

# Water Flea (*Daphnia lumholtzi*)

## Ecological Risk Screening Summary

U.S. Fish & Wildlife Service, February 2011

Revised, November 2016

Web Version, 3/30/2018



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## 1 Native Range and Status in the United States

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### Native Range

From Benson et al. (2016):

“Tropical and subtropical lakes in east Africa, east Australia, and the Asian subcontinent of India (Havel and Hebert 1993).”

### Status in the United States

From Benson et al. (2016):

“*Daphnia lumholtzi* has been detected in 56 reservoirs in the southern and midwestern United States. The earliest record is from Texas in 1990 (Havel, pers. comm.). It has since been found in localized waters leading into major river drainages such as the: Arkansas, Cumberland, Illinois, Mississippi, Missouri, South Atlantic-Gulf, Tennessee, and Texas-Gulf. Occurrences of *D.*

*lumholtzi* in these waters fall in the following states: Alabama, Arizona, Arkansas, California, Florida, Illinois, Kansas, Kentucky, Louisiana, Minnesota/Wisconsin, Mississippi, Missouri, North Carolina, Oklahoma, Ohio, South Carolina, Tennessee, Texas, and Utah (Havel and Shurin 2004; D. Jackson; J. A. Stoeckel; M. A. Pegg; J. S. Kuwabara). In August of 1999 it was discovered for the first time in the Great Lakes, Lake Erie, just north of Lakeside, Ohio (Muzinic, 2000).”

## Means of Introduction into the United States

From Benson et al. (2016):

“It is uncertain how *D. lumholtzi* was introduced into the U.S. It is suspected that it may have been transported with shipments of Nile perch from Lake Victoria in Africa where it is a dominant zooplankton. Nile perch was originally introduced into Texas as early as 1983 (Havel and Hebert 1993). The continuing discovery of *D. lumholtzi* in new locations could be due to contaminated stockings of fish through international commercial trade. At the same time, the close proximity of affected reservoirs in Missouri and in Texas might lead to the conclusion that *D. lumholtzi* may have spread by recreational boating from the initially infested reservoirs.

“Dzialowski et al. (2000) found that non-human dispersal mechanisms had little to do with the spread of *D. lumholtzi* in Kansas. *D. lumholtzi* was not detected in small ponds inaccessible to boats, even though the ponds were within watersheds where *D. lumholtzi* was established (Dzialowski et al. 2000).”

## Remarks

From Benson (2016):

“It is most likely that *D. lumholtzi* has become a successful invader because of its ability to avoid predation, not because it is a better competitor for the available food supply. Stomach samples of fish from Norris Reservoir contained no *D. lumholtzi* (Goulden et al. 1995). Work and Gophen (1999) note three aspects of *D. lumholtzi* that have most likely contributed to its success as an invader in North America. First, due to its tropical to subtropical native range, *D. lumholtzi* is adapted to higher temperatures than its native *Daphnia*. Second, *D. lumholtzi* is adapted to disturbed areas, giving it an invasion advantage (according to invasion theory). Third, the long helmet and tail spine helps *D. lumholtzi* avoid predation.”

“Nutrient and resource levels in lakes likely play a large role in the presence and spread of *D. lumholtzi* throughout the United States, though research on mechanism is unclear. Dzialowski et al. (2000) suggested that low resource (algae) levels aid *D. lumholtzi* invasion because it is better able to take advantage of low quality food resources than small competitors, but Havel et al. (1995) found that reservoirs invaded by *D. lumholtzi* had much higher levels of nutrients than non-invaded reservoirs. Further research is warranted to clarify discrepancies.”

## 2 Biology and Ecology

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### Taxonomic Hierarchy and Taxonomic Standing

From ITIS (2016):

“Kingdom Animalia – Animal, animaux, animals  
Subkingdom Bilateria  
Infrakingdom Protostomia  
Superphylum Ecdysozoa  
Phylum Arthropoda – Artrópode, arthropodes, arthropods  
Subphylum Crustacea Brünnich, 1772 – crustacés, crustáceo, crustaceans  
Class Branchiopoda Latreille, 1817 – branchiopods, branchiopodes  
Subclass Phyllopoda Preuss, 1951  
Order Diplostraca Gerstaecker, 1866  
Suborder Cladocera Latreille, 1829 – water fleas, cladocères, puces d'eau  
Infraorder Anomopoda Stebbing, 1902  
Family Daphniidae Straus, 1820  
Genus *Daphnia* O. F. Müller, 1785  
Species *Daphnia lumholtzi* G. O. Sars, 1885”

“Current Standing: valid”

### Size, Weight, and Age Range

From Benson et al. (2016):

“3.5 mm in length”

From Fofonoff et al. (2003):

“Female *D. lumholtzi* at 20-25 C, on average, [...] lived for up to 30 days.”

“[...] generation time of 6-9 days [...]”

### Environment

From GISD (2016):

“Most water bodies invaded by *D. lumholtzi*, reservoirs in the southern regions of the U.S., tend to be more eutrophic than lakes and reservoirs in the north.”

“[...] the species can exist in waters that experience periodic pulses of salinity.”

From Fofonoff et al. (2003):

“Nontidal Limnetic-Oligohaline”

“This cladoceran has also been found in inland saline lakes (e.g. Lake Texoma, OK-TX, 1.4 ppt; Work and Gophen 1995, Mobile Bay, 1.4 PSU), but the full extent of its salinity tolerance is unknown. Some *Daphnia* species can tolerate high salinities in inland salt lakes (Hairston et al. 1999), but this genus is a rare straggler in estuarine environments (Johnson and Allen 2005).”

## Climate/Range

From Fofonoff et al. (2003)

“Warm temperate-Tropical”

“It appears to be more tolerant of high temperatures than most other *Daphnia* (Tifnouti et al. 1993; Fey and Cottingham 2011; Engel and Tollrian 2012).”

From GISD (2016):

“*D. lumholtzi* takes advantage of late summer thermal niches when the water temperature surpasses 25C and will subsequently continue to colonize lakes and reservoirs across North America. It has been shown, though, that *D. lumholtzi* performs poorly at water temperatures below 10C which may inhibit the range of its expansive [*sic*] into more northern waters\” (Lenon et al. 2001).”

## Distribution Outside the United States

### Native

From Benson et al. (2016):

“Tropical and subtropical lakes in east Africa, east Australia, and the Asian subcontinent of India (Havel and Hebert 1993).”

### Introduced

From Fofonoff et al. (2003):

“In 2000, *Daphnia lumholtzi* was reported in the Três Irmãos reservoir, on the Tiete River (tributary of the Parana River), in Sao Paulo state, Brazil (Zanata et al. 2003). In 2003, and 2008, it was found in two floodplain lakes of the Upper Parana River, Parana State. It is expected to spread extensively in Brazil (Simões et al. 2009). In Mexico, *D. lumholtzi* was collected in Sonora (Elías-Gutiérrez et al. 2008), and the Presa El Salto reservoir, in Sinaloa in 2003 (Silva-Briano et al. 2010). The spotty nature of these tropical occurrences could reflect the scarcity of sampling or else a very scattered pattern of dispersal.”

From GISD (2016):

“Canada > Ontario”

From Kotov and Taylor (2014):

“*D. lumholtzi* was collected in a pool (coordinates: 31.6631°S; 60.5935°W) adjacent to the Paraná River, between Paraná and Santa Fe, Santa Fe Province [Argentina] on 19 February 2006 [...]”

## Means of Introduction Outside the United States

From Zanata et al. (2003):

“Some authors have suggested that intercontinental dispersion of cladocerans is rare, although the production of resting eggs and the parthenogenetic reproduction mode have been facilitating dispersion (Dodson & Frey, 1991). According to Havel & Hebert (1993), another dispersion agent could be the introduction into reservoirs of fishes for angling purposes. Once the species reaches the new continent, its dispersal could be by means of boats used for recreational activities.”

From Kotov and Taylor (2014):

“Since *D. lumholtzi* is known to disperse by river systems, the simplest hypothesis for the immediate source of the Argentinian *D. lumholtzi* is dispersal from the Brazilian populations of the Upper Paraná River detected in 2003 (Simões et al., 2009).”

## Short Description

From Fofonoff et al. (2003):

“*Daphnia lumholtzi* is morphologically distinctive. Its head-spine (helmet) is larger than that of any native species and its tail spine is equal to, or greater than, its body length. There is a depression (cervical sinus) separating the dorsal base of the head from the rest of the body. The posterior part of the head bears two projecting structures called fornices (fornix = arch or fold), which in this species are projected into sharp points. The ventral carapace bears about 10 sharp spines on each side (Havel and Hebert 1993).”

“Male *D. lumholtzi* usually have a head without a helmet, or occasionally with a small spike-shaped crest. The tail spine is about two-thirds the carapace length (Zanata et al 2003). The ephippia (resting egg capsules) of *D. lumholtzi* have a long point on each end and a dorsal surface covered with fine hairs (Havel and Hebert 1993).”

## Biology

From CABI (2016):

“*Daphnia* spp. can be found in almost any permanent body of water. They are mainly freshwater and densely populate most lakes and ponds. They live as plankton in the open water of lakes, or live either attached to vegetation or near the bottom of the body of water (Miller, 2000).”

From Fofonoff et al. (2003):

“Cladocerans of the genus *Daphnia* can develop parthenogenetically from unfertilized eggs in a female's brood pouch. The juveniles have the basic form of miniature adults, and molt and grow as they feed. After a period of growth, parthenogenetic eggs are deposited in the female's brood pouch. For *D. lumholtzi* at 15-25 C, the eggs were produced at 8.7-4.7 days after birth, and took 1.9- 1.1 days to develop (Tifnouti et al. 1993). When the embryos hatch, the female molts, and a new batch of eggs are deposited in the brood pouch. A female may have several successive broods. Female *D. lumholtzi* at 20-25 C, on average, had 6.9 - 6.4 broods, consisting of 2.2-2.4 eggs each, and lived for up to 30 days. With parthenogenetic development, and a generation time of 6-9 days, *D. lumholtzi* is capable of rapid population growth (Tifnouti et al. 1993).”

“*Daphnia* spp. can reach high population densities by parthenogenetic reproduction, developing populations that are all female or female-dominated. Environmental factors such as temperature, day-length, the presence of predators, etc., appear to stimulate the production of males. Females, when fertilized, produce large resting eggs, in pairs, enclosed in a capsule formed by modifications of the brood chamber (called an ephippium). The ephippium is cast off when the female molts. It settles into the sediment, but may be stimulated to development by favorable conditions of light and temperature. Sexual reproduction of resting eggs provides a means of surviving winter, droughts, or other adverse conditions, as well as providing new genotypes for potentially altered conditions (Barnes 1983).”

“*Daphnia* sp. are filter-feeders, creating a current and filtering out phytoplankton in the water column. They have limited capacity for selective feeding (Barnes 1983), but may reduce filtering rates in the presence of large chains of diatoms, or large colonies of toxic organisms, such as cyanobacteria of the genus *Microcystis* sp. (Gifford et al. 2007; Davis and Gobler 2011).”

## Human Uses

From CABI (2016):

“Research model”

From Cáceres et al. (2014):

“In the last few decades, zooplankton (especially *Daphnia*) have emerged as a model system for examining the ecological and evolutionary roles of parasites in populations, communities and ecosystems.”

## Diseases

From Searle et al. (2016):

“The fungus *Metschnikowia bicuspidata* (Duffy et al. 2010; Hall et al. 2010) is a common, environmentally transmitted parasite of the native host. When *Daphnia* ingest spores of this parasite, it penetrates the gut wall and proliferates in the host's hemolymph. It is highly virulent; infected individuals experience reduced fecundity and reduced life span (Ebert et al. 2000; Duffy

and Hall 2008). Infections are easily identified because they turn the normally transparent hosts opaque (Duffy and Hall 2008); spores are only released when infected *Daphnia* die.”

From Cáceres et al. (2014):

“[...] infection by *Pasteuria* (M.A. Duffy, unpubl. data) [...]”

## Threat to Humans

No information available.

## 3 Impacts of Introductions

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From Benson et al. (2016):

“The impacts of this invader are not yet fully understood. It competes with native daphnia for food and of [*sic*] its ability to avoid predation (U.S.EPA 2008).”

“Studies that have compared native *Daphnia* to the exotic *D. lumholtzi* have found that competition between these species is lower than expected. *D. lumholtzi* is a tropical species, and is adapted to warmer temperatures than native North American *Daphnia*. Thus *D. lumholtzi* population sizes tend to rise in late summer when native *Daphnia* populations are dropping. Thus *D. lumholtzi* tends to fill a vacant "temporal niche" in the warmer summer months (Johnson and Havel 2001; Work and Gophen 1999; Dzialowski et al. 2000; Goulden et al. 1995; East et al. 1999). Dzialowski et al. (2000) hypothesized that by occupying a niche that was previously unexploited by *Daphnia*, *D. lumholtzi* competed with non-daphnid zooplankton otherwise able to obtain resources during that time. One such zooplankton was *Diaphanosoma*, whose population was found to be significantly lower in reservoirs of Kansas where *D. lumholtzi* had invaded (Dzialowski et al. 2000). If *D. lumholtzi* has a negative impact on other native zooplankton populations in late summer, this may have a detrimental effect on fishes that depend on zooplankton at that time period but are not able to handle the spines of *D. lumholtzi*.”

“Larval and juvenile stages of fish that overlap with high *D. lumholtzi* populations are more likely to be negatively impacted by *D. lumholtzi* due to gape limitation (Kolar and Wahl 1998). L[ie]nesch and Gophen (2001) noted that fish large enough to handle *D. lumholtzi* spines would have a new prey item with a larger overall body size than the zooplankton normally present in the later summer months. Lemke et al. (2003) studied four fish species that consumed more *D. lumholtzi* as fish size increased (blue gill, white bass, white crappie, and black crappie of Lake Chautauqua, Illinois). Silversides (*Menidia beryllina*) may be able to utilize this new prey item and survive longer during their late summer spawning period (L[ie]nesch and Gophen 2001). L[ie]nesch and Gophen (2001) hypothesized that when growing juvenile fish become capable of handling *D. lumholtzi*, the fish can grow more rapidly and reduce their risk of predation.”

From Fofonoff et al. (2003):

“Mesocosm experiments in Missouri showed that *D. lumholtzi* suppressed the increase of the native *D. parvula* in late summer and fall, but not birth rates, suggesting that the suppression of

*D. parvula* resulted from increased death rates, possibly due to juvenile starvation (Johnson and Havel 2001). However, field surveys and experiments in Missouri reservoirs indicate that relations between *D. lumholtzi* and native *Daphnia* are largely complementary, with *D. lumholtzi* co-occurring with natives, and dominating in summer conditions when native species are normally scarce, while natives dominate in cooler periods, as they had prior to the *D. lumholtzi* invasion (Havel and Graham 200[6]).”

“Differential predation also plays a role in zooplankton interactions. In Lake Springfield, IL, the invasion of *D. lumholtzi* was followed by a change in species composition, with decreased abundance of native cladocerans. Kolar et al. (199[7]) speculated that competition with native cladocerans in late summer and fall, may affect spring recruitment of the native species. The species co-occur only briefly, but during this time competition, combined with differential predation, may be affecting native cladocerans, which then are overwintering or producing resting eggs, and providing next spring's generations. Predation by fishes may reinforce the effects of competition, since fishes tend to select the less spiny native cladocerans (Kolar et al. 199[7]). In experiments with mesocosms containing *D. lumholtzi*, native *D. pulex*, with and without juvenile Pumpkinseed (*Lepomis gibbosus*) fish, *D. lumholtzi* predominated at higher temperature in the presence of fish, because of its higher [sic] temperature tolerance, predator defenses, and the increasing rates of predation at higher [sic] temperatures (Fey and Herren 2014).”

“Initial research suggests that this spiny cladoceran may be altering the available food supply for juvenile fishes, potentially affecting recruitment (Swaff[a]r and O'Brien 1996; Kolar et al. 199[7]). Larval Bluegill Sunfish in laboratory feeding trials preferred the native, shorter-spined *D. magna* or *D. pulex* to *D. lumholtzi*, which were often visually rejected. Visual observation indicated that smallest fish had the greatest trouble ingesting *D. lumholtzi* (Kolar and Wahl 1998; Swaff[a]r and O'Brien 1996).”

From Havens et al. (2012):

“We found that in most of the studied lakes in Florida, *D. lumholtzi* occurred less often and at lower densities than the native *D. ambigua*. [...] we found little evidence that *D. lumholtzi* can out-compete *D. ambigua*, its smaller congener, despite their co-occurrence for years in lakes with phytoplankton that is dominated by cyanobacteria, water temperatures that become very high in mid-summer, and high concentrations of suspended solids – all factors that previous research suggested would favour *D. lumholtzi*.”

“Lake Jesup, in the St Johns River system, is an outlier among our results. It is the one lake where *D. lumholtzi* periodically attained very high population densities, even after periods of apparent absence from the plankton, and at higher densities than *D. ambigua* on several occasions. [...] The periodic high densities of *D. lumholtzi* in Lake Jesup suggest that although Florida lakes typically do not provide conditions suitable for *D. lumholtzi* to attain high densities, there may be a potential for this to occur.”

## 4 Global Distribution



**Figure 1.** Known global established locations of *D. lumholtzi*. Map from GBIF (2016). Points in Australia outside Queensland and the Northern Territory were not included in climate matching due to locational inaccuracy (CABI 2016). Although the native range of *D. lumholtzi* includes locations in Africa and Asia, GBIF (2016) does not have any georeferenced occurrences reported on those continents.

## 5 Distribution Within the United States

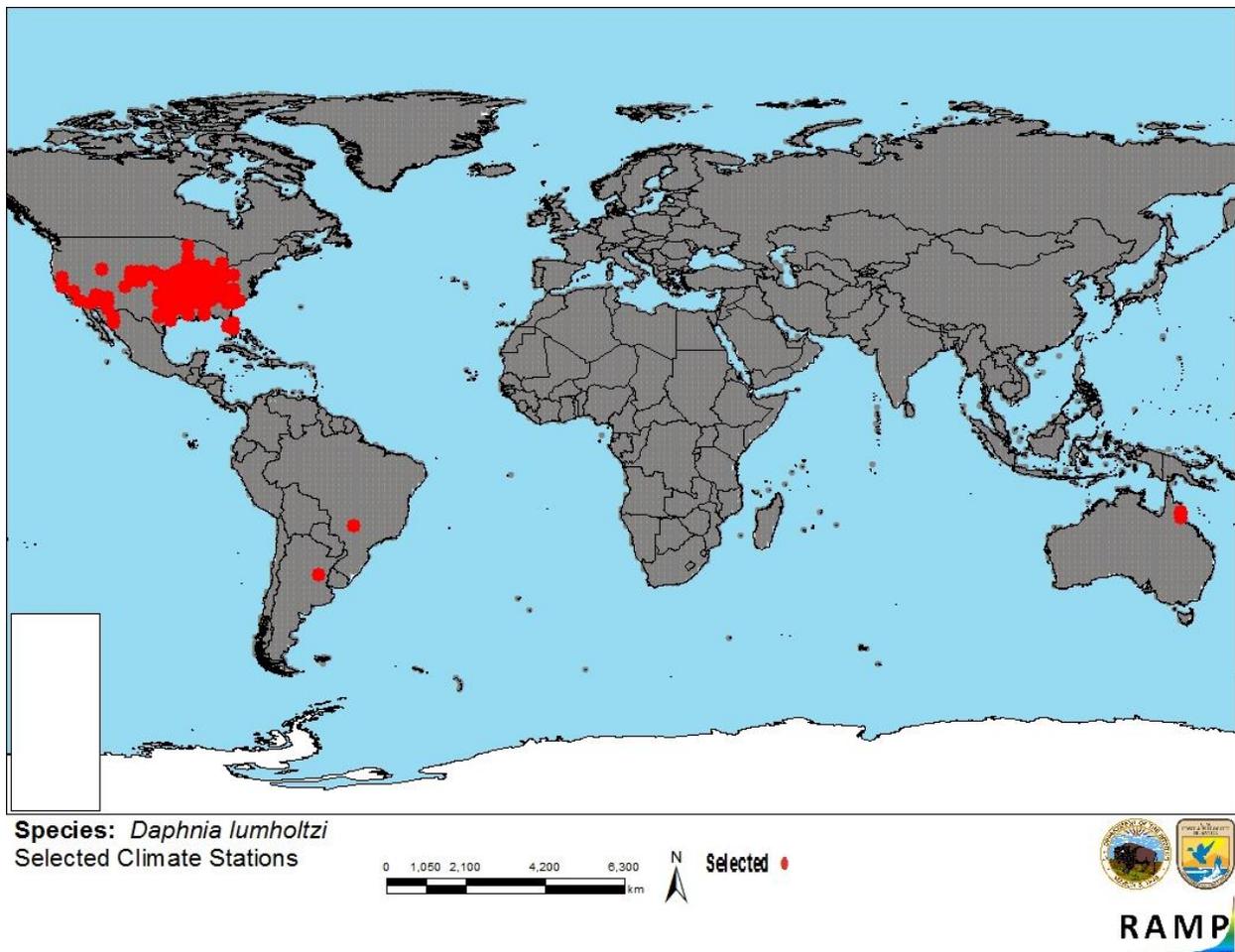


**Figure 2.** Known distribution of *D. lumholtzi* in the United States. Map from Benson et al. (2016).

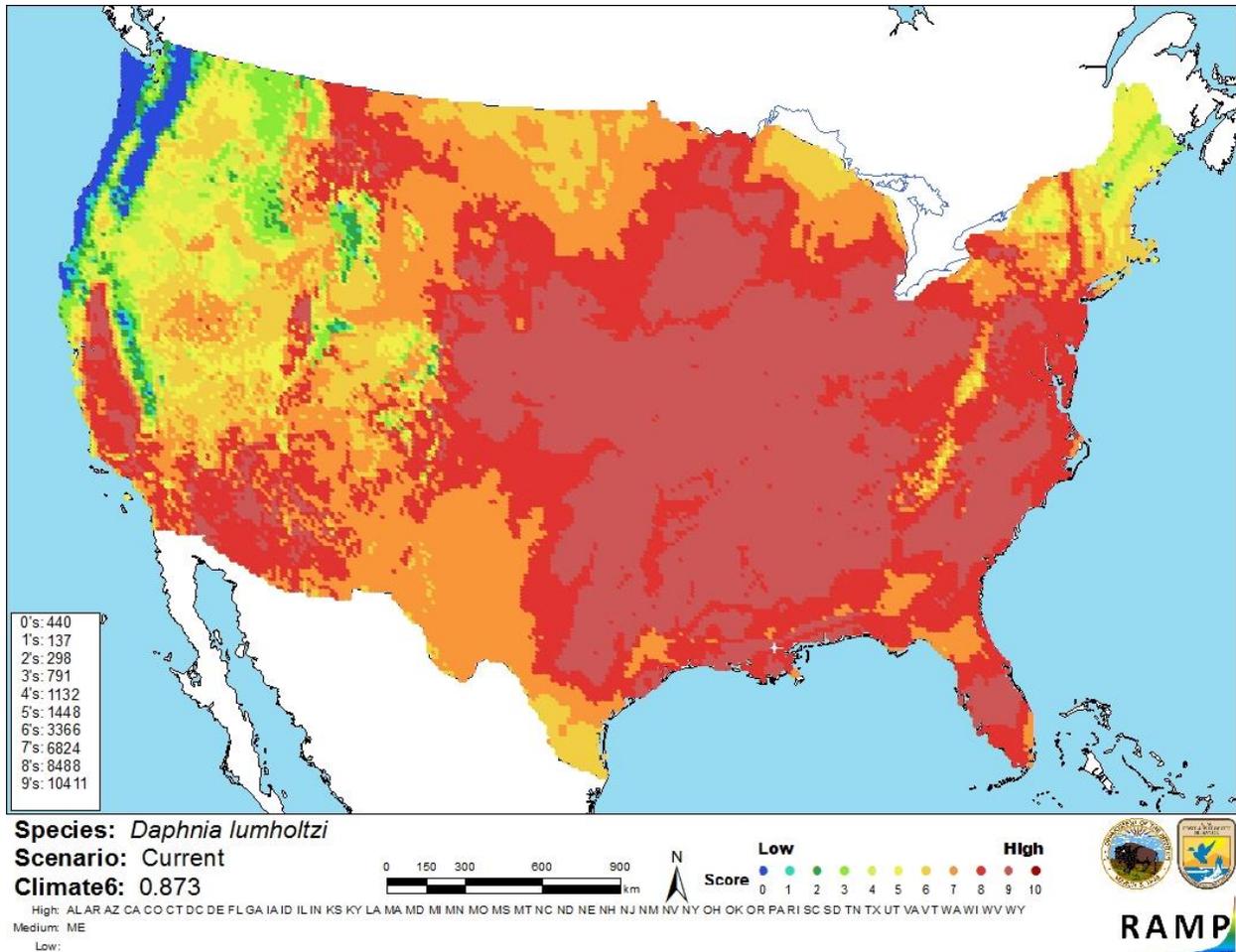
## 6 Climate Matching

### Summary of Climate Matching Analysis

The climate match (Sanders et al. 2014; 16 climate variables; Euclidean Distance) was high across nearly all of the eastern and central U.S., the Southwest, and California. Climate match was also high in patches of the Interior West. Climate match was moderate in the Northeast, parts of the Great Lakes region, the North-Central U.S., much of the Interior West, and western and southern Texas. Climate match was low in the Pacific Northwest. Climate 6 score indicated that the contiguous US has a high climate match. The range of scores indicating a high climate match is 0.103 and greater; Climate 6 score for *D. lumholtzi* was 0.873. This score, although high, may still be an underestimate of *D. lumholtzi* climate match to the continental U.S., as much of the native range of *D. lumholtzi* was not represented in the source locations for matching.



**Figure 3.** RAMP (Sanders et al. 2014) source map showing weather stations selected as source locations (red) and non-source locations (gray) for *D. lumholtzi* climate matching. Source locations from GBIF (2016) and Benson et al. (2016). Additional locations from Zanata et al. (2003; Brazil) and Kotov and Taylor (2014; Argentina).



**Figure 4.** Map of RAMP (Sanders et al. 2014) climate matches for *D. lumholtzi* in the contiguous United States based on source locations reported by GBIF (2016), Benson et al. (2016), Zanata et al. (2003), and Kotov and Taylor (2014). 0= Lowest match, 10=Highest match. Counts of climate match scores are tabulated on the left.

The “High”, “Medium”, and “Low” climate match categories are based on the following table:

Climate 6: Proportion of (Sum of Climate Scores 6-10) / (Sum of total Climate Scores)	Climate Match Category
$0.000 \leq X \leq 0.005$	Low
$0.005 < X < 0.103$	Medium
$\geq 0.103$	High

## 7 Certainty of Assessment

Information on the biology and ecology of *D. lumholtzi* is available. The distribution in the U.S. is well-described, but range expansion may be ongoing and few data exist on the distribution of *D. lumholtzi* outside the U.S. Several peer-reviewed studies have been published on the impacts of *D. lumholtzi* invasion, but authors have come to varying conclusions about the seriousness of these impacts. Certainty of assessment is medium.

## 8 Risk Assessment

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### Summary of Risk to the Contiguous United States

*Daphnia lumholtzi* is a cladoceran native to parts of Africa, Asia, and Australia. It has recently become established in numerous locations in the United States, as well as scattered locations in Canada, Mexico, Brazil, and Argentina. Although competition between *D. lumholtzi* and native *Daphnia* in the U.S. is reduced by differences in phenology, competition can occur in certain circumstances and differential predation may reinforce the effects of competition. *D. lumholtzi* has also been associated with declines in the zooplankton *Diaphanosoma*. *D. lumholtzi* is less available to juvenile fish predators than native *Daphnia* because of its larger size and prominent spines. Climate match is very high and potential pathways of introduction are not well understood or managed, so further range expansion in the United States is likely. Overall risk posed by *D. lumholtzi* is high.

### Assessment Elements

- **History of Invasiveness: High**
- **Climate Match: High**
- **Certainty of Assessment: Medium**
- **Overall Risk Assessment Category: High**

## 9 References

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**Note: The following references were accessed for this ERSS. References cited within quoted text but not accessed are included below in Section 10.**

- Benson, A., E. Maynard, D. Raikow, J. Larson, T. H. Makled, and A. Fusaro. 2016. *Daphnia lumholtzi*. USGS Nonindigenous Aquatic Species Database, Gainesville, Florida. Available: <https://nas.er.usgs.gov/queries/FactSheet.aspx?SpeciesID=164>. (November 2016).
- CABI. 2016. *Daphnia lumholtzi* [original text by J. Stoeckel]. Invasive Species Compendium. CAB International, Wallingford, United Kingdom. Available: <http://www.cabi.org/isc/datasheet/107777>. (November 2016).
- Cáceres, C. E., A. J. Tessier, M. A. Duffy, and S. R. Hall. 2014. Disease in freshwater zooplankton: what have we learned and where are we going? *Journal of Plankton Research* 36(2):326-333.
- Fofonoff, P. W., G. M. Ruiz, B. Steves, and J. T. Carlton. 2003. *Daphnia lumholtzi*. National Exotic Marine and Estuarine Species Information System. Available: <http://invasions.si.edu/nemesis/browseDB/SpeciesSummary.jsp?TSN=-210>. (November 2016).

- GBIF (Global Biodiversity Information Facility). 2016. GBIF backbone taxonomy: *Daphnia lumholtzi* Sars, 1885. Global Biodiversity Information Facility, Copenhagen. Available: <http://www.gbif.org/species/2234817>. (November 2016).
- GISD (Global Invasive Species Database). 2016. Species profile: *Daphnia lumholtzi*. IUCN Invasive Species Specialist Group, Gland, Switzerland. Available: <http://www.iucngisd.org/gisd/speciesname/Daphnia+lumholtzi>. (November 2016).
- Havens, K. E., J. R. Beaver, T. L. East, K. Work, E. J. Phlips, M. F. Cichra, A. C. Croteau, A. J. Rodusky, R. S. Fulton III, and T. C. Rosati. 2012. The outcome of the invasion of Florida lakes by *Daphnia lumholtzi*. *Freshwater Biology* 57(3):552-562.
- ITIS (Integrated Taxonomic Information System). 2016. *Daphnia lumholtzi* G. O. Sars, 1885. Integrated Taxonomic Information System, Reston, Virginia. Available: [https://www.itis.gov/servlet/SingleRpt/SingleRpt?search\\_topic=TSN&search\\_value=684652#null](https://www.itis.gov/servlet/SingleRpt/SingleRpt?search_topic=TSN&search_value=684652#null). (November 2016).
- Kotov, A. A., and D. J. Taylor. 2014. *Daphnia lumholtzi* Sars, 1885 (Cladocera: Daphniidae) invades Argentina. *Journal of Limnology* 73(2):369-374.
- Sanders, S., C. Castiglione, and M. Hoff. 2014. Risk Assessment Mapping Program: RAMP. U.S. Fish and Wildlife Service.
- Searle, C. L., M. H. Cortez, K. K. Hunsberger, D. C. Grippi, I. A. Oleksy, C. L. Shaw, S. B. de la Serna, C. L. Lash, K. L. Dhir, and M. A. Duffy. 2016. Population density, not host competence, drives patterns of disease in an invaded community. *The American Naturalist* 188(5):554-566.
- Zanata, L. H., E. L. G. Espíndola, O. Rocha, and R. H. G. Pereira. 2003. First record of *Daphnia lumholtzi* (Sars, 1885), exotic cladoceran, in São Paulo State (Brazil). *Brazilian Journal of Biology* 63(4):717-720.

## 10 References Quoted But Not Accessed

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**Note: The following references are cited within quoted text within this ERSS, but were not accessed for its preparation. They are included here to provide the reader with more information.**

- Barnes, R. D. 1983. *Invertebrate zoology*. Saunders, Philadelphia.
- Davis, T. W., and C. J. Gobler. 2011. Grazing by mesozooplankton and microzooplankton on toxic and non-toxic strains of *Microcystis* in the Transquaking River, a tributary of Chesapeake Bay. *Journal of Plankton Research* 33:415-430.
- Dodson, S. I., and D. G. Frey. 1991. Cladocera and other Branchiopoda. Pages 723-786 in J. H. Thorpe, and A. P. Covich, editors. *Ecology and classification of North American freshwater invertebrates*. Academic Press, San Diego, California.

- Duffy, M. A., C. E. Cáceres, S. R. Hall, A. J. Tessier, and A. R. Ives. 2010. Temporal, spatial, and between-host comparisons of patterns of parasitism in lake zooplankton. *Ecology* 91:3322-3331.
- Duffy, M. A., and S. R. Hall. 2008. Selective predation and rapid evolution can jointly dampen effects of virulent parasites on *Daphnia* populations. *American Naturalist* 171:499-510.
- Dzialowski, A. R., W. J. O'Brien, and S. M. Swaffar. 2000. Range expansion and potential dispersal mechanisms of the exotic cladoceran *Daphnia lumholtzi*. *Journal of Plankton Research* 22(12):2205-2223.
- East, T. L., K. E. Havens, A. J. Rodusky, and M. A. Brady. 1999. *Daphnia lumholtzi* and *Daphnia ambigua*: population comparisons of an exotic and a native cladoceran in Lake Okeechobee, Florida. *Journal of Plankton Research* 21(8):1537-1551.
- Ebert, D., M. Lipsitch, and K. L. Mangin. 2000. The effect of parasites on host population density and extinction: experimental epidemiology with *Daphnia* and six microparasites. *American Naturalist* 156:459-477.
- Elías-Gutiérrez, M., F. M. Jerónimo, N. V. Ivanova, M. Valdez-Moreno, and P. D. N. Hebert. 2008. DNA barcodes for Cladocera and Copepoda from Mexico and Guatemala, highlights and new discoveries. *Zootaxa* 1839:1-42.
- Engel, K., and R. Tollrian. 2012. Competitive ability, thermal tolerance and invasion success in exotic *Daphnia lumholtzi*. *Journal of Plankton Research* 34:91-97.
- Fey, S. B., and K. L. Cottingham. 2011. Linking biotic interactions and climate change to the success of exotic *Daphnia lumholtzi*. *Freshwater Biology* 56:2196-2209.
- Fey, S. B., and C. M. Herren. 2014. Temperature-mediated biotic interactions influence enemy release of nonnative species in warming environments. *Ecology* 95:2246-2256.
- Gifford, S. M., G. Rollwagen-Bollens, and S. M. Bollens. 2007. Mesozooplankton omnivory in the upper San Francisco Estuary. *Marine Ecology Progress Series* 348:33-46.
- Goulden, C. L., D. Tomljanovich, D. Kreeger, and E. Corney. 1995. The invasion of *Daphnia lumholtzi* Sars (Cladocera, Daphniidae) into a North American reservoir. Pages 9-38 in S. W. Hamilton, D. S. White, E. W. Chester, and A. F. Scott, editors. *Proceedings of the sixth symposium on the natural history of the lower Tennessee and Cumberland River Valleys*. The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.
- Hairston, N. G., Jr., L. J. Perry, A. J. Bohonak, M. Q. Fellows, C. Kearns, D. R. Engstrom. 1999. Population biology of a failed invasion: paleolimnology of *Daphnia exilis* in upstate New York. *Limnology and Oceanography* 44:477-486.

- Hall, S. R., R. Smyth, C. R. Becker, M. A. Duffy, C. J. Knight, S. MacIntyre, A. J. Tessier, and C. E. Cáceres. 2010. Why are *Daphnia* in some lakes sicker? Disease ecology, habitat structure, and the plankton. *BioScience* 60:363-375.
- Havel, J. E., and J. L. Graham. 2006. Complementary population dynamics of exotic and native *Daphnia* in North American reservoir communities. *Archiv fur Hydrobiologie* 167:245-264.
- Havel, J. E., and P. D. N. Hebert. 1993. *Daphnia lumholtzi* in North America: another exotic zooplankton. *Limnology and Oceanography* 38:1837-1841.
- Havel, J. E., W. R. Mabee, and J. R. Jones. 1995. Invasion of the exotic cladoceran *Daphnia lumholtzi* into North American reservoirs. *Canadian Journal of Fisheries and Aquatic Sciences* 52:151-160.
- Havel, J. E., and J. B. Shurin. 2004. Mechanisms, effects, and scales of dispersal in freshwater zooplankton. *Limnology and Oceanography* 49:1229-1238.
- Johnson, W. S., and D. M. Allen. 2005. Zooplankton of the Atlantic and Gulf coasts. Johns Hopkins Press, Baltimore.
- Johnson, J. L., and J. E. Havel. 2001. Competition between native and exotic *Daphnia*: *in situ* experiments. *Journal of Plankton Research* 23(4):373-387.
- Kolar, C. S., J. C. Boase, D. F. Clapp, and D. H. Wahl. 1997. Potential effect of invasion by an exotic zooplankton, *Daphnia lumholtzi*, *Journal of Freshwater Ecology* 12:521-530.
- Kolar, C. S., and D. H. Wahl. 1998. Daphnid morphology deters fish predators. *Oecologia* 116:556-564.
- Lemke, A. M., J. A. Stoekel, and M. A. Pegg. 2003. Utilization of the exotic cladoceran *Daphnia lumholtzi* by juvenile fishes in an Illinois River floodplain lake. *Journal of Fish Biology* 62:938-954.
- Lenon, J. T., V. H. Smith, and K. Williams. 2001. Influence of temperature on exotic *Daphnia lumholtzi* and implications for invasion success. *Journal of Plankton Research* 23(4):425-434.
- Lienesch, P. W., and M. Gophen. 2001. Predation by inland silversides on an exotic cladoceran, *Daphnia lumholtzi*, in Lake Texoma, U.S.A. *Journal of Fish Biology* 59:1249-1257.
- Miller, C. 2000. *Daphnia pulex*. Animal Diversity Online. Available: [http://animaldiversity.ummz.umich.edu/site/accounts/information/Daphnia\\_pulex.html](http://animaldiversity.ummz.umich.edu/site/accounts/information/Daphnia_pulex.html). (January 2005).

- Muzinic, C. J. 2000. First record of *Daphnia lumholtzi* Sars in the Great Lakes. *Journal of Great Lakes Research* 26(3):352-354.
- Silva-Briano, M., G. Arroyo-Bustos, R. Beltrán-Álvarez, A. Adabache-Ortiz, and R. G. de la Rosa. 2010. [*Daphnia Ctenodaphnia lumholtzi* G. O. Sars, 1885 (Crustacea: Cladocera)]; an exotic cladoceran in Mexico]. *Hidrobiológica* 20:275-280.
- Simões, N. R., B. A. Robertson, F. A. Lansac-Tôha, E. M. Takahashi, C. C. Bonecker, L. F. M. Velho, and C. Y. Joko. 2009. Exotic species of zooplankton in the Upper Paraná River floodplain, *Daphnia lumholtzi* Sars, 1885 (Crustacea: Branchiopoda). *Brazilian Journal of Biology* 69:551-558.
- Swaffar, S. M., and J. W. O'Brien. 1996. Spines of *Daphnia lumholtzi* create feeding difficulties for juvenile bluegill sunfish (*Lepomis macrochirus*). *Journal of Plankton Research* 18:1055-1061.
- Tifnouti, A., R. Pourrio, and C. Rougier. 1993. Influence de la temperature sur le developpement et la fecondite de quatre especes de Cladoceres. *Planctoniques (Crustaces) en presence de ressources naturelles. Annales de Limnologie* 29:3-13.
- U.S. EPA (Environmental Protection Agency). 2008. Predicting future introductions of nonindigenouse species to the Great Lakes. EPA/600/R-08/066F. National Center for Environmental Assessment, Washington, DC. Available: <http://www.epa.gov/ncea>.
- Work, K., and M. Gophen. 1995. Invasion of *Daphnia lumholtzi* (Sars) into Lake Texoma (USA). *Archiv fur Hydrobiologie* 133:287-303.
- Work, K. A., and M. Gophen. 1999. Factors which affect the abundance of an invasive cladoceran, *Daphnia lumholtzi*, in U.S. reservoirs. *Freshwater Biology* 42:1-10.