

Food web structure provides biotic resistance against plankton invasion attempts

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Abstract It is generally accepted that native communities provide resistance against invaders through biotic interactions. However, much remains uncertain about the types of ecological processes and community attributes that contribute to biotic resistance. We used experimental mesocosms to examine how zooplankton community structure, invertebrate predation, and nutrient supply jointly affected the establishment of the exotic *Daphnia lumholtzi*. We predicted that establishment would increase with declining biomass and diversity of native zooplankton communities and that an invertebrate predator (IP) would indirectly facilitate the establishment of *D. lumholtzi* due to its relatively long predator-detering spines. Furthermore, we hypothesized that elevated nutrient supply would increase algal

food availability and facilitate establishment. Only when the biomass and diversity of native zooplankton were significantly reduced, was *D. lumholtzi* able to successfully invade mesocosms. Although invertebrate predation and resource supply modified attributes of native zooplankton communities, they did not influence the establishment of *D. lumholtzi*. Overall, our results are consistent with observed population dynamics in invaded reservoirs where *D. lumholtzi* tends to be present only during the late summer, coinciding with historic mid-summer declines in native zooplankton populations. Lakes and reservoirs may be more susceptible to invasion not only by *D. lumholtzi*, but also by other planktonic species, in the late summer when native communities exhibit characteristics associated with lower levels of biotic resistance.

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Introduction

Exotic species threaten the biological integrity of virtually all ecosystems. As such, elucidating the mechanisms involved in the establishment of exotic species in native ecosystems has emerged as a major ecological research priority (Mack

et al. 2000). It is generally accepted that native communities provide resistance against invaders through biotic interactions (Elton 1958; Levine and D'Antonio 1999). However, much remains unclear about the types of ecological processes and community attributes that contribute to biotic resistance (Levine et al. 2004; Smith et al. 2004; Romanuk and Kolasa 2005), and it is unknown during which phase of the invasion process (i.e., establishment, spread, impact) biotic resistance is most effective (Levine et al. 2004).

Competition and predation are two types of interactions that potentially contribute to biotic resistance. It has long been assumed, for example, that competition between exotic and native species confers resistance to invasion (Elton 1958; Levine and D'Antonio 1999; van Ruijven et al. 2003; Levine et al. 2004). Similarly, native predators can provide strong biotic resistance through direct predation on potential invaders (Crawley 1986; Schoener and Spiller 1995; Miller et al. 2002). Conversely, the establishment of exotic species may be facilitated if predators prey preferentially or exclusively upon native species (Swaffar and O'Brien 1996; Maron and Vila 2001; Keene and Crawley 2002).

Relationships between invasibility and biotic interactions such as competition and predation may be further affected by resource availability. Communities may be more susceptible to invasion if competitive interactions become less intense with increasing resource levels (Davis et al. 2000; Davis and Pelsor 2001; Jiang and Morin 2004). In natural systems such increases in resource availability can result from: (a) changes in external resource inputs (e.g., eutrophication); (b) altered predation intensity (e.g., trophic cascades); and/or (c) disturbances that reduce the ability of resident communities to consume limiting resources (Burke and Grime 1996; Davis et al. 2000).

Surprisingly, few experimental studies have directly measured the interactive effects of multiple species interactions on invasion dynamics. In this study, we examined how competition, predation, and resource supply jointly affected the establishment success of the exotic cladoceran *Daphnia lumholtzi*. Since first being reported in a Texas reservoir in the late 1980s (Sorenson and Sterner 1992), *D. lumholtzi* has appeared in

waterbodies throughout the United States and its range continues to expand (see Havel and Shurin 2004 for its current U.S. distribution). *Daphnia lumholtzi* often peaks in plankton communities during the late summer when native zooplankton assemblages typically experience declines in population densities and diversity (Lennon et al. 2001; Lemke et al. 2003). Strong competitive interactions with native species may prevent *D. lumholtzi* from occupying plankton communities at other times of the year and from invading additional systems. Furthermore, *D. lumholtzi* possesses unique morphological defences that may influence its invasion success. Spines, helmets, and neckteeth are common among many species in the genus *Daphnia*; however, *D. lumholtzi* possesses spines that are longer than those of native daphnids (Tollrian and Dodson 1999). As a result, *D. lumholtzi* is less susceptible to some predators than native competitors (Swaffar and O'Brien 1996). Once *D. lumholtzi* has invaded a new community, predators may selectively feed upon native species, allowing the invader to experience relatively faster population growth and reductions in the intensity of resource competition.

We experimentally manipulated: (1) native zooplankton community structure, (2) the presence and absence of an invertebrate predator (IP), and (3) nutrient supply in a series of experimental mesocosms to explore how different community attributes influence the establishment of *D. lumholtzi*. We predicted that *D. lumholtzi* establishment would increase with declining biomass and diversity of native zooplankton communities, and that an IP would indirectly facilitate the establishment of *D. lumholtzi* due to its long predator-detering spines. Furthermore, we hypothesized that elevated nutrient supply would increase algal food availability and facilitate establishment of *D. lumholtzi*.

Methods

Experimental mesocosms

We used 24 experimental mesocosms to determine how native zooplankton community structure,

invertebrate predation, and nutrient supply influenced the establishment of *D. lumholtzi*. The mesocosms were located at the Indoor Mesocosm Facility at the University of Kansas Field Station and Ecological Reserves (KSR), 4 km north of Lawrence, KS. The mesocosms were white polyethylene tanks that held roughly 300 l of water (0.6 m height; 1.0 m width). A 1-m long shop light was attached to the top of each mesocosm to provide approximately $125 \mu\text{E m}^{-2} \text{s}^{-1}$ of light on a 16:8 light–dark cycle. The temperature in the facility was maintained at approximately 24°C , which is within the optimum temperature range of *D. lumholtzi* (Lennon et al. 2001).

Food web manipulations

We experimentally manipulated native plankton communities to create three food web treatments, each of which was replicated in quadruplicate mesocosms: (1) Low Zooplankton (LZ), (2) Ambient Zooplankton (AZ), and (3) AZ + an IP (IP). Each of the food web treatments were also exposed to two nutrient supply treatments (see *Nutrient supply treatments* below). Initially, we filled all 24 mesocosms with filtered ($80 \mu\text{m}$) water from a single source pond. The filtering removed most of the macrozooplankton present in the source pond water. Eight of the mesocosms containing this filtered pond water served as the LZ treatment, and no additional native organisms were added to these mesocosms. All 16 of the remaining mesocosms were inoculated with a diverse assemblage of native macrozooplankton consisting of cladocera (*Daphnia parvula*, *Diaphanasoma birgei*, *Bosmina longirostris*, *Ceriodaphnia lacustris*, *Chydorus sphaericus*, and *Simocephalus vetulus*) and copepods (*Cyclops bicuspidatus*, *Diaptomus pallidus*, and *Diaptomus scillioides*). All of these species were also present in the original source water. Native zooplankton were added to the mesocosms at a biomass that was roughly 50% of the total zooplankton biomass in each of the two source ponds. Eight of the 16 mesocosms that were inoculated with native zooplankton served as the AZ manipulation. We created the final food web manipulation (IP) by adding the IP *Notonecta undulata* to the remaining eight

mesocosms that were inoculated with native zooplankton. Notonectids were added to the mesocosms at densities similar to those found in nature (8 individuals/mesocosm, or $0.027 \text{ individuals l}^{-1}$; Shurin 2001). We used notonectids in this study because they are size-selective predators that tend to consume large-bodied zooplankton, and they can have strong impacts on zooplankton community structure (Murdoch et al. 1984; Shurin 2001). After the food web manipulations were established, we added four snails to each mesocosm to inhibit periphyton growth (Lennon et al. 2003).

Nutrient supply treatments

Each of the three food web treatments was exposed to two different nutrient supplies. One half of the 24 mesocosms received no supplemental phosphorus at the beginning of the experiment, and the ambient pond water ($\text{TP} = 22.5 \mu\text{g l}^{-1}$) served as the target low-phosphorus concentration. The remaining 12 high-nutrient supply mesocosms received supplements of inorganic phosphorus (KH_2PO_4) sufficient to raise the total phosphorus (TP) concentration to $100 \mu\text{g l}^{-1}$. Inorganic nitrogen (KNO_3) was also added to the mesocosm to increase total nitrogen (TN) from ambient concentrations ($\sim 650 \mu\text{g l}^{-1}$) to a target concentration of $800 \mu\text{g l}^{-1}$ for all 24 mesocosms.

Daphnia lumholtzi additions

Daphnia lumholtzi were collected from Clinton Reservoir, a large multi-purpose reservoir located 3 km west of Lawrence, Kansas, which was colonized by *D. lumholtzi* prior to 1995 (Dzialowski et al. 2000). Live zooplankton samples were collected from the reservoir using a $250 \mu\text{m}$ plankton net and individual *D. lumholtzi* were isolated into filtered lake water. We added 15 adult *D. lumholtzi* to all 24 of the mesocosms, achieving an initial density of 0.05 l^{-1} and initial biomass of $0.25 \mu\text{g l}^{-1}$. The density of *D. lumholtzi* added to the mesocosms was intentionally low in order to simulate the small propagule size that is likely associated with natural invasion attempts (Lennon et al. 2003).

Mesocosm sampling

For 4 weeks, we sampled the mesocosms at weekly or bi-weekly intervals for nutrients, chlorophyll *a* (proxy for algal biomass), and a variety of zooplankton response variables. A 1-L grab sample was collected from the center of each mesocosm for analysis of TP, TN, and chlorophyll *a*. TP and TN were determined spectrophotometrically after persulfate digestion (Prepas and Rigler 1982; Bachmann and Canfield 1996; respectively). Chlorophyll *a* concentrations were determined fluorometrically after samples were filtered onto GF/F filters and extracted in 90% methanol (APHA 1995).

We collected zooplankton samples from the mesocosms using a PVC depth-integrated tube sampler (740 ml). Nine (6.7 l) to sixteen (11.8 l) randomly placed samples were taken from each mesocosm per sampling event. In addition, we collected a larger 75 l sample from each mesocosm on the final sampling date using a 20 l bucket to increase the likelihood of including rare species in our samples (Lennon et al. 2003). Zooplankton samples were filtered onto an 80 μm mesh net and preserved in ~70% ethanol. These samples were returned to the laboratory, where zooplankton from sub-samples (5–10% of the total sample volume) were identified and enumerated. The entire volume of each zooplankton sample was also examined under $25\times$ magnification to determine whether *D. lumholtzi* was present at low densities. Length measurements of up to 50 individuals of the most common taxa were used to estimate zooplankton biomass based on published length–weight regression formulas (McCauley 1984; Eisenbacher 1998).

Statistical analyses

We evaluated the effects of our nutrient and food web manipulations over the duration of the experiment using repeated measures analysis of variance (RM-ANOVA). We used TN, TP, chlorophyll *a*, cladoceran biomass, and zooplankton richness as response variables, all of which were \log_{10} -transformed in order to meet assumptions of normality and homogeneity of variance. Greenhouse-Geiser corrections were

used to account for potential violations of the assumptions of sphericity (von Ende 2001). Tukey's HSD test ($P = 0.05$) was used to detect differences between treatments when significant differences were found with RM-ANOVA. We characterized zooplankton community structure on the final sampling date using principal components analysis (PCA) with a correlation matrix of \log_{10} -transformed biomass data from the eight most abundant taxa. RM-ANOVA and PCA were conducted using Sigma Stat (v. 3.1) and Minitab (v. 12.0), respectively.

We evaluated the establishment of introduced *D. lumholtzi* using abundance, biomass, and presence–absence data. We defined successful establishment as the presence of *D. lumholtzi* on the final sampling date at a density greater than the initial stocking density (0.05 l^{-1}). In other words, *D. lumholtzi* did not successfully establish within a mesocosm unless it could both increase when rare and persist throughout the duration of the experiment. We used a multiple factor contingency table to evaluate the effects of the food web manipulations and the nutrient supply treatment on establishment. Presence–absence data from the final sampling date were used in this analysis, which was an extension of the chi-square test. Test statistics (G^2) were calculated using weighted natural logarithms (Lowry 2005). A summary of the experimental treatments and the interpretations of potential invasion outcomes are presented in Table 1.

Results

Responses to nutrient supply and food web manipulations

TP was $7.5\times$ greater ($P < 0.001$, $F_{1,18} = 1173$) in the high-nutrient supply treatment than in the low-nutrient supply treatment (Fig. 1), but TP was not affected by food web manipulations ($P = 0.96$). TN was not affected by the nutrient supply treatment ($P = 0.58$) or food web manipulations ($P = 0.61$) (Fig. 1).

There were no main effects of nutrient supply ($P = 0.073$) or food web manipulations ($P = 0.27$) on chlorophyll *a*. However, there was a significant

Table 1 Description of experimental food web manipulations and interpretation of potential invasion scenarios

Treatment and description	Potential outcomes and interpretations of invasion scenarios
LZ: 80 µm-filtered pond water	<i>D. lumholtzi</i> fails to invade LZ → environmental factors (e.g., temperature, alkalinity) or microbial factors (e.g., pathogens) inhibit invasion
AZ: 80 µm-filtered pond water + native macrozooplankton	<i>D. lumholtzi</i> invades LZ, but not AZ → species interactions (e.g., resource or interference competition) inhibits invasion
IP: 80 µm-filtered pond water + native macrozooplankton + invertebrate predator	<i>D. lumholtzi</i> invades LZ and AZ, but not IP → predator inhibits invasion <i>D. lumholtzi</i> invades LZ and IP, but not AZ → predator facilitates invasion
Nutrient supply: Above treatments crossed by low- and high-nutrient levels	<i>D. lumholtzi</i> invades LZ, but not AZ or IP → predator has no effect on invasion <i>D. lumholtzi</i> invades LZ and AZ and IP → food web structure provides no resistance to invasion Differential invasion success of <i>D. lumholtzi</i> in low vs. high-nutrient supply → invasibility of different food web structures is dependent on nutrient supply; importance of resource limitation or overall ecosystem productivity

interaction between nutrient supply and food web manipulation ($P = 0.044$, $F_{2,18} = 3.73$), such that there was elevated chlorophyll *a* in the LZ treatment with high nutrients, but not in the LZ treatment with low nutrients (Fig. 1).

The nutrient and food web treatments had significant effects on native zooplankton community structure. Cladoceran biomass ($P = 0.027$, $F_{1,18} = 5.83$) was significantly greater in the high-nutrient supply treatment than the low-nutrient supply treatment (Fig. 1). Furthermore, cladoceran biomass ($P < 0.001$, $F_{2,18} = 108.4$) was lower in the LZ treatment than in the AZ and IP treatments. Native zooplankton richness was also lower in the LZ treatment than in the other two food web manipulations ($P < 0.001$, $F_{2,18} = 44.33$), particularly at high-nutrient supply (food web × nutrient treatment interaction; $P < 0.001$, $F_{2,18} = 12.44$; Fig. 2).

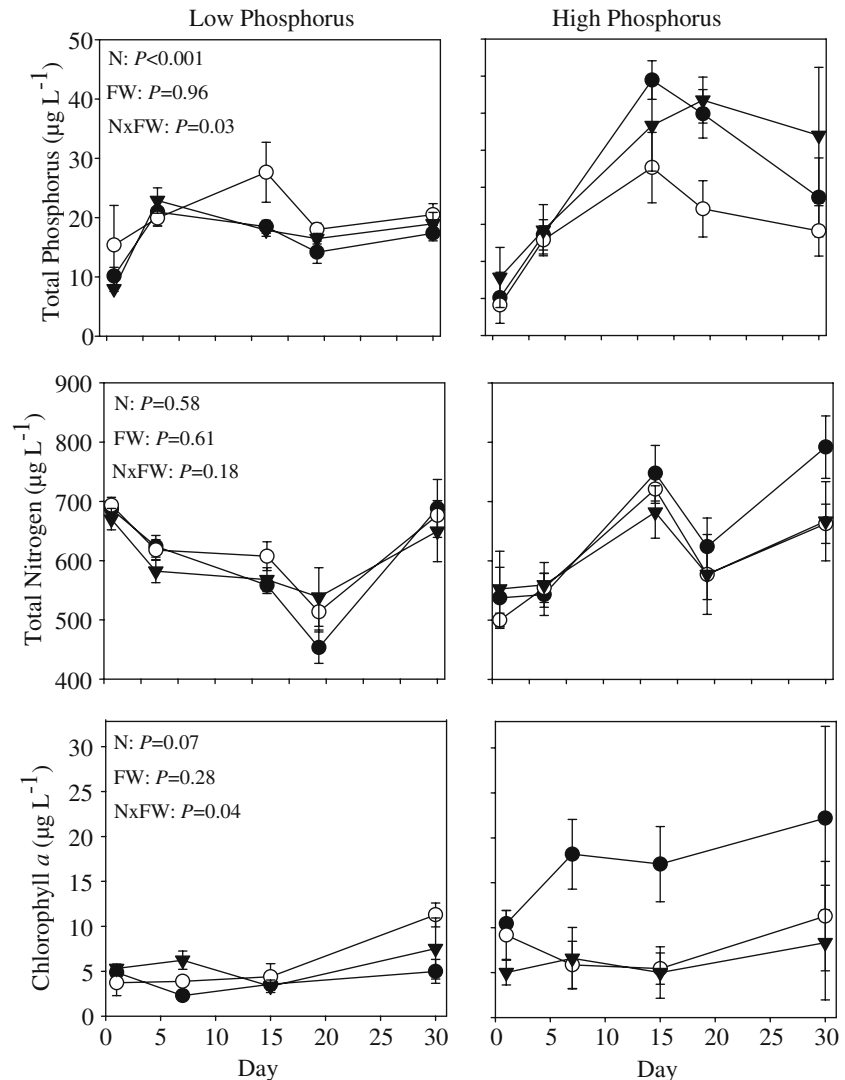
The PCA analysis indicated that native zooplankton composition was affected more by food web manipulations (i.e., LZ, AZ, and IP) than by nutrient supply (Table 2; Fig. 3). Zooplankton composition separated along PC axis 1 (“native cladoceran biomass” axis) in response to the food web manipulations. In particular, zooplankton from the LZ mesocosms had low native cladoceran biomass, while mesocosms from the AZ and

IP treatments had high native cladoceran biomass (Fig. 3).

Establishment of *D. lumholtzi*

D. lumholtzi establishment was affected by food web manipulations ($P = 0.005$, $G^2 = 10.52$), but not by nutrient supply ($P = 1.0$; $G^2 = 0.02$). *D. lumholtzi* did not establish in any mesocosms from the AZ or IP treatments. In fact, *D. lumholtzi* was never detected in any of the samples collected from the 16 mesocosms in these two food web manipulations during the entire course of the experiment. In contrast, *Daphnia lumholtzi* was present in four of the eight LZ mesocosms (including two low- and two high-nutrient supply mesocosms) on the final sampling date at densities that exceeded the initial stocking density. The median and interquartile range of *D. lumholtzi* biomass in these mesocosms on the final sampling date were $14 \mu\text{g l}^{-1}$ and $3\text{--}526 \mu\text{g l}^{-1}$, respectively (Fig. 4). Within the LZ treatment, the invasion of *D. lumholtzi* was affected by native zooplankton biomass. Native cladocerans attained a higher maximum biomass (Mann–Whitney test; $P = 0.06$) in non-established mesocosms ($96 \pm 81.5 \mu\text{g l}^{-1}$) than they did in established mesocosms ($0.8 \pm 0.50 \mu\text{g l}^{-1}$). The increase in native

Fig. 1 Total phosphorus (TP), total nitrogen (TN), and chlorophyll *a* in the experimental mesocosms from the three food web manipulations (FW) receiving low (left column) and high (right column) nutrient supply (N): ● = Low Zooplankton (LZ), ○ = Ambient Zooplankton (AZ), and ▼ = Ambient Zooplankton + Invertebrate Predation (IP). Statistical results were calculated using RM-ANOVA. Error bars represent the standard error of the mean



cladoceran biomass corresponded with an increase in the biomass of a single competitor (either *Bosmina* or *Ceriodaphnia*) in several of these non-invaded LZ mesocosms, particularly under high-nutrient supply (Fig. 4).

Discussion

It is generally perceived that native communities provide biotic resistance against invaders through species interactions such as competition and predation (Levine and D'Antonio 1999; Levine et al. 2004). However, much remains uncertain about the ecological processes and

community characteristics that contribute to biotic resistance (Cleland et al. 2004; Levine et al. 2004; Smith et al. 2004). In this study, we experimentally manipulated plankton food webs to determine how competition, predation, and resource supply affected the establishment of *Daphnia lumholtzi*, an exotic species that has successfully invaded freshwater habitats throughout the United States (Havel and Shurin 2004). Despite altering different aspects of plankton food web structure, *D. lumholtzi* was unable to establish in any of the mesocosms from the AZ or IP treatments; however it did successfully establish in several of the LZ mesocosms, which had significantly lower biomass

Fig. 2 Cladoceran biomass and zooplankton richness in the experimental mesocosms from the three food web manipulations (FW) receiving low (left column) and high (right column) nutrient supply (N): ● = Low Zooplankton (LZ), ○ = Ambient Zooplankton (AZ), and ▼ = Ambient Zooplankton + Invertebrate Predation (IP). Statistical results were calculated using RM-ANOVA. Error bars represent the standard error of the mean

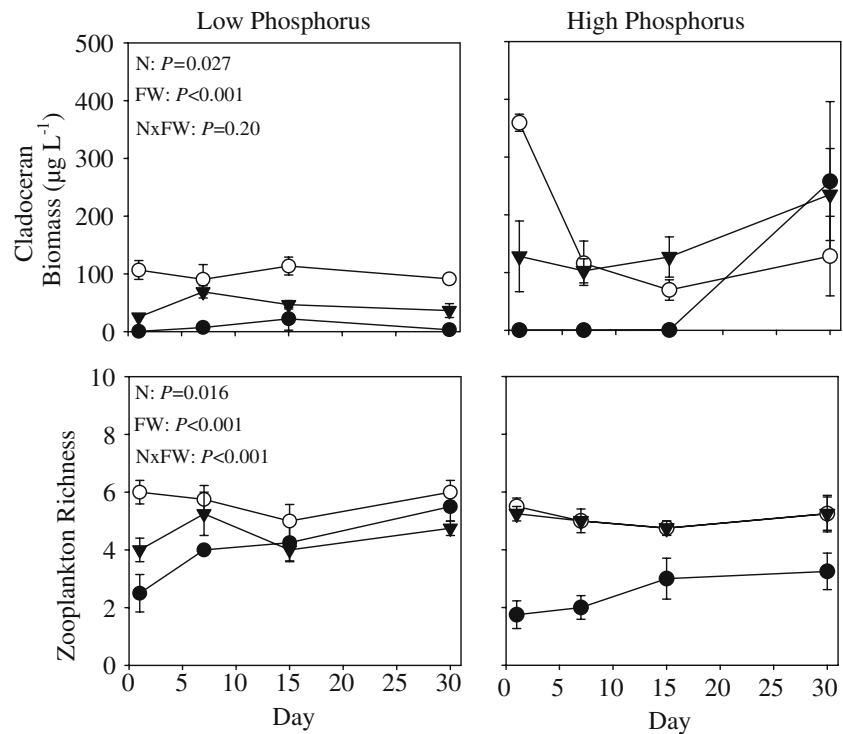


Table 2 Principal component weightings for the eight dominant zooplankton taxa on the final mesocosm sampling date

Zooplankton taxa	PCA 1	PCA 2	PCA 3
<i>Bosmina longirostris</i>	- 0.343	- 0.062	0.587
Calanoid copepods	- 0.287	0.269	0.410
<i>Ceriodaphnia lacustris</i>	0.306	- 0.416	0.036
<i>Chydorus sphaericus</i>	- 0.342	0.054	- 0.543
Cyclopoid copepods	0.232	- 0.586	- 0.050
<i>Daphnia lumholtzi</i>	0.386	0.459	0.085
<i>Diaphanasoma birgei</i>	- 0.491	0.016	- 0.370
Nauplii	- 0.382	- 0.440	0.210
Percent explained variance	28.4	24.2	18.6
Cumulative explained variance	28.4	52.6	71.2

and diversity of native zooplankton (Fig. 2). These results suggest that native zooplankton communities provided biotic resistance against *D. lumholtzi* through strong species interactions (Table 1). In contrast, the presence of an invertebrate predator or nutrient additions had no measurable effect on the invasion of *D. lumholtzi*.

Native communities may provide biotic resistance against invaders during different stages of the invasion process (Levine et al. 2004). *Daphnia lumholtzi* was not present in any of the mesocosms from the AZ treatment after its initial

introduction, suggesting that native communities provided a barrier that prevented establishment. These results are in contrast to a recent meta-analysis (Levine et al. 2004), which found that plant communities were incapable of completely repelling invaders. Instead, native communities were often only able to contain and regulate the abundance or impact of invaders after they had become established. The absence of *D. lumholtzi* from the AZ treatment in the current study indicates that native zooplankton communities can provide barriers during establishment through strong biotic interactions.

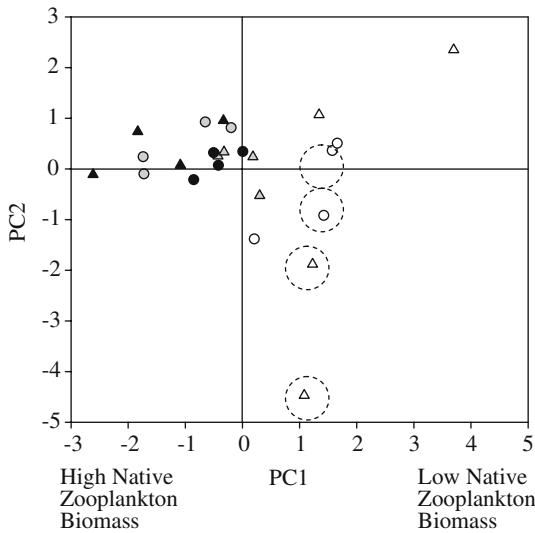


Fig. 3 Principal components analysis (PCA) for zooplankton communities from the experimental mesocosms from the three food web manipulations receiving low (circles) and high (triangles) nutrient supply: white = Low Zooplankton (LZ), gray = Ambient Zooplankton (AZ), and black = Ambient Zooplankton + Invertebrate Predation (IP); Circles = low-nutrient supply, and triangles = high-nutrient supply. The dashed circles identify those mesocosms in which *D. lumholtzi* successfully established

There are many characteristics of native communities that can potentially contribute to biotic resistance. Mesocosms in the AZ treatment had significantly higher native zooplankton biomass and native zooplankton diversity than mesocosms from the LZ treatment (Fig. 2). Therefore, it is difficult to conclude whether establishment was affected by biomass, diversity, or a combination of both (Fig. 3). However, recent research suggests that the biomass or abundance of native species may contribute more to biotic resistance than the diversity of native species (Huston 1994; Crawley et al. 1999; Wardle 2001). In a similar study, *D. lumholtzi* was found to be more likely to establish in zooplankton communities with low biomass and high diversity, than zooplankton communities with high biomass and low diversity (Lennon et al. 2003). Furthermore, Smith et al. (2004) showed that dominance by individual species played a more important role in determining establishment of grassland invaders than native diversity. Additional invasion experiments conducted across gradients of native zooplankton

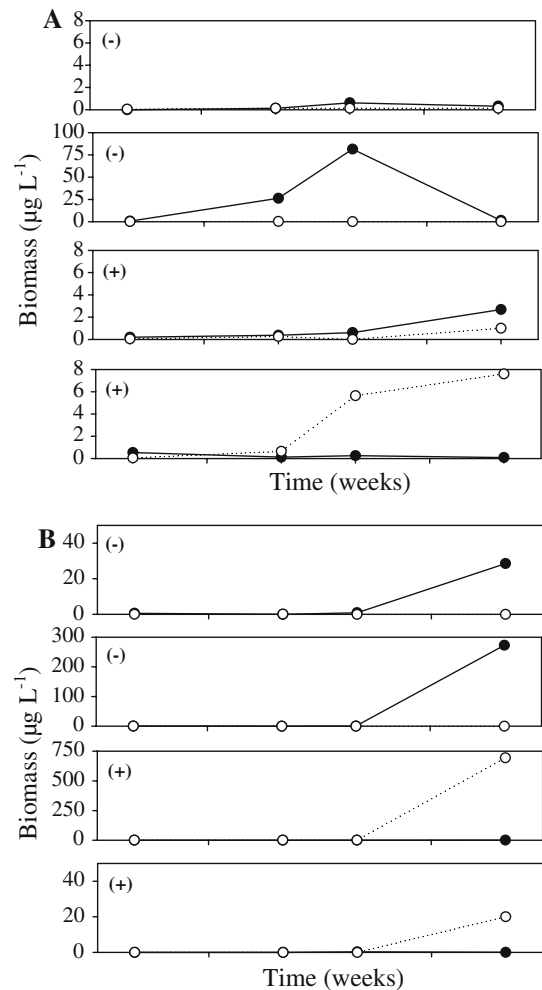


Fig. 4 Biomass of native cladocerans (●) and *D. lumholtzi* (○) in the eight replicate mesocosms from the Low Zooplankton (LZ) treatment receiving low (A) and high (B) nutrient supply. Note differences in scale between replicates. *Daphnia lumholtzi* was considered to have successfully established within a mesocosm (+) if it was present on the final sampling data at a density greater than the initial stocking density (0.05 ind. l^{-1} which equal $25 \mu \text{ l}^{-1}$ biomass); if it was not present at this initial stocking density, it did not successfully establish within a mesocosm (-)

biomass are needed to further evaluate the importance of native biomass to biotic resistance (Cottingham et al. 2004; Sommer et al. 2001).

Although establishment was generally high in the LZ treatment, *D. lumholtzi* did not establish in all of the mesocosms from this treatment (Fig. 4). Several hypotheses may help to explain the lack of establishment in these four LZ

mesocosms. For example, the density at which *D. lumholtzi* was added to the mesocosms was intentionally low in order to mimic natural invasion events (Veltman et al. 1996; Marchetti et al. 2004). Stochastic processes associated with this small propagule size, therefore, may have influenced invasion success in the absence of strong competitive interactions (Liebhold and Bascompte 2003). Alternatively, biotic resistance may have been important in some of the LZ mesocosms as well. For example, experimental reductions of zooplankton biomass and diversity in the LZ treatment allowed for a single competing native species (either *Ceriodaphnia* or *Bosmina*) to increase in biomass in several mesocosms, particularly under high-nutrient supply (Fig. 4). As a result, native cladoceran attained higher biomass in LZ mesocosms where *D. lumholtzi* did not establish, suggesting that competition with native zooplankton may have inhibited establishment in these four LZ mesocosms. However, since there were only four mesocosms within the LZ treatment in which *D. lumholtzi* did not establish (Fig. 4), it is difficult to determine which hypothesis might explain the observed patterns.

Effects of predation on invasion

The presence of an IP did not affect *D. lumholtzi*'s ability to establish within mesocosms. We predicted that *D. lumholtzi* would experience a reduction in the intensity of competition if there was selective predation on native species due to *D. lumholtzi*'s long spines (Swaffar and O'Brien 1996). The addition of *Notonecta* did have significant effects on native zooplankton, but these effects varied over the course of the experiment and zooplankton biomass was similar in the AZ and IP treatments, particularly at high nutrients (Fig. 2). Furthermore, we did not witness an increase in the availability of food resources (i.e., chlorophyll *a*) with the addition of *Notonecta* (Fig. 2). Therefore, while we predicted that the presence of an IP would facilitate establishment through a reduction of native zooplankton biomass due to selective predation on native species, this did not occur in our experiment. The native zooplankton communities present in the mesocosms were generally small-bodied, and may have

been outside the size class of prey that are commonly selected by *Notonectids* (Murdoch et al. 1984; Shurin 2001). As a result, mesocosms from the IP treatment were associated with intermediate to high levels of native zooplankton biomass and were more similar in species composition to communities from the AZ treatment than the LZ treatment (Fig. 4).

Effects of nutrient supply on invasion success

While biotic interactions such as competition and predation may influence establishment, these interactions may be modified by variations in resource supply rates (Davis et al. 2000). Nutrient additions increased chlorophyll *a* in the LZ treatment only, which happened to be the treatment where establishment was high (Fig. 4). In contrast, chlorophyll *a* did not increase with nutrient supply in the AZ or IP treatments. It is likely that much of the increase in primary production due to nutrient additions was grazed and converted to native zooplankton biomass, and if anything, may have resulted in stronger competitive interaction due to increases in native zooplankton biomass (Lennon et al. 2003). As such, there did not appear to be an overall reduction in the intensity of competition with the addition of nutrients in the AZ and IP treatments.

Although there was no apparent effect of nutrient supply on the establishment of *D. lumholtzi* in this study, recent research suggests that *D. lumholtzi* may be more successful under low to moderate nutrient conditions. A comparative survey of 35 eastern Kansas reservoirs (Dzialowski et al. 2000) revealed that reservoirs successfully invaded by *D. lumholtzi* exhibited lower chlorophyll and nutrient concentrations than non-invaded reservoirs. Likewise, Lennon et al. (2003) found that experimental invasions of *D. lumholtzi* were more likely to be successful in nutrient-poor than in nutrient-rich mesocosms. Interestingly, workers exploring plant community structure in terrestrial ecosystems have found similar results; for example, Foster et al. (2004) found that species were less likely to establish in highly productive sites, in part, due to stronger competitive interactions.

Conclusion

Native zooplankton communities provided biotic resistance against the establishment of the exotic *D. lumholtzi*. Only when the biomass and diversity of native zooplankton were significantly reduced in the LZ treatment, was *D. lumholtzi* able to successfully invade mesocosms. Our data in combination with additional experimental and comparative studies suggest that pre-invasion native zooplankton biomass may be a more important component of biotic resistance than pre-invasion zooplankton diversity per se. In contrast, while the addition of an IP and resource supply did modify some attributes of native zooplankton communities, they did not influence the establishment of *D. lumholtzi*. Overall, our data are consistent with observed population dynamics in invaded reservoirs where *D. lumholtzi* tends to be present only during the late summer, coinciding with historic mid-summer declines in the biomass of native zooplankton populations (Havel et al. 1995; East et al. 1999; Lennon et al. 2001). Therefore, lakes and reservoirs may be more susceptible to invasion not only by *D. lumholtzi*, but also by other planktonic species, in the late summer when native communities exhibit characteristics associated with lower levels of biotic resistance.

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