Regional versus local processes in determining zooplankton community composition of Little Rock Lake, Wisconsin, USA

Yolanda Lukaszewski, Shelley E. Arnott and Thomas M. Frost

Center for Limnology, University of Wisconsin, Madison, WI 53706, USA

1Present address: Ministry of Environment, PO Box 39, Dorset, Ontario P0A 1E0, Canada

Abstract. The species present within a community result from a combination of local and regional processes. We experimentally tested the importance of these two processes for lake zooplankton communities by examining the ability of additional species to persist when introduced into mesocosms in Little Rock Lake, Wisconsin, from other nearby lakes in the Northern Highland Lake District. We established a control treatment with only Little Rock Lake zooplankton and two treatments that supplemented the Little Rock communities with zooplankton from nearby lakes. Species richness declined during the 3 weeks of the experiment so that, at the end of the third week, the treatments with added zooplankton species had the same number of species as the controls; increasing the initial number of species in the community did not increase its final species richness. A plot of the mean species richness in the local habitat against the mean species richness of the regional pool fell below a 1:1 slope. This suggested that local processes were more important in structuring Little Rock Lake zooplankton communities.

Introduction

A central objective of community ecology is to understand what controls the distribution of organisms. Species distributions are influenced by factors operating at both regional and local scales (Ricklefs, 1987; Minns, 1989; Ricklefs and Schluter, 1993). At the regional scale, species occurrence patterns can be associated with dispersal or the movement of organisms across the landscape. Once organisms have arrived within a habitat, biotic interactions with established species and the suitability of the abiotic environment determine community composition. Here we examine the importance of regional versus local processes in structuring the zooplankton communities of lakes using experimental manipulations.

Few previous studies have attempted to test the importance of regional and local processes in structuring zooplankton communities experimentally. Dispersal has been particularly difficult to evaluate for zooplankton, but it could be an important factor in structuring zooplankton communities (Jenkins, 1995). Copepods, cladocerans and rotifers disperse by means of resting eggs or diapausing stages that are carried by wind, fish and waterfowl (Maguire, 1963; Dodson, 1992), as well as by surface water connections (Stemberger, 1995). While resistant resting eggs and a variety of transport mechanisms suggest that zooplankton have high immigration rates (Dodson, 1992), the occurrence of some copepod species appears to be limited by dispersal (Stemberger, 1995). In a survey of lakes in the northeastern USA, Stemberger (1995) found that some species of copepods were ubiquitous, suggesting no dispersal limitations. Other species, however, were found only in drainages that were once covered by glaciers, and were absent from high-elevation lakes, suggesting that the presence of some species was limited by dispersal.
We asked whether regional or local processes were more important in structuring zooplankton communities, i.e. are zooplankton dispersal limited, unable to reach new habitats, or is it that, once they arrive, they cannot tolerate local conditions? One approach to answering this question is to determine whether a community is saturated or unsaturated with species (Cresswell and Vidal-Martinez, 1995). Cornell (1993) defined saturation as ‘an upper limit to local richness that is independent of the size of the regional colonization pool in the sense that further increases in regional richness will have little influence on local richness’. An unsaturated community suggests that zooplankton are dispersal limited. If a zooplankton is able to survive in a habitat, this provides evidence for the importance of regional processes. The importance of regional and historical factors in shaping communities has been discussed by Holt (1993) and by Ricklefs and Schluter (1993). Local processes structure zooplankton communities abiotically (Locke and Sprules, 1993), biotically (DeMott and Kerfoot, 1982; Vanni, 1986; Black and Hairston, 1988), or both abiotically and biotically ( Arnott and Vanni, 1993; Rodriguez et al., 1993; Sierszen and Frost, 1993; González and Frost, 1994). Local processes would be more influential than regional processes in a saturated community where co-existing species compete for space and food resources.

To assess the roles of regional and local processes in structuring zooplankton communities, we tested the abilities of zooplankton communities to support additional species in a series of mesocosm experiments in Little Rock Lake. Little Rock Lake was the site of a whole-lake acidification experiment that divided the lake into treatment and reference basins (Brezonik et al., 1993). The treatment basin was manipulated in three, 2-year acidification levels to pH 5.6, 5.2 and 4.7. Biological recovery in the treatment basin of Little Rock Lake was incomplete at the time of our experiments (Sampson et al., 1995; Frost et al., 1998). This provided an opportunity to examine the invasibility of stressed and unstressed communities. Stressed communities have been postulated to be more susceptible to invasion (Pimm, 1989; Lodge, 1993) and we anticipated that introduced species would be more likely to persist in the Little Rock Lake treatment basin.

**Method**

We used three treatments for our mesocosm experiments, which were conducted in both the treatment and the reference basins of Little Rock Lake. They included: (i) a control with species only from the treatment or reference basin of Little Rock Lake; (ii) a low-species-richness treatment that supplemented Little Rock Lake zooplankton communities with zooplankton from three additional lakes; (iii) a high-species-richness treatment that supplemented Little Rock Lake communities with zooplankton from seven additional lakes. The control represented Little Rock Lake zooplankton communities with no dispersal to the lake; the low- and high-species-richness treatments simulated low- and high-dispersal-level situations, respectively, to the ambient Little Rock Lake community. We used three replicates for each treatment. The enclosures consisted of 309 l polyethylene bags, 1.35 m in length and 0.64 m in diameter, suspended from wooden
and styrofoam frames. The bags were open to the atmosphere, but sealed off from the sediments. We pumped Little Rock Lake water into all the bags, filtering out zooplankton through an 80-µm-mesh net. We stocked all mesocosms with Little Rock Lake zooplankton at approximately ambient density from the respective basin with one vertical tow from 2.0 m depth with a 50-cm-diameter, 80-µm-mesh Wisconsin net.

To establish the treatments with supplemented zooplankton, we stocked the mesocosms with zooplankton from the North Temperate Lakes, Long-Term Ecological Research (NTL-LTER) primary study lakes (Magnuson et al., 1984). These lakes lie within 10 km of Little Rock Lake in the Northern Highland Lake District in northern Wisconsin (http://www.limnology.wisc.edu/). We stocked the low-species-richness treatment with zooplankton from Allequash, Big Muskel-lunge and Sparkling Lakes, adding four new crustacean species to the mesocosms and increasing the densities of Little Rock Lake species (Table I). The high-species-richness treatment contained zooplankton from Allequash, Big Muskel-lunge, Crystal, Sparkling and Trout Lakes, and Trout and Crystal Bogs. This accounted for five additional crustacean species beyond the control and further increased the densities of Little Rock Lake and introduced species (Table I). Using a 12 l Schindler–Patalas trap, we collected zooplankton from the pelagic regions of the LTER lakes from 0.5 and 1.0 m, and stocked them at 8% of their ambient density in the mesocosms. We chose this density to simulate low-density invasion yet also to collect a diverse assemblage of zooplankton. By stocking the introduced species in the mesocosms, we eliminated any dispersal problems for them and were able to focus instead on what happened once they arrived in a lake they normally did not inhabit.

We sampled the zooplankton in the mesocosms once a week for 3 weeks during late June and early July 1995, using a 1.2-m-long, 0.05-m-wide tube that held 2.45 l

**Table I.** Crustacean zooplankton stocked into the three treatments at the beginning of the experiment. ‘All treatments’ lists the species common to the controls and the low- and high-species-richness treatments, including those not initially detected. ‘Low’ and ‘High’ include the species introduced to the low- and high-species-richness treatments, respectively

<table>
<thead>
<tr>
<th></th>
<th>All treatments</th>
<th>Low</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alona spp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bosmina longirostris</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chydorus sphaericus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daphnia catawba</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daphnia dubia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daphnia parvula</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diacyclops thomasi</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diaphanosoma birgei</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eucyclops spp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Holopedium gibberum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acanthocyclops spp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceriodaphnia spp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daphnia galeata mendotae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Skistodiaptomus spp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leptodiaptomus spp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesocyclops edax</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polyphemus pediculus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scapholeberis kingi</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tropocyclops extensus</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

993
of water (DeVries and Stein, 1991). To avoid transferring zooplankton, we sampled the controls first, then the low-species-richness treatments and finally the high-species-richness treatments. We lowered the tube into the bag and corked it below the surface, then filtered the contents through an 80-µm-mesh net. After repeating this three times, we pooled the samples together in one jar. We preserved the samples with Lugol’s solution for later identification and enumeration. We identified zooplankton to species using Dodson and Frey (1991), Williamson (1991), Balcer et al. (1984), Pennak (1978) and Brooks (1957), but grouped the following to genera: Acanthocyclops, Alona, Eucyclops, Leptodiaptomus, and Skistodiaptomus. The only copepods counted were adults. In samples where we could not positively identify Leptodiaptomus sp. and Skistodiaptomus sp., we excluded these species from statistical analysis.

We used a two-way analysis of variance (ANOVA) to test for differences between basins and among colonization treatments. Variables were (i) the difference between initial and end species richness, (ii) species richness at the end of the experiment and (iii) community similarity between basins and among treatments from the beginning to the end of the experiment. We calculated a similarity index using Jaccard’s Coefficient \( \text{CC}_J = c/(s_1 + s_2 - c) \) (Brower and Zar, 1984). This test uses species presence/absence data, where \( c \) is the number of species common to both basins, and \( s_1 \) and \( s_2 \) are the numbers of species in the treatment basin and reference basins, respectively. Possible values range from zero to one, with zero indicating that communities are completely different and one indicating that communities are exactly the same. We plotted residuals to test equality of variances. Variances were equally distributed across treatments, except for our comparison of end species richness. As a result, we used the Kruskal–Wallis one-way ANOVA, a non-parametric test.

**Results**

Overall species richness decreased from the beginning to the end of the experiment in the low- and high-species-richness treatments (Figure 1; Table II). The difference between the number of species present at the beginning and the end was significant (ANOVA; \( P < 0.001 \)). Species richness at the end of the experiment did not differ significantly between the treatment and reference basins (Kruskal–Wallis; \( P = 0.320 \)), nor did species richness at the end of the experiment differ significantly among the three treatments (Kruskal–Wallis; \( P = 0.524 \)). Roughly the same number of species survived in all three treatments in both basins (Figure 1). The zooplankton communities in both basins behaved similarly from start to finish (ANOVA; \( P = 0.278 \)). The results of Jaccard’s Coefficient confirmed that the mesocosm communities of the treatment and reference basins were similar to each other from beginning to end (ANOVA; \( P = 0.822 \)) with no interaction between the lake and treatments (ANOVA; \( P = 0.881 \)).

To determine zooplankton saturation levels, we used the mean number of species initially present in each treatment as the regional richness and the mean number present in each treatment at the end as local richness, and plotted these points. A slope of less than one would indicate a saturated community more
**Regional versus local processes and community composition**

![Graph showing species richness](image)

**Fig. 1.** The mean number of species at the beginning and end of the experiment in both basins ($n = 3$). Error bars represent 1 SEM. Beginning species richness excludes Little Rock Lake species that were undetected initially.

**Table II.** Summary of ANOVA results

<table>
<thead>
<tr>
<th>Test</th>
<th>d.f.</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Two-way ANOVA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Difference in species richness from beginning to end</td>
<td>1</td>
<td>1.289</td>
<td>0.278</td>
</tr>
<tr>
<td>Between basins</td>
<td>1</td>
<td>1.289</td>
<td>0.278</td>
</tr>
<tr>
<td>Among treatments</td>
<td>2</td>
<td>59.711</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Community similarity</td>
<td>1</td>
<td>0.053</td>
<td>0.822</td>
</tr>
<tr>
<td>Between basins</td>
<td>1</td>
<td>0.053</td>
<td>0.822</td>
</tr>
<tr>
<td>Lake × treatment interaction</td>
<td>2</td>
<td>0.002</td>
<td>0.881</td>
</tr>
<tr>
<td>Kruskal–Wallis one-way ANOVA $^a$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>End species richness</td>
<td>1</td>
<td>29.500</td>
<td>0.320</td>
</tr>
<tr>
<td>Between basins</td>
<td>1</td>
<td>29.500</td>
<td>0.320</td>
</tr>
<tr>
<td>Among treatments</td>
<td>2</td>
<td>1.292</td>
<td>0.524</td>
</tr>
</tbody>
</table>

$^a$Kruskal–Wallis test statistic for among-treatments comparison and Mann–Whitney $U$-test statistic for between-basins comparison.
strongly affected by local conditions; a line with a 1:1 slope would indicate an unsaturated community that is influenced by regional factors (Cornell, 1985; Minns, 1989; Cornell and Lawton, 1992; Figure 2). Our species richness curves fell below the 1:1 slope (Figure 3), indicating the importance of local conditions.

The three introduced species that disappeared from all treatments after 3 weeks were cladocerans (Daphnia galeata mendotae, Daphnia retrocurva and Ceriodaphnia), whereas the two that persisted were copepods (Acanthocyclops and Skistodiaptomus) (Figure 4). Acanthocyclops was present in four replicates of the low-species-richness treatment: two in the treatment basin and two in the reference basin. We also detected it in one of the controls in the reference basin. In four of these five replicates Acanthocyclops density increased. Skistodiaptomus survived in at least six replicates, but in three other replicates could not be positively identified. The surviving Skistodiaptomus populations decreased in density.

**Discussion**

Evidence is strong that local processes determined which species survived in Little Rock Lake. The inability of the three cladocerans to colonize the mesocosms supports this. At first glance, the persistence of Acanthocyclops and Skistodiaptomus could reflect unsaturated zooplankton communities. The decline in Skistodiaptomus populations during the experiment, however, suggests that they would be unsuccessful in colonizing the mesocosms, while the increase in Acanthocyclops abundance could be copepodids maturing into adults, not necessarily recruitment of a new generation. Recruitment of a new generation would indicate

![Regional Species Richness](image)

**Fig. 2.** A schematic diagram showing the possible relationship between local and regional processes. Regional species richness represents the number of zooplankton within an entire region. Local species richness represents the number of zooplankton within individual communities. Unsaturated, or Type I, communities have a 1:1 slope, where species additions from the regional pool result in proportional increases at the local level. In saturated, or Type II communities, species additions from the regional pool will not increase the number of species in the local community.
unsaturation. Because copepods have longer generation times than cladocerans (Allan, 1976), 3 weeks was probably insufficient time for reproduction. Zooplankton seem unlikely to be dispersal limited because of their many vectors of transport (but see Stemberger, 1995). The potential for high mobility by zooplankton suggests that these communities should tend to be saturated. In the Northern Highland Lake District, where an abundance of lakes provide many sources of colonizing zooplankton, high rates of dispersal seem likely.

Several studies report biotic and abiotic factors working together to determine which zooplankton species survive in a given body of water. For example, in fishless bog lakes in Northern Wisconsin and Michigan, pH and predation by invertebrates restrict small-bodied zooplankton species from colonizing (Arnott and Vanni, 1993). Neill (1978) attributed the absence of *Daphnia pulex* in one montane lake to unknown abiotic conditions, food limitation and *Chaoborus* predation. While most likely a combination of biotic and abiotic factors influenced which species survived in our enclosures, based on the evidence available to us, we believe that biotic factors played a secondary role to abiotic factors. Although fish can be important predators on zooplankton, we excluded them from the enclosures, and therefore did not evaluate their impact on the introduced zooplankton species. We observed *Chaoborus punctipennis*, an important invertebrate predator in Little Rock Lake (Fischer and Frost, 1997), in several of

![Graph](image_url)

**Fig. 3.** Relationship of mean local species richness versus mean regional species richness. Regional species richness represents the number of species present at the beginning of the experiment. Local species richness represents the number of zooplankton species present at the end of the experiment. Each point represents the control, low- and high-species-richness treatments, respectively. An unsaturated community would theoretically have a 1:1 slope, whereas the slope of a saturated community would fall below the 1:1 line, as it does here.
the enclosures. We believe that *Chaoborus* had a minor impact on the introduced species because their consumption rates are relatively low during July (Fischer, 1994). Furthermore, in July, the lake is numerically dominated by early instars, which are relatively inefficient predators (Moore and Gilbert, 1987). These instars tend to prey on small organisms such as rotifers and flagellated phytoplankton (Moore *et al.*, 1994); therefore, the large-bodied zooplankton that we introduced were probably not susceptible to *C. punctipennis* predation. We did not directly test for competition between native and introduced species, and are unable to comment on its role.

Abiotic conditions and/or food resources may have been more instrumental in determining species richness than biotic conditions. A qualitative analysis of
representative samples revealed similar food resources between basins. Large-bodied, inedible species were present in both basins of Little Rock Lake. We observed *Rhabdoderma, Aphanocapsa, Gloeоthece* and *Staurastrum* in the treatment basin, and *Gloeоthece* and *Aphanocapsa* in the reference basin. However, we also observed edible algae such as diatoms and *Pediastrum* in the enclosures, suggesting that suitable food resources were available to introduced species.

Ultraviolet radiation of the surface waters may have influenced the survival of introduced zooplankton species to a small extent as well. The mesocosms were 1.3 m deep and may have prevented zooplankton from escaping UVB radiation by restricting vertical migration. UVB radiation has been shown to increase zooplankton mortality (Williamson *et al*., 1994), and potentially toxic levels appear to penetrate to 1.0 m in Little Rock Lake (Williamson *et al*., 1996). Using equations from Morris *et al*. (1995), we calculated the 1% attenuation depths for UVB in both basins of Little Rock Lake and each of the source lakes. The 1% attenuation depth for UVB in both basins of Little Rock Lake was 0.5 m, less than half the depth of the enclosures. Four of the source lakes had UVB penetration depths greater than that for Little Rock Lake, suggesting that zooplankton taken from the surface waters of those lakes would not be adversely affected by UVB in Little Rock Lake. Three of the source lakes, Allequash, Crystal Bog and Trout Bog, had low penetration depths of 0.4, 0.2 and 0.1 m, respectively (LTER, unpublished data), indicating that UVB-sensitive zooplankton could suffer from the decreased UVB protection offered by Little Rock Lake. However, our enclosures extended beyond the 1% attenuation depth, thus providing zooplankton a refuge in the bottom half of the enclosures. Therefore, we believe that UVB radiation was not an important factor preventing the establishment of non-native zooplankton populations in our experimental enclosures.

The most probable explanation for the decline in species richness is pH intolerance. For example, *D.galeata mendotae*, one of the introduced species in this experiment, has demonstrated sensitivity to pH < 6.0, with decreasing biomass near pH 6.0 (Keller *et al*., 1990). In another study, *D.galeata mendotae, Skistodiaptomus oregonensis* and *D.retrocurva* showed sensitivity to pH < 6.0, with a 50% mortality at pH 5.7, 5.9 and 5.9, respectively, in laboratory experiments (Havens *et al*., 1993). The pH of Little Rock Lake treatment and reference basins in late June 1995 was 5.8 and 6.23, respectively (LTER, unpublished data), suggesting that pH may be a limiting factor for these species of zooplankton.

While our results indicate that local processes most strongly influenced zooplankton community composition, we would need to repeat this experiment at a whole-lake scale over a longer period of time to get a more complete answer. Two drawbacks to mesocosm experiments are reduced spatial and temporal scales (Carpenter, 1996; Drake *et al*., 1996). For example, zooplankton in enclosures were unable to take advantage of extensive habitat partitioning that might enable their co-existence in a lake (Makarewicz and Likens, 1975). Mesocosms, however, allowed us to conduct an experiment that would otherwise be logistically and ethically impossible. Considering the deleterious effects of non-native zooplankton species additions in other systems (Spencer *et al*., 1991; Yan and Pawson, 1997), we chose to conduct our experiment in enclosures that could be
dismantled at the end, without the risk of introducing non-native species into the lake. Using enclosures also enabled us to replicate treatments, something that would have been impossible at a larger scale.

The use of mesocosms may be problematic if they somehow inhibit the growth of zooplankton populations. We addressed this by comparing the development of the zooplankton in the control enclosures to the zooplankton in the lake during the experimental time period. The zooplankton in the treatment basin enclosures mostly followed the same trends as those in the lake, while only several species in the reference basin enclosures reflected the trends in the lake. Three of the five species we introduced successfully established populations in other enclosure experiments, demonstrating that enclosures do not inhibit their population growth. These species were *Ceriodaphnia* (Vanni, 1986), *D.galeata mendotae* (Vanni, 1988; Havens and Heath, 1989; Fischer, 1997) and *D.retrocurva* (although it declined in acidified enclosures) (Fischer, 1997).

Zooplankton communities generally recover following water quality improvements, but recovery times depend on the severity and duration of stress on the body of water, current water chemistry and colonization rates by common species (Keller and Yan, 1991; Keller et al., 1992; Locke et al., 1994; Yan et al., 1996). Recovery can take as long as a decade (Keller and Yan, 1991; Keller et al., 1992; Locke et al., 1994). Because the treatment basin zooplankton community had not returned to pre-acidification composition and density, we anticipated that introduced species would be better able to persist in the Little Rock Lake treatment basin. Introduced species, however, did not survive. This suggested that abiotic or biotic conditions created an unsuitable environment for regional species to colonize Little Rock Lake. Additionally, Little Rock Lake’s treatment basin is surrounded by many lakes (including the adjacent reference basin) that could provide it with colonists. Thus, composition and density differences between the treatment and reference basins were probably not because of colonization or dispersal restrictions. Our results suggest that, by 1995, the species that could survive the biotic and abiotic conditions in Little Rock Lake had already colonized it.

In conclusion, the addition of new species to the mesocosms did not increase species richness in either basin, indicating that communities were saturated and that local processes determined community composition. This contrasts previous studies which found that some plant and animal communities were unsaturated, and that regional processes were more important in determining community composition (Cornell and Lawton, 1992; Cornell, 1993; Caley and Schluter, 1997; Tilman, 1997). In this region, however, where there is a high density of lakes, dispersal rates of zooplankton among lakes are probably high and therefore regional processes are not important drivers. It is the local conditions that ultimately determine species composition.

**Acknowledgements**

helped with zooplankton identification. J. Magnuson, J. Fischer, D. Lewis, B. Greenfield, T. O’Keefe and two anonymous reviewers provided thoughtful comments and advice on several revisions of this manuscript. This research was supported by funds from the National Science Foundation Research Experience for Undergraduates, Long-Term Research in Environmental Biology and Long-Term Ecological Research programs.

References


Regional versus local processes and community composition


Received on June 24, 1998; accepted on December 31, 1998