

Portage connectivity does not predict establishment success of canoe-mediated dispersal for crustacean zooplankton

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Abstract Although community structure may be largely determined by local abiotic and biotic conditions under moderate levels of dispersal, anthropogenic activities can enhance dispersal rates far beyond what would otherwise occur in natural systems. We investigated the potential impact of recreational canoeing on crustacean zooplankton community structure in Killarney Provincial Park, Canada, where canoes that are transported between lakes via portage routes may enhance zooplankton community

connectivity by providing a dispersal “short-cut.” We conducted a study to (1) quantify zooplankton attachment to canoe hulls after paddling through a lake and assess the importance of canoes to overall seasonal dispersal within a lake relative to other means of dispersal, (2) test the prediction that zooplankton survivorship is negatively correlated with portage duration using a mesocosm experiment, and (3) test whether variation in lake community composition was better explained by models based on reduced portage-corrected distances or true edge-to-edge distances between lakes along popular canoe routes. Here, we report the findings that canoes have the potential to act as frequent dispersal vectors, but appear to have little impact on community structure in portage-connected lakes. Substantial numbers of adult zooplankton became attached to canoe hulls and were able to establish viable populations even after exposure to portage conditions for 30 min. However, canoe-mediated dispersal only accounted for a very small proportion (<1% in this case) of overall seasonal dispersal. Moreover, environmental variables explained the greatest amount of variation in community composition among park lakes. Nevertheless, this study indicates that canoe dispersal could be more effective for specific species such as *Sida crystallina* than is evident by analysis of entire communities and could facilitate the spread of invasive species amenable to attaching to boat hulls. Thus, the debate about whether community composition is more strongly influenced by local environmental conditions or

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regional dispersal may vary depending on the scale of consideration (i.e., individual species vs. whole community).

Keywords Community structure · Metacommunity · Anthropogenic vectors · Spatial autocorrelation

Introduction

The metacommunity concept (Hanski and Gilpin 1991; Leibold and Norberg 2004; Leibold et al. 2004) is important for understanding the distribution of freshwater aquatic organisms, where communities exist in a network of lakes separated by terrestrial habitat. In accordance with this concept, communities are structured by the regional processes that govern dispersal across a landscape to a new water body, as well as by the local factors (abiotic and biotic conditions) that vary between habitat patches and govern species interactions within local communities (Leibold et al. 2004).

For crustacean zooplankton, multiple routes of natural passive dispersal among waterbodies have been identified for both adults and diapausing eggs, including wind and precipitation (Cáceres and Soluk 2002; Cohen and Shurin 2003; Vanschoenwinkel et al. 2008), stream connections (Michels et al. 2001), and animal vectors that act at different spatial scales (e.g., short distances by amphibians, Bohonak and Whiteman 1999; intermediate distances by mammals and invertebrates, Bohonak 1999, Allen 2007; long distances by waterfowl, Green and Figuerola 2005). Recreational motor boats have also been identified as a common anthropogenic dispersal vector (Havel and Stelzleni-Schwent 2000). Despite the seemingly ready nature of zooplankton to disperse across a landscape, the extent to which local and regional processes shape the distribution of crustacean zooplankton within a metacommunity is currently under debate (reviewed in Havel and Shurin 2004) and the role of dispersal in particular is poorly understood (Cohen and Shurin 2003). Several studies have suggested that dispersal limitation plays a greater role in structuring communities than local interactions (Jenkins and Buikema 1998; Jenkins and Underwood 1998; Shurin et al. 2000), while other studies have posited that abiotic conditions and strong local interactions are a greater structuring force (e.g., Lukaszewski et al. 1999; Arnott

et al. 2006). These studies point to survival, rather than arrival, as the limiting step in zooplankton distributions.

Several studies have identified a number of local exclusion mechanisms at work even in the face of frequent dispersal, including biological resistance from native and non-native predatory macroinvertebrates (Arnott and Vanni 1993; Keller et al. 2002; Arnott et al. 2006; Strecker and Arnott 2010) and competitive interactions with the resident zooplankton community (Lukaszewski et al. 1999; Shurin 2000; De Meester et al. 2002; Binks et al. 2005). Moreover, dispersal is often haphazard in the sense that only a few colonists are likely to disperse to the same location at any one time, making small colonist populations vulnerable to extinction via Allee effects (Stephens et al. 1999; Kramer et al. 2008). Together, these multiple exclusion mechanisms suggest that local processes, including interactions with the community already established in a water body, may be the dominant force that acts to structure zooplankton communities regardless of dispersal rates.

However, neither local interactions nor dispersal limitation can be considered in isolation if we are to fully understand zooplankton distributions and community structure. The degree of establishment success may differ among species due to the combined effects of local and regional processes. The arrival of a species in a new habitat is a result of both its dispersal ability and its regional abundance, while its persistence in a habitat is a result of both its competitive and dispersal abilities. Thus, a poor competitor may persist in a given habitat patch simply because it has a high dispersal rate, while a good competitor that would be able to survive in a new habitat patch may not arrive there because it has a poor dispersal capacity or occurs in very low abundances (Cohen and Shurin 2003; Leibold et al. 2004; Hessen and Walseng 2008; Louette et al. 2008). Thus, inter-species variation in abundances and dispersal capacities also plays a role in forming regional species occurrence patterns. Moreover, trade-offs between competitive and colonization abilities could result in species composition shifts in disturbed systems (Cadotte 2007), highlighting the complexity of the processes that determine crustacean zooplankton community structure.

Killarney Provincial Park in Ontario, Canada, presents a useful opportunity to study the effects of local and regional processes on zooplankton

distribution. Lake acidification, largely from industrial emissions of sulfur and nitrogen oxides, caused the loss of thousands of invertebrate populations in boreal lakes and resulted in widespread changes in crustacean zooplankton community structure (Keller et al. 1990; Minns et al. 1990; Schindler 1998). Despite the extensive chemical recovery of lake waters that has since occurred, biological recovery has been slower than expected (Keller et al. 2007). In light of this, questions about what controls crustacean zooplankton distributions and dispersal become particularly important for predicting the recovery trajectories of damaged communities.

Killarney Provincial Park is a popular wilderness recreation destination that experiences a high degree of canoe traffic between lakes. There are over 600 waterbodies within the park's watershed (55,980 ha), many of which are connected by an extensive network of portage trails that are commonly used during canoe excursions to access multiple lakes within the same day. Previous studies have found that humans can act as dispersal vectors when zooplankton become attached to recreational motor boats (Havel and Stelzl-Schwent 2000), but the degree of spread depends on both the propagule load (number of individuals dispersed per event) and survivorship during transport (Havel and Shurin 2004). The use of recreational motor boats is restricted within the confines of many conservation areas and parks, including Killarney Provincial Park, unlike the relatively uncontrolled use of canoes, which could potentially act as a dispersal vector when they are carried (portaged) between lakes.

We used Killarney Provincial Park to investigate the importance of canoe-mediated dispersal in a metacommunity where canoes act as a frequent dispersal vector. We accomplished this using three separate studies that built upon each other in a stepwise fashion. Firstly, we quantified the zooplankton dispersal occurring at two lakes within the park that experience heavy canoe traffic by rinsing canoe hulls from simulated canoe trips and actual portage users. We tested whether lake taxa abundances were a significant predictor of canoe hull abundances. We also assessed the relative importance of canoes to overall seasonal zooplankton dispersal within a lake by comparing the amount of zooplankton transported by canoe to the amount transported by additional vectors (wind, stream, and diapausing egg bank). Secondly, we examined the effect of portage

duration (i.e., time out of the water) on the ability of zooplankton to survive and subsequently establish a viable population in mesocosms created with cattle drink tanks filled with 50 μm filtered lake water. We tested the prediction that zooplankton survivorship and establishment would be negatively correlated with portage duration. Thirdly, we evaluated whether canoe traffic contributed to lake zooplankton community composition along popular canoe routes by providing a dispersal "short-cut" to adjacent lakes. To do this, we calculated reduced measures of between-lake distances based on the frequency of canoe traffic and tested whether models based on these canoe-based distance measures explained more variation in community structure than true edge-to-edge distances. The results may give further insight into the impact of human recreational activities on the recovery process of damaged lakes, as well as indicate the potential for non-native aquatic invertebrates to disperse in the park by hitchhiking on canoes.

Materials and methods

Study 1: Quantifying dispersal by canoe

To quantify canoe zooplankton dispersal, we sampled canoe hulls removed from George Lake, Carlyle Lake, and at the George-Freeland portage in Killarney Provincial Park, Ontario, Canada (46° 01'N, 81° 24'W) between June 9, 2008, and August 20, 2008. George Lake and Carlyle Lake are two of the main launch points from which campers begin canoe trips into the interior lakes of the park. The lakes were acidified in the 1960s, but have since chemically recovered to preindustrial conditions with a pH above 6.0 (Keller et al. 2003).

We simulated the activities associated with canoe portages by paddling a canoe in George or Carlyle Lake for approximately 5 min then transported the canoes to a washing station on shore where they were placed on a frame and immediately rinsed with 50 μm filtered lake water. Rinse water fell onto a polyethylene sheet suspended from the frame and was collected into a bucket and preserved in >70% ethanol. Simulations were conducted on 7 different days at George ($n = 68$) and 6 different days at Carlyle ($n = 57$). In addition, on July 19, 2008, and August 14 and 15, 2008, canoeists at the George-Freeland portage ($n = 30$)

were intercepted and asked whether they would volunteer to have their canoes rinsed to verify that our 5-min simulations were a true representation of what would become attached to a canoe hull on a trip across the entire lake. Zooplankton in rinse samples were counted using a Leica M165C dissecting scope and a Leica DM E compound microscope (Leica Microsystems (Canada) Inc., Richmond Hill, ON). The entire samples were counted. Copepods were identified to orders Calanoida and Cyclopoida, while cladocerans were identified to genus or family according to the taxonomic guide of Edmondson (1959). Ehippia (cladoceran resting stages), nauplii (the juvenile stage of copepods), and adults carrying subitaneous eggs were also enumerated.

Dispersal of zooplankton to George Lake via additional vectors was also measured for a separate study conducted during the summer of 2008 (Gray and Arnott 2011). Dispersal vectors evaluated were (1) movement via streams, quantified by the number of individuals captured by in-stream drift nets; (2) movement overland via wind and animals, quantified by colonization of dispersal traps placed at lake edges; and (3) dispersal through time via historically deposited diapausing eggs, quantified by the number of individuals hatched from sediment within in situ emergence traps. We used these data to determine the relative contribution of canoe dispersal to overall seasonal dispersal of zooplankton at George Lake.

The average number of zooplankton dispersing per canoe and standard deviation were calculated at George, Carlyle, and the George-Freeland portage, using total number of individuals per canoe at each respective lake. To test the accuracy of the simulations to real-life portagers, a *t* test between the number of zooplankton dispersed per canoe at the George Lake simulations ($n = 20$) and at the George-Freeland portage ($n = 20$) was conducted. Levene's test was used to determine whether variance between simulations and actual portagers differed. The average number of zooplankton dispersing by canoe at the George-Freeland portage was not significantly different from simulated portage events conducted on canoes at the George Lake shoreline (*t* test, $t = -1.95$, $df = 38$, $P = 0.059$), and Levene's test indicated that the variance between simulations and actual portagers was not significantly different ($F = 2.8$, $P = 0.10$).

A correlation analysis between the relative abundances of pelagic zooplankton taxa in George Lake

and the relative abundances of zooplankton attached to canoe hulls was performed to determine whether lake abundances were a significant predictor of canoe hull abundances. George Lake zooplankton relative abundances were determined from three pelagic hauls of the entire water column with a 35-cm diameter, 80- μm mesh zooplankton net taken in May, June, and July 2008. A repeated measures ANOVA was also conducted to identify differences in the amount of dispersal occurring at various life stages throughout the season, where the categorical predictor was lake (George or Carlyle) and the repeated measure was month (June, July, August). Sampling dates were pooled by month. The response variable was a $\log(x + 1)$ transformation of the total number of zooplankton individuals found per canoe for each group of interest (adults without eggs, adults with subitaneous eggs, and ehippia). Tukey HSD post hoc comparisons followed the ANOVA.

To evaluate the relative importance of canoe dispersal versus other zooplankton dispersal vectors into George Lake, we compared the total number of individuals transported per season by each vector using our data and that of Gray and Arnott (2011). To quantify dispersal by canoes over the open-water season (May–October), we estimated the number of canoes entering George using the number of people camping on George Lake and two surrounding lakes (Killarney and O.S.A.) for which George is a starting and finishing point. We divided this number in half since two people typically travel per canoe. This number was then multiplied by the average number of zooplankton per canoe hull rinsed from George Lake.

Study 2: Effect of portage duration on dispersal

We hypothesized that zooplankton survivorship would be negatively correlated with portage duration (i.e., time out of the water) due to a prolonged exposure of adult zooplankton to harsh conditions (e.g., heat, UV radiation, and desiccation). We tested this using a mesocosm experiment that was conducted between June 22, 2009, and August 4, 2009. Mesocosms were created by filling 378 L cattle drink tanks (Rubbermaid Agricultural Products, Ltd.) with George Lake water that had first been filtered (50 μm) to exclude crustacean zooplankton. The tanks were seeded with zooplankton rinsed from the hulls of canoes that had been paddled one at a time in the pelagic zone of George

Lake for 5 min (see study 1). Portaging was simulated by placing the canoes onshore in the shade with the hull facing upward for treatments of 5, 10, 15, 20, or 30 min. These treatment times were considered representative of the times it would take to complete the majority of the portages within Killarney Provincial Park, as estimated from portage distance and personal experience (median park portage length = 257 m). When the allotted time was finished, canoes were brought to the washing station used in study 1. The rinse water from three canoes was immediately used to inoculate each cattle tank. There were five tanks (replicates) per portage duration treatment as well as five controls for a total of 30 tanks. Controls did not receive rinse water from canoes and any zooplankton present in these tanks would be indicative of colonization from overland dispersal. Cattle tanks were placed in a shaded area approximately 400 m from lakeshore. The tanks were covered with 1-mm mesh to minimize egg laying by adult insects (thus minimizing the introduction of insect larvae to the tank community) and to exclude other animals that could act as dispersal vectors (Allen 2007).

The rinse water from three canoes was separately filtered (80 μm) and any captured animals were immediately preserved in 70% ethanol as an estimate of the abundance and identity of initial zooplankton rinsed into a single tank. A pelagic haul of the entire water column was taken in June 2009 using a 35-cm diameter, 80- μm zooplankton net, as well as a littoral sample using an 8.3-cm diameter, 60-cm-long tube sampler to identify zooplankton species living in George Lake.

Temperature and dissolved oxygen (DO) were measured weekly at midday with a YSI 550A Dissolved Oxygen Instrument (YSI (USA) Inc., Yellow Springs, OH). Nitrogen (270 $\mu\text{g/L}$) and phosphorus (3 $\mu\text{g/L}$) were added to each cattle tank at two-week intervals using NaNO_3 and KH_2PO_4 solutions, respectively, to maintain nutrient levels similar to ambient George Lake conditions (Shead 2007; S. Arnott unpublished data). Tanks were sampled after six weeks with successive hauls of a 35-cm diameter, 80- μm mesh zooplankton net until the volume of water sampled was equal to the volume of the tank. Captured animals were preserved in 70% ethanol. Each sample was standardized to 100 mL volume and examined in successive subsamples until a minimum of 200 adults were enumerated (resting eggs were not included in

the 200-count total since it was impossible to identify whether they were rinsed from canoe hull or deposited by transported adults during the incubation period). If a new taxon was discovered in the final subsample, additional subsamples were counted until no new taxa were found in the final two subsamples. Species accumulation curves were constructed for each sample to ensure that an asymptote in species richness was reached. Thus, the counted portion adequately captured the tank's diversity and raw species richness counts could be validly compared as suggested by Gotelli and Colwell (2001). The remainder of the sample was then scanned for rare species. Samples that contained less than 200 individuals were processed entirely. Adult crustacean zooplankton were identified to species using the taxonomic guides of Hudson et al. (1998), Witty (2004), and Edmondson (1959). However, *Bosmina leideri* and *Bosmina (Eubosmina) freyi* were grouped into one category (*Bosmina* spp.) due to difficulties in distinguishing taxonomic differences, and cyclopoid copepods were identified to species for only one randomly selected replicate per treatment for the sake of efficiency. For all other samples, cyclopoid copepods were grouped into one category (Unidentified Cyclopoid sp.). The commonly found *Leptodiptomus minutus* was identified and counted separately for every tank in which it occurred. Juvenile cladocerans were identified to family level when possible, while copepod juveniles were identified to order (copepodites) or class (nauplii).

Cattle tank community structure was investigated using three indices: abundance, species richness, and Simpson's Diversity Index. Total tank abundances were estimated using species densities in the counted portion of each tank sample, except for rare species whose actual counts were used as a measure of abundance (since the entire tank samples were scanned for rare species). Rare species were included in the calculation of species richness and Simpson's Diversity Index.

Single factor analysis of variance (ANOVA) was used to investigate the effects of portage duration on \log_{10} -transformed abundances, richness, and Simpson's diversity from 2009 data only (i.e., the canoe hull rinse samples from the survey in study 1 were not included). Data transformations were used when they improved normality. Welch's ANOVA was used when the assumption of homogeneity of variance was not met, as suggested by Quinn and Keough (2002).

To enhance statistical power, the results of the ANOVAs were combined with ordered heterogeneity tests following Rice and Gaines (1994) to test against directional alternative hypotheses (i.e., expected trends with increasing portage duration). This yielded a new test statistic ($r_s P_c$).

To investigate differences in the community structure among portage duration treatment tanks, principal components analysis (PCA) was performed on the collective abundance data from all tanks, centered by species. PCA is an unconstrained approach that summarizes community composition variability (Lepš and Šmilauer 2003). All counts were subjected to Hellinger transformation (Legendre and Gallagher 2001) prior to PCA, and species occurring in ≤ 2 tanks were removed to avoid placing too much weight on rare species (Legendre and Gallagher 2001). A single factor ANOVA combined with an ordered heterogeneity test was used to investigate the effects of portage duration on PCA1 and PCA2 axis scores. Parametric multivariate analysis of variance based on permutations (PERMANOVA; Anderson 2001; McArdle and Anderson 2001) was also performed on the collective abundance data from all cattle tanks to test for differences in community composition among portage duration treatments. As in the PCA, all counts were Hellinger-transformed and rare species (those which occurred in two or less tanks) were removed prior to analyses. The PERMANOVA used 9999 unrestricted Monte Carlo permutations of raw data units to test statistical significance at $P < 0.05$, while 999 unrestricted permutations were used for pairwise a posteriori comparisons.

To make comparisons between what was initially rinsed from canoe hulls and the final community structure of the portage duration treatment tanks, PCA was performed on the relative abundance of species in three hull samples taken in 2009, 26 hull samples taken in June 2008 (study 1), and the final cattle tank communities. Data from 2008 (study 1) was identified only to family level, and thus, data from 2009 was classified at the same level for comparison. Three measures of frequency, adapted from Hessen and Walseng (2008), were calculated for each species in order to explore patterns of dominance. First, treatment frequency was calculated as the proportion of ponds in which a species was present within a treatment (out of five). This gives an estimate of how much the pond communities vary within a

treatment. Second, global frequency was calculated as a measure of the proportion of ponds in which a species is present in all treatment ponds, excluding control (out of 25), which gives an estimate of how successful each species is at colonizing in total. Third, the highest relative abundance at which each species occurred, throughout all treatments, was recorded to give an estimate of each species' dominance success potential. These were categorized as <1 , 1–10, 10–50, >50 , and 100%.

To test the prediction that littoral species were associated with canoe hulls with a greater frequency relative to pelagic species, we compared the presence or absence of species in the initial hull samples and in George Lake. The George Lake species list was compiled from littoral and pelagic samples taken in June 2009, as well as from samples taken in 1999 (B. Walseng, unpublished) and 2008 (Derek Gray, unpublished) since cumulative multiple year species lists are better estimates of species richness than single-year samples (Arnott et al. 1998). The proportion of the species list that was classified as littoral was compared between George Lake and all treatment tanks using a two-tailed single sample t test (Zar 1999) to test the hypothesis that treatment tanks have different proportions of littoral species than the lake. Tanks where no zooplankton were found were excluded from the analysis. Cyclopoid copepods were also excluded from species lists prior to analysis since cyclopoids were only identified to species for one replicate tank in each treatment. For this same reason, the general category Unidentified Cyclopoid sp. was used in the calculation of community indices, PCA, ANOVAs, and treatment and global frequencies. We believe this still captures the majority of variation in tanks since cyclopoids only comprised 6 out of 38 species and generally occurred in low abundances.

Zooplankton were found in control tanks (which had initially received no canoe hull rinse water), indicating that unintentional colonizers were present in the cattle tanks. A two-tailed t test was used to compare mean \log_{10} -transformed abundances in pooled treatment tanks and pooled control tanks. We used randomization tests to assess whether *Scapholeberis kingi* and *Ophryoxus gracilis* occurred in control tanks in higher abundances than would be expected at random, as we observed higher abundances of *S. kingi* and *O. gracilis* in controls, but the near absence of these species in treatment tanks. The

abundance of each species was randomly assigned to treatment or control tanks, and then, ANOVAs were used to compare pooled abundance data from all treatments tanks and pooled abundance data from all control tanks, testing each species separately. Species abundances were randomized 4999 times and each randomization was assessed against the F-ratio of the original data to determine how frequently the randomized abundances of species differed between treatment and control tanks.

PCAs were performed in Canoco ver. 4.5 (ter Braak and Šmilauer 2002), PERMANOVAs were performed in PERMANOVA ver. 1.6 (Anderson 2005), randomizations were performed in R ver. 2.12 (R Development Core Team 2010), and all other statistical analysis in studies 1 and 2 were performed using JMP 6 (SAS Institute Inc. 2005).

Study 3: Lake community connectedness by canoe traffic

Lake connectedness (based on canoe traffic), environmental characteristics, and zooplankton community composition for 45 lakes in Killarney Provincial Park (Shead 2007) were used to evaluate the relative contribution of environmental and spatial (canoe traffic) predictors to zooplankton community structure. Killarney Provincial Park provided data on the total number of campers at canoe campsites on each lake between April 1 and November 7, 2008. There were a total of 25 lakes on portage routes for which environmental and species abundance data were available. Data were also available for an additional twenty lakes, which were not accessible by maintained portage routes.

Three matrices were created for the 45 survey lakes to test the effect of canoe dispersal on zooplankton community structure. The first matrix, users (U), was constructed from a map of portage routes in the park, knowledge of starting points and most likely canoe routes, and frequency of canoe campsite use. From this, each portage was ranked according to an estimated amount of canoe traffic. Portage routes were assigned a number from one (no portage connection, i.e., least connected) to six (well-used portage connection, i.e., most connected). The second matrix, distance (D), was an edge-to-edge Euclidean distance matrix between all lakes in the study derived from maps in ArcGIS ver. 10. The third matrix,

portage (P), was derived from $P = D/U$, whereby distance between lakes is downscaled if the portage is heavily traversed, indicating the greater potential for dispersal with a greater number of portage users.

We constructed a set of synthetic variables at different spatial scales from both D and P using the distance-based eigenvector method of Dray et al. (2006). Using matrix D for illustration, the matrix of geographic distances (d_{ij}) between sample sites is created and truncated by a connectivity matrix. Here, we chose to leave all sites in the matrix connected, as zooplankton can disperse long distances and are not necessarily constrained by directional processes (i.e., waterfowl movement between waterbodies). Next, the matrix D was weighted by the function $(1 - d_{ij}/\max(d_{ij}))$ to give higher weight to lakes that are closer together. Finally, the matrix D is centered and eigenvectors are computed using a principal coordinates analysis (PCoA). This was repeated for the P matrix. The eigenvectors are then synthetic variables that represent spatial autocorrelation at different scales (Dray et al. 2006, Griffith and Peres-Neto 2006). For example, the eigenvector with the largest positive eigenvalue represents positive spatial autocorrelation at the landscape scale, whereas eigenvectors with smaller eigenvalues represent more local spatial patterns.

To examine the influence of portage-mediated dispersal in shaping zooplankton communities, we separately examined the spatial variables created from both the D and P matrices in a multivariate analysis. We analyzed both sets of spatial variables to account for the fact that overland dispersal of zooplankton may occur that is independent of portage users and will be reflected by distances between lakes (i.e., we expect that lakes that are closer together will experience greater overland dispersal). If the spatial variables from D and P yield similar results, we would conclude that canoe-mediated dispersal is indistinguishable from other modes of dispersal that are influenced by proximity; however, if the variables from P explain more variation than D, we can then conclude that canoe-mediated dispersal influences zooplankton community structure.

In addition to spatial variables, we also examined the influence of environmental variables in our multivariate analyses. Variables used included maximum depth, pH, presence of the invasive predatory invertebrate *Bythotrephes*, presence of fish, area,

Secchi depth, total phosphorus, calcium, total nitrogen, SO_4 , K, Cu, and Fe. Some variables were \log_{10} -transformed to improve normality and all variables were standardized via z -score prior to analysis. Correlated environmental variables were removed prior to analysis ($r > 0.8$). When a correlation of two or more variables was found, one variable was retained to represent the others. Species abundance data were converted to relative abundances and Hellinger-transformed prior to analysis (Legendre and Gallagher 2001), in addition to removing rare species (occurrence in $<5\%$ of lakes). A preliminary analysis with a detrended correspondence analysis indicated that redundancy analysis (RDA) was most appropriate for the species abundance data (Legendre and Legendre 1998). Variable inclusion was determined by forward selection with criteria of $P < 0.05$. Variation explained in zooplankton community structure with RDA was then partitioned into that attributable to purely environmental, purely spatial, or spatially structured environmental variation following Peres-Neto et al. (2006), which accounts for the bias of increasing numbers of variables. The significance of fractions was assessed by permutation tests (Legendre and Legendre 1998). Thus, we performed two RDAs, one each with spatial variables from the P and D matrix, and partitioned variation in each analysis, which we will refer to as portage RDA and distance RDA, respectively. All distance-based eigenvector maps and multivariate analyses were performed in R ver. 2.12 using the *vegan*, *spdep*, and *spacemaker* libraries (R Development Core Team 2010).

Results

Study 1: Quantifying dispersal by canoe

An average of 11.2 ± 2.1 zooplankton individuals per canoe were detected on canoes from George Lake, 12.9 ± 1.4 individuals per canoe were detected at Carlyle Lake, and 10.0 ± 2.5 individuals per canoe were collected from canoes at the George-Freeland portage. The most common taxonomic groups found dispersing per canoe in descending order were Sidiidae, Cyclopoida, Chydoridae, Bosminidae, nauplii, Polyphemidae, and Calanoida (Fig. 1). Correlations between relative abundances of zooplankton taxa in George Lake versus abundances on canoe hulls

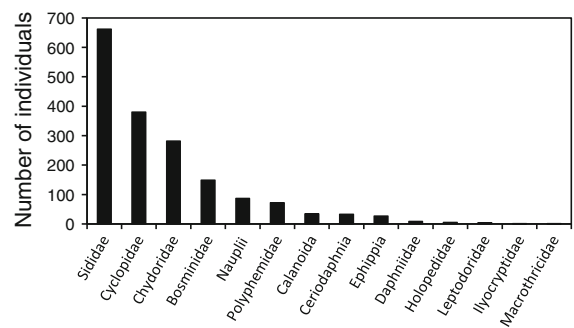


Fig. 1 Total number of individuals of different taxonomic groups found attached to canoe hulls during the 2008 canoe hull survey at both George and Carlyle lakes combined ($n = 125$)

indicated that lake abundances are a poor predictor of dispersal by canoe ($r = 0.34$, $P = 0.30$). Adults without eggs were dispersed significantly more than adults with eggs or ephyppia across all months and at both lakes (Fig. 1; Tukey HSD, $P < 0.05$). At George Lake, zooplankton dispersal to the lake during the open-water season (May–October) was dominated by individuals arriving from the egg bank (59,670,000 individuals; 87% of total dispersal), followed by stream dispersal (8,352,600 individuals; 12% of total dispersal), canoe dispersal (40,359 individuals; 0.06% of total dispersal), and overland dispersal (0 individuals; Gray and Arnott 2011).

Study 2: Effect of portage duration on dispersal

Community indices including total number of individuals, Simpson's diversity, and richness were variable both among and within treatments (Online Resource 1). Portage duration had no directional effect on richness, Simpson's diversity, community structure (as indicated by PCA1 and PCA2 axis scores), or abundance, as indicated by the ordered heterogeneity test (Fig. 2; Online Resource 2).

Zooplankton community structure in cattle tanks displayed considerable variation among treatments as well as between treatment replicates (Fig. 3). The PCA comparing cattle tank communities using only 2009 data revealed that variation among portage duration treatment tanks was most strongly driven by *Bosmina* spp. and *Sida crystallina*, while control tank communities were less variable and had higher relative abundances of Unidentified Cyclopoid sp., copepodids, *Ophryoxus gracilis*, and *Scapholeberis*

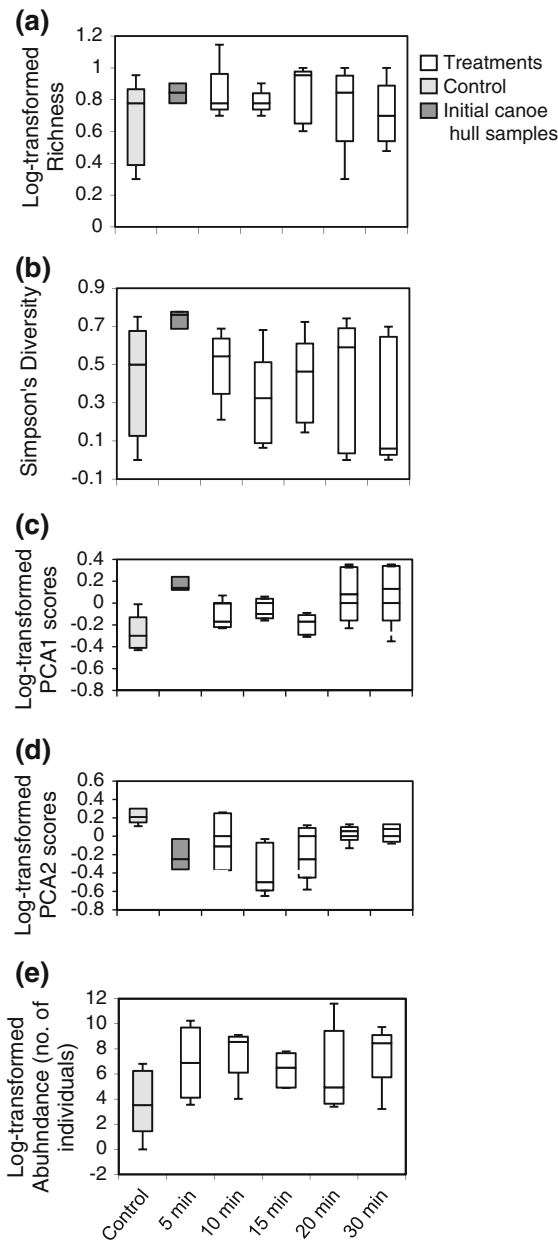


Fig. 2 Boxplots of **a** \log_{10} -transformed richness, **b** Simpson's diversity, **c** \log_{10} -transformed PCA1 axis scores, **d** \log_{10} -transformed PCA2 axis scores, and **e** \log_{10} -transformed abundances of crustacean zooplankton communities by treatment. Boxes represent the interquartile range with a line at the median. Whiskers extend to the outermost data point. Ordered heterogeneity tests (Rice and Gaines 1994) indicated that portage duration had no significant directional effect on any of the plotted community indices, and the corresponding results (significant at $p_{(OH)} < 0.05$) are indicated in each panel

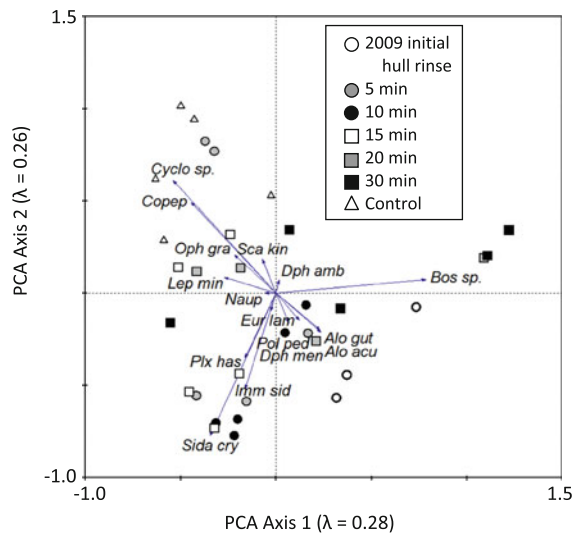


Fig. 3 Ordination biplots of the first and second axis scores of a principal components analysis (PCA) based on abundance of crustacean zooplankton in cattle tanks, as well as crustacean zooplankton rinsed from canoe hulls without tank incubation in 2009. Species name codes are as follows: Alo acu, *Alonella acutirostris*; Alo gut, *Alona guttata*; Bos sp., *Bosmina* spp.; Copep, Copepodids; Cyclo sp., unidentified Cyclopoid spp.; Dph amb, *Daphnia (Daphnia) ambigua*; Dph men, *Daphnia (Hyalodaphnia) mendotae*; Eur lam, *Eurycercus lamellatus*; Imm sid, immature Sidaeae; Lep min, *Leptodiptomus minutus*; Naup, nauplii; Oph gra, *Ophryoxus gracilis*; Plx has, *Pleuroxus hastatus*; Pol ped, *Polyphemus pediculus*; Sca kin, *Scapholeberis kingi*; Sida cry, *Sida crystallina*

kingi (Fig. 3). A PERMANOVA indicated there were significant differences in community structure between portage duration treatments (5 time treatments + control; $F_5 = 2.23$, $P = 0.003$), and pairwise a posteriori comparisons revealed that these differences in community composition existed between the control tanks and each of the 10, 15, 20, and 30 min portage duration treatments (Table 1). A full list of species and their respective presence and frequencies in treatment and control tanks is provided in Online Resource 3.

The PCA comparing initial canoe hull rinse data from 2009 and 2008 to final cattle tank abundances also revealed high interannual variation in the zooplankton composition rinsed from canoes (2008 vs. 2009 initial hull rinse), and these also differed from the composition of zooplankton that successfully

Table 1 Results of pairwise comparisons following a single-factor permutational multivariate analysis of variance (PERMANOVA) of collective zooplankton abundances from all portage duration treatment tanks, using 999 unrestricted Monte Carlo permutations (significant at $P < 0.05$)

Group comparisons		t	p
5 min	× 10 min	1.07	0.336
	15 min	0.78	0.584
	20 min	1.08	0.328
	30 min	1.15	0.279
	Control	1.51	0.094
10 min	× 15 min	1.0	0.414
	20 min	1.48	0.095
	30 min	1.43	0.121
	Control	2.33	0.006
15 min	× 20 min	1.66	0.057
	30 min	1.58	0.082
	Control	2.07	0.012
20 min	× 30 min	0.34	0.919
	Control	1.98	0.022
30 min	× Control	1.85	0.031

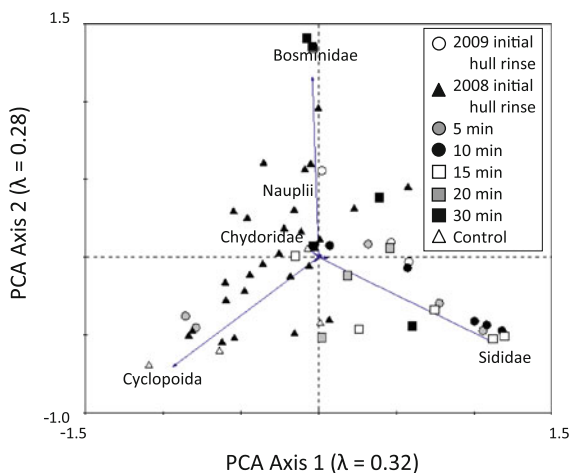


Fig. 4 Ordination biplot of the first and second axis scores of a principal components analysis (PCA) based on the relative abundance of crustacean zooplankton in cattle tanks, as well as crustacean zooplankton rinsed from canoe hulls without tank incubation in 2009 and in 2008. Vectors for zooplankton families that were small and close to the origin have been removed for clarity

established in the 2009 cattle tanks largely due to higher relative abundances of Sididae and lower abundances of Cyclopoida in tanks (Fig. 4; Online

Resource 3). It is interesting to note that the variation among rinse samples highlights the high potential for cattle tanks to be inoculated with unique species assortments, both within and among years.

Sida crystallina had the highest global frequency of 0.92 in treatment ponds (Online Resource 2). *Ophryoxus gracilis* and *S. kingi* shared the lowest global frequency of 0.04, but their high frequencies of occurrence in the control tanks relative to treatment tanks suggest that their arrival may not have been associated with canoes (see below). Of 40 species found in George Lake, 15 were not found in any cattle tank, and only nine were found on the initial canoe hull samples taken at the beginning of the experiment in June 2009. This may, however, reflect some seasonal effects as some of the samples for the George Lake species surveys used in this study were taken at a different time of year (Hessen and Walseng 2008). In addition, the proportion of species on the George Lake species list classified as littoral was not significantly different from treatment tanks (single sample t test, $t_{27} = 1.19$, $P > 0.05$).

All control tanks contained at least one species of crustacean zooplankton (Online Resource 1). Only seven of 33 species found in treatment tanks were also found in control tanks. Pooled total species abundances were significantly higher in treatment tanks than in control tanks (t test, $t = 2.05$, $df = 28$, $P = 0.015$). Tests against a null model revealed that *Scapholeberis kingi* occurred in control tanks in higher abundances than treatment tanks more often than would be expected at random ($P = 0.01$), although *Ophryoxus gracilis* did not ($P = 1.0$).

Cattle tank water temperatures varied throughout the incubation period, with a minimum recorded temperature of 15.7 °C and a maximum of 18.8 °C. Dissolved oxygen (DO) also varied widely, with a minimum of 3.79 mg L⁻¹ and a maximum of 8.01 mg L⁻¹. However, there was no significant difference between tanks for temperature (repeated measures ANOVA, $F_{5,25} = 1.30$, $P = 0.17$) or DO ($F_{5,25} = 1.38$, $P = 0.13$). Final tank pH varied between 5.8 and 7.03; however, only three tanks, all in different treatments, reached a pH < 6.0. Considering that the threshold for biological recovery from acidification is generally accepted as 6 (Holt and Yan 2003), it is not expected that pH affected zooplankton colonization.

Study 3: Lake community connectedness by canoe traffic

Both the portage and distance RDAs on zooplankton community structure were significant (portage: $F = 2.70$, $P = 0.005$; distance: $F = 2.62$, $P = 0.005$). As the effects of environmental variables on zooplankton in Killarney Park have been reported previously (Derry et al. 2009), here we focus on the variation partitioning results that test our hypothesis on the influence of canoe-mediated dispersal on community structure. Using variation partitioning, we determined that environmental variation is the primary driver of differences in zooplankton community composition, explaining 29% of variation in the distance RDA ($F = 2.46$, $P < 0.001$) and 32% of variation in the portage RDA ($F = 2.67$, $P < 0.001$; Fig. 5). Spatial variables explained greater variation in the portage RDA (5%) compared with the distance RDA (<1%), but were not significant in either analysis (portage: $F = 1.32$, $P = 0.21$; distance: $F = 0.91$, $P = 0.51$; Fig. 5). Spatially structured environmental variation, which is indicative of a spatial gradient in environmental conditions, explained small amounts of additional variation in community composition (portage RDA = 4%, distance RDA = 7%; note that the significance of this fraction cannot be tested; Fig. 5).

Discussion

While several studies have documented and quantified the potential for aquatic organisms to be carried between water bodies by recreational boat hulls and trailers that have been fouled or carry residual water (e.g., Havel and Stelzleni-Schwent 2000; Johnson et al. 2001), few have directly investigated how harsh transport conditions affect the establishment and structuring of communities after transport, or the ultimate effect that transport of individuals from the regional species pool has on the receiving community. We have demonstrated that crustacean zooplankton become attached to canoes and can survive portages of at least 30 min and thus can be transported between lakes as a result of recreational canoeing. Despite the potential for canoes to transport tens of thousands of individuals in a season, however, lake connectedness by portage did not explain a significant portion of the variation in zooplankton community composition

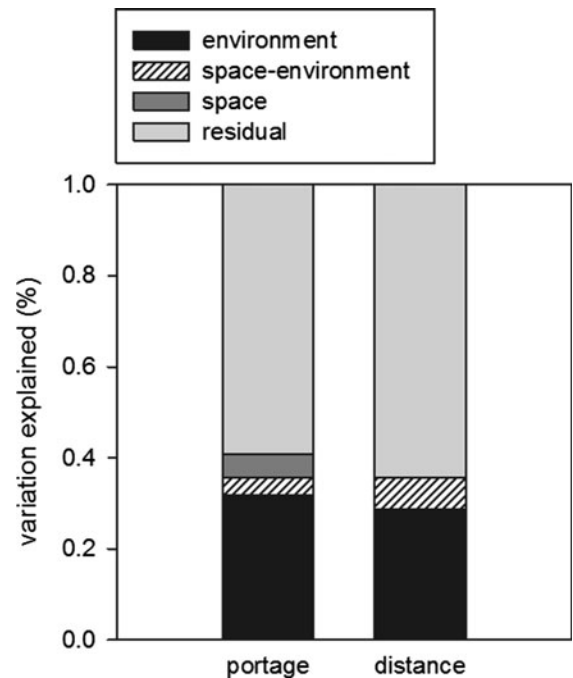


Fig. 5 Variation (%) in zooplankton community composition explained by purely environmental, purely spatial, and spatially structured environmental (space-environment) variables in the portage RDA and distance RDA

among Killarney Park lakes. Spatial variables based on portage-corrected distances did not explain a significantly greater proportion of variation among lake communities than those based on edge-to-edge distances. Rather, we found that environmental variation was the primary determinant of community composition in park lakes. Moreover, we found that even heavy canoe traffic may only account for a small (<1%) proportion of the overall seasonal dispersal received by a lake relative to other sources, such as through streams or hatching from the egg bank (Gray and Arnott 2011), which may partially explain the apparent lack of canoe impact on community composition. Alternatively, canoes could simply be transporting regionally common species, making it difficult to detect the degree of inter-lake transport. Thus, canoes are a frequent dispersal vector for crustacean zooplankton, but appear to have a weak influence on community composition in portage-connected lakes.

Potential for canoe-mediated dispersal

Not only were substantial numbers of zooplankton attached to canoes, but they also appeared to be able to

survive harsh portage conditions for 30 min, as portage duration did not affect the abundance, richness, or diversity of the transported communities incubated in the tanks. We predicted that communities would be more diverse and species rich in the shorter duration treatments where the hulls did not dry completely because there would presumably be less mortality. However, no such pattern was found in this study.

Colonists from an unknown source (likely from aerial dispersal, see Cáceres and Soluk 2002; Cohen and Shurin 2003; Vanschoenwinkel et al. 2008) were found in the control tanks and may have concealed portage effects by influencing community structure in treatments that received colonists rinsed from canoe hulls. However, important biological differences existed between treatment and control tanks that indicate that canoe-mediated dispersal was an important factor in determining treatment tank community composition. Pooled species abundances were significantly greater in treatment tanks than in control tanks, and only a single species, *Scapholeberis kingi*, was found in control tanks in greater abundance than would be expected at random. Indeed, it was the most abundant species in control tanks, while being practically absent in treatment tanks. Moreover, PERMANOVA revealed that there were significant differences in community composition between control tanks and every other portage duration treatment besides the shortest (5 min). Thus, while conclusions cannot be made about differences in portage treatment survivorship because of possible interference by unintentional colonists, we believe that our findings still provide evidence that zooplankton can survive harsh portage conditions for up to 30 min and that canoe traffic can move significant numbers of zooplankton individuals between waterbodies.

Although canoe-mediated transport of species from the regional species pool does not appear to influence community structure, there is strong potential for canoes to transport invasive species, which could in turn have an impact on community structure beyond that caused by the introduction of native colonizers. For example, the invasive predatory cladoceran *Bythotrephes longimanus* has established in several Killarney Park lakes (Shead 2007). *B. longimanus* has been associated with significant changes in native zooplankton community structure following invasion in lakes across North America, including decreased

species richness and abundance (e.g., Boudreau and Yan 2003; Barbiero and Tuchman 2004). On the other hand, canoe-mediated transport of native colonizers could buffer against the extirpation of native taxa in the face of invasion or aid the recovery of damaged communities. For instance, Strecker and Arnott (2010) found the dispersal of native crustacean zooplankton taxa helped restore the abundance, richness, and species composition of communities invaded by *B. longimanus* in experimental enclosures constructed in Killarney Park lakes. We did not explicitly test the potential for canoes to transport *B. longimanus* since our aim was to characterize the effect of canoe-mediated transport on the structuring of native crustacean zooplankton communities rather than the effect of adding a stressor such as an invasive species. However, it seems intuitive that if canoes are an effective dispersal vector for native crustacean zooplankton, they are likely effective for some invasive species as well.

Our study also provides some evidence that canoes may act as species-specific dispersal vectors. *Sida crystallina* is relatively rare in George Lake (B. Walseng unpublished data; Schartau et al. 2007), but it was the most common and dominant species in cattle tanks and the most abundant zooplankton family to become attached to canoe hulls from George Lake (Fig. 1; Online Resource 2). Similarly, *Bosmina* spp. have only moderate relative abundances in George Lake but were dominant and common in cattle tanks. These findings suggest that canoe dispersal may be considered more important for *S. crystallina* and *Bosmina* spp. than it is for most other species in George Lake, perhaps due to unknown species-specific characteristics that affect canoe attachment probability. For instance, the substrate attachment behavior of *S. crystallina* may be partly responsible for its high abundance on canoes. Fairchild (1981) observed that *S. crystallina* would swim rapidly toward and readily attach to opaque Plexiglas blocks after being disturbed, indicating the potential for *S. crystallina* to intentionally attach to canoes. Knowledge of other species-specific traits that could be associated with canoe dispersal is limited, although it is well recognized that zooplankton vary in their dispersal and colonization abilities (Cáceres and Soluk 2002; Cohen and Shurin 2003; Allen 2007; Louette et al. 2008). Alternatively, high species abundances within tanks may have been a result of high population

growth rates during the incubation period rather than due to high initial canoe attachment. This may be more likely for *Bosmina* spp. that have higher temperature-specific egg development rates than several other cladoceran taxa (Kuns and Sprules 2000). One must also keep in mind that canoes are only exposed to zooplankton near the surface and that the composition of this “surface community” can change drastically throughout a single day. For instance, species that exhibit diel vertical migration are much less likely to be transported between lakes by canoes since canoe traffic is generally much higher during daylight hours. Our findings suggest that dispersal capabilities may be a product of both species characteristics (e.g., body size, morphology, behavior) and how they are able to interact with the particular landscape situation (e.g., abundance of animal or human dispersal vectors, exposure to wind, proximity of water bodies).

Consequences of canoe-mediated dispersal

Our survey of canoe hulls and incubation of canoe rinse water indicated a high potential for portage events to frequently transport viable individuals between lakes although our spatial analysis revealed that local environmental factors are a more important determinant of zooplankton colonization success than canoe traffic. It might be expected that transport by canoe would have some advantage for establishment over other, more erratic forms of dispersal such as wind because canoes provide directed dispersal by consistently transporting individuals to the same location (the portage landing in the next lake), thereby reducing Allee effects by increasing colonist density in that specific habitat patch. As well, canoes transport high abundances of adult zooplankton, which would be advantageous over resting eggs because adults can immediately begin reproducing (Allen 2007). Although resting eggs are much more likely to survive desiccation, resting eggs were relatively rare in samples rinsed from canoe hulls compared with adults without eggs. This could be linked to the tendency for some resting eggs to sink to lake sediments while free-swimming adults achieve higher densities and are present in the water column for longer periods of time (Brendonck and DeMeester 2003; Cáceres et al. 2007), allowing more opportunity for canoe attachment. Resting egg production can also be seasonal and our summer sampling may have missed peak egg

production. Any advantages of adult dispersal, however, may be rendered null by the high variation in the species composition that becomes attached to canoe hulls or by inhospitable biotic and abiotic conditions in the receiving lake.

Inhospitable conditions could be shaped by strong gradients in local environmental factors (e.g., pH), which may limit zooplankton colonization despite frequent dispersal and conceal any effects that canoe traffic would otherwise have in an undisturbed system (e.g., Keller et al. 2002; Cottenie et al. 2003). Biological resistance could also play a role by preventing establishment in an otherwise hospitable environment. For instance, priority effects can allow the resident zooplankton community to inhibit further colonization through resource monopolization (Boileau et al. 1992; Lukaszewski et al. 1999; Shurin 2000; De Meester et al. 2002; Binks et al. 2005). Predation by macroinvertebrates has also been shown to significantly reduce zooplankton abundance, diversity, and species richness in some acid-recovering lakes (Arnott et al. 2006) and can play a role in restricting colonization when fish are not present (Arnott and Vanni 1993; but see Shurin 2001). The lack of effects related to canoe traffic may thus be due to factors that prevent local establishment rather than to issues of transportation, although the low contribution of canoes to overall annual dispersal (<1% in George Lake) likely plays a role as well.

Moreover, high variation in the composition of the dispersing community could prevent transported individuals from establishing viable populations by promoting Allee effects despite directed dispersal. Variation in the dispersing community may indicate that zooplankton become attached to canoes by random chance that is not necessarily related to encounter rates. This is supported by the surprising finding that neither the cattle tanks nor the canoe hulls possessed a consistently higher proportion of littoral versus pelagic species. We predicted that most species attaching to and surviving on canoes would be littoral since the canoes used in this experiment were dragged through littoral habitat immediately before being removed from the water, as is standard practice at portage route landings. This prediction was reinforced when we found that abundances on canoes were not representative of the pelagic George Lake community during the canoe hull survey in study 1. However, cattle tank communities in study 2 had lower

proportions of littoral species than the George Lake community (B. Walseng unpublished data; Schartau et al. 2007). This could be due to an inability of some littoral species to survive in cattle tanks without macrophytes or sediment that provide necessary habitat structures (DeClerck et al. 2007), although Pedruski and Arnott (2011) found that substrate had no significant effect on local zooplankton richness in cattle tanks identical to the ones used in this study. It could also be due to the effects of unintentionally introduced aerial colonizers. Discrepancies between proportions of littoral and pelagic species on canoes and in George Lake could also be a result of species-specific traits related to canoe attachment.

Conclusion

Although we have demonstrated that canoes can act as dispersal vectors for viable adult crustacean zooplankton, the consequences must be considered in the context of natural systems. Canoe dispersal may be more important for distributing particular species such as *S. crystallina* and *Bosmina* spp., but the overall realized effect of canoe dispersal appears very limited. Nevertheless, there is potential for canoes to transport invasive species, which could in turn have an impact on community structure beyond that caused by the introduction of colonizers from the regional species pool. Further research into the species-specific traits that are involved in dispersal and how they interact with environmental factors is needed before the degree of dispersal occurring at any particular location can truly be understood or estimated.

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References

- Allen MR (2007) Measuring and modeling dispersal of adult zooplankton. *Oecologia* 153:135–143
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- Anderson MJ (2005) PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand
- Arnott SE, Vanni MJ (1993) Zooplankton assemblages in fishless bog lakes: influence of biotic and abiotic factors. *Ecology* 74:2361–2380
- Arnott SE, Magnuson JJ, Yan ND (1998) Crustacean zooplankton species richness: single- and multiple-year estimates. *Can J Fish Aquat Sci* 55:1573–1582
- Arnott SE, Jackson AB, Alarie Y (2006) Distribution and potential effects of water beetles in lakes recovering from acidification. *J N Am Benthol Soc* 25:811–824
- Barbiero RP, Tuchman ML (2004) Changes in the crustacean communities of Lakes Michigan, Huron, and Erie following the invasion of the predatory cladoceran *Bythotrephes longimanus*. *Can J Fish Aquat Sci* 61:2111–2125
- Binks JA, Arnott SE, Sprules WG (2005) Local factors and colonist dispersal influence crustacean zooplankton recovery from cultural acidification. *Ecol Appl* 15:2025–2036
- Bohonak AJ (1999) Effect of insect-mediated dispersal on the genetic structure of postglacial water mite populations. *Heredity* 82:451–461
- Bohonak AJ, Whiteman HH (1999) Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): effects of hydroperiod and salamanders. *Limnol Oceanogr* 44:487–493
- Boileau MG, Hebert PDN, Schwartz SS (1992) Non-equilibrium gene frequency divergence: persistent founder effects in natural populations. *J Evol Biol* 5:25–39
- Boudreau SA, Yan ND (2003) The differing crustacean zooplankton communities of Canadian Shield lakes with and without the nonindigenous zooplanktivore *Bythotrephes longimanus*. *Can J Fish Aquat Sci* 60:1307–1313
- Brendonck L, DeMeester L (2003) Egg banks in freshwater zooplankton: evolution and ecological archives in the sediment. *Hydrobiologia* 491:65–84
- Cáceres CE, Soluk DA (2002) Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia* 131:402–408
- Cáceres CE, Christoff AN, Boeing WJ (2007) Variation in ephippial buoyancy in *Daphnia pulicaria*. *Freshw Biol* 52:313–318
- Cadotte MW (2007) Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology* 88:823–829
- Cohen GM, Shurin JB (2003) Scale-dependence and mechanisms of dispersal in freshwater zooplankton. *Oikos* 103:603–617
- Cottenie K, Michels E, Nuytten N, DeMeester L (2003) Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology* 84:991–1000

- De Meester LA, Gómez A, Okamura B, Schwenk K (2002) The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Oecologia* 23:121–135
- DeClerck S, Vanderstukken M, Pals A, Muylaert K, DeMeester L (2007) Plankton biodiversity along a gradient of productivity and its mediation by macrophytes. *Ecology* 88:2199–2210
- Derry AM, Arnott SE, Shead JA, Hebert PDN, Boag PT (2009) Ecological linkages between community and genetic diversity in zooplankton among boreal shield lakes. *Ecology* 90:2275–2286
- Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol Model* 196:483–493
- Edmondson WT (1959) Fresh-water biology. Wiley, New York
- Fairchild GW (1981) Movement and microdistribution of *Sida crystallina* and other littoral microcrustaceans. *Ecology* 62:1341–1352
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391
- Gray DK, Arnott SE (2011) Does dispersal limitation impact the recovery of zooplankton damaged by a regional stressor? *Ecol App* 21:1241–1256
- Green AJ, Figuerola J (2005) Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. *Diversity Distrib* 11:149–156
- Griffith DA, Peres-Neto PR (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology* 87:2603–2613
- Hanski I, Gilpin M (1991) Metapopulation dynamics: brief history and conceptual domain. *Biol J Linn Soc* 42:3–16
- Havel JE, Shurin JB (2004) Mechanisms, effects, and scales of dispersal in freshwater zooplankton. *Limnol Oceanogr* 49:1229–1238
- Havel JE, Stelzleni-Schwent J (2000) Zooplankton community structure: the role of dispersal. *Verh Int Ver Theor Angew Limnol* 27:3264–3268
- Hessen DO, Walseng B (2008) The rarity concept and the commonness of rarity in freshwater zooplankton. *Freshw Biol* 53:2026–2035
- Holt C, Yan ND (2003) Recovery of crustacean zooplankton communities from acidification in Killarney Park, Ontario, 1971–2000: pH 6 as a recovery goal. *Ambio* 32:203–207
- Hudson PL, Reid JW, Lesko LT, Selgeby JH (1998) Cyclopoid and harpacticoid copepods of the Laurentian Great Lakes. *Bull Ohio Biol Surv NS* 12:21–50
- Jenkins DG, Buikema AL Jr (1998) Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecol Monograph* 68:421–443
- Jenkins DG, Underwood MO (1998) Zooplankton may not disperse readily in wind, rain, or waterfowl. *Hydrobiologia* 387(388):15–21
- Johnson LE, Ricciardi A, Carlton JT (2001) Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. *Ecol Appl* 11:1789–1799
- Keller W, Yan ND, Holtze KE, Pitblado JR (1990) Inferred effects of lake acidification on *Daphnia galeata mendotae*. *Environ Sci Technol* 24:1259–1261
- Keller W, Yan ND, Somers KM, Heneberry JH (2002) Crustacean zooplankton communities in lakes recovering from acidification. *Can J Fish Aquat Sci* 59:726–735
- Keller W, Heneberry JH, Dixit SS (2003) Decreased acid deposition and the chemical recovery of Killarney, Ontario lakes. *Ambio* 32:183–189
- Keller W, Yan ND, Gunn JM, Heneberry JH (2007) Recovery from acidified lakes: lessons from Sudbury, Ontario. *Water Air Soil Poll Focus* 7:317–322
- Kramer AM, Sarnelle O, Knapp RA (2008) Allee effect limits colonization success of sexually reproducing zooplankton. *Ecology* 89:2760–2769
- Kuns MM, Sprules WG (2000) Zooplankton production in Lake Ontario: a multistrata approach. *Can J Fish Aquat Sci* 57:2240–2247
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam
- Leibold MA, Norberg J (2004) Biodiversity in metacommunities: plankton as complex adaptive systems? *Limnol Oceanogr* 49:1278–1289
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- Lepš J, Šmilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge
- Louette G, De Meester L, Declerck S (2008) Assembly of zooplankton communities in newly created ponds. *Freshw Biol* 53:2309–2320
- Lukaszewski Y, Arnott SE, Frost TM (1999) Regional versus local processes in determining zooplankton community composition of Little Rock Lake, Wisconsin, USA. *J Plankton Res* 21:991–1003
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290–297
- Michels E, Cottenie K, Neys L, De Gelas K, Coppin P, De Meester L (2001) Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. *Mol Ecol* 10:1929–1938
- Minns CK, Moore JE, Schindler DW, Jones ML (1990) Assessing the potential extent of damage to inland lakes in Eastern Canada due to acidic deposition. III. Predicted impacts on species richness in seven groups of aquatic biota. *Can J Fish Aquat Sci* 47:821–830
- Pedruski MT, Arnott SE (2011) The effects of habitat connectivity and regional heterogeneity on artificial pond metacommunities. *Oecologia* 166:221–228
- Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614–2625
- Quinn G, Keough M (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

- R Development Core Team (2010) R: a language and environment for statistical computing. In: R Foundation for Statistical Computing. Vienna, Austria
- Rice WR, Gaines SD (1994) Extending nondirectional heterogeneity tests to evaluate simply ordered alternative hypotheses. *P Natl Acad Sci USA* 91:225–226
- Schartau AK, Halvorsen G, Walseng B (2007) Northern lakes recovery study—microcrustaceans: reference conditions, acidification, and biological recovery. NINA Report 235, Oslo
- Schindler DW (1998) A dim future for boreal waters and landscapes. *Bioscience* 48:157–164
- Shead J (2007) Chemical and biological recovery of Killarney Park, Ontario lakes (1972–2005) from historical acidification. Dissertation, Queen's University
- Shurin JB (2000) Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81:3074–3086
- Shurin JB (2001) Interactive effects of predation and dispersal on zooplankton communities. *Ecology* 82:3404–3416
- Shurin JB, Havel JE, Leibold MA, Pinel-Alloul B (2000) Local and regional zooplankton species richness: a scale-dependent test for saturation. *Ecology* 81:3062–3073
- Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the allee effect? *Oikos* 87:185–190
- Strecker AL, Arnott SE (2010) Complex interactions between regional dispersal of native taxa and an invasive species. *Ecology* 91:1035–1047
- Ter Braak CJF, Šmilauer P (2002) Canoco for windows ver. 4.54. Biometris Plant Research In, Wageningen
- Vanschoenwinkel B, Gielen S, Seaman M, Brendonck L (2008) Any way the wind blows—frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* 117:125–134
- Witty LM (2004) Practical guide to identifying freshwater zooplankton, 2nd edn. Cooperative Freshwater Ecology Unit, Sudbury
- Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, New Jersey