

Environmental limits to a rapidly spreading exotic cladoceran¹

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Abstract: Invasion of exotic species may be regulated either by regional factors (dispersal limitation) or by local site characteristics that influence colonization success (invasibility). To address the latter question, we surveyed crustacean zooplankton and abiotic features of 171 lakes in Missouri, Arkansas, and Oklahoma and examined features associated with presence of the exotic cladoceran *Daphnia lumholtzi*. The data set was also used to examine variation in zooplankton species composition in this region. Canonical Correspondence Analysis revealed that zooplankton distributions were most strongly correlated with lake fertility and conductivity. Logistic regression analyses showed that *D. lumholtzi* was more likely to invade larger and more fertile lakes and appeared unaffected by native zooplankton species richness or presence of particular species. Thus, the current study suggests that physico-chemical characteristics are better predictors than zooplankton communities for explaining the regional spread of *D. lumholtzi*. Nevertheless, the underlying causes for these trends are unclear, as landscape features correlated to the same physical features may also influence dispersal processes, and other unknown differences between lakes may also be important for colonization success.

Keywords: biological invasions, colonization, *Daphnia lumholtzi*, exotic species, invasibility, reservoirs, zooplankton.

Résumé : L'invasion d'espèces exotiques peut être influencée par des facteurs régionaux (contraintes à la dispersion) ou par des caractéristiques locales qui ont un impact sur le succès de colonisation. Nous avons étudié l'influence des caractéristiques abiotiques locales sur les crustacés zooplanctoniques de 171 lacs du Missouri, de l'Arkansas et de l'Oklahoma. Nous avons en outre examiné les caractéristiques associées à la présence du cladocère exotique *Daphnia lumholtzi*. Les données qui ont été récoltées ont également servies à l'étude des variations de la composition en espèces zooplanctoniques. L'analyse des correspondances canoniques indique que la répartition du zooplancton est fortement corrélée à la fertilité des lacs et à leur conductivité. Les analyses de régression logistique montrent que *D. lumholtzi* est plus susceptible d'envahir les grands lacs très fertiles. Cette daphnie ne semble pas affectée par la richesse en espèces du zooplancton indigène ou par la présence d'espèces particulières. Cette étude suggère qu'il est plus approprié d'utiliser les caractéristiques physicochimiques des lacs que les communautés de zooplancton pour prédire l'expansion régionale de *D. lumholtzi*. Les causes de ces tendances sont toutefois plus ou moins claires. En effet, les caractéristiques du paysage, qui sont corrélées aux caractéristiques physiques des lacs, peuvent aussi influencer les processus de dispersion. On peut également émettre l'hypothèse qu'il y a d'autres caractéristiques associées aux lacs, encore inconnues, qui jouent un rôle important dans le succès de colonisation.

Mots-clés : colonisation, *Daphnia lumholtzi*, degré d'envahissement, espèces exotiques, invasions biologiques, réservoirs, zooplancton.

Nomenclature: see Appendix 1.

Introduction

Species invasions represent one of the most pressing threats to freshwater ecosystems. Aquatic habitats have experienced extensive "biotic exchanges", which have contributed to widespread extinctions of native fauna (Ricciardi & Rasmussen, 1999; Sala *et al.*, 2000). The enormous number of introduced aquatic species has had major impacts on biodiversity, ecosystem stability, and the human economy (Carlton & Geller, 1993; Lodge, 1993). The expanding crisis of freshwater invasive species has led

ecologists to address the causes of invasions, although the processes that allow some species to become invasive and certain habitats to become invaded remain elusive.

The spread of exotic species depends upon both dispersal and availability of suitable environments. In aquatic habitats, propagules can be introduced by a variety of processes (Carlton & Geller, 1993; Johnson, Ricciardi & Carlton, 2001; Havel & Shurin, 2004). Following introduction, the susceptibility of the environment to invasion (invasibility) depends on several factors. First, climatic similarity to the native habitat of potential invaders should provide a hospitable environment (Williamson, 1996; Sakai *et al.*, 2001). Second, habitat disturbance (perturbation) has been shown to promote colonization by new species (Vitousek *et al.*, 1996; Williamson, 1996). Third,

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communities with greater native species richness may show greater resistance to invasion (Baltz & Moyle, 1993; Levine, 2000; Shurin, 2000). However, correlations among the physical environment, diversity of native species, and the processes that introduce invaders (dispersal vectors) may confound the interpretation of processes controlling the spread of invaders (Lonsdale, 1999; Stohlgren *et al.*, 1999; Havel, Lee & Vander Zanden, 2005). Despite extensive study, the relative importance of the physical environment and biotic interactions for governing invasions remains poorly understood.

Recent invasions of lake communities by exotic cladocerans provide an opportunity to study this question. Cladocerans have several characteristics of successful invaders (Sakai *et al.*, 2001), including dormant life history stages, asexual reproduction, rapid population growth, and phenotypic plasticity (Dodson & Frey, 2001). One particularly successful invader in North America is the tropical cladoceran *Daphnia lumholtzi* Sars, a native to the Old World tropics. First appearing in North America in 1990 (Sorensen & Sterner, 1992), *D. lumholtzi* has recently invaded a wide variety of North American aquatic habitats, including natural lakes, reservoirs, and riverine habitats. Over the past decade, this species has rapidly expanded its range over much of the United States (Havel & Shurin, 2004). Time-series data from a large number of Missouri reservoirs have revealed that most populations persist from year to year (Havel, Shurin & Jones, 2002). The success of *D. lumholtzi* in warm-water reservoirs may be linked both to its defensive morphology (Swaffar & O'Brien, 1996) and its dominance during summer (Havel, Mabee & Jones, 1995), a period when native *Daphnia* are generally at low abundance (Havel & Graham, unpubl. data).

In the current study, we used a survey of 171 lakes in the south-central United States (Figure 1) to explore relationships among the abiotic environment, zooplankton composition, and invasion by *D. lumholtzi*. Reservoirs are the dominant lake type in this region and are quite variable in size, fertility, and dissolved and suspended sediments (Thornton, Kimmel & Payne, 1990; Jones & Knowlton, 1993). These strong physical gradients provide a good stage for empirical studies of invasibility. We used Canonical Correspondence Analysis (CCA) to examine the relationship between major environmental gradients and zooplankton community composition. We then used multiple logistic regression analysis to explore the roles of limnological features and the presence of other zooplankton species for predicting colonization of lakes by *D. lumholtzi*.

Methods

STUDY LAKES

We sampled 171 lakes over a broad geographic region in Arkansas, Missouri, and Oklahoma, USA (Figure 1). These lakes occur in numerous physiographic regions (OWRB, 1990; Jones & Knowlton, 1993) and show a wide range in size, fertility, and concentrations of dissolved and suspended solids (Table I). Most (96%) of these lakes are reservoirs, ranging in size from small storage reservoirs to large main-stem impoundments. The

remainder are productive oxbow lakes. For convenience, we refer to both reservoirs and oxbows as "lakes".

We used a sampling strategy to maximize our chance of detecting the presence of *D. lumholtzi*. Previous work showed that *D. lumholtzi* is most abundant during the middle of summer in this region (Havel, Mabee & Jones, 1995). We therefore sampled all 171 lakes during June-August 1995, starting in the southern locations and working north during the summer. Each lake was sampled on one date and all samples were collected in daylight hours. Smaller lakes were sampled in mid-channel near the dam (or levee), whereas larger lakes were usually sampled from an up-reservoir site, where *D. lumholtzi* tends to be most abundant (J. Havel and E. M. Eisenbacher, pers. observ.).

PHYSICO-CHEMICAL SAMPLING AND ANALYSIS

In order to examine the effect of local environmental features on invasion, we measured 13 physico-chemical characteristics in most of the lakes. These features include physical features (depth, surface area, surface and bottom temperature), transparency (Secchi depth, turbidity, volatile and non-volatile suspended solids), indicators of fertility (total nitrogen, phosphorus, and chlorophyll), and dissolved ions (conductivity, pH) (Table I).

Lake surface areas (at conservation pool) were obtained from USGS topographic maps or from US Army Corps of Engineers brochures. Depth was recorded at each sample site by sonar (Humminbird Wide Eye, Techsonic Industries, Eufaula, Alabama, USA). Depth profiles of temperature and oxygen were measured with a YSI Model 50B oxygen meter and conductivity with a YSI model 33 meter (YSI Inc., Yellow Springs, Ohio, USA). For statistical models (below), we used maximum and minimum temperatures in the epilimnion and hypolimnion, respectively. Whether or not the hypolimnion was hypoxic (< 1 ppm O₂) was used as a categorical variable. Transparency was measured with a Secchi disk and turbidity with a Hach 2100P turbidimeter (Hach, Loveland, Colorado, USA).

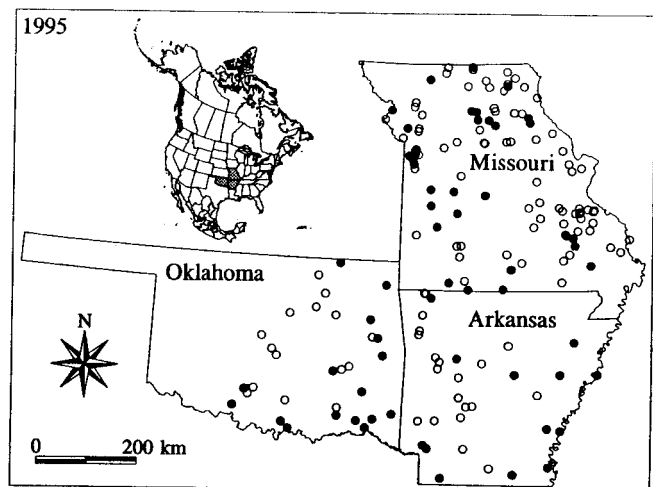


FIGURE 1. Map of 171 lakes sampled from Arkansas, Missouri, and Oklahoma in 1995, showing presence (closed circles) or absence (open circles) of *Daphnia lumholtzi*. A total of 56 populations were detected.

TABLE I. Summary statistics for characteristics of lakes in the current study. NVSS: non-volatile suspended solids.

| Variable (units) | Code | Number of lakes | Median | Minimum | Maximum |
|---|-----------|-----------------|--------|---------|---------|
| PHYSICAL | | | | | |
| Surface area (ha) | Area | 167 | 106 | 2 | 57,871 |
| Depth (m) | Depth | 163 | 6.1 | 0.4 | 35.4 |
| Bottom temperature (°C) | TempBot | 159 | 23.2 | 7.6 | 32.2 |
| Surface temperature (°C) | TempTop | 159 | 29.2 | 17.9 | 36.3 |
| Secchi depth (m) | Secchi | 165 | 0.9 | 0.1 | 5.8 |
| Turbidity (NTU) | Turbidity | 164 | 7.4 | 0.9 | > 100 |
| CHEMICAL | | | | | |
| Conductivity (µS) | Cond | 167 | 200 | 25 | 600 |
| pH | pH | 167 | 7.8 | 5.2 | 10.0 |
| Total nitrogen (µg·L ⁻¹) | TN | 145 | 685 | 135 | 1,680 |
| Total phosphorus (µg·L ⁻¹) | TP | 145 | 46 | 7 | 249 |
| Total chlorophyll (µg·L ⁻¹) | Chl | 146 | 15 | 1 | 82 |
| NVSS (mg·L ⁻¹) | NVSS | 145 | 4.1 | 0.2 | 54.9 |
| VSS (mg·L ⁻¹) | VSS | 145 | 3.7 | 0.7 | 14.1 |
| BIOLOGICAL | | | | | |
| Species richness | SpRich | 171 | 9 | 2 | 22 |

Because our goal was to examine associations between zooplankton and the local physical environment, we measured conditions at the same site where zooplankton samples were collected. In larger reservoirs, these sites were generally located up-reservoir in the transition between riverine and lacustrine zones (Thornton, Kimmel & Payne, 1990). Such sites tend to be shallower and to have higher nutrients and weaker vertical stratification than sites closer to the dam.

Samples for water chemistry analysis were taken by combining four 1-L grab samples, each taken at *ca* 0.5 m depth from the same site as the zooplankton sample. Whole water samples for total nitrogen and total phosphorus were placed on ice and stored frozen at -10 °C. Total suspended solids samples were collected by filtering duplicate 250-1,000 mL samples on tared Whatman GFC filters, with volume depending on the turbidity of the samples. For chlorophyll, duplicate 250-mL samples were filtered through GFC filters, placed in desiccant on ice, and stored frozen with desiccant until analysis.

Laboratory analysis followed standard methods (APHA, 1985) for non-volatile suspended solids (NVSS), volatile suspended solids (VSS), and total phosphorus (TP). Total chlorophyll (Chl) was extracted in heated ethanol (Sartory & Grobbelaar, 1984) and analyzed by fluorometry (Knowlton, 1984). Total nitrogen (TN) was analyzed by second derivative spectroscopy following persulfate oxidation (Crumption, Isehart & Mitchell, 1992).

ZOOPLANKTON SAMPLING AND ANALYSIS

Samples of crustacean zooplankton were collected with two or more vertical tows (total length 20 m), using a 25-cm-diameter zooplankton net (mesh = 200 µm). This large mesh likely misses the smallest taxa (*e.g.*, juvenile *Bosmina*), but was necessary to prevent clogging by suspended clays. Shallow sites (< 4 m) were sampled with oblique tows from 1 m above the bottom. The sample volume (982 L) should detect densities of *D. lumholtzi* over 1·m⁻³. The tows were pooled into one sample, anaesthetized with carbonated water, and preserved with buffered sugar-formalin. In order to avoid transmitting

zooplankton between lakes, nets were thoroughly rinsed at each site, then soaked in ammonia cleanser between sites. The entire sample from each site was later screened at 30X for *D. lumholtzi*, using distinctive characteristics (Havel & Hebert, 1993).

Zooplankton community composition was determined by examining at least 200 individuals or, if less abundant, all individuals in the sample. Cladocerans and copepods were identified to species using standard keys (Edmondson, 1959; Dodson & Frey, 2001; Williamson, 2001) plus more detailed keys (listed at <http://www.cnas.missouris-tate.edu/zooplankton/default.htm>). All individuals were scored as present or absent.

STATISTICAL ANALYSES

We first used data on the 13 physico-chemical variables to examine their importance in explaining variation in zooplankton species richness and composition. To examine the effects of these abiotic factors on zooplankton species richness, we used multiple stepwise regression with a backwards elimination procedure (SAS, version 8.01, SAS Institute Inc., Cary, North Carolina, USA).

We used Canonical Correspondence Analysis (CCA, CANOCO, version 4) with the species-by-site matrix to determine which of the 13 physico-chemical features most clearly separate the different zooplankton communities. CCA allows us to test the strength of the relationship between zooplankton species composition and measured physical factors. CCA is a form of direct gradient analysis that assumes a unimodal relationship between the species and the environmental factors. We assumed a unimodal rather than a linear relationship because of the very broad environmental gradients present among the lakes in our survey and because our species-by-site matrix was relatively sparse (*i.e.*, there were many zeros) (Jongman, ter Braak & van Tongeren, 1995). The CCA axes are constrained to be linear combinations of the explanatory variables. Bi-plots showing the loadings of environmental variables and species on the CCA axes allow us to interpret the associations among the species and the physical factors. We restricted the CCA analysis to the matrix including the 30 common species (present in ≥ 5% of lakes). The significance of each explanatory variable was tested by comparing the observed *F* statistic with those generated by 999 unrestricted Monte Carlo permutations (Jongman, ter Braak & van Tongeren, 1995).

We next explored the features that best explain the occurrence of *D. lumholtzi*, by analyzing the physico-chemical features (Table I) and the zooplankton presence/absence data in a logistic regression (SAS, version 8.01, SAS Institute Inc., Cary, North Carolina, USA). To select the best model of physical control of invasion by the 13 limnological variables, we used multiple logistic regression with a backwards elimination procedure. Normality of the independent variables was tested by a Kolmogorov-Smirnov test, and those showing deviations from normality were log_e-transformed. To ask whether the richness of the zooplankton assemblage predicted invasion by *D. lumholtzi*, we included the number of zooplankton taxa identified (not including *D. lumholtzi*) as an independent variable in the multiple regression.

To test associations between *D. lumholtzi* invasion and other zooplankton species, we performed 2×2 contingency table analyses with chi-square tests. This procedure was used to select species for inclusion in a multiple regression model; therefore, no correction for multiple comparisons was used. The factors in the contingency table were the presence of *D. lumholtzi* and that of each of the other common species identified in the survey (43 separate tests).

Once we determined which species showed non-random (either positive or negative) associations with *D. lumholtzi*, those species were introduced as categorical variables into a second logistic regression analysis. We used stepwise model selection (backwards elimination procedure) to identify the minimal model of biotic control. Those species that contributed significantly in this model were then included in a third model of physical and biotic controls of invasion. The contribution to the fit of the models indicates the relative importance of biotic and abiotic variables in predicting the occurrence of *D. lumholtzi*.

Results

ENVIRONMENTAL VARIATION

The 171 lakes in our survey covered a wide range in physical and chemical characteristics (Table I). Area ranged over four orders of magnitude. Transparency ranged from clear (Secchi depth 5.8 m) to highly murky (0.1 m), and as expected, these observations showed an inverse correlation with turbidity ($r = -0.46$). High quantities of mineral turbidity ($> 10 \text{ mg} \cdot \text{L}^{-1}$ nonvolatile suspended solids) were present in 10% of the lakes. Most lakes were neutral to slightly alkaline, and conductivity measurements indicated a wide range in salinity. Total phosphorus and chlorophyll measurements (Table I) indicated that fertilities varied from oligotrophic to hypereutrophic. Almost half were eutrophic: 47% had chlorophyll concentrations $> 15 \mu\text{g} \cdot \text{L}^{-1}$, the lower bound for eutrophic lakes (Wetzel, 2001). With the exception of one small hypolimnetic-release lake, all the lakes had warm surface temperatures (median 29°C). Deeper lakes ($> 4 \text{ m}$) were thermally stratified, and of these, 52% were already anoxic in the hypolimnion by our midsummer sampling period. Presumably, some other lakes became anoxic later in the summer, so this is likely an underestimate of the proportion that were anoxic.

ZOPLANKTON SPECIES COMPOSITION AND RICHNESS

A total of 63 species of cladocerans and copepods were identified in the survey (Appendix I). In addition, the dipteran *Chaoborus punctipennis* was present in most (79%) of the lakes. Although collections focused on the pelagic zone, littoral-benthic species comprised 40% of the fauna (Appendix I). Species richness in the study lakes ranged from 2 to 22 (median 9) species per lake. Species richness depended on area (Figure 2), as well as surface temperature and two measures of fertility (total nitrogen and volatile suspended solids) (Table II). Although most species were rare (Appendix I), some were very common in the survey. Widespread cladocerans included *Diaphanosoma birgei* (89% of the lakes), *Ceriodaphnia*

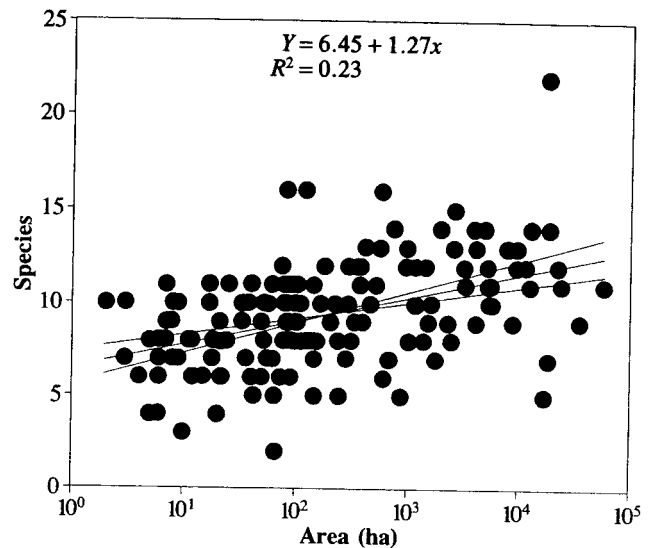


FIGURE 2. Species-area curve for crustacean zooplankton from 167 lakes surveyed in 1995.

TABLE II. Multiple regression model to predict species richness. Volatile suspended solids (VSS) is a measure of particulate organic matter and so includes algal chlorophyll.

| Source | Estimate | F | P |
|------------|--------------------|-------|------------|
| Constant | 33.31 ± 9.85 | 11.44 | 0.0010 |
| ln area | 0.44 ± 0.09 | 22.67 | < 0.0001 |
| ln TempTop | 7.59 ± 2.88 | 6.95 | 0.0095 |
| ln TN | -0.003 ± 0.001 | 10.54 | 0.0015 |
| ln VSS | 1.26 ± 0.47 | 7.20 | 0.0083 |

lacustris (82%), *Bosmina* cf. *longirostris* (68%), and *Daphnia parvula* (65%). Widespread copepods included *Mesocyclops edax* (94%) and the fish parasite *Ergasilus chautauquensis* (62%). The exotic *D. lumholtzi* appeared in 33% of the lakes and was found in many different environmental conditions (see "Environmental predictors of *Daphnia lumholtzi* occurrence" below). This species occurred in lakes covering a wide range of latitude and in most physiographic provinces of the region (Figure 1). Of the eight *Daphnia* species identified, *D. lumholtzi* was the second most widespread species (Appendix I).

PHYSICO-CHEMICAL ASSOCIATIONS WITH ZOOPLANKTON ASSEMBLAGES

The Canonical Correspondence Analysis (CCA) using the matrix containing only the 30 common species (those present in $> 5\%$ of the lakes) found that 14 abiotic variables explained 48% percent of the variance in zooplankton species composition (Table III). The primary axis of variation was most strongly associated with measures of lake fertility such as Secchi depth, dissolved nutrient and suspended solids concentrations, and phytoplankton biomass (as chlorophyll-a) (Figure 3). This indicates that variation in trophic status is the most important factor that we measured for controlling zooplankton community membership. The second axis of variation was associated with conductivity and pH, measures of dissolved ions. Physical features such as surface area, depth, top and bottom temperature, and the presence of an anoxic hypolimnion

generally explained less variation in zooplankton composition (Figure 3). These patterns suggest that the supply of limiting nutrients and chemical composition of lake water play a major role in shaping zooplankton communities in this region. Similar patterns were revealed when all 63 species found in the survey were included in the analysis.

TABLE III. Results from Canonical Correspondence Analysis, indicating environmental variables most important in explaining zooplankton species assemblages. Shown are the eigenvalues (λ), F -statistics, and associated P -values for each variable. The P -values were determined by resampling the F -statistics.

| Variable | λ | F | P |
|--------------|-----------|------|-------|
| Secchi | 0.15 | 5.92 | 0.001 |
| Conductivity | 0.10 | 3.73 | 0.001 |
| TempBot | 0.06 | 2.38 | 0.001 |
| TN | 0.05 | 2.06 | 0.001 |
| Depth | 0.05 | 2.34 | 0.003 |
| TempTop | 0.05 | 1.90 | 0.006 |
| pH | 0.04 | 1.73 | 0.02 |
| TP | 0.04 | 1.52 | 0.074 |
| NVSS | 0.04 | 1.43 | 0.134 |
| Turbidity | 0.03 | 1.38 | 0.156 |
| Chlorophyll | 0.03 | 1.36 | 0.115 |
| VSS | 0.03 | 1.18 | 0.176 |
| Anoxic | 0.03 | 1.09 | 0.316 |
| Area | 0.01 | 0.50 | 0.907 |

The association of individual species with environmental variables is illustrated by their position along multivariate axes associated with physical gradients (Figure 3). The length of the axes (the arrows in Figure 3) indicates the strength of their correlation with the species data. Several common species showed clear trends with environmental gradients. *Holopedium amazonicum* and *Epishura nordenskioldi* were found only in deep lakes, and *Daphnia pulicaria* and *Daphnia rosea* were found only in clear, unproductive lakes. *Daphnia lumholtzi* tended to be found in larger, more productive lakes (upper left quadrant of Figure 3).

ENVIRONMENTAL PREDICTORS OF *DAPHNIA LUMHOLTZI* OCCURRENCE

Logistic regression showed that both area and total phosphorus were important predictors of *D. lumholtzi* occurrence (Table IV). Larger lakes had a higher likelihood of being invaded than smaller lakes. However, invaded lakes ranged in area from 2 to 36,000 ha (Figure 4), indicating that smaller lakes were occasionally invaded. Similarly, lakes with higher total phosphorus were more likely to be invaded (Table IV), despite the large range for invaded lakes (17-249 $\mu\text{g} \cdot \text{L}^{-1}$) (Figure 4). Species richness showed no significant association with *D. lumholtzi* invasion.

Pairwise contingency table tests identified five zooplankton species that showed significant associations with

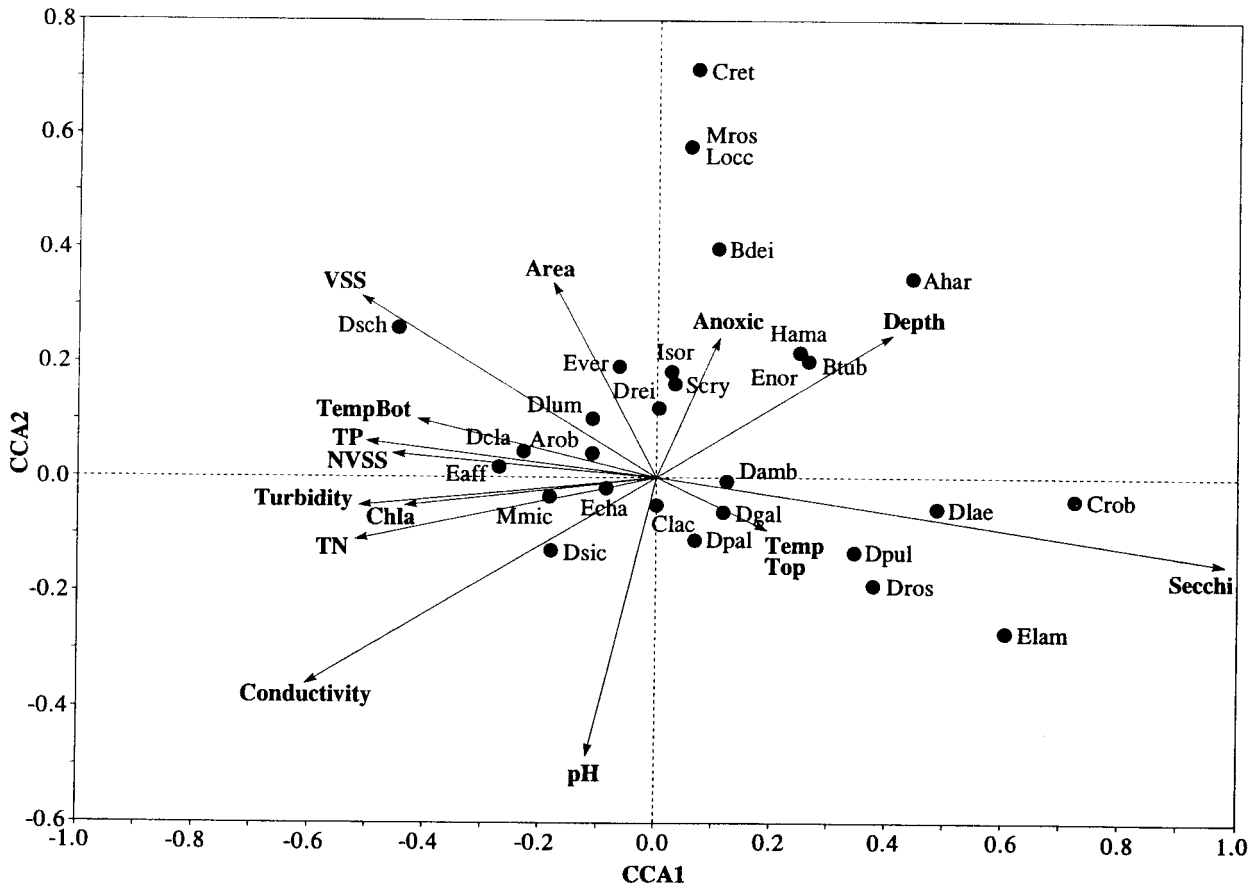


FIGURE 3. Results of Canonical Correspondence Analysis. Only significant environmental features are shown. Physico-chemical codes are listed in Table I, species codes in Appendix I. The proportion of variation explained by each factor is illustrated by the length of the arrows.

TABLE IV. Logistic regression models to predict the occurrence of *D. lumholtzi*, based on a) abiotic variables and b) biotic variables (other species). Species codes: Mmic, *Moina micrura*; Ever, *Ergasilis versicolor*; Drei, *Diaptomus reighardi*; Dsic, *Diaptomus siciloides*. The optimal models were selected by a multiple logistic regression using a backwards elimination procedure. The 13 abiotic variables (Table I) and the eight species that showed significant or marginally-significant associations with *D. lumholtzi* in univariate contingency tables (Table V) were entered separately into the full models. When the two abiotic and four biotic variables were entered together to select the optimal model with all variables, all four species were eliminated by the backwards selection procedure. The optimal model with both biotic and abiotic factors was therefore the same as the optimal abiotic model (a). AIC: Akaike Information Criterion (Hilborn & Mangel, 1997); when comparing models, the model with the smaller AIC is preferred. Regression coefficients ± 1 SE.

| Source | Estimate | χ^2 | P |
|--------------------------|------------------|----------|----------|
| a) ABIOTIC; AIC = 142.52 | | | |
| Constant | -7.26 \pm 1.65 | 19.26 | < 0.0001 |
| ln area | 0.38 \pm 0.10 | 14.01 | 0.0002 |
| ln TP | 1.13 \pm 0.34 | 11.15 | 0.0008 |
| b) BIOTIC; AIC = 197.85 | | | |
| Constant | -0.78 \pm 0.46 | 2.94 | 0.086 |
| Mmic | 0.50 \pm 0.23 | 4.68 | 0.031 |
| Ever | 0.99 \pm 0.42 | 5.47 | 0.019 |
| Drei | 0.49 \pm 0.21 | 5.40 | 0.020 |
| Dsic | 0.56 \pm 0.24 | 5.46 | 0.019 |

the occurrence of *D. lumholtzi*, and three more were marginal (Table V). *Daphnia lumholtzi* showed a positive association with all of these species except *Diaptomus pallidus*, with which it tended not to co-occur (Figure 3). When these species were added together as categorical variables in a logistic regression to predict the occurrence of *D. lumholtzi*, the backwards elimination procedure retained four species (Table IVb). However, when these species were entered into a logistic regression model along with the minimal abiotic model of invasibility, none of the species contributed significantly to the fit of the model. The model selection procedure retained only lake area and total phosphorus as the minimal model of biotic and abiotic control. The biotic model showed considerably weaker agreement with the data than the abiotic model (Table IV).

Discussion

We found strong evidence that community structure of crustacean zooplankton and invasion by *Daphnia lumholtzi* are both influenced by lake morphometry and water chemistry. Fourteen habitat variables explained 48% of the variation in zooplankton composition, with the most important explanatory features being measures of trophic status and salinity (conductivity). Lakes invaded by *D. lumholtzi* tended to be larger and more productive. Overall, the correlations between the physical environment with zooplankton community composition and with invasion likelihood were quite strong. By contrast, observational support for the role of species interactions was more equivocal. Contingency table analysis found that the incidence of *D. lumholtzi* was associated with eight other

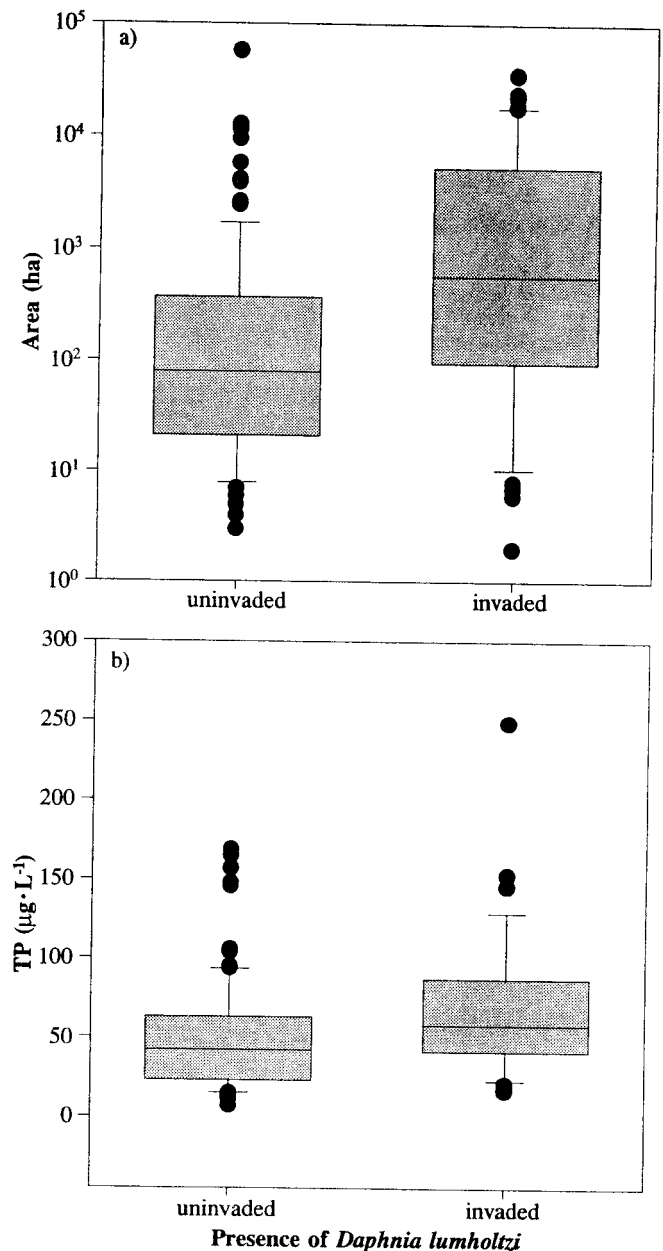


FIGURE 4. Box plots for variables that were significantly associated with presence of *Daphnia lumholtzi*. a) area. b) total phosphorus (TP). The dots indicate extreme values, those beyond 3X the interquartile range.

species. However, when these species were included as categorical variables in logistic regression models along with surface area and total phosphorus, none significantly improved the fit of the model. Thus, it seems likely that the association between *D. lumholtzi* and other zooplankton is driven by similar environmental tolerances or demands. Below we discuss each of these results in detail and their significance for the control of zooplankton community structure and invasibility.

Daphnia lumholtzi invasion was strongly associated with the physical and chemical environment in lakes. *Daphnia lumholtzi*'s position in the CCA shows that it was found mainly in large, eutrophic lakes (Figure 3). Similarly, logistic regression found that surface area and

TABLE V. Contingency table results for association between occurrence of zooplankton species and *Daphnia lumholtzi*. Only species which show significant or marginally significant associations are listed. The direction of the association between each species with *D. lumholtzi* is indicated in the last column.

| Species | χ^2 | P | Association |
|---------------------------------|----------|----------|-------------|
| <i>Moina micrura</i> | 13.632 | < 0.0001 | + |
| <i>Ergasilus versicolor</i> | 10.767 | 0.001 | + |
| <i>Diaptomus pallidus</i> | 8.407 | 0.004 | - |
| <i>Diaptomus reighardi</i> | 7.075 | 0.008 | + |
| <i>Ergasilus chautauquensis</i> | 5.983 | 0.014 | + |
| <i>Sida crystallina</i> | 3.163 | 0.075 | + |
| <i>Bosmina cf. longirostris</i> | 3.057 | 0.08 | + |
| <i>Diaptomus siciloides</i> | 2.832 | 0.092 | + |

total phosphorus were the best predictors of invasion. Nevertheless, the 56 lakes containing this species showed high variation in these environmental features (Figure 4). Similarly, smaller surveys in Missouri and Kansas also found broad ranges in the characteristics of invaded habitats (Havel, Mabee & Jones, 1995; Dzialowski, O'Brien & Swaffar, 2000), indicating that *D. lumholtzi* has a broad tolerance for a wide variety of freshwater environments.

The greater invasion rate in large lakes provides insights into the causes of the positive association between zooplankton species richness and lake area (Dodson, 1992) (Figure 2). Large lakes may contain more species either because they have more suitable habitats or because they are more likely to receive colonists. For instance, large lakes typically have more launch areas for recreational boats, a vector known to transmit zooplankton (Havel & Stelzleni-Schwent, 2000). In reservoirs, position in the landscape also contributes to this area effect, as large reservoirs are often downstream from smaller reservoirs, allowing dispersal via river transport (Shurin & Havel, 2002). The fact that area predicted *D. lumholtzi* invasion after accounting for other abiotic factors suggests that greater propagule pressure accounts for part of the higher invasion rate in large lakes. The observation that proximity to sources also predicts invasion (Havel, Shurin & Jones, 2002) also supports the idea that dispersal is in part responsible for constraining the spread of this species, as well as other freshwater invertebrates, such as zebra mussels (Johnson, Ricciardi & Carlton, 2001; Karatayev *et al.*, 2003). Nevertheless, it seems likely that local conditions in large lakes may also increase colonization success relative to small lakes. Such differences might include larger local populations that are less prone to stochastic extinction, larger pelagic zones, or greater habitat heterogeneity (Angermeier & Schlosser, 1989). For instance, large reservoirs exhibit broad longitudinal gradients in environmental characteristics such as depth, turbidity, and fertility (Thornton, Kimmel & Payne, 1990).

Increased fertility (and its variability) may increase the susceptibility of a community to invasion by providing more resources to colonizing species (Davis, Grime & Thompson, 2000). Results from the current survey of reservoir invasion by *D. lumholtzi* support this prediction, as invasion likelihood increased with phosphorus levels (Table IV). These results differ from those of a survey of 35 Kansas reservoirs, where those invaded by *D. lumholtzi*

were lower in chlorophyll, total nitrogen, and total phosphorus than non-invaded lakes (Dzialowski, O'Brien & Swaffar, 2000). The difference in these two studies may be partly because many of the Kansas lakes were higher in fertility than those in the current study. Increases in fertility may increase invasion likelihood only when lakes are below the eutrophic end of the productivity gradient. In a recent 7-y study of Missouri lakes that combined both spatial position and physico-chemistry, we found no detectable effect of these fertility features on *D. lumholtzi* invasion probability (Havel, Shurin & Jones, 2002). Overall, these differences in outcomes suggest that the effect of fertility on *D. lumholtzi* invading reservoirs is less important than other features, such as size and spatial position. Indeed, we found a broad range of fertilities for invaded lakes (Table I), indicating that both oligotrophic and eutrophic systems are susceptible to invasion. A recent mesocosm experiment also found weak effects of fertility on invasion success. Lennon, Smith, and Dzialowski (2003) manipulated nutrient concentrations with a natural pond assemblage and introduced *D. lumholtzi* to half of the tanks. Although total zooplankton biomass showed a clear positive response to nutrient enrichment, invasibility was similar across all nutrient treatments. Overall, these studies suggest that fertility may sometimes affect colonization success, but its effects are generally weaker than those of lake size.

Several species were associated with invasion success by *D. lumholtzi*. Contingency table analysis identified eight candidate species for playing a role in generating invasion resistance or facilitation. However, these species no longer showed any significant association with invasion after accounting for physico-chemical characteristics (Table IV). This result suggests that the associations of *D. lumholtzi* with other species were due to shared responses to the physical environment rather than direct pair-wise interactions. This result agrees with studies of invasion in stream fish communities, where human modification of flow and temperature were more important for determining invasibility than resident composition (Baltz & Moyle, 1993). Nevertheless, we must be careful when interpreting single-date surveys such as used in the current study. It is possible that these exotic species invade communities that were originally different in species composition, but then later converged through species replacement. Excluding this possibility requires data from before-after studies, such as those used to examine food web impacts by the predaceous cladoceran *Bythotrephes* (Yan, Girard & Boudreau, 2002).

The results of our observational study of invasion by an exotic species contrast with recent experimental studies of invasion, which demonstrated large effects of zooplankton community composition on invasibility. In mesocosm experiments where multiple species from the same region were introduced into natural pond zooplankton communities, Shurin (2000) found that communities were nearly saturated with species and resisted most invaders. Perturbing the local communities greatly increased the number and biomass of invasive species, indicating a major role for species interactions in generating invasion resistance. These experimental results suggest that zoo-

plankton community composition can confer resistance to future invasions.

The way in which species interactions were incorporated in our analysis may partially explain the disparity between the current study and experimental work. Our analysis examined species interactions in pair-wise fashion, whereas interactions may be more diffusely distributed. That is, *D. lumholtzi* may not be strongly affected by any particular zooplankton species, but the overall strength and number of interactions may be important. There may be little difference, for instance, between lakes with one species or another, but other aspects of the plankton assemblage may be very important. In this case, our analysis would likely fail to detect a role of species interactions. Perhaps most important, we lacked data on a number of important community members, particularly planktivorous forage fish. Most reservoirs are extensively managed by state game agencies, with frequent introductions of forage and game fishes (Stein, DeVries, & Dettmers, 1995). Unknown differences in the effects of planktivory among lakes may contribute to their susceptibility to zooplankton invasions.

Finally, the strength and qualitative effect of species interactions often depend on the local environment (Goldberg *et al.*, 1999). Our simple analysis may have failed to detect context-dependent species interactions. For example, our study focused on zooplankton communities coexisting during midsummer, the period when *D. lumholtzi* is most common (Havel, Mabee & Jones, 1995) and native *Daphnia* are less abundant (J. Havel & J. Graham, unpubl. data). The timing of invasion thus may be critical to its success.

Our study also found no association between native zooplankton species richness and likelihood of invasion by *D. lumholtzi*. Although invaded lakes tended to have more resident species than uninvaded lakes (Figure 4), the difference between the two groups was not statistically significant. In other words, the higher species richness in larger lakes does not appear to exclude invaders. However, we should view these data with caution, as our single-year survey may have underestimated species richness in these lakes. Analyses of long-term zooplankton data from other lakes reveal a high turnover in species composition among years (Arnott *et al.*, 1999). Furthermore, we sampled during a single season (summer), likely missing species that are more common during cooler months. Thus, our single-year survey has likely underestimated the species pool in this region. If more of the regional species pool is indeed present within individual lakes, then differences between communities in composition would be small, making it more difficult to detect the effects of native communities on invasibility. Future research is needed to examine the relative importance of temporal *versus* spatial variation in zooplankton assemblages in this region.

Studies of the relationship between community diversity and invasibility have yielded equivocal results in other studies. Whereas some experiments have found negative effects of diversity on invasion success (Levine, 2000; Shurin, 2000; Kennedy *et al.*, 2002), some observational studies have found positive associations (Stohlgren

et al., 1999). Levine and D'Antonio (1999) explain this disparity as a result of the context-dependence of the effects of diversity on invasibility. If diversity *per se* has negative effects on invasion, but covaries with environmental features such as productivity that enhance invasibility, then correlational studies may reflect the indirect effects of the environment more than the direct effects of diversity on invasion. The slightly greater invasion rate in diverse lakes in our data may be driven by the species-area relation (Figure 4). Large lakes may be invaded more often by *D. lumholtzi* for the same reason that they contain more native species; they receive a greater supply of propagules, have more local habitat heterogeneity, and support larger local populations.

In conclusion, the current study reveals that the pattern of invasions by the exotic *D. lumholtzi* in the central US is best explained by physico-chemical features of the lakes. Discerning the relative importance of dispersal and local site characteristics for this pattern will require future analyses of time-series data and carefully designed experiments.

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APPENDIX I. Species codes for 1995 zooplankton survey. A total of 171 lakes were surveyed and 63 species of cladocerans and copepods detected.

| Species | Authority | Code | Frequency of occurrence |
|--|------------------------------------|------|-------------------------|
| CLADOCERA | | | |
| <i>Acroperus harpae</i> | Baird, 1843 | Ahar | 2 |
| <i>Alona affinis</i> | Leydig, 1660 | Aaff | 3 |
| <i>Alona guttata</i> | Sars, 1862 | Agut | 7 |
| <i>Alona rectangula</i> | Sars, 1861 | Arec | 1 |
| <i>Alonella diaphana</i> | King, 1853 | Adia | 2 |
| <i>Alonella globulosa</i> | Daday, 1898 | Aglo | 1 |
| <i>Bosmina</i> cf. <i>longirostris</i> | O. F. Müller, 1785 | Blon | 116 |
| <i>Bosmina tubicen</i> | Brehm, 1953 | Btub | 6 |
| <i>Bosminopsis deitersi</i> | Richard, 1985 | Bdei | 3 |
| <i>Camptocercus rectirostris</i> | Schödler, 1862 | Crec | 4 |
| <i>Ceriodaphnia lacustris</i> | Birge, 1893 | Clac | 141 |
| <i>Ceriodaphnia quadrangula</i> | O. F. Müller, 1785 | Cqua | 3 |
| <i>Ceriodaphnia reticulata</i> | Jurine, 1820 | Cret | 1 |
| <i>Chydorus</i> cf. <i>sphaericus</i> | O. F. Müller, 1785 | Csph | 28 |
| <i>Daphnia ambigua</i> | Scourfield, 1947 | Damb | 26 |
| <i>Daphnia galeata mendotae</i> | Birge, 1918 | Dgal | 57 |
| <i>Daphnia laevis</i> | Birge, 1879 | Dlae | 6 |
| <i>Daphnia lumholtzi</i> | Sars, 1885 | Dlum | 56 |
| <i>Daphnia parvula</i> | Fordyce, 1901 | Dpar | 111 |
| <i>Daphnia pulicaria</i> | Forbes, 1896, emend. Hrbáček, 1913 | Dpul | 15 |
| <i>Daphnia retrocurva</i> | Forbes, 1882 | Dret | 20 |
| <i>Daphnia rosea</i> | Sars, 1862, emend. Richard, 1896 | Dros | 10 |
| <i>Daphnia schodleri</i> | Sars, 1862 | Dsch | 1 |
| <i>Diaphanosoma birgei</i> | Kořínek, 1970 | Dbir | 152 |
| <i>Diaphanosoma brachyurum</i> | Liéven, 1848 | Dbra | 5 |
| <i>Eurycercus lamellatus</i> | O. F. Müller, 1785 | Elam | 1 |
| <i>Graptoleberis testudinaria</i> | Fischer, 1863 | Gtes | 2 |
| <i>Holopedium amazonicum</i> | Zaddach, 1904 | Hama | 28 |
| <i>Ilyocryptus sordidus</i> | Liéven, 1848 | Isor | 21 |
| <i>Ilyocryptus spinifer</i> | Herrick, 1884 | Ispi | 3 |
| <i>Kurzia latissima</i> | Kurz, 1874 | Klat | 3 |
| <i>Latonopsis occidentalis</i> | Birge, 1891 | Locc | 1 |
| <i>Leptodora kindtii</i> | Focke, 1844 | Lkin | 39 |
| <i>Leydigia acanthocercoides</i> | Fischer, 1854 | Laca | 4 |
| <i>Leydigia quadrangularis</i> | Leydig, 1860 | Lqua | 4 |
| <i>Macrothrix rosea</i> | Jurine, 1820 | Mros | 1 |
| <i>Moina affinis</i> | Birge, 1893 | Maff | 2 |
| <i>Moina micrura</i> | Kurz, 1874 | Mmic | 29 |
| <i>Oxyurella tencicaudis</i> | Sars, 1862 | Oten | 1 |
| <i>Pleuroxus denticulatus</i> | Birge, 1878 | Pden | 3 |
| <i>Pleuroxus hamulatus</i> | Birge, 1910 | Pham | 10 |
| <i>Scapholeberis kingi</i> | Sars, 1903 | Skin | 5 |
| <i>Sida crystallina</i> | O. F. Müller, 1875 | Scry | 15 |
| <i>Simocephalus exspinosus</i> | Koch, 1841 | Sexs | 3 |
| <i>Simocephalus serrulatus</i> | Koch, 1841 | Sser | 4 |
| <i>Simocephalus vetulus</i> | Schödler, 1858 | Svet | 1 |
| COPEPODA | | | |
| <i>Acanthocyclops robustus</i> | Sars, 1965 | Arob | 58 |
| <i>Canthocamptus robertcokeri</i> | M. S. Wilson, 1958 | Crob | 1 |
| <i>Cyclops bicolor</i> | Sars, 1963 | Cbic | 36 |
| <i>Diacyclops thomasi</i> | Forbes, 1898 | Dtho | 18 |
| <i>Diaptomus clavipes</i> | Schacht, 1897 | Dcla | 6 |
| <i>Diaptomus pallidus</i> | Herrick, 1879 | Dpal | 79 |
| <i>Diaptomus reighardi</i> | Marsh, 1895 | Drei | 76 |
| <i>Diaptomus saltillinus</i> | Brewer, 1989 | Dsal | 1 |
| <i>Diaptomus siciloides</i> | Lilljeborg, 1889 | Dsic | 36 |
| <i>Epishura nordenskioldi</i> | Lilljeborg, 1889 | Enor | 14 |
| <i>Ergasilus chautauquensis</i> | Fellows, 1911 | Echa | 106 |
| <i>Ergasilus versicolor</i> | C. B. Wilson, 1911 | Ever | 10 |
| <i>Eucyclops agilis</i> | Koch, 1963 | Eagi | 10 |
| <i>Eurytemora affinis</i> | Poppe, 1880 | Eaff | 14 |
| <i>Macrocyclus ater</i> | Herrick, 1882 | Mate | 1 |
| <i>Mesocyclops edax</i> | S. A. Forbes, 1880 | Meda | 160 |
| <i>Orthocyclops modestus</i> | Herrick, 1883 | Omod | 10 |