Invasibility of plankton food webs along a trophic state gradient

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Biological invasions are becoming more common, yet the majority of introduced exotic species fail to establish viable populations in new environments. Current ecological research suggests that invasion success may be determined by properties of the native ecosystem, such as the supply rate of limiting nutrients (i.e. trophic state). We examined how trophic state influences invasion success by introducing an exotic zooplankter, *Daphnia lumholtzi* into native plankton communities in a series of experimental mesocosms exposed to a strong nutrient gradient. We predicted that the attributes of nutrient-enriched communities would increase the likelihood of a successful invasion attempt by *D. lumholtzi*. Contrary to our original predictions, we found that *D. lumholtzi* was often absent from mesocosms that developed under high nutrient supply rates. Instead, the presence of *D. lumholtzi* was associated with systems that had low nutrients, low zooplankton biomass, and high zooplankton species diversity. Using generalized estimating equations (GEE) and multivariate species data, we found that the presence–absence of *D. lumholtzi* could be explained by variations in zooplankton community structure, which was itself strongly influenced by nutrient supply rate. We argue that the apparent invasion success of *D. lumholtzi* was inhibited by the dominance of another cladoceran species, *Chydorus sphaericus*. These results suggest that the interaction between trophic state and species identity influenced the invasion success of introduced *D. lumholtzi*.

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Human-mediated movement of organisms has broken down dispersal barriers for many species. This is evidenced by the exponential rise in the number of biological invasions over the past century (Cohen and Carlton 1998, Mack et al. 2000, Pimentel et al. 2000, Ruiz et al. 2000). Nevertheless, approximately 90% of all introduced species fail to establish viable populations in new environments (Williamson and Fitter 1996). Such a low colonization rate implies that local abiotic and biotic factors influence the invasion success of many non-native species. One local factor that may determine invasion success is trophic state (Dukes and Mooney 1999, Pärtel et al. 2000, Foster 2001). Trophic state refers to the fertility of an ecosystem and is determined by the supply rate and availability of limiting nutrients.

Nutrient supply may influence the susceptibility of a community to invasion via two mechanisms. First, enhancing the fertility of oligotrophic ("poorly fed") ecosystems may facilitate invasions by relaxing resource limitation (Tilman 1982, Huston and DeAngelis 1994, Davis et al. 2000, Miller et al. 2002). For example, phosphorus (P) additions increased the prevalence of exotic plants in California grasslands (Huenneke et al. 1990) and nitrogen (N) additions favored exotic C_3 plants over native C_4 plants in Minnesota grasslands (Wedin and Tilman 1996). Second, biological invasions may be facilitated in eutrophic ('well fed') ecosystems when excess nutrients modify community structure. Generally, eutrophic ecosystems have a reduced number of trophic links (Jenkins et al. 1992, Spencer and Warren 1996) and low species diversity (Waide et al.

1999, Mittelbach et al. 2001). Theory suggests that such communities are susceptible to biological invasion (Case 1990). Recent empirical evidence supports these theoretical expectations: experimentally simplified communities (i.e. low species- or functional- richness) are often prone to invasion by non-native species (Levine and D'Antonio 1999, Stachowicz et al. 1999, Naeem et al. 2000). Together, this evidence suggests that an ecosystem's trophic state may influence the success of introduced exotic species.

The potential relationship between nutrient supply and biological invasion is of particular interest because human activities modify global biogeochemical cycles. For example, it is estimated that anthropogenic activities have doubled N inputs to terrestrial ecosystems (Vitousek et al. 1997). Likewise, human activities are responsible for increasing N and P supply from terrestrial to aquatic ecosystems (Carpenter et al. 1998). Recipient freshwater ecosystems are particularly sensitive to increasing nutrient supply: the composition, biomass, and productivity of planktonic communities are driven to a large extent by nutrient loading (Brooks 1969, Pace 1986, Crisman et al. 1995, Smith 1998, Dodson et al. 2000). Do changes in trophic state associated with nutrient supply account for the marked invasion success of exotic species in freshwater ecosystems (Mills et al. 1994, Ricciardi 2001)? Surprisingly, very few studies have addressed this question (but see Gophen et al. 1999, Jensen et al. 2001).

The recent invasion of North American waters by the exotic cladoceran *Daphnia lumholtzi* (Sars) provides an opportunity to explore whether trophic state influences the invasibility of plankton communities. *Daphnia lumholtzi* is an herbivorous zooplankter native to tropical and subtropical regions of Africa, India, and Australia (Havel and Hebert 1993). This aggressive invader has been documented in at least 125 lakes and reservoirs in North America since its first U.S. sighting in 1990 (Sorenson and Sterner 1992, Havel and Hebert 1993, Swaffar and O'Brien 1996, J. Havel, pers. comm.). Most waterbodies invaded by *D. lumholtzi* are reservoirs in the southern regions of the U.S., which tend to be more eutrophic than lakes and reservoirs in the north (Thornton 1987). Comparative studies of midwestern reservoirs have suggested that the establishment of exotic *D. lumholtzi* may be linked to trophic state (Havel et al. 1995, Dzialowski et al. 2000), but this hypothesis has not yet been rigorously tested.

We used experimental mesocosms to determine whether the invasibility of plankton communities is affected by trophic state. Based upon the theoretical and experimental evidence discussed above, we predicted that nutrient enrichment would facilitate the invasion success of a one-time invasion attempt by *D. lumholtzi*. In addition, we sought to determine whether a successful invasion event would lead to ecological impacts on zooplankton community structure and ecosystem function, measured here as changes in algal biomass and nutrient concentrations in the water column. If so, the invasion and rapid range expansion of *D. lumholtzi* could have significant impacts on North American freshwater ecosystems.

Methods

Mesocosm facility

We used a factorial designed mesocosm experiment to test whether nutrient supply rate influenced the invasion success of *D. lumholtzi*. The mesocosms consisted of 24 circular cattle tanks (300 l operating volume, 0.6 m in height, 1.0 m $\varnothing$) and were housed indoors at the Nelson Environmental Studies Area (NESA), Univ. of Kansas. We filled the mesocosms with filtered (220 μm) pond water from a nearby fishless reservoir that serves as the source water for the entire experimental pond network at NESA. The water filtration retained most macrozooplankton, but allowed microzooplankton and phytoplankton to pass through. We maintained temperature within the optimal range for exotic *D. lumholtzi* throughout the six-week experiment (24 ± 1.0°C, Lennon et al. 2001). We provided light on a 16:8 light-dark cycle with a pair of forty-watt, cool-white fluorescent bulbs wired to the top of each mesocosm. The average concentration of photosynthetically active radiation (77 ± 3.3 μE m^{-2} s^{-1}) was typical for the turbid epilimnia of many midwestern U.S. reservoirs (F.J. de Noyelles, pers. comm.). We added three adult snails, *Planorbella trivolis*, to each tank at the beginning of the experiment to retard periphyton growth.

Trophic state treatments and chemical analyses

We used three levels of nutrient supply in order to capture a gradient of N and P concentrations found in Midwestern U.S. reservoirs. The low nutrient treatment consisted of eight replicate mesocosms with source water having ambient concentrations of N and P (TN = 589 ± 19 μg/l; TP = 24.6 ± 1.60 μg/l; TN:TP = 24 by mass). We then added sufficient volumes of dissolved KNO_3 and KH_2PO_4 to the remaining 16 mesocosms to achieve eight replicates of the medium nutrient treatment (target TP = 50 μg/l) and eight replicates of the high nutrient treatment (target TP = 75 μg/l). The target nutrient concentrations were maintained over the course of the experiment by adding dissolved N and P every seven days assuming a loss rate of 5% per day due to sedimentation (V.H. Smith, unpubl.). These nutrient amendments ensured that the supply ratio of nitrogen and phosphorus was the same for all treatments. We assumed that all mesocosms in this study were P-limited based upon empirically established N:P ratio criteria (Smith 1982).

Once a week, we took separate surface grab samples from the middle of each mesocosm for measurements of total nitrogen (TN), total phosphorus (TP), soluble reactive phosphorus (SRP), total inorganic nitrogen (TIN), and chlorophyll a. N and P concentrations were determined simultaneously using a Lachat 4200 auto-analyzer at the Ecotoxicology Laboratory, Univ. of Kansas. TN and TP were determined on unfiltered water samples using automated colorimetric procedures after persulfate digestion (Ebina et al. 1983). TIN and SRP were determined on 0.45 μm-filtered samples but were not digested. TIN was estimated as the sum of nitrate-N ($NO_3 + NO_2$-N) plus ammonium-N (NH_4-N). We measured phaeopigment-corrected chlorophyll a after cold methanol extraction using an Optical Technologies fluorometer (APHA 1998).

Zooplankton inoculations, treatments, and sampling

We inoculated all 24 mesocosms with a native zooplankton community from West Campus Pond at the Univ. of Kansas five days after filling the mesocosms. West Campus Pond (2 ha surface area, mean depth 4 m) has not been invaded by *D. lumholtzi* and supports a small- to medium-sized zooplankton community consisting of: *Asplanchna* sp., *Bosmina longirostris*, *Ceriodaphnia lacustris*, *Chydorus sphaericus*, *Daphnia parvula*, *Diaphanasoma birgei*, *Scapholebris kingi*, *Simocephalus vetulus*, *Chaoborus punctipennis*, *Cyclops bicuspidatus thomsai*, *Diaptomus pallidus*, and *Diaptomus scilliodies*. We obtained zooplankton from approximately 4000 l of lake water by taking replicate vertical tows. A standard aliquot of the well-mixed zooplankton concentrate was then added to each mesocosm. This inoculum (0.04 mg/l) was equivalent to 25% of the total zooplankton density found in West Campus Pond. We removed all observable individuals of the invertebrate predator *Chaoborus* from the zooplankton concentrate prior to inoculation. No fish were added to the mesocosms.

We collected *Daphnia lumholtzi* from Clinton Reservoir located approximately 3 km west of the Univ. of Kansas. This 2 800 ha, multipurpose impoundment has supported populations of invasive *D. lumholtzi* since at least 1994 (W. J. O'Brien, pers. commun.). From live samples, we isolated a total of 1200 gravid *D. lumholtzi* under a dissecting microscope. One-hundred *D. lumholtzi* were then randomly assigned to four replicate tanks in each of the three nutrient treatments; these 12 mesocosms served as the invasion treatment. The relatively low inoculum size (0.33 animals/l) was intended to simulate the propagule pressure of a natural invasion (Neill 1978, Vanni 1986). The remaining 12 mesocosms not inoculated with *D. lumholtzi* served as the invasion reference.

We used two methods for sampling zooplankton from the mesocosms. On weeks one through five, we took a 6.4 l zooplankton sample (2.1% of total mesocosm volume) from each mesocosms using a 400 ml PVC-pipe sampler. On week six, in order to detect potentially low densities of *D. lumholtzi*, we took a 64 l destructive zooplankton sample (~21% of the total mesocosm volume) from each mesocosm using an 8 l polyethylene bucket. Samples from each tank were filtered through 220 μm mesh, preserved with 4% formalin, and identified according to Edmondson (1959). Estimates of zooplankton biomass were determined using length-weight regressions. We measured the lengths of 100 individuals for each of the most abundant taxa using an ocular micrometer under 40 × magnification. We converted mean lengths to average biomass per individual using literature reported formulae (Dumont et al. 1975, McCauley 1984, Eisenbacher 1998).

The detection limit of *D. lumholtzi* was important in this study because we used presence–absence as a criterion for invasion success. The volumetric detection limit of *D. lumholtzi* was 0.156 animals/l with the column sampler and 10 fold lower with the bucket sampling method, assuming 100% mesh filtration efficiency. We applied the techniques of Green and Young (1993) to determine the probability of detecting *D. lumholtzi* at a density of 2 animals/l (average density found in the source population, Clinton Reservoir, Lennon et al. 2001). Their method assumes that the population approximates a Poisson distribution and that the probability of obtaining at least one individual is:

$$P_{>0,n} = 1 - e^{-mn}$$

where m is the mean density and n is the number of independent samples. Using this formula, we determined that, if *D. lumholtzi* were present in a given mesocosm, there would be an 87% chance of capturing one individual using the column sampler and > 99% chance using the bucket sampling method. *Daphnia lumholtzi* was deemed "present" if it was recovered using either of the two sampling methods. If *D. lumholtzi* was not present on a given sampling date, the invader may have (1) been present, but below detection, or (2) gone extinct from the mesocosm ("absent"). It is difficult to distinguish between these two scenarios. Therefore, we inferred that *D. lumholtzi* was present on an earlier sampling date if the invader was detected in the same mesocosm on a later sampling date.

Statistical analyses

We used univariate two-way repeated measures analysis of variance (RM-ANOVA) to test for main effects of the nutrient and invasion treatments and their interac-

tions over the course of the experiment. TP, TN, SRP, TIN, chlorophyll a, and zooplankton biomass were considered independently as response variables for the RM-ANOVA. Univariate RM-ANOVA requires that the data meet the assumption of sphericity, i.e. the variance-covariance matrix must be equal or else the test is biased. The assumption of sphericity for RM-ANOVA was violated for all of our response variables. We remedied this by applying the Greenhouse-Geiser correction, a conservative factor that makes adjustments to the F-ratio degrees of freedom (von Ende 2001). We interpreted a significant interaction term to mean that *D. lumholtzi* had differentially affected one of the response variables among the three nutrient supply treatments.

We also used multiple regressions for week five data to describe plankton responses (i.e. chlorophyll a, zooplankton biomass, and zooplankton species diversity) as a function of mesocosm nutrient concentrations (continuous variable) and invasion treatment (dummy variable, Neter et al. 1996). We calculated zooplankton species diversity from biomass data using the Shannon-Wiener index of diversity (Magurran 1988). We used $\log_{10}$ transformations when residuals did not meet the assumptions of normality or equal variance.

We analyzed multivariate species data using principal components analysis (PCA) to characterize the differences in zooplankton communities where *D. lumholtzi* was present or absent. We used a correlation matrix of $\log_{10}$ transformed biomass data for the seven most abundant zooplankton taxa. A correlation matrix was used instead of a covariance matrix because it standardizes the data (mean = 0; $\sigma^2 = 1$) and thus does not overemphasize large values.

The invasion success of introduced *D. lumholtzi* was evaluated by its patterns of presence and absence over the duration of the experiment. We used PROC GENMOD for analyzing the repeated sampling of categorical response variables (SAS 1999). PROC GENMOD relies upon generalized linear models that use a nonlinear link function to allow for the analysis of a binary response variable (Stokes et al. 2001). This type of repeated measures analysis uses generalized estimating equations (GEE) and requires that the user specify the structure of the response variable correlation matrix (Agresti 2002). We opted for an autoregressive correlation matrix because it assumes that the correlation between longitudinal observations (i.e. time) decreases with distance (Stokes et al. 2001). We used both categorical (ordinal nutrient treatment) and continuous predictors (nutrient concentrations, chlorophyll a, zooplankton biomass, zooplankton diversity, and principal components scores) to explain patterns of *D. lumholtzi* presence-absence over the duration of the six-week experiment. We loaded each of the predictor variables into the GENMOD models separately because a) many of the predictors were correlated, and b)

the GEE method becomes less reliable when there are many predictors and a relatively small number of subjects (Stokes et al. 2001). We used type 3 likelihood ratio statistics to determine the significance of predictor variables and time interactions. All statistical procedures were conducted using SAS v8.0 (SAS 1999).

Results

Nutrient treatments

Inorganic nutrient additions had significant and persistent effects on N and P concentrations over the duration of the experiment (Fig. 1). Results from RM-ANOVA indicate there was a significant time × nutrient effect for TP (P = 0.029, $F_{5.9,\ 52.8} = 2.6$), TN (P < 0.0001, $F_{5.8,\ 52.2} = 82.6$), SRP (P < 0.0001, $F_{3.8,\ 34.0} = 24.0$), and TIN (P < 0.0001, $F_{2.6,\ 23.7} = 83.3$). In addition, there was a significant time × introduction effect on TN concentrations (P = 0.006, $F_{2.9,\ 52.2} = 4.69$). On average, TN concentrations were 155 µg /l lower in systems with added *D. lumholtzi* when pooled across all nutrient treatments. This suggests that the introduction of *D. lumholtzi* affected N cycling. Despite this, there were no significant time × introduction × nutrient effects (P > 0.05).

Phytoplankton biomass

There was no significant difference between chlorophyll a concentrations across the three nutrient treatments over time (RM-ANOVA, P = 0.255, $F_{2.5,\ 21.2} = 1.46$). There was also no relationship between TP and chlorophyll a at the end of the experiment (P = 0.53). Chlorophyll a was typically below 4 µg/l (range = 0.04–86 µg/l), even when water column TP concentrations exceeded 75 µg/l. These results are consistent with predictions for "dominant even-link" predator-prey relationships represented in our simple phytoplankton-herbivore system (Mazumder 1994). In addition, *D. lumholtzi* introductions had no effect on chlorophyll a over time (RM-ANOVA, P = 0.41) or on week five (dummy variable parameter, P = 0.40).

Zooplankton biomass

Total zooplankton biomass (B_z) increased exponentially over time and responded significantly to nutrient enrichment (RM-ANOVA, P = 0.005, $F_{1.7,\ 30.7} = 47.4$). The introduction of *D. lumholtzi* had no effect on this relationship (RM-ANOVA, P = 0.81). At the end of the experiment (week five), approximately half of the variability in total zooplankton biomass in all 24 mesocosms could be explained by TP in these putatively P-limited systems (Fig. 2):

Fig. 1. Nutrient concentrations (mean ± SEM) in experimental mesocosms with and without *D. lumholtzi*: total phosphorus (TP), total nitrogen (TN), soluble reactive phosphorus (SRP), and total inorganic nitrogen (TIN); ● = low nutrient supply, ○ = medium nutrient supply, ▼ = high nutrient supply. There was a significant (RM-ANOVA, $P < 0.05$) time × nutrient effect for TP, TN, SRP, and TIN; there was also a significant time × *Daphnia* effect for TN ($P = 0.006$, $F_{2.9, 52.2} = 4.69$). Estimated inorganic nutrient-limitation values for phytoplankton from SAS (1989). Note logarithmic scales.
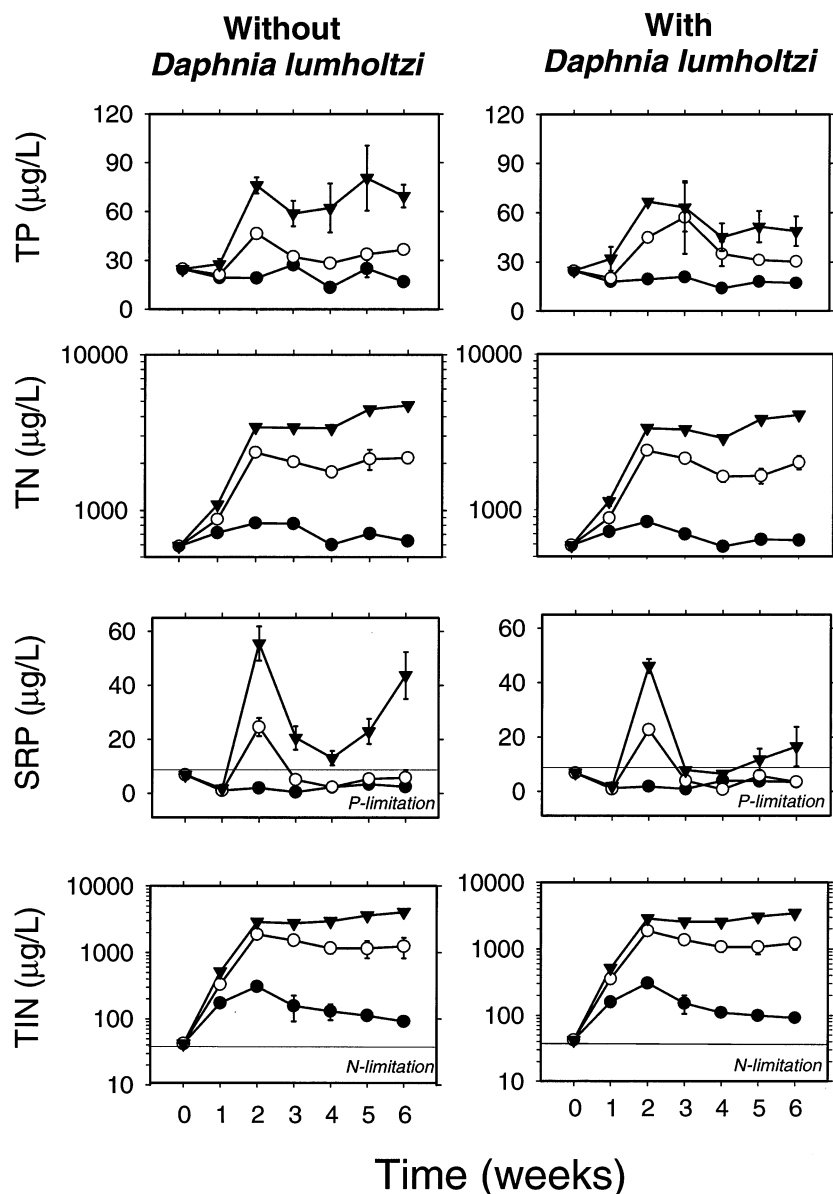
$$\log_{10} B_z = 1.66 + 1.18(\log_{10} TP), \quad R^2 = 0.49, \quad P < 0.0001 \tag{1}$$

The introduction of *D. lumholtzi* had no effect on this relationship (dummy variable parameter, $P = 0.78$).

Enrichment and zooplankton community structure

The biomass of the seven dominant species were analyzed to determine whether zooplankton community structure was altered by our experimental treatments. Cladoceran biomass was ~ 8% of the total biomass on week one, but comprised 85–99% of the total zooplankton biomass on week five. This was due pri-marily to the success of one species, *Chydorus sphaericus*, which comprised 45–87% of the total zooplankton biomass by the end of the experiment. *Chydorus sphaericus* biomass increased with TP (Fig. 3), but was not affected by the *D. lumholtzi* invasion (dummy variable parameter, $P = 0.37$):

$$Chydorus \ biomass = 228.9 + 67.1(TP),$$
$$R^2 = 0.56, \quad P < 0.0001 \tag{2}$$

This strong biomass response resulted in a five-fold increase in the relative biomass of *C. sphaericus* across the trophic state gradient, with near-monocultures of *Chydorus* occurring at the highest TP concentrations (Fig. 3b).
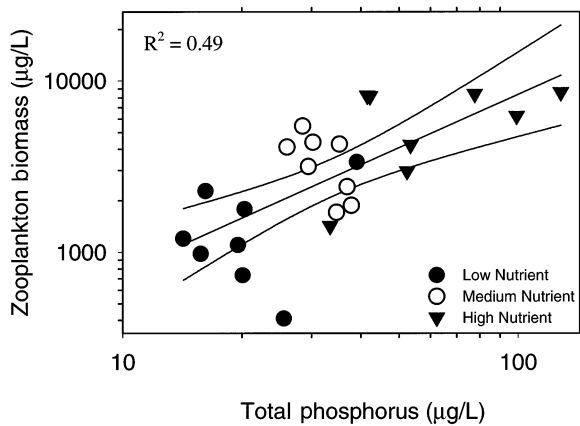
Fig. 2. Zooplankton biomass (B_z) vs total phosphorus (TP) concentrations observed in mesocosms on week five (with 95% confidence intervals). There was no significant effect of *D. lumholtzi* introduction on this relationship (P = 0.78). Note logarithmic scales.
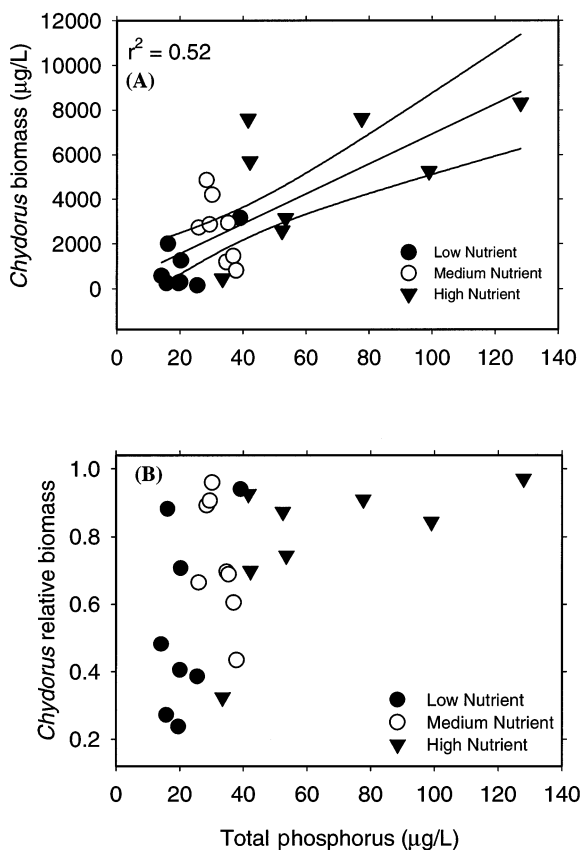

Fig. 3. (A) Biomass of *Chydorus sphaericus* vs total phosphorus (TP) concentrations observed in mesocosms on week five (with 95% confidence intervals). There was no significant effect of *D. lumholtzi* introduction on this relationship (P = 0.37). (B) Relationship between *C. sphaericus* relative biomass and TP for the different nutrient supply rates.

Nutrient enrichment caused a decrease in zooplankton species diversity (Shannon-Wiener Index, H′). Diversity declined significantly with TP, but total zooplankton biomass was a better single predictor:

$$H' = 4.35 + 1.04(\log_{10} B_z), \ R^2 = 0.77, \ P < 0.0001 \quad (3)$$

This relationship primarily reflects shifts in relative dominance that occurred across the experimental treatments. Species richness (S) alone only ranged between four and eight species on week five and S was not significantly related to B_z (Fig. 4). The introduction of *D. lumholtzi* had no effect on the diversity-biomass relationship expressed in Eq. (3) (dummy variable parameter, P = 0.62).

D. lumholtzi invasion success

Introduced *D. lumholtzi* achieved densities that were comparable to those found in its local source population (Lennon et al. 2001). *Daphnia lumholtzi* reached its peak relative-abundance (2.6%) in a medium nutrient level replicate on week three, with a density of 2.19 animals/l. On the same sampling date, *D. lumholtzi* reached a density of 1.88 animals/l in a low-nutrient replicate, resulting in the highest relative biomass attained by *D. lumholtzi* during the experiment (6.0%). However, trophic state indicators such as nutrient concentrations, chlorophyll a, zooplankton biomass, or zooplankton diversity could explain neither the abundance nor biomass of *D. lumholtzi* (P > 0.05, RM-ANOVA and simple linear regression for week 5 data).

These results lead us to evaluate invasion success using the presence-absence of *D. lumholtzi*. *Daphnia lumholtzi* was detected in 83% of the mesocosms that it
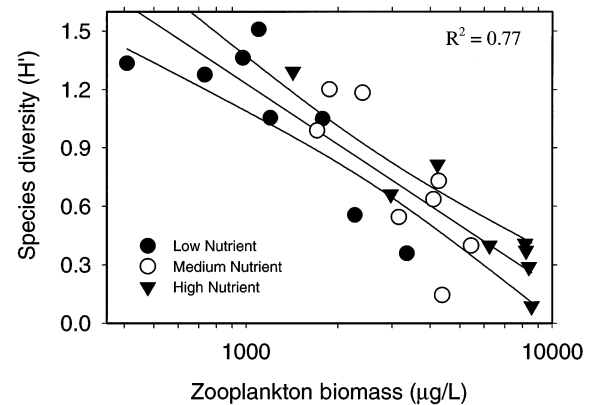

Fig. 4. Zooplankton species diversity (Shannon-Wiener Index, H′) as a function of zooplankton biomass (B_z) on week five (with 95% confidence intervals). Species diversity significantly decreased with TP, but zooplankton biomass was a better predictor. There was no significant effect of *D. lumholtzi* introduction on this relationship (P = 0.62). Note logarithmic scale.

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Table 1. Principal component weightings for the first three principal components generated from a zooplankton species matrix. Species data represent the log$_{10}$ transformed biomasses of the seven dominant zooplankton found in the mesocosms that had been inoculated with *D. lumholtzi* at the beginning of the six-week long experiment.

Zooplankton taxa	PCA 1	PCA 2	PCA 3
Calanoid copepods	0.504	0.114	0.042
Diaphanosoma birgei	0.337	0.557	−0.045
Cyclopoid copepods	0.003	0.566	−0.608
Bosmina longirostris	0.358	0.241	0.498
Simocephalus vetulus	−0.469	0.159	0.101
Ceriodaphnia lacustris	−0.250	0.397	0.606
Chydorus sphaericus	−0.470	0.339	−0.035
Percent variance explained	41	24	14

was introduced to over the six-week experiment. Generalized estimating equations (GEE) revealed that a number of trophic state variables were good predictors of *D. lumholtzi* presence-absence. There was a significant time × nutrient interaction indicating that *D. lumholtzi* was found less under high nutrient concentrations later in the experiment (time × TP, P = 0.039; time × TN, P = 0.027); however, qualitative nutrient treatments (i.e. low, medium, high) were not useful in predicting presence-absence of the invader (P = 0.36). Chlorophyll a was a poor predictor of invader presence-absence (P = 0.32). Zooplankton biomass and zooplankton species diversity were marginally significant (time × log$_{10}$ biomass, P = 0.079; H′, P = 0.065) and thus somewhat useful for predicting invasion success over the duration of the experiment.

A principal components analysis (PCA) was used to assess whether the presence-absence of *D. lumholtzi* was associated with zooplankton community structure. The first three principal components axes of the PCA analysis (PC1, PC2, and PC3) explained 79% of the variation in biomass of the seven dominant zooplankton taxa in the 12 invaded mesocosms over the six-week duration of the experiment (Table 1). In general, the probability of detecting *D. lumholtzi* increased along PC1 ("invasion axis") and this invader was found more often in communities dominated by calanoid copepods and *Bosmina longirostris* (Fig. 5). These communities had low zooplankton biomass and high zooplankton species diversity (Fig. 6). In contrast, *D. lumholtzi* was less likely to be found in communities dominated by *Chydorus sphaericus* and *Simocephalus vetulus*, which were communities with high zooplankton biomass and low zooplankton species diversity (Fig. 6). Using the GEE method again, we found a significant time × PC1 interaction suggesting that *D. lumholtzi* was found less in communities with *Chydorus sphaericus* and *Simocephalus vetulus* later in the experiment (time × PC1, P = 0.028).

Discussion

The primary aim of this study was to determine whether trophic state influenced the success of a one-time invasion attempt by an exotic crustacean zoooplankter, *Daphnia lumholtzi*. The experimental trophic state gradient, which we created by amending mesocosms with inorganic nutrients, significantly altered plankton community structure. Nutrient enrichment increased zooplankton biomass (Fig. 2) and created shifts in plankton composition (Fig. 3) that led to an overall reduction in zooplankton species diversity (Fig. 4). Together, these changes allowed us to test

Fig. 5. Principal components analysis (PCA) for the seven dominant zooplankton taxa in the 12 "invaded" mesocosms for all data obtained over the duration of the experiment. Different data points refer to the presence-absence of *D. lumholtzi* that were introduced at the beginning of the experiment. *D. lumholtzi* was considered: 'present' (●) if it was identified in a sample, 'inferred present' (◉) for an earlier sampling date if it was identified in the same mesocosm on a later sampling date; 'absent' (○) if it was not detected in a given sample and was not detected in the same mesocosm at a later sampling date.
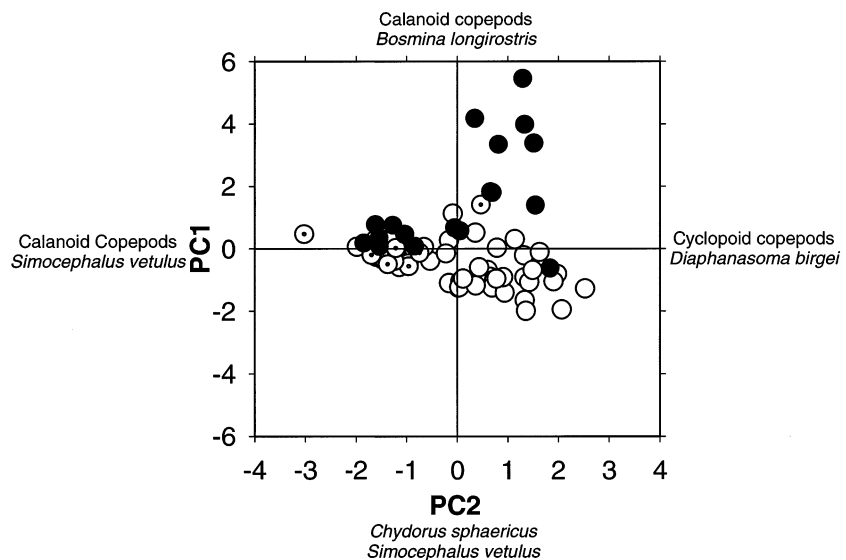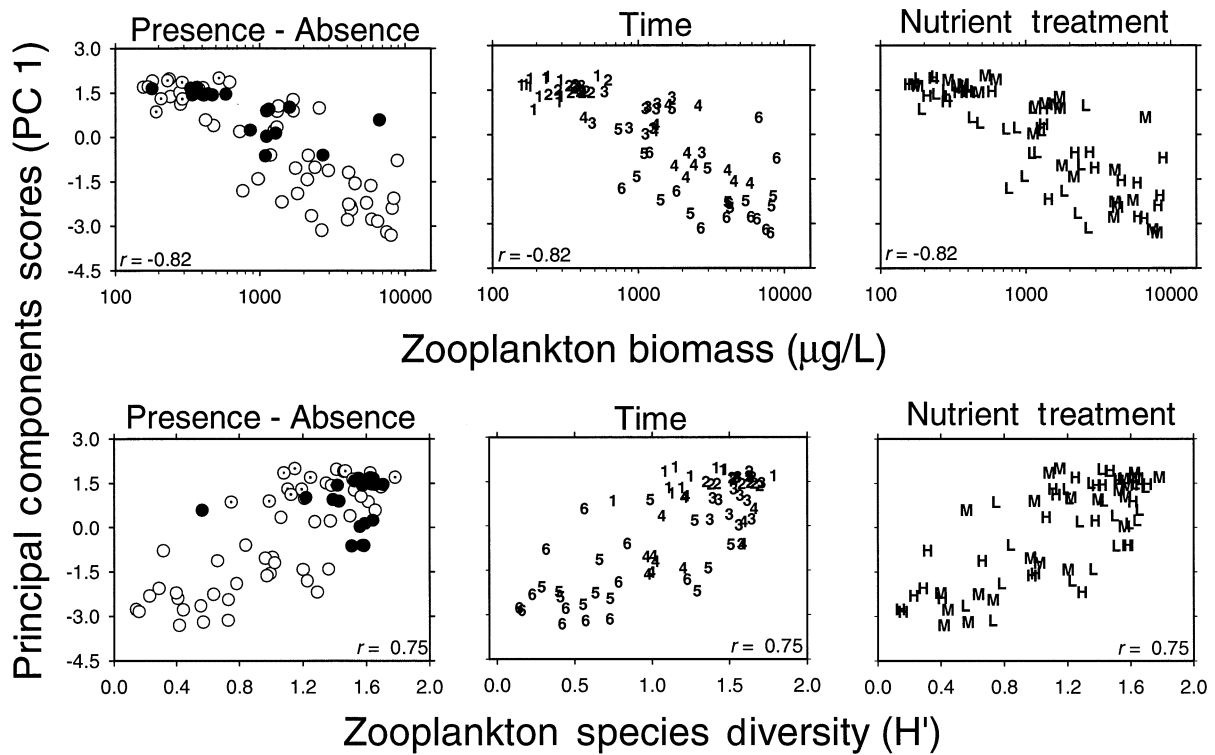
Fig. 6. PCA scores from the first principal component axis plotted against $\log_{10}$ zooplankton biomass (upper panels) and zooplankton species diversity (lower panels). From left to right, the same data are plotted, but are coded for *D. lumholtzi* presence-absence (see Fig. 5 for legend descriptors), time of sampling (weeks 1–6), and categorical nutrient treatment (L = low, M = medium, H = high). Zooplankton species diversity was calculated with the Shannon-Weiner Index (H′). Pearson's correlation coefficients (r) were calculated, but no P values were assigned since the samples are not independent.

whether trophic state may be contributing to the rapid range expansion of exotic *D. lumholtzi* in North America (Dzialowski et al. 2000, Havel et al. 2000, Muzinic 2000).

For two reasons, we predicted that *D. lumholtzi* invasion success would increase along a trophic state gradient. First, as noted earlier, nutrient enrichment can directly facilitate invasion success by relaxing resource limitation (Tilman 1982, Davis et al. 2000). Second, species diversity typically declines in nutrient-rich communities (Leibold 1999, Waide et al. 1999), potentially making these systems more susceptible to biological invasions (Levine and D'Antonio 1999, Naeem et al. 2000). However, in contrast to our original predictions, we found that *D. lumholtzi* was often absent from mesocosms that developed under high nutrient supply rates. Instead, the invader was found in mesocosms with low nutrients, low zooplankton biomass, and high zooplankton species diversity. These experimental results are consistent with a recent comparative survey (Dzialowski et al. 2000), which reported that oligo-meostrophic midwestern waterbodies were more susceptible to invasion by *D. lumholtzi* than eutrophic systems. Potential mechanisms that may help account for these empirical results are discussed below.

Trophic state, resource limitation and invasion success

Resource limitation is one characteristic that may influence invasion success in some aquatic ecosystems. For example, Neill (1978) questioned why the cosmopolitan *Daphnia pulex* was absent from the plankton of oligotrophic montane lakes within its native range of British Columbia, Canada. In order to rule out dispersal limitation, *D. pulex* was experimentally introduced into zooplankton communities under ambient and enriched P concentrations. P enrichment increased algal resources, and as a result, the relative abundance of *D. pulex* increased from 4 to 50% over a three-month period. Similarly, *D. pulex* invasion success was facilitated by nutrient enrichment in an oligo-mesotrophic midwestern U.S. lake (Vanni 1986). In the latter study, inorganic N and P additions resulted in a 10-fold peak increase in *D. pulex* abundance. The rapid-growing *D. pulex* population reduced phytoplankton biomass by an order of magnitude and also reduced the abundance of resident zooplankton species.

In contrast to the studies of Neill (1978) and Vanni (1986), we found no numerical response of introduced *D. lumholtzi* to the nutrient supply gradient in this

study. *Daphnia lumholtzi* never exceeded 2.19 animals/l or 6% of the total community biomass over the duration of the experiment. Thus, our results suggest that relaxing resource limitation via nutrient enrichment did not facilitate *D. lumholtzi* invasion success.

Trophic state, food web structure and invasion success

Variation in community structure can influence the susceptibility of an ecosystem to biological invasions (Lodge 1993). It has been suggested since the time of Elton (1958) that diverse communities are inherently resistant to exotic invasion attempts. Ecological theory predicts that high diversity systems have fewer "niche opportunities" for invading species (Shea and Chesson 2002), and several empirical studies tend to support this diversity-invasibility hypothesis (Naeem et al. 2000, Hector et al. 2001). Because species diversity typically declines at high levels of resource supply (Schindler 1990, Leibold 1999, Dodson et al. 2000), we predicted that communities receiving the highest nutrient loads would be the most susceptible to *D. lumholtzi* invasion.

As we anticipated, zooplankton species diversity declined with nutrient enrichment (Fig. 4). However, invasion success did not in turn increase with nutrient supply-mediated changes in community structure. Instead, the high-nutrient, low-diversity communities were most resistant to *D. lumholtzi* invasion based on presence–absence data (Figs. 5 and 6).

We suggest here that our resource supply gradient caused shifts in species dominance that resulted in increased ecological resistance to invasion. Typically, only a few species become numerically abundant under conditions of high resource supply (Rosenzweig 1995). These specialists often competitively exclude native species from the community, but their dominance may also inhibit colonization by invading species (Huston 1994). In such cases, species- or functional- identity may be important and explain why high pre-invasion diversity does not always confer resistance to introduced species (Wardle 2001). For example, in English grasslands, species identity was found to be more important than species richness in warding off invading species (Crawley et al. 1999). Similarly, in California grasslands, the invasion success of a noxious weed (*Centaurea solstitialis*) was hindered by one species (*Hemizonia congesta*) far more than other native grasses (Dukes 2002). Finally, species richness has been found to be relatively unimportant for invasion success in experimental aquatic microcosms: the identity of resident species determined whether introduced protist species could establish persistent populations (Law et al. 2000). Species identity may generate biotic resistance if a given native species inherently has strong negative interactions with a potential invading species (Case 1990). This biotic resistance can be achieved 1) if a native species has a disproportionately large influence on the invader relative to the native species' own biomass (i.e. it is a keystone species), or 2) if a native species interacts less strongly with the invader, but attains high relative biomass in the community.

Our results suggest that the identity of one species, *Chydorus sphaericus*, strongly influenced the success of introduced *D. lumholtzi*. Under high nutrient supply rates, the zooplankton assemblages became strongly dominated by *C. sphaericus* (Fig. 3a and Fig. 3b); these systems exhibited the greatest resistance to *D. lumholtzi* invasion. A principal components analysis (PCA) revealed that the presence-absence of *D. lumholtzi* could be explained by changes in community structure that accompanied experimental nutrient enrichment. Along the first principal components axis ('invasion axis'), *D. lumholtzi* was almost always absent from communities dominated by *C. sphaericus* (Fig. 5). In contrast, communities dominated by calanoid copepods and *Bosmina longirostris* were significantly more vulnerable to invasion by *D. lumholtzi* over the duration of our study (GEE, time × PC1, P = 0.022, Fig. 5). These same communities also had lower zooplankton biomass (Fig. 6a), which has been experimentally shown to facilitate zooplankton invasion success (Shurin 2000). Thus, it is possible that *D. lumholtzi* was deterred by zooplankton biomass alone, however multiple lines of evidence indicate that *C. sphaericus* is an ecologically important species in eutrophic freshwater ecosystems.

In general, chydorids are considered littoral species (Whiteside et al. 1978). However, early limnologists recognized that *Chydorus sphaericus* is often found in pelagic regions of lake ecosystems (Birge 1897). In addition, it appears that *C. sphaericus* has an affinity for fertile waterbodies: fossil records, comparative studies, and whole-lake experiments all demonstrate that it is a major player in the pelagic regions of nutrient-rich lakes (Kerfoot 1981, Kitchell and Sanford 1992, Cottingham et al. 1997). For example, following the experimental P enrichment of an Ontario lake, plankton diversity drastically declined and *C. sphaericus* comprised 97% of the total zooplankton biomass (Yan and Lafrance 1984). Mechanistically, *C. sphaericus* may do well under eutrophic conditions because it has high grazing rates and is tolerant of filamentous algae (Brooks 1969, Balcer et al. 1984, Nörberg 2000). Filamentous algae are considered a low quality resource, in part because they interfere with zooplankton filtration (Fulton and Paerl 1988, Leibold 1999). DeMott et al. (2001) suggest that the absence of large *Daphnia* from hypereutrophic Dutch lakes is attributed to physical interference of filtering by filamentous algae. It is feasible that *C. sphaericus* outperformed *D. lumholtzi* under high nutrient supply due to low quality food resources. However, we do not have the data required to directly test this hypothesis.

Impacts of *D. lumholtzi* on ecosystem function

Most biological invasions result in a low impact on native communities. It has been reported that only 10% of established exotic populations have a discernable impact on structure or function of invaded systems (Williamson and Fitter 1996). Nevertheless, the potential exists for invasive species to dramatically alter fundamental properties of an ecosystem, including its physical features, community structure, biogeochemical cycles, and overall productivity (Mack et al. 2000). For example, total zooplankton biomass and zooplankton species richness declined sharply in Harp Lake, Ontario following its invasion by the predatory cladoceran, *Bytotrephes cederstromi* (Yan et al. 2001). Because *Daphnia* are often considered keystone herbivores (Stockner and Porter 1988, Ives et al. 1999), we wanted to document any changes that *D. lumholtzi* invasions imposed on the structure and function of our study systems.

Initially, it seemed questionable whether *D. lumholtzi* invasions could impact natural freshwater ecosystems. In general, the abundance of *D. lumholtzi* is low within both its native and introduced ranges (Swar and Fernando 1979, King and Greenwood 1992, Havel et al. 1995, Davidson and Kelso 1997, East et al. 1999, Work and Gophen 1999). However, small-scale predation studies indicate that bluegill sunfish feed preferentially on native *Daphnia* over *D. lumholtzi* (Kolar and Wahl 1998) because *D. lumholtzi* is equipped with head spines that can nearly double its total body size. If these patterns of size selective predation scale to whole ecosystems, then it is possible that *D. lumholtzi* invasions may cause shifts in zooplankton community composition. A recent comparative survey of 35 Kansas reservoirs indicates that *D. lumholtzi* invasions may impact zooplankton community composition. Dzialowski et al. (2000) found that zooplankton communities of seven reservoirs, which were newly invaded by *D. lumholtzi* between 1994 and 1997, exhibited less similarity than 22 reservoirs that were not invaded during the same sampling period.

We found no evidence of *D. lumholtzi* impact on three measures of the plankton structure (algal biomass, zooplankton biomass, or zooplankton species diversity). However, the introduction of *D. lumholtzi* did have a significant effect on nutrient cycling. TN concentrations were 8% lower in systems that were inoculated with *D. lumholtzi*. We argue that *D. lumholtzi* invasion success is impeded in systems with high nutrients, but it appears that *D. lumholtzi* may also have the ability to reduce water column nutrient concentrations. Future studies should investigate how *D. lumholtzi* alters N cycling and determine whether this mechanism aids in the establishment of newly invaded ecosystems.

Implications for *D. lumholtzi* invasion success in lakes and reservoirs

The results reported here allow us to speculate whether lake trophic state may be contributing to the rapid range expansion of exotic *D. lumholtzi* in North American waterbodies (Dzialowski et al. 2000, Havel et al. 2000, Muzinic 2000). Although *Daphnia lumholtzi* was first reported in North America in the early 1990s (Sorenson and Sterner 1992, Havel and Hebert 1993), this invader has now established itself throughout much of the southern United States (J. Havel, pers. comm.) and is dispersed from Florida (East et al. 1999) to Arizona and Utah (J.J. Elser and C. Luecke, pers. comm.). These observations suggest that like many other zooplankton species, *D. lumholtzi* may be dispersal limited at large spatial scales (Shurin 2000). If so, we anticipate that *D. lumholtzi* will continue to expand its geographic range in North America.

However, empirical studies have shown that local factors contribute to zooplankton invasion dynamics (Lukaszewski et al. 1999, Shurin 2000). Our results suggest that once dispersed into a new system, lake trophic state may contribute to the local invasion success of *D. lumholtzi*. Dzialowski et al. (2000) found that *D. lumholtzi* was present primarily in oligotrophic rather than eutrophic reservoirs. That is, invaded reservoirs had significantly lower N and P concentrations, lower chlorophyll a, and higher water column transparency when compared to uninvaded reservoirs (however, see Havel et al. 1995, 2002). Our experimental results agree with the trends reported by Dzialowski et al. (2000). Nutrient concentrations were good predictors of *D. lumholtzi* invasion success in our mesocosms, as were a number of biotic factors affected by our nutrient supply gradient. In particular, the identity of one zooplankton species seemed to be important in determining invasion success. It appears that *C. sphaericus*, which became the dominant zooplankter under high nutrient supply, may have prevented the establishment of *D. lumholtzi*. Our results thus suggest that nutrient-mediated changes in aquatic community structure have the potential to strongly influence zooplankton invasion success.

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