Wind and rain dispersal results

Sample date	Sampling interval (days)	UIS Wind	UIS Rain	SS Wind	SS Rain
22 Oct 94	14	0/1	0/4	Bdell 1/1	Bdell 1/1 Lleon 1/4
12 Nov 94	21	0/1	0/4	Bdell 1/1	0/4
19 Nov 94	7	0/1	0/4	Bdell 1/1	Bdell 1/4
14 Mar 95	115	0/1	Bdell 1/4	Bdell 1/1	0/4
28 Mar 95	14	0/1	0/4	Bdell 1/1	0/4
12 Apr 95	15	0/1	0/4	0/1	0/4
24 Apr 95	12	0/1	0/4	0/1	0/4
14 Aug 95	112	Bdell 1/1	Bdell 3/3 Kcoch 1/3	0/1	Bdell 1/3 Kcoch 1/3 Lclos 1/3
29 Aug 95	15	0/1	0/3	Bdell 1/1	Bdell 2/3
18 Sep 95	20	0/1	0/3	0/1	Bdell 2/3
4 Dec 95	77	0/1	0/3	Bdell 1/1	Bdell 1/3
TOTAL	422	Bdell 1/11	Bdell 4/40 Kcoch 1/40	Bdell 7/11	Bdell 8/40 Kcoch 1/40 Lleon 1/40 Lclos 1/40

UIS site was on rooftop at University of Illinois at Springfield campus, SS site was near Shick Shack Pond, 80 km away from UIS. Bdell, bdelloid rotifer; Lleon, *Lecane leontina*; Lclos, *Lecane closterocerca*; Kcoch, *Keratella cochlearis*. Data represent the fraction of samples collected that contained each species. One windsock and four rain samplers were located at each site through 24 April 95, after which three rain samplers were used.

Table 2. Organisms incubated from sediments by same procedures used for wind, rain, and waterfowl fecal samples

	UIS Campus Pond	Shick Shack Pond
Rotifera	Bdelloid *Lecane leontina* *Lecane* sp. *Lepadella ovalis* *Lepadella patella* *Lepadella rhomboides* *Platyias patulus* *Platyias quadricornis* *Testudinella* sp.	Bdelloid *Lecane copeis* *Lecane closterocerca* *Lecane leontina* *Lepadella triptera*
Copepoda	*Cyclops bicuspidatus thomasi nauplii*	
Cladocera	*Alona guttata* *Ceriodaphnia quadrangula* *Kurzia latissima* *Pleuroxus denticulatus*	
Ostracoda	Two unidentified species	*Candona biangulata*

Discussion

Only four species were detected as dispersing by wind and rain during one year of sampling at two sites 80 km apart. All four species were rotifers: no crustaceans were observed in cultured wind or rain samples, nor were ephippia or diapaused copepods observed.

The two sample sites were intended to sample dispersal differently. Although both sites collected very limited sets of dispersing zooplankton, the site intended to be more remote (UIS) collected propagules less frequently than the site intended to be near a potential source pool (SS). This result may be due to several factors: (1) proximity of samplers to water (150 m at SS versus 1 km at UIS; (2) elevation (up to 2.5 m at SS versus 16 m at UIS); and/or (3) position of samplers relative to the prevailing wind direction and the pond. Although spatial pattern of dispersal canot be adequately analyzed with two sample sites, our results suggest that distances on the order of a kilometer severely restrict wind and rain dispersal of zooplankton.

Keratella cochlearis was observed in rain samples collected on the same day but 80 km apart. Rain samples were collected after precipitation events, and it is possible that *K. cochlearis* were dispersed by one storm front to both sites. However, this was the only such occurrence during the year.

No zooplankton were incubated from duck fecal material. Previous studies of zooplankton passing through waterfowl (Malone, 1965; Mellors, 1975; Proctor, 1964; Proctor & Malone, 1965; Proctor et al., 1967) were conducted in laboratories, with zooplankton eggs or adults fed to birds in the lab and feces then collected and incubated. None of the studies involved collection of feces from birds feeding in the wild. Clearly, birds can *potentially* transport zooplankton internally, but our results indicate that such events may not be naturally common. In addition, natural dispersal events would depend on compound probabilities: ingestion of viable propagules, survival of propagules in the gut, transport to a site within the gut passage time, and deposition in the site.

Limited species diversity in incubated samples was not due to poor incubation conditions, as evidenced by species collected from identically incubated pond sediments. It is possible that some propagules were present that did not hatch or break diapause in our experimental conditions. May (1986) used three temperatures to incubate sediments, with great success. We used one temperature, but the diversity of species from pond sediments and the paucity of species in wind, rain, and fecal samples indicates that incubation conditions did not cause low diversity.

Based on the results of this study, zooplankton are *not* readily dispersed by wind, rain, and duck feces. Wind and rain may play an occasional role in the dispersal of bdelloid rotifers but do not play a significant role in the dispersal of monogonant rotifers or other zooplankton. Aquatic organisms may be transported externally on waterfowl and other animals (Swanson, 1984), but actual rates, distances, and species involved are not clear.

Note that we do not say wind, rain, and internal transport by waterfowl does not happen, only that it appears to happen infrequently and for a few species. Our results are consistent with genetic and biogeographic studies that indicate species ranges change at geologic time scales (Boileau & Hebert, 1991; Carter et al., 1980; Stemberger, 1995). Obviously, more studies of zooplankton dispersal are warranted, but our results have important implications for the forces that shape zooplankton communities:

Abiotic conditions

Limited dispersal may impede our ability to use rotifers and other zooplankton as indicators of water quality (Pejler, 1995; Pontin & Langley, 1993). Instead, community composition, or the presence/absence of certain species may be confounded by chance dispersal events. Of course, the older the system and the more interconnections with other water bodies, the more likely it is that regional species would have been dispersed to a site. The problem is that so little empirical data exists on natural dispersal rates that the magnitude of this confounding factor remains largely unknown.

Biotic interactions

Competition and predation can be significant forces in community composition and seasonal successions of zooplankton communities. Dispersal may also be important, by virtue of its function as a 'rate-limiting step.' Ricklefs (1987) argued that unsaturated communities are shaped more by regional processes (speciation and dispersal) than by local processes (e.g., competition and predation). Models and empirical studies of rocky intertidal communities have indicated that settlement rate is the controlling parameter in determining those community dynamics (Roughgarden, 1989; Roughgarden et al., 1987; Underwood et al., 1983). When settlement rates are high, post-settlement processes (e.g., competition, predation) determine community composition (Connell, 1961; Paine, 1974); but when settlement rates are low, community composition is strongly influenced by settlement rate. This 'supply-side ecology' (Lewin, 1986) may be a common theme among different ecosystems.

Invasions

If zooplankton communities are not saturated by regionally available species, then local abiotic and biotic processes act on but a subset of potential community members. The addition of a new member by a rare dispersal event could have major consequences for community composition, especially if that species has strong interactions with existing species. Therefore, changes in community structure and function may occur that could rival or exceed changes that occur due to local processes. This is essentially the problem with invading species (Drake et al., 1991), although exotic species transferred among continents by humans have typically received most attention. Our results suggest that similar 'invasions' could occur intra-continentally by species native to a region, although the results may go unrecognized if zooplankton are presumed to have cosmopolitan distributions.

Succession

Robinson & Dickerson (1987) experimentally manipulated inoculation sequence and found sequence was important to resulting community structure, especially at low arrival rates. If many zooplankton species rarely disperse overland, the sequence of colonization will have lasting priority effects on subsequent community structure, especially given the ability of many zooplankton to develop large populations quickly and produce dormant life stages. Variation among zooplankton communities of regional, even closely-spaced ponds (Fryer, 1985) may be due to such effects.

Population genetics

Dispersal is significant to the maintenance of regional metapopulations (Taylor, 1990). Given low dispersal rates among water bodies, populations founded by single or few propagules may exhibit lasting founder effects (Berg & Garton, 1994; Boileau & Hebert, 1991; Thier, 1994). Therefore, egg banks (DeStasio,

1987) may store little genetic variation, and populations may be subject to inbreeding or outbreeding depression (Brown, 1991). Zooplankton populations among isolated water bodies may not operate as metapopulations.

Disturbance

Without minimal dispersal to provide a 'rescue effect' (Gotelli, 1991), local extinctions may occur, potentially changing community dynamics. Although local extinction risk is mitigated by an egg bank, the genetic bottleneck involved in colonization by one of few propagules may render some populations susceptible to disturbances that would be relatively innocuous to other, more diverse populations. Different populations may then respond to disturbance differently.

In summary, we did not find zooplankton to be readily dispersed by wind, rain, and waterfowl. Bdelloid rotifers alone were wind dispersed, but infrequently at distances of 1 km from a water body. Limited dispersal has important ramifications for common perceptions about processes regulating zooplankton community structure in freshwaters.

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