Article

Predicting impacts of an invading copepod by ecological assessment in the animal's native range

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Abstract

We assembled data from 11 years of observational research on zooplankton in subtropical Florida, USA, lakes to determine potential impacts of the copepod *Arctodiaptomus dorsalis* on biodiversity and biomass of co-occurring crustacean zooplankton. This synthesis provided insight into how the species might impact plankton in limnologically similar lakes that it invades outside of its native range. *A. dorsalis* recently was found in the Philippines, and it was suggested that it could invade lakes in Asia and reduce biodiversity. In 7 shallow eutrophic lakes in Florida, we found no relationship between relative biomass of *A. dorsalis* and number of species of crustacean zooplankton, and we were equally likely to find a similar-sized copepod *Diaptomus floridanus* in lakes with or without *A. dorsalis*. In Lake Okeechobee, where a 7-year dataset existed for crustacean zooplankton, we found no evidence that *A. dorsalis* impacts the biomass of cladocerans or other dominant copepods. Gut analysis and grazing experiments documented that *A. dorsalis* is capable of eating bacteria and nearly all phytoplankton taxa, including cyanobacteria. This ability to exploit a broad range of resources and to execute rapid escape maneuvers to avoid fish predation may explain why *A. dorsalis* often is dominant in shallow eutrophic lakes with high densities of omnivorous fish. We conclude that *A. dorsalis* will not negatively affect the biodiversity of plankton in similar lakes of Asia; instead, it may fill a vacant niche in lakes with high fish predation where other copepods cannot survive. Further research is needed to determine how *A. dorsalis* will influence the plankton in less enriched lakes where food resources may be limiting.

Key words: copepods, ecological impacts, invading species, native range, zooplankton

Introduction

Nonindigenous species invade freshwater ecosystems at a high frequency, with thousands of reported examples (Ruiz and Carlton 2003). The animals or their resting eggs are transported by the ballast water of ships, on the hulls of recreational boats, by migratory waterfowl, and by various other mechanisms such as hydrological connections in reservoir systems. In zooplankton communities, there are 2 well-known examples. The predatory cladoceran *Bythotrephes longimanus*, native to northern Europe and Asia, invaded the Laurentian Great Lakes from ballast water in the 1980s and spread to lakes throughout the Canadian Shield, causing a large-scale change in the size distribution of zooplankton (Tuchman and Barbiero 2004, Strecker et al. 2006). The herbivorous cladoceran *Daphnia lumholtzi*, native to Australia and Asia, invaded a lake in Texas in the early 1990s (Sorensen and Sterner 1992) and then spread across North America (Tudorancea et al. 2009). It seems to have filled a vacant niche (e.g., East et al. 1999, Walker et al. 2013), and in the only long-term assessment to date, displayed a lack of persistence in the plankton (Havens et al. 2012). A variety of lakes, reservoirs, and rivers also have been invaded by copepods: for example, Asian copepods in the Snake River (Cordell et al. 2008) and Lower Columbia River (Bollens et al. 2012) of the United States; nonindigenous copepods of unknown origin in the Saratov Reservoir of

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Russia (Popov 2011); and estuarine copepods in a variety of freshwater habitats (e.g., Lee 1999, Walker et al. 2013).

We found only one published account of a copepod invasion negatively effecting resident zooplankton; Papa et al. (2012) reported that the calanoid *Arctodiaptomus dorsalis* had invaded lakes in the Philippines and suggested that it caused a loss of copepod biodiversity. The authors qualified this conclusion, however, noting that the lakes also experienced eutrophication and fish introduction during the years between contemporary and past plankton samplings. Although this finding creates uncertainty about invasion impacts, the authors concluded that *A. dorsalis* might impact other zooplankton communities in Asia.

A. dorsalis originally was described by Marsh (1907) from lakes in Louisiana, USA, and its native range includes the southern United States, Central America, and northern South America, but it has been recently found in eutrophic reservoirs in Arizona and Hawaii, USA (Beaver, unpubl. data). In a synoptic survey (Reid 2007), *A. dorsalis* also was found in the northeastern United States, in several locations in the Mississippi drainage basin, in California, and in Mexico. Reid (2007) concluded that *A. dorsalis* "has the potential to extend its range farther into suitable eutrophic waterbodies," and clearly this has occurred. Based on their collections from the Philippines, illustrations of taxonomic features of *A. dorsalis* by Papa et al. (2012) clearly indicate that it is the same species found in Florida. In Florida, *A. dorsalis* was found in the earliest quantitative plankton surveys (Blancher 1984, Elmore et al. 1984), dominating the zooplankton in hardwater eutrophic lakes, whereas its congener *A. floridanus* was more common in softwater mesotrophic lakes. Recent plankton studies in Florida, including our own, have been restricted to eutrophic lakes, and we consistently find dominance by *A. dorsalis* (Havens and Beaver 2011).

For more than a decade, we have studied the zooplankton of Florida lakes (Havens et al. 2007, 2011, Havens and Beaver 2011). In this study we extract information from a large dataset to determine how *A. dorsalis* might affect biodiversity and biomass of other crustacean plankton. This approach of assessing potential impacts of an invader by studying its dynamics in the native range has been widely used to predict potential effects of invasion by plants (Hierro et al. 2005, Pysek et al. 2009), mollusks (Loo et al. 2007), amphibians (Ficetola et al. 2007), and other organisms. To our knowledge, this is the first study to use this approach to predict invasion impacts on zooplankton.

Florida lakes are similar in a number of ways to lowland lake, pond, and reservoir ecosystems in Asia. In the Philippines, China, Korea, and other nations, such lakes often are highly eutrophic and have high densities of omnivorous fish (Eng et al. 1989, Fernando 1991, Kim et al. 2001, Xie and Liu 2001, Papa and Mamaril 2011). Thus, we can reasonably conclude that impacts (or lack thereof) observed in Florida will occur (or not) in invaded lakes in Asia with a similar trophic state.

Methods

Data were assembled from studies conducted between 1996 and 2007 in Lake Okeechobee and the Kissimmee Chain-of-Lakes in Florida, USA (Table 1). The lakes are shallow (1–4 m mean depth), eutrophic, and have dense populations of omnivorous fish (Allen et al. 2000, Rogers and Allen 2008) including gizzard shad (*Dorosoma cepedianum*) and threadfin shad (*Dorosoma petenense*) that exert strong predation pressure on the zooplankton (Havens and Beaver 2011). Historical plankton sampling was conducted by the South Florida Water Management District, and enumeration and identification was conducted by BSA Environmental Services. Here we provide an overview of the methodology and provide references to published literature with detailed methods.

A comparative analysis of zooplankton communities in Florida lakes was conducted by Havens and Beaver (2011), who considered nearshore and offshore regions of Lake Okeechobee separately. In that study, the lakes were sampled monthly for 2 years to describe the crustacean zooplankton. Samples were collected with vertical tows through the entire water column (from 0.5 m off the bottom) using a 30 cm diameter conical plankton net with a mesh of 153 µm. Animals were preserved in sucrose-formalin until counting. Enumeration of animals and conversion of population densities to units of carbon biomass (µg L^{-1} C) were conducted according to the methods described in Havens et al. (2007) and were identical to methods used by Auer et al. (2004) to allow comparison of results from other lakes.

A comprehensive time series analysis of crustacean zooplankton also was conducted in Lake Okeechobee from 2000 to 2007 (Havens et al. 2011), with quarterly or more frequent sampling at a nearshore and offshore site. Methods were identical to those identified above. From those data, we examined the relationship between biomass of *A. dorsalis* and (1) cladocerans and (2) the other dominant copepod in this lake, *Mesocyclops edax*.

Work and Havens (2003) examined the diet habits of zooplankton in Lake Okeechobee, including *A. dorsalis*, performing grazing experiments at the same nearshore and offshore sites on 5 occasions between July 1998 and July 1999. Grazing occurred *in situ* with a 2 L Haney chamber at mid-depth for 5 minutes, with the grazers being

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Table 1. Physical and chemical features of the study lakes in Florida, USA. Data are 2-year means ±95% confidence intervals. TP = total phosphorus, Chl-*a* = chlorophyll *a*, NS = nearshore, and OS = offshore.

Lake	Latitude (°N)	Area (km^2)	Depth (cm)	Secchi (cm)	TP ($\mu g\ L^{-1}$)	Chl-*a* ($\mu g\ L^{-1}$)
Fells Cove	28	5	230	79 ± 3	36 + 1	3 ± 0.3
East Tohopekaliga	28	51	440	115 ± 4	31 ± 1	6 ± 0.4
Tohopekaliga	28	76	260	61 ± 2	60 ± 2	23 ± 2
Cypress	28	27	190	55 ± 2	84 ± 4	31 ± 2
Hatchineha	28	49	210	72 ± 6	76 ± 5	20 ± 2
Kissimmee	28	144	340	50 ± 2	52 ± 2	27 ± 2
Okeechobee (NS)	27	432	150	50 ± 5	110 ± 21	24 ± 1
Okeechobee (OS)	27	865	380	22 ± 2	140 ± 6	15 ± 1

provided with cultured native bacterial cells fluorescently labeled with 5-[4,6-(dichlorotriazin-2-yl)] amino fluorescein (DTAF). After killing with sucrose-formalin, the animal guts were examined with an epifluorescent microscope for presence of DTAF-labeled bacteria; gut contents also were visually inspected with a light microscope to determine species of algae consumed.

Results

In the survey of 7 Florida lakes, relative biomass of *A. dorsalis* ranged from 53 to 92% (Fig. 1). The lakes collectively had 15 species of cladocerans and 5 species of copepods, including *A. dorsalis* and the native calanoid *D. floridanus*. There was no relationship between the total number of zooplankton species or the number of copepod species and the relative biomass of *A. dorsalis* (Table 2); the lowest number of species occurred both in the lakes with the lowest and highest relative biomass of *A. dorsalis*. Finding the 2 calanoids together in a lake was equally as likely as finding just one, although when only one was found it always was *A. dorsalis*. The biomass of *A. dorsalis* was typically 2 orders of magnitude higher than *D. floridanus* in any given sample. Although it occurs in many Florida lakes, *A. floridanus* densities and biomass tend to be low. In Florida lakes there are just 2 species of *Daphnia*: the small native *D. ambigua* and the invasive *D. lumholtzi*. Although they co-occurred in all 7 lakes, the population density and biomass of *D. ambigua* consistently was higher.

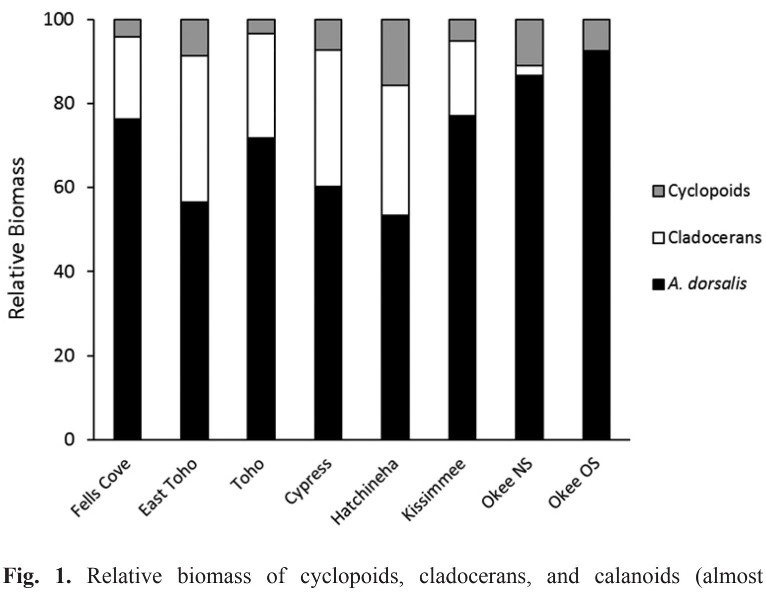

Fig. 1. Relative biomass of cyclopoids, cladocerans, and calanoids (almost exclusively *Arctodiaptomus dorsalis*) in 7 Florida lakes, including the nearshore and offshore sites in Lake Okeechobee.

Using data from the 7-year study of crustacean zooplankton in Lake Okeechobee, we found that the biomass of cladocerans and *M. edax* both were positively correlated with biomass of *A. dorsalis* (Fig. 2). Pearson's correlation coefficients on the log-transformed data were positive and had p values ranging from 0.01 to 0.10.

In the grazing experiments, *A. dorsalis* at the nearshore site sometimes had fluorescent bacteria in its gut (39% of the animals examined), while at the offshore site it almost always grazed bacteria (92%). We also found that *A. dorsalis* consumed cyanobacteria, including *Lyngbya*, *Planktothrix*, *Anabaena*, and *Microcystis*. More than 60% of the phytoplankton found in *A. dorsalis* guts was cyanobacteria. These results only reflect consumption and do not determine whether these food items were digested and assimilated.

Table 2. Presence (+) vs. absence (o) of crustacean zooplankton species in 9 Florida lakes, and total number of crustacean zooplankton species found during 2-year long monthly sampling regimes. FC = Fells Cove, ET = East Tohopekaliga, TO = Tohopekaliga, CY = Cypress, HA = Hatchineha, KI = Kissimmee, ON = Okeechobee nearshore, and OS = Okeechobee offshore.

	FC	ET	TO	CY	HA	KI	ON	OS
Cladocerans								
Alona guttata	+	+	+	+	+	+	+	+
Bosminopsis deitseri	+	+	+	o	+	o	+	o
Camptocercus recirostris	+	o	+	+	+	+	o	o
Ceriodaphnia rigaudi	+	+	+	+	+	+	+	+
C. reticulata	o	o	o	o	o	o	o	o
Chydorus cf sphaericus	o	o	+	+	+	+	+	+
Daphnia ambigua	+	+	+	+	+	+	+	+
D. lumholtzii	+	+	+	+	+	+	+	+
Diaphanosoma brachyurum	+	+	+	+	+	+	+	+
Eubosmina tubicen	+	+	+	+	+	+	+	+
Holopedium gibberum	+	+	+	+	o	o	o	o
Ilyocryptus spinifer	o	o	o	+	+	o	+	o
Macrothrix rosea	o	o	o	o	+	o	o	o
Pleuroxus striatus	+	o	o	o	o	o	o	o
Sida crystallina	o	o	o	+	o	o	o	o
Copepods								
Acanthocyclops cf vernalis	+	o	+	+	+	+	+	+
Mesocyclops edax	+	+	+	+	+	+	+	+
Tropocyclops prasinus	o	o	+	+	+	+	+	+
Diaptomus floridanus	+	o	o	+	o	+	+	o
Arctodiaptomus dorsalis	+	+	+	+	+	+	+	+
Total # Species	14	10	14	16	15	13	14	11

Discussion

The main focus of research dealing with nonindigenous zooplankton has been on cladocerans, in particular *Bythotrephes longimanus* (Tuchman and Barbiero 2004, Strecker et al. 2006) and *Daphnia lumholtzi* (Havel and Hebert 1993, Havel and Shurin 2004, Havens et al. 2012). Yet there are recent examples of copepod invasions in estuaries (e.g., Bollens et al. 2012), lakes (e.g., Banks and Duggan 2009, Popov 2011), and reservoirs (Walker et al. 2013). Most recently, Papa et al. (2012) suggested that a massive invasion by *A. dorsalis* is threatening the biodiversity of lakes in the Philippines, and that it could spread into mainland Asia. In a recent study of 2 ponds in the Himalayas, Kumar et al. (2012) found this species in both ecosystems. Papa et al. (2012) conducted a comprehensive survey of 27 Philippine lakes between 2006 and 2011 and found *A. dorsalis* in most of the lakes, but their comparison with prior studies indicated "no primary literature" existed for 17 of the lakes; therefore, changes in biodiversity could not be determined. Further, the suggested source of the nonindigenous copepod was from aquaculture operations that had developed over recent decades for intensive fish production to provide affordable food for the Philippine population; thus, changes in biodiversity might be attributed to increased predation by fish.

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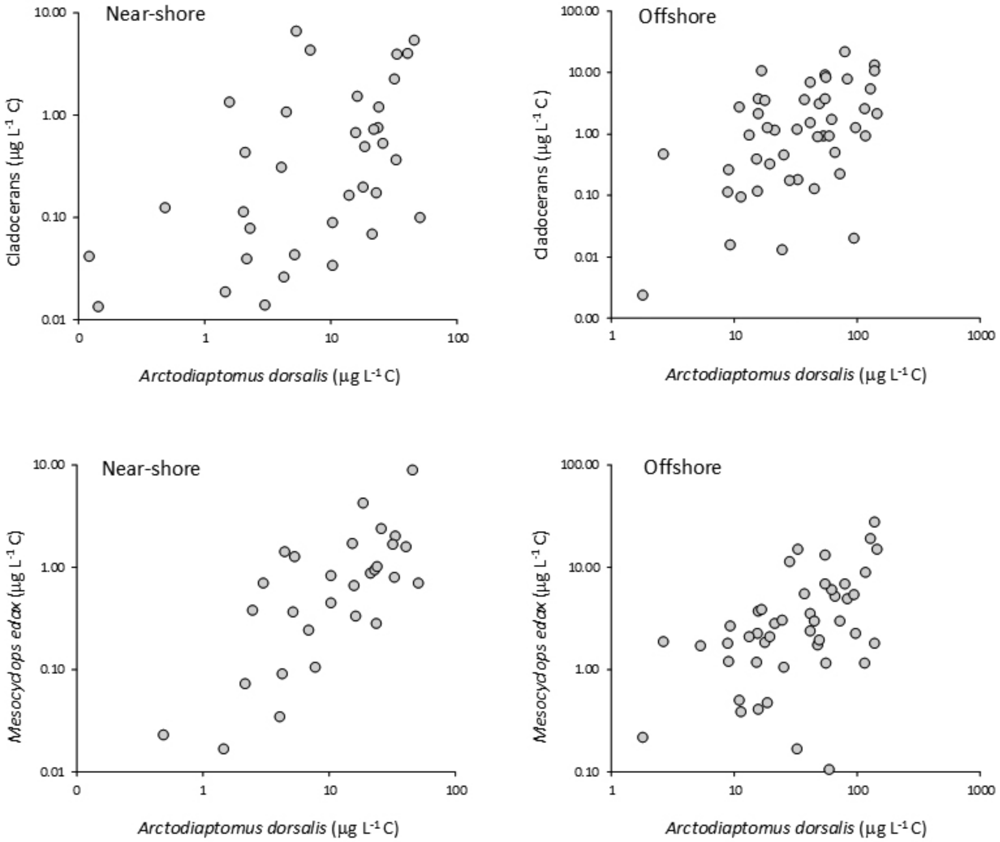

Fig. 2. Relationships between the biomass of *Arctodiaptomus dorsalis* with total biomass of cladocerans and the other dominant copepod, *Mesocyclops edax*, at a nearshore and offshore sampling site in Lake Okeechobee.

Low biodiversity and biomass of zooplankton is typically found in subtropical lakes, even in the absence of aquaculture, because they naturally support a high biomass of small planktivorous and omnivorous fish (Crisman and Beaver 1990, Jeppesen et al. 2007, Iglesias et al. 2008, Havens and Beaver 2011).

One approach to assess impacts of a nonindigenous species after its introduction is to examine changes in the ecosystem from a long-term dataset, as has been done in the Laurentian Great Lakes for *B. longimanus* (Tuchman and Barbiero 2004) and in Florida for *D. lumholtzi* (Havens et al. 2011). Where such long-term data are not available, either because an invasion has just occurred or because historical information is sparse or lacking, we may gain insight into potential future impacts by examining how the species affects ecosystems in its native range. Florida is an ideal location to conduct such an assessment for *A. dorsalis* because it is at the core of the home range (Reid 2007), the species occurs in nearly every lake that we have sampled, and there is considerable observational and experimental research to document *A. dorsalis* interactions with other crustacean zooplankton. Many lakes in the Philippines, China, Korea, and other lowland areas of Asia also are shallow, eutrophic, and have high densities of small fish (Allen et al. 2000), so the results from Florida can be generalized to the Asian region where copepod invasion is occurring.

Contrary to the expectations based on findings by Papa et al. (2012), we found no relationship between the dominance of *A. dorsalis* and biodiversity of other crustacean zooplankton. The species with the greatest niche overlap, *D. floridanus*, was just as likely to occur in lakes with *A. dorsalis* as in lakes without it. Likewise, we found no evidence of a negative influence of *A. dorsalis* on the biomass of cladocerans or a dominant cyclopoid based on 7 years of data from nearshore and offshore sampling stations in Lake Okeechobee; on the contrary, we found that the biomasses were positively correlated. In this eutrophic ecosystem, it is unlikely that food is limiting given the high biomass of phytoplankton, bacteria, ciliates, and flagellates (Havens et al. 2007), so this finding is not unexpected.

Grazing experiments indicated that *A. dorsalis* can use a wide range of food resources, including bacteria and nearly all species of phytoplankton found in the lake. This attribute, along with its ability to implement rapid escape maneuvers when approached by fish (Bays and Crisman 1983), may explain why *A. dorsalis* is so successful in highly eutrophic lakes, co-occurring (albeit usually at low densities) with dense blooms of *Anabaena*, *Microcystis*, and other noxious cyanobacteria. One of the earliest studies of zooplankton in Florida lakes (Blancher 1984) found that *A. dorsalis* was the dominant species in eutrophic lakes, whereas *D. floridanus* was more likely to dominate in oligotrophic lakes. In Florida, there is a strong correlation between fish density and trophic state (Bachmann et al. 1996), and we know that in the state's eutrophic lakes, fish predation is so intense that ratios of zooplankton to phytoplankton biomass are among the lowest recorded from any global location (Havens and Beaver 2011), a result that is typical of the subtropics (Jeppesen et al. 2007, Iglesias et al. 2008).

Our research on *A. dorsalis* in Florida lakes suggests that if this species invades shallow eutrophic lakes, ponds, and reservoirs in Asia, the outcome for biodiversity and biomass of other crustacean zooplankton will depend more on what also happens with fish predators than on interactions between *A. dorsalis* and native zooplankton. The experimental and observational research of Jeppesen et al. (2007) and Meerhoff et al. (2007), and our own work in Florida (Havens and Beaver 2011) suggests that high predation by small planktivorous and omnivorous fish in subtropical lakes drive the zooplankton to low densities and nearly eliminate certain species such as large members of the genus *Daphnia*. The finding that *A. dorsalis* biomass correlates with total biomass of cladocerans and with biomass of *M. edax* suggests that all the crustacean zooplankton are controlled by fish in Lake Okeechobee. Further, a comparison of data from Florida lakes, based on ratios of biomass of zooplankton to phytoplankton (Fig. 3), suggests intense fish predation compared to similar lakes in Denmark (Jeppesen et al. 2007) and Germany (Auer et al. 2004). Based on our research, *A. dorsalis* is best equipped to deal with intense fish predation (and thus is the most common species), but even then it can only attain low densities relative to available resources in Florida lakes.

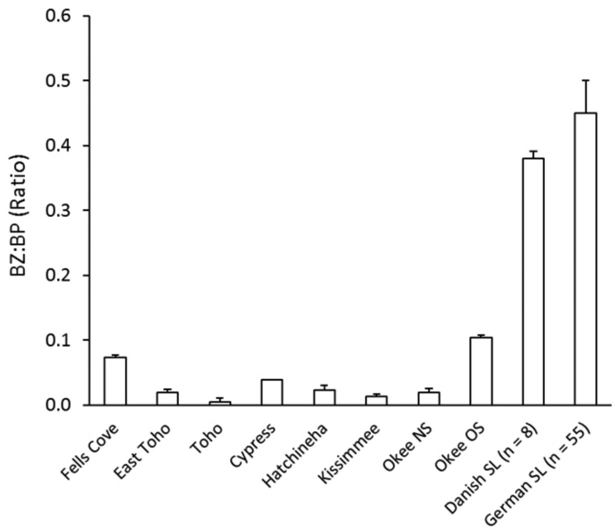

Fig. 3. Ratio of total zooplankton biomass to phytoplankton biomass in 7 Florida lakes compared to 8 shallow eutrophic Danish lakes and 55 shallow lakes in Germany ranging from mesotrophic to hypereutrophic (the Florida lakes are eutrophic and shallow).

Our study demonstrates that application of known ecological characteristics of a copepod species in its native habitat can be valuable in assessing the potential impacts of invasion. The results of Papas et al. (2012), who found only *A. dorsalis* and no native species of copepods in Philippine lakes, probably reflects the impacts of predation by cultured fish in those lakes, not an effect of *A. dorsalis*. This interpretation is consistent with our findings in Florida where *A. dorsalis* is the only crustacean species that can coexist at moderately high densities along with omnivorous fish. Because many eutrophic lakes, ponds, and reservoirs in Asia have high densities of introduced omnivores (Fernando 1991, Kim et al. 2001, Xie and Liu 2001), *A. dorsalis* may simply fill a niche vacated by large zooplankton eliminated by predation. We recognize that our results may apply only to eutrophic lakes where food resources of zooplankton are not limiting. Controlled experiments or long-term observations of invaded lakes will be required to elucidate effects of the invader in less productive ecosystems.

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