

The role of dispersal levels, Allee effects and community resistance as zooplankton communities respond to environmental change

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Summary

1. Worldwide, freshwater zooplankton communities have been subjected to multiple environmental stressors including acidification, invasive species introductions, habitat alteration and climate change. Understanding the factors that affect zooplankton community responses in the face of environmental change is an important goal if ecologists expect to make predictions regarding the impact of current and future stressors. The acidification and recovery of lakes provides a well-studied example of the impacts of environmental change.

2. For this study, we conducted a field enclosure experiment using zooplankton communities that are recovering from the effects of acidification to determine whether dispersal levels, Allee effects and biotic interactions could influence community responses as pH levels increase. The experiment involved the introduction of four acid-sensitive colonist species (*Daphnia retrocurva*, *Skistodiaptomus oregonensis*, *Epischura lacustris* and *Tropocyclops extensus*) into enclosures stocked with recipient communities. The experiment was a factorial design with colonists introduced at three starting densities (low, medium and high) and enclosures being stocked with either diverse communities typical of neutral lakes or relatively depauperate communities dominated by the acid-tolerant copepod *Leptodiantomus minutus*. *Per capita* growth rates (r) for colonist species were measured by sampling communities in enclosures over a 10-week period. Factorial ANOVAS were conducted to determine whether r differed according to starting densities, recipient community type or their interaction.

3. Our results indicated that r for the copepods *E. lacustris* and *S. oregonensis* were greater when introduced at high initial densities, suggesting an Allee effect based on mate limitation. In addition, r for *S. oregonensis* was lower when introduced to acid communities, suggesting biotic interactions with the resident community were important for these species. *Per capita* growth rates for *T. extensus* and *D. retrocurva* did not differ among treatments.

4. *Synthesis and applications.* These results suggest that community response to environmental change can be influenced by dispersal, Allee effects and community interactions. Studies evaluating the ongoing recovery of zooplankton communities from acidification, or their response to other stressors, should take these factors into account. If rapid community responses are desired, dispersal rates for sexual zooplankton species (copepods) may need to be artificially increased.

Key-words: acidification, biotic resistance, environmental stressors, lakes, mate limitation, zooplankton

Introduction

The response of aquatic communities to environmental change can be influenced by both local and regional vari-

ables (Berg *et al.* 2010; Westley *et al.* 2010). Changes to local abiotic conditions, such as temperature or water pH, may alter community structure by causing shifts in relative species abundances or changes in species composition based on physiological tolerances (Keller & Yan 1998; Cottenie & De Meester 2004). Community changes driven by abiotic factors may eventually lead to altered competition and predation regimes, resulting in further shifts in community composition attributable to ecological pro-

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cesses (Shurin 2000; Cottenie *et al.* 2003). Regional variables that impact dispersal rates, such as habitat connectivity and the vagility of species in the regional species pool, may also be important because they can influence the capacity for communities to respond to environmental change (Shurin 2000; Shurin & Allen 2001; Cottenie & De Meester 2004). Low dispersal levels may hinder the ability of communities to adapt to changing conditions, while high dispersal levels allow communities to better track local conditions (Cottenie & De Meester 2004; Leibold *et al.* 2004).

Dispersal processes are key to providing the 'building blocks' of a community for local selective forces to act upon (Cottenie & De Meester 2004). However, to gain a better understanding of the true contribution of metacommunity processes during environmental change, it is necessary to couple knowledge of dispersal rates with local population dynamics (Gray & Arnott 2011a). After dispersing to a new environment, the growth and establishment of small introduced populations can be affected by both Allee effects and demographic stochasticity (Allee 1931; Grevstad 1999). Allee effects occur when there is 'a positive relationship between any component of fitness and numbers or density of conspecifics' (Stephens, Sutherland & Freckleton 1999). For example, in sexual species, reproductive output may depend on the availability of suitable mates (Stephens, Sutherland & Freckleton 1999). Demographic stochasticity may also be important for small populations as stochastic fluctuations in survival and reproductive rates can increase extinction probabilities (Dennis 2002). While both Allee effects and demographic stochasticity are important for sexual zooplankton species, seasonally parthenogenetic species may be impacted less by mate limitation due to the opportunity for bouts of asexual reproduction before the production of sexual resting eggs (Drake 2004).

Gaining an understanding of the factors that influence the response of communities to environmental change is an important prerequisite to making informed management decisions and predictions regarding the impacts of future environmental stressors. The acidification and subsequent pH recovery of lakes in the area surrounding Sudbury, Ontario, Canada, provides an ideal system with which to evaluate the role of dispersal and local variables as communities respond to a changing environment (Gray & Arnott 2011b). Decreased pH levels in many lakes caused decreases in species richness and species diversity of zooplankton communities (Marmorek & Korman 1993). Acid-sensitive zooplankton species such as *Daphnia mendotae*, *Epischura lacustris* and *Skistodiaptomus oregonensis* are typically absent from acidified lakes (Keller & Yan 1998). Instead, acidic lakes are numerically dominated by the acid-tolerant calanoid copepod *Leptodiaptomus minutus* (Keller & Yan 1998). Fortunately, reductions in sulphur dioxide and nitrogen oxide emissions beginning in the 1950s and 1960s has allowed for pH recovery in many lakes (Stoddard *et al.* 1999). As pH levels have increased, ecologists have studied the recovery of

zooplankton communities intensively (Yan *et al.* 2004; Monteith *et al.* 2005; Arnott, Jackson & Alarie 2006).

Most studies on acidified lakes have found a noticeable time lag in the response of zooplankton communities after pH levels have increased (Gray & Arnott 2009). Field experiments have suggested that these time lags may occur owing to a variety of local factors, including community resistance by acid-structured zooplankton communities (community resistance hypothesis; Binks, Arnott & Sprules 2005). Recent studies have also documented spatial structure in recovering zooplankton communities across the landscape, suggesting that dispersal could play a role as pH levels change (Valois, Bill Keller & Ramcharan 2010; Gray & Arnott 2011b). A recent study by Gray *et al.* (2011a) also documented Allee effects for the acid-sensitive calanoid copepod *E. lacustris*. While these studies provide evidence that both local factors and dispersal can influence community change in response to a stressor, they had several limitations. Binks, Arnott & Sprules (2005) tested community resistance using only one acid-structured recipient community (Swan Lake, Sudbury, Ontario), making it difficult to generalize about the importance of this factor. Gray & Arnott (2011a) described Allee effects for only one copepod species (*E. lacustris*), leaving questions about whether other acid-sensitive copepod species respond similarly or if other species might have noticeably different Allee thresholds (Gerritsen 1980). Moreover, Gray & Arnott (2011a) did not provide an assessment of how likely Allee effects were to occur given levels of zooplankton dispersal to acidified lakes. Finally, past studies were not able to examine the effects of dispersal and community resistance together, making it difficult to determine whether there could be cumulative or interactive effects of these two factors.

For this study, we conducted a field experiment to test if dispersal levels, community resistance and their interaction could influence the growth and establishment of colonists introduced to communities that are responding to environmental changes associated with recovery from regional acidification. This study was designed to address some of the limitations of past research described in the previous paragraph. To test the generality of the community resistance hypothesis (Binks, Arnott & Sprules 2005), we collected four acid-structured and four neutral-structured zooplankton communities from eight different lakes for use as recipient communities in our experiment. In addition, the influence of Allee effects was tested for two additional acid-sensitive copepod species in addition to the previously studied *E. lacustris*. Furthermore, the experiment was a full factorial design allowing for an examination of the potential cumulative or interactive effects of dispersal and community resistance on the growth and establishment of introduced colonists. Lastly, experimental results were coupled with field data collected by Gray & Arnott (2011b) to assess whether dispersal levels measured in the field are likely to lead to Allee effects for copepod populations colonizing recovering lakes.

Materials and methods

FIELD ENCLOSURE EXPERIMENT

To determine whether dispersal levels, community resistance and their interaction could influence the growth and establishment of acid-sensitive zooplankton populations we conducted a factorial design field enclosure experiment. The experiment involved the introduction of four acid-sensitive species into enclosures stocked with recipient communities. There were two recipient community types (acid, neutral) and three colonist propagule pressure levels (low, medium and high). Community types were replicated at the lake level by collecting four acid-structured and four neutral-structured recipient communities from eight different lakes (i.e. communities from the eight lakes were not mixed or combined). In summary, there were 2 community types \times 3 propagule pressure levels \times 4 replicates per community, for a total of 24 experimental enclosures. A control enclosure was also included that contained only filtered lake water. This enclosure allowed us to assess whether contamination had occurred during the course of the experiment. Enclosures were numbered from 1 to 25 and each community type by propagule pressure treatment combination was assigned to an enclosure using a random number generator.

The enclosure experiment was run in Killarney Provincial Park, Ontario. Zooplankton communities in many of the park's lakes were damaged as a result of acidification caused by SO_2 and NO_x emissions from nearby industrial activity (Holt & Yan 2003). Four acid-sensitive species native to the region were selected as colonists: *Daphnia retrocurva*, *E. lacustris*, *S. oregonensis* and *Tropocyclops extensus* (Keller & Yan 1998). *Daphnia retrocurva* is a cladoceran zooplankton that can reproduce parthenogenetically and therefore would not be hindered by mate availability during introduction events. *Epischura lacustris*, *S. oregonensis* and *T. extensus* are copepod zooplankton that must reproduce sexually and therefore could be affected by mate limitation when introduced at low densities.

To select recipient communities representative of those found under acid and neutral conditions, we referred to the results of a principal components analysis (PCA) conducted by Gray *et al.* (2012) using data from 45 Killarney Park lakes collected in 2005. The analysis indicated a separation of zooplankton communities along PCA axis 1, with most acidic lakes having high axis 1 values and most neutral communities having low axis 1 values. Acid communities were dominated by the calanoid copepod *Leptodiatomus minutus*, while neutral communities had a more even mix of species (Gray *et al.* 2012). We selected four lakes with low PCA axis 1 scores (neutral communities) and four with high PCA axis 1 scores (acidic communities) for use as recipient communities in our experiment (Table 1). Zooplankton community data collected in 1990, 2000 and 2005, suggested that our four colonist species were not present in the eight study lakes we selected (Sprules 1975; Holt & Yan 2003; Gray *et al.* 2012).

The experiment was conducted using floating enclosures on Carlyle Lake (N46°03', W81°17') in Killarney Provincial Park, between 3 June and 5 August 2010. The pH of Carlyle Lake water in July 2011 was 6.1 (Shelley E. Arnott, unpublished data). Enclosures were constructed following the methodology of Arnott & Vanni (1993). Each enclosure consisted of a 1 m diameter cylindrical polyethylene tube that was closed off from the lake at the bottom and suspended approximately 30 cm above the water surface with a floating wooden frame. Each tube was approxi-

mately 1.8 m in length and was filled with lake water to a depth of 1.5 m (1178L volume). Lake water added to enclosures was filtered consecutively through an 80 μm and then 50 μm mesh to remove crustacean zooplankton. Enclosures were covered with tulle fabric (approximately 1.2 mm mesh size) to prevent contamination from diapausing eggs transported by waterbirds and large insects.

Recipient communities were collected from 8 lakes (four acid-structured and four neutral-structured; Table 1) and added to enclosures on 26 and 27 May. Three vertical zooplankton hauls (one for each propagule pressure treatment) were collected from each lake using a 35 cm diameter, 50 μm , mesh size zooplankton net. To stock the enclosures with an ambient density of zooplankton, each net haul was pulled from 16 m depth so as to sample approximately 1.5 m^3 of water. Zooplanktons collected from each haul were placed in approximately 2 L of lake water in a Nalgene container for transport to enclosures on Carlyle Lake. Recipient communities were released into their assigned enclosures by partially submerging the Nalgene containers and opening them at the air-water interface.

When introducing colonist species to our enclosures, we aimed to choose population sizes that were low enough that sexual species might experience Allee effects but high enough to avoid extinction. To calculate a rough approximation of the density of individuals required to meet this goal, we calculated critical densities using a mate finding model from Gerritsen (1980) that is described in Appendix S1 (Supporting Information). Estimated critical densities ranged between approximately 2–6, 3–9 and 6–245 m^{-3} for *E. lacustris*, *S. oregonensis* and *T. extensus*, respectively. The wide range for *T. extensus* resulted from uncertainty regarding its swimming speed (see Appendix S1, Supporting Information). To achieve densities within the calculated range for these species, we introduced 4, 8 and 16 individuals to our low, medium and high propagule pressure treatments, respectively. Given that each mesocosm contained approximately 1.17 m^{-3} of water, this resulted in initial densities of 3.4, 6.8 and 13.7 individuals per cubic metre, for low, medium and high treatments, respectively. It is important to note that N_C values calculated using this method should be viewed only as very rough estimates because behavioural and physiological processes can significantly alter estimates of critical density (Kramer, Sarnelle & Yen 2011).

Table 1. Location of Killarney Park lakes from which recipient communities were collected for enclosure experiment. Recent pH measurements and the type of community structure based on results of a principle components analysis are also indicated

Lake	Latitude (N)	Longitude (W)	pH*	Community structure
Bell	46°07'	81°12'	6.6	Neutral
Clearsilver	46°07'	81°15'	5.2	Acid
George	46°01'	81°24'	6.6	Neutral
Great Mountain	46°09'	81°21'	6.0	Neutral
Johnnie	46°05'	81°14'	6.2	Neutral
Lumsden	46°01'	81°25'	5.6	Acid
O.S.A.	46°03'	81°23'	5.1	Acid
Ruth Roy	46°05'	81°15'	5.1	Acid

*Data from Gray *et al.* (2012).

Colonist species used for our experiment were collected from nearby lakes where they had been found during past surveys. *Daphnia retrocurva* was collected from Richard Lake (N46°26', W80°55'), and *E. lacustris*, *S. oregonensis* and *T. extensus* were collected from Tyson Lake (N46°07', W 81°07'). The zooplankton communities of both lakes were sampled on 2 June 2010 using an 80- μ m conical zooplankton net and live samples were transported to the laboratory for sorting. In the laboratory, colonist species were extracted from petri dishes using pipettes, placed on glass microscope slides in drops of water, identified under a dissecting microscope and transferred into 250-mL sample containers that had been previously filled with filtered (50 μ m) lake water. To correspond with the three propagule pressure treatments, 4, 8 or 16 individuals were placed into the 250-mL sample containers during sorting. For *E. lacustris* and *S. oregonensis*, equal numbers of males and females were placed in each sample container. Owing to their speed and small size, individual *T. extensus* could not be sexed and were therefore placed in containers at the existing sex ratio. Ovigerous females of all species were excluded. *Epischura lacustris*, *S. oregonensis* and *T. extensus* were added to enclosures on 2 June, while *D. retrocurva* individuals were introduced on 3 June.

The growth of the introduced colonist populations was monitored through time by sampling our enclosures after 4, 6, 8 and 10 weeks. No sampling occurred during the first 4 weeks to allow for the reproduction of introduced colonists. Sampling at weeks 4, 6 and 8 consisted of a single vertical haul from the bottom to top of each enclosure using a 30-cm diameter 80- μ m zooplankton net. More extensive sampling was conducted at week 10 by taking 13, 1.5-m vertical hauls from each enclosure with a 30-cm diameter 80- μ m zooplankton net. Given this sampling scheme, approximately 12% of the existing zooplankton population was sampled at weeks 4, 6 and 8, while 82% was sampled at week 8. Analyses that estimate the influence of sampling error on the calculation of r are described in Appendix S2 (Supporting Information).

DATA ANALYSIS

The *per capita* population growth rate (r) of colonist species in each of the 24 stocked enclosures was determined by calculating the natural logarithm of the estimated population size at each time interval (weeks 0, 4, 6, 8 and 10) and fitting a least-squares linear regression model to determine the slope of the line. The slope of a semi-logarithmic plot of population size vs. time represents r (Gotelli 2001). Exponential growth was assumed because colonist populations introduced at the highest population sizes (16 individuals) did not appear to reach a carrying capacity over the course of the experiment (Appendix S3, Supporting Information). The population size in each enclosure at time 0 was assumed to be the number of individuals introduced and therefore did not account for mortality that could have occurred following the introduction of colonists. Zeros for weeks 4, 6 and 8 were excluded when fitting the regressions because the failure to collect individuals on those dates was assumed to be a reflection of the low probability of detection with one vertical net tow (individuals were often collected from the same enclosures at subsequent sampling dates).

For logistical reasons, our four colonist species were introduced into the same enclosures for our experiment. This cohabitation allowed for interspecific interactions among colonist species that could have influenced our results. For example, if

one colonist went extinct consistently in one of our treatments, it could have released the other colonist species from competition, thereby biasing our results. To determine whether there were any consistent patterns of extinction, we created a 2×3 contingency table for each species containing counts of the number of populations that reached extinction for each propagule pressure \times community treatment combination. We then ran a Fisher's exact test in *R* to determine whether there was an association of these extinction counts with our experimental treatments.

To analyse the structure of the recipient zooplankton communities added to our enclosures, and to ensure that recipient communities did not contain colonist species, zooplankton samples were collected from enclosures before the start of the experiment (1 June) using a 15-cm diameter zooplankton net. Only one colonist species was detected in our enclosures prior to the start of experiments: *E. lacustris* was found in the recipient communities collected from George Lake. As a result, *E. lacustris* data obtained from these three enclosures were excluded during analyses. A survey conducted in the year following these experiments (2011) found *D. retrocurva* in Bell and Johnnie Lakes, while *E. lacustris* was collected from Johnnie Lake (Shelley E. Arnott, unpublished data). Colonists remained absent from all other lakes used as sources for recipient communities. To avoid potential bias owing to contamination, we excluded data for *D. retrocurva* introduced to Bell and Johnnie communities. Similarly, data for *E. lacustris* introduced to Johnnie communities were not used in analyses. The overall conclusions of the study were the same regardless of whether these data were excluded from analyses or not.

To analyse the structure of our recipient communities, we used PCA. PCA is a linear ordination technique that allows for the visualization of the differences among communities along the most variable axes. The data used for the PCA included a survey of 45 lakes conducted in 2005 (Gray *et al.* 2012), as well as the data that were collected from the eight communities introduced to our enclosures. Species abundances were Hellinger-transformed to reduce the influence of rare species (Legendre & Gallagher 2001). The PCA was conducted on the species covariance matrix using the `pca{labdsv}` function in *R* (Roberts 2010). To aid with the interpretation of the PCA biplot, lakes were divided into three categories based on their acidification histories and current pH levels as determined by water chemistry data collected in 1972–73 and 2005 (Gray *et al.* 2012): (i) Circumneutral lakes that have always had a pH > 6; (ii) Recovered lakes that dropped to <6 during acidification but have subsequently recovered; and (iii) Acidic lakes that currently remain at pH levels <6.

A factorial analysis of variance (ANOVA) was conducted separately for each of the four colonist species to determine whether r differed significantly among propagule pressure treatments or between community types, and if variation among treatments was based on an interaction between propagule pressure and community type. ANOVAs were followed by *post hoc* Tukey Honestly Significant Different (HSD) tests to determine where significant differences existed. Assumptions of normality were violated for r in *D. retrocurva*, *S. oregonensis* and *T. extensus* (Shapiro-Wilk's Test, P -values > 0.05) and transformation of r for each species failed to yield a normal distribution. As ANOVA is robust to violations of normality when sample sizes are equal, we chose to present the factorial ANOVA results for these species. However, we also conducted permutation tests intended for factorial ANOVA designs that do not require the assumption of

normality. The test recommended by Manly (2007) allows for the unrestricted permutation of data over all cells in the experimental design. The permutation procedure was repeated 5000 times for each species to provide a distribution of F -values that could occur under the null hypothesis. The F -value calculated from our experimental data (F_{exp}) was then compared with the F -distribution obtained from the resampling approach to determine the percentage of replications under which the resampled F exceeded F_{exp} . The percentage of replications that exceed F_{exp} represents the probability of obtaining F_{exp} assuming that the null hypothesis is true (similar to the P -value in a conventional ANOVA). The assumption of homogeneity of variances for r was met for all four colonist species (Levene's test, P -values > 0.05).

MEASURED DISPERSAL LEVELS AND THE POTENTIAL FOR ALLEE EFFECTS

Although our enclosure experiment provided the opportunity to document Allee effects and estimate Allee thresholds, this information alone does not allow for a determination of whether Allee effects are likely to occur given natural dispersal rates. To assess the likelihood that our study species might experience Allee effects during the colonization of new habitat, we used dispersal data collected by Gray & Arnott (2011b). In this previous study, we measured overland dispersal of zooplankton to four lakes in Killarney Provincial Park from May to August 2009. Fifteen small (0.85 m² surface area) plastic bins were placed approximately 10 m from the shoreline of each of the study lakes and were sampled every 10 days to collect incoming zooplankton. Over 110 days, we collected only 19 adult copepods (*Leptodiaptomus minutus* and *Macrocyclus albidus*) and two unidentified copepod nauplii (Gray & Arnott 2011b). However, given the small surface area of the plastic bins, it is likely that other species were dispersing across the landscape but were not sampled. To determine the probability that our study species were dispersing at high enough levels to overcome Allee effects, but were not captured by the traps because of their small surface area, we made two simplifying assumptions: (i) zooplankton dispersing across the landscape rain down uniformly on the surface of recipient lakes; and (iii) the arrival of individuals through time follows a Poisson distribution,

$$p(x) = \frac{\lambda^x e^{-\lambda}}{x!},$$

where $p(x)$ is the probability of x occurrences in a particular time frame given an expected number of occurrences, λ . The expected number of occurrences per season was determined by calculating the number of individuals that would need to rain down on each of the four study lakes used by Gray & Arnott (2011b) in order to achieve densities ranging from 1 to 15 individuals m⁻³ in the epilimnion and then scaling this down to the surface area of the 15 bins used at each lake. Using the `dpois{stats}` function in *R*, we then calculated the probability of zero occurrences per season of our study species ($x = 0$) in all 15 traps used at each lake assuming that individuals were raining down at the expected number of occurrences (dispersal rates) required to achieve the aforementioned densities (1–15 individuals m⁻³). Although these calculations rely on a simplistic conception of overland dispersal, this method allowed us to assess if Allee effects might be a common or rare phenomenon for our study species in Killarney Park.

Results

Samples collected from our enclosures prior to the introduction of colonists revealed that the recipient communities within our enclosures were representative of acid-structured and neutral-structured communities found in Killarney Park (Fig. 1). Acid communities were dominated by *Leptodiaptomus minutus*, while neutral communities had a variety of acid-sensitive species (Fig. 1). We did not detect the colonization of any acid-sensitive species into our acid-structured enclosures over the course of the experiment, suggesting that the essential difference between our two community treatments was maintained. None of the four colonist species were found in our control enclosure consisting of filtered lake water.

Over the course of the experiment, *E. lacustris*, *S. oregonensis* and *T. extensus* populations experienced positive growth rates, while *D. retrocurva* populations experienced negative growth rates (Fig. 2). Of the 24 introduced populations for each species, there were 6, 0, 5 and 17 extinctions for *E. lacustris*, *S. oregonensis*, *T. extensus* and *D. retrocurva*, respectively. All extinctions for *E. lacustris* occurred in the low propagule pressure treatments, while no consistent patterns of extinction occurred for *T. extensus* and *D. retrocurva*. The results of our Fisher exact tests revealed that the number of extinctions for each colonist species were not significantly associated with our experimental treatments (P -values > 0.6 in all cases).

Results of the factorial ANOVAS using data on *per capita* growth rates for each species found significant main effects for *E. lacustris* and *S. oregonensis* (Table 2). For *E. lacustris*, r differed significantly among propagule pressure treatments, but not according to community type (Table 2). Follow-up Tukey HSD tests indicated that r was significantly higher for *E. lacustris* in the high propagule pressure treatment compared with the low propagule pressure treatment ($P < 0.05$), but differences between low and medium and medium and high propagule pressure were not significant ($P > 0.05$). For *S. oregonensis*, r differed according to both propagule pressure and community type (Table 2). Follow-up Tukey HSD tests indicated that r was significantly higher in medium and high propagule pressure treatments than in low propagule pressure treatments (P -values < 0.05), but r did not differ significantly between medium and high propagule pressure treatments ($P > 0.05$). For *T. extensus* and *D. retrocurva*, there were no significant differences in r based on either community type or propagule pressure (Table 2). Results of permutation tests designed for factorial experiments mirrored the results found in our parametric ANOVAS (Table 2).

Calculations using data from Gray & Arnott (2011b) indicated that it was unlikely that *E. lacustris*, *S. oregonensis* and *T. extensus* were dispersing to the four study lakes examined by Gray & Arnott (2011b) at rates required to achieve densities between 1 and 15 individu-

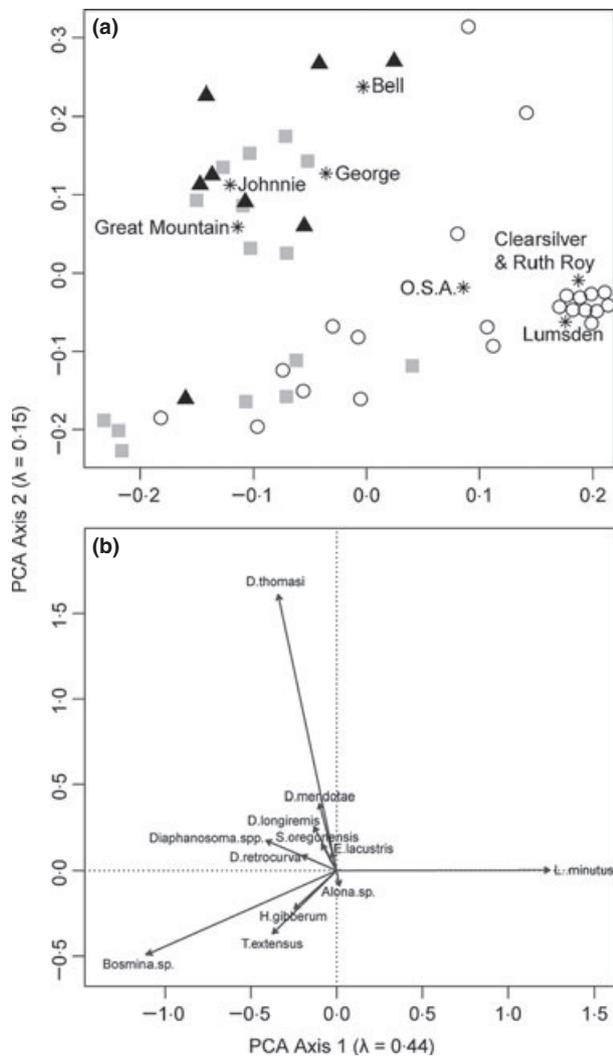


Fig. 1. Principal components analysis of zooplankton communities for 45 lakes in Killarney Park collected in 2005. (a) Site scores: squares = recovered lakes, circles = acidic lakes, triangles = circumneutral lakes. Communities sampled from enclosures representing neutral and acidic communities were also included in the PCA (asterisks). (b) Species scores.

als m^{-3} in the epilimnion. For all four study lakes examined, the probabilities that our study species were arriving at rates required to reach even 1 individual m^{-3} , but were not sampled by the overland dispersal traps used by Gray & Arnott (2011b), were <0.001 .

Discussion

This study provides further evidence of the potential importance of dispersal limitation as communities respond to environmental change. In our experiment, *per capita* growth rates for both *E. lacustris* and *S. oregonensis* were higher when populations were introduced at high density than at low density, suggesting an Allee effect. Given the environmental conditions in our enclosures, the Allee threshold between growth and extinction occurred some-

where between 3.4 and 6.8 individuals m^{-3} for *E. lacustris* and was <3.4 individuals m^{-3} for *S. oregonensis*. To achieve the threshold required for *E. lacustris* would require relatively high dispersal rates. For example, to reach a density of approximately 3.4 individuals m^{-3} in a hypothetical 10-ha lake that is 10 m deep, 3.4×10^6 individuals would need to disperse and survive to reproduce during the ice-free season. Given the low overland dispersal rates measured by Gray & Arnott (2011b) for Killarney Park lakes, the arrival of this many *E. lacustris* individuals seems unlikely. During a 110 day study, *E. lacustris* was not found in 60 overland dispersal traps that were placed around the circumference of four Killarney lakes (Gray & Arnott 2011b). Furthermore, our calculations based on data from Gray & Arnott (2011b) indicated that it was unlikely that *E. lacustris* was dispersing at rates high enough to exceed Allee thresholds, but was missed by dispersal traps placed around their four study lakes. Unfortunately, our data do not allow us to estimate an Allee threshold for *S. oregonensis* because growth rates were positive even in our low propagule pressure treatment. However, no *S. oregonensis* were collected in the overland dispersal traps used by Gray & Arnott (2011b), and distributional data collected by Stemberger (1995) suggests that the species might be a poor disperser because there is little evidence that it has spread beyond its postglacial distribution. Recolonization of *S. oregonensis* and *E. lacustris* from the diapausing egg bank may be possible, but the contribution of the egg bank in some lakes could be limited owing to burial, ageing and Allee effects (Sarnelle & Knapp 2004; Gray & Arnott 2009). Dispersal through stream connections may also provide an opportunity for recolonization, but would require the presence of a neutral upstream lake. Owing to the regional nature of acidification, very few stream connections exist between neutral lakes and acidified lakes in Killarney Park (Gray & Arnott 2011b). Taken together, our results suggest that the addition of copepod species to zooplankton communities recovering from acidification may be hindered by a combination of dispersal limitation and Allee effects.

Our results add to a growing body of evidence suggesting that dispersal processes and Allee effects can play an important role in determining the distribution of zooplankton species. The current study along with Valois, Bill Keller & Ramcharan (2010), Gray & Arnott (2011a,b) and Gray *et al.* (2012) provide evidence for the importance of dispersal limitation and Allee effects during recovery from acidification, while Sarnelle & Knapp (2004), Knapp & Sarnelle (2008) and Kramer, Sarnelle & Knapp (2008) have documented the impacts of dispersal and Allee effects for copepods recolonizing alpine lakes after removal of an introduced predator. Interestingly, while these recovery studies seem to highlight the importance of dispersal limitation, conclusions from more general studies of zooplankton colonization and dispersal are mixed. Some studies that have observed the colonization of sterile habitats have

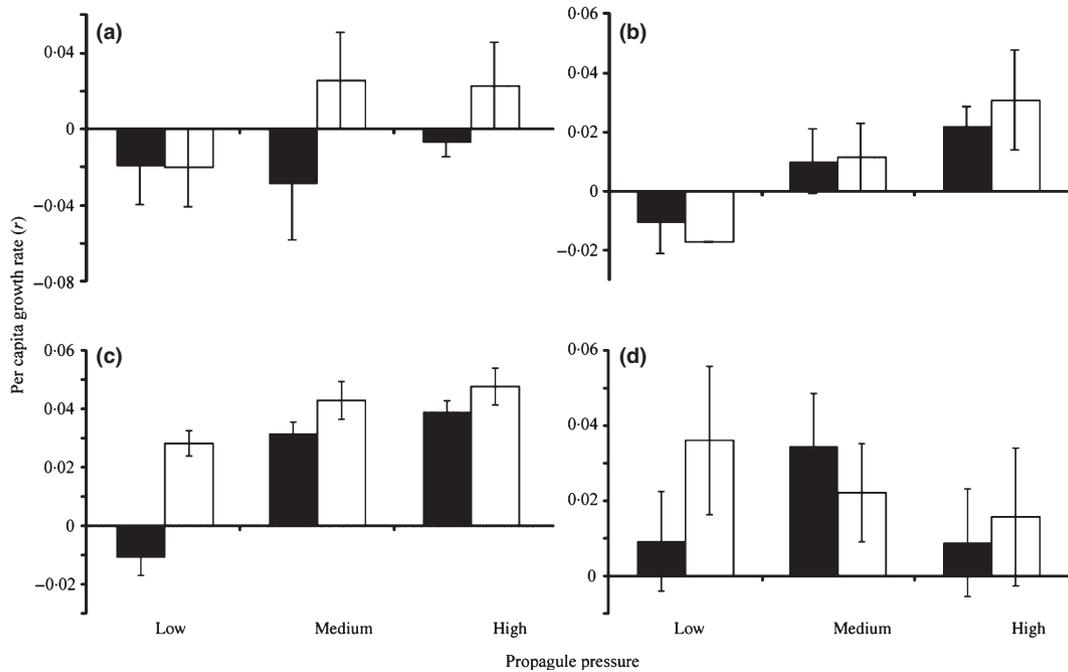


Fig. 2. Per capita population growth rates vs. propagule pressure and community type for four species colonizing acid-structured (filled bars) and neutral-structured (open bars) zooplankton communities. (a) *Daphnia retrocurva*; (b) *Epischura lacustris*; (c) *Skistodiptomus oregonensis*; (d) *Tropocyclops extensus*. Low, medium and high propagule pressure treatments consisted of individuals introduced at 3.4, 6.8 and 13.7 individuals per cubic metre, respectively.

Table 2. Results of factorial ANOVAS conducted to determine whether *per capita* growth rates for four colonist species differed significantly based on propagule pressure and community resistance treatments. Results of the additional analyses based on permutation tests are also included

Dependent variable	Source	Degrees of freedom	Sum of squares	Mean square	F-value	P-value	Permutation test P-value
<i>Per capita</i> growth rate of <i>Daphnia retrocurva</i>	Community	1	0.0031	0.0031	3.7	0.076	0.068
	Propagule pressure	2	0.0015	0.0007	0.9	0.418	0.423
	Community × propagule pressure	2	0.0020	0.0010	1.2	0.643	0.319
	Error	12	0.0100	0.0008			
<i>Per capita</i> growth rate of <i>Epischura lacustris</i>	Community	1	7×10^{-6}	6.7×10^{-6}	0.01	0.899	0.898
	Propagule pressure	2	0.0043	0.0021	5.3	0.021	0.021
	Community × propagule pressure	2	0.0001	7.6×10^{-5}	0.2	0.830	0.831
	Error	12	0.0048	0.0004			
<i>Per capita</i> growth rate of <i>Skistodiptomus oregonensis</i>	Community	1	0.0006	0.0006	8.5	0.009	0.009
	Propagule pressure	2	0.0015	0.0007	9.5	0.001	0.001
	Community × propagule pressure	2	2.5×10^{-5}	1.3×10^{-5}	0.1	0.855	0.857
	Error	18	0.0014	8×10^{-5}			
<i>Per capita</i> growth rate of <i>Tropocyclops extensus</i>	Community	1	0.0002	0.0002	0.3	0.590	
	Propagule pressure	2	0.0009	0.0004	0.5	0.598	
	Community × propagule pressure	2	0.0012	0.0006	0.6	0.519	
	Error	18	0.0160	0.0008			

concluded that colonization occurs rapidly, and therefore dispersal is unlikely to be a limiting factor (Cohen & Shurin 2003; Louette & De Meester 2005; Vanschoenwinkel *et al.* 2008), while others conclude the exact opposite (Jenkins 1995; Jenkins & Underwood 1998; Cáceres & Soluk

2002; Allen 2007). Analyses using large data sets also come to contrasting conclusions regarding the importance of dispersal processes (Beisner *et al.* 2006; Shurin *et al.* 2009). **2** The wide range of results obtained by the aforementioned studies may stem from regional differences in factors that

could affect dispersal rates such as landscape structure, the availability of dispersal vectors or some other unmeasured variable (Bohonak & Jenkins 2003; Allen 2007; Gray *et al.* 2011b).

Our results also provide evidence that community interactions, such as competition, may play a role as communities respond to changing environmental conditions. *Per capita* growth rates for *S. oregonensis* were higher when introduced into neutral communities than when they were introduced into acid-structured communities dominated by *Leptodiatomus minutus*. Experiments conducted by Binks, Arnott & Sprules (2005) found similar results: *S. oregonensis* populations introduced into an acid-structured community had lower establishment success compared with those introduced to enclosures that contained only filtered lake water. While Binks, Arnott & Sprules (2005) did not have replicate acid-structured communities for their experiment, the present study involved the use of four acid-structured and four neutral-structured communities, suggesting that community resistance may be a general phenomenon during recovery from acidification. The reasons that *S. oregonensis* appeared to be more successful when introduced to neutral-structured communities are unclear; however, *S. oregonensis* is herbivorous, leading Binks, Arnott & Sprules (2005) to speculate that community resistance might occur owing to competition for algal resources. Many past studies have also documented evidence of community resistance in zooplankton resulting from priority effects and alternate stable states (Mouquet *et al.* 2003; Louette, De Meester & Declerck 2008; Allen & VanDyke 2011). The mechanisms behind priority effects can be complex, including joint effects of resource depletion, competition and predation (Price & Morin 2004; Gerla *et al.* 2009). Therefore, a more detailed study of potential interactions between acid-structured communities and *S. oregonensis* is needed before proposing a definitive explanation for our results.

The results of this study have practical implications in terms of setting expectations for the recovery of zooplankton communities from acidification and for understanding the factors that may hinder zooplankton community responses in the face of environmental change. One of the main goals behind emissions reduction agreements was the recovery of biota damaged by acid deposition (Menz & Seip 2004). As a result, aquatic ecologists have extensively studied acidified zooplankton communities looking for signs of recovery (Gray & Arnott 2009). The results of this study indicate that dispersal limitation and community interactions may significantly delay the recovery of copepod communities and that short-term expectations should be adjusted to account for these processes. Our results also indicate that mate limitation and community interactions can hinder the response of communities to environmental change by affecting the colonization/extinction dynamics of species that might be better suited to current environmental conditions. Cottenie & De Meester (2004) describe dispersal processes as ‘fuel’ burned by

local selective forces as they shape communities to correspond with changing environmental conditions. Unfortunately, our results suggest that mate limitation may quell the fire lit by dispersal processes, resulting in slower rates of community change and less predictability in the face of changing environmental conditions.

Acknowledgements

Three anonymous reviewers provided comments that significantly improved the manuscript. C. Ostic, C. Symons, T. Nash and K. Turner provided assistance in the field. Funding was provided by an NSERC Discovery grant and the Friends of Killarney Provincial Park.

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Received 20 April 2012; accepted 17 August 2012

Handling Editor: M. Cadotte

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Calculation of critical densities for colonist species.

Appendix S2. Simulations to determine the influence of sampling error on estimates of r .

Appendix S3. Growth of colonist populations in enclosures that received initial population sizes of 16 individuals per species.

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