BioInvasions Records (2014) Volume 3, Issue 2: 89–95
doi: http://dx.doi.org/10.3391/bir.2014.3.2.06

Research Article

Invasion of the Allegheny River in Pennsylvania by the spiny water flea (*Bythotrephes longimanus* Leydig, 1860)

David G. Argent*, William G. Kimmel, Derek K. Gray, Brian Deleonibus and David Drescher
California University of Pennsylvania, 250 University Avenue, California, PA 15419, USA
**Corresponding author*
E-mail: argent@calu.edu

Received: 25 January 2014 / Accepted: 20 March 2014 / Published online: 14 April 2014

Handling editor: Ian Duggan

Abstract

The spiny water flea (*Bythotrephes longimanus*), has successfully established populations in North American reservoirs and lakes, but little is known of its movement between lake and river systems. Here we document the first longitudinal movement of this aquatic invader in the Allegheny River, Pennsylvania. During spring 2013 we collected samples from the tailrace of Kinzua Dam to the confluence of Oil Creek, Oil City Pennsylvania, a distance of 100 km. The spiny water flea was present along 24 km of the sampled reach, comprising from 10 to 30% of the total zooplankton assemblage. In addition we collected two species of *Daphnia,* the dominant taxon, and *Leptodora kindtii*. All three developmental stages of the spiny water flea were present in samples collected (Instars I, II, and III). This study presents one of the first documented expansions of this species from an impoundment to downstream riverine reaches. Its presence warrants further monitoring and appropriate strategies to curb its spread and to investigate its potential impact on the lotic food web.

Key words: Allegheny River, Kinzua Dam, *Bythotrephes*, spiny water flea, river invasion

Introduction

There is increasing concern among biologists regarding the ecological impacts of aquatic invasive species. Among the more difficult to detect are those not readily seen by the naked eye from field collections - that is, until large aggregations form. One such invader, the spiny water flea (*Bythotrephes longimanus* Leydig, 1860), has successfully established populations in North American reservoirs and lakes (Branstrator et al. 2006; Cullis and Johnson 1988; Kelly et al.2013; Lange and Cap 1986; USGS 2013a). First detected in Lake Huron (Bur et al. 1986), this species quickly spread to all of the Great Lakes (Bur et al. 1986; Lange and Cap 1986; Cullis and Johnson 1988; Evans 1988), a likely result of Euro-Asian ship ballast water exchanges (Sprules et al. 1990; Berg et al. 2002; Colautti et al. 2005). Since its initial discovery, the spiny water flea has moved inland to a number of reservoirs and lakes (MacIsaac et al. 2000, 2004; Branstrator et al. 2006; Kelly et al. 2013), a probable consequence of recreational boaters (MacIsaac et al. 2004; Johnson et al. 2008).

Reaching 12 mm in length when sexually mature (Branstrator 2005), *B. longimanus* has been implicated as causing major shifts in resident zooplankton, phytoplankton, and macroinvertebrate community composition (Lehman and Cáceres 1993; Foster and Sprules 2009; Strecker et al. 2011; Yan et al. 2002, 2011). By consuming native cladocerans, copepods, and rotifers, the spiny water flea directly competes with larval fish (Berg and Garton 1988; Coulas et al. 1988; Evans 1988; Vanderploeg et al. 1993). However, due to its abundance in some systems, it has also become a significant food source for a variety of fish species during various portions of their life cycles (Nilsson 1979; Bur et al. 1986; Makarewicz and Jones 1990; Branstrator and Lehman 1996; Amtstaetter 2000; McRae 2001) while deterring consumption by others with its long spine

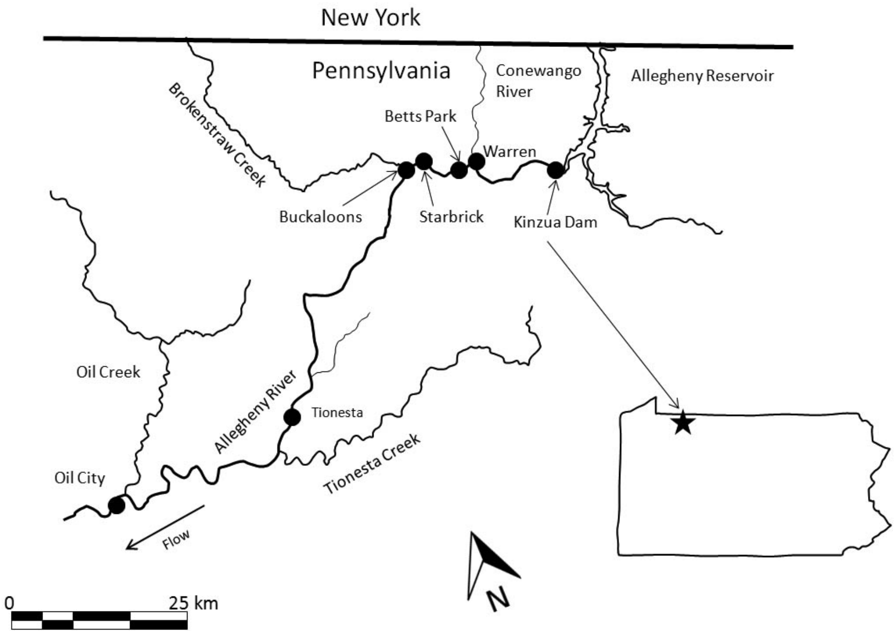

Figure 1. Map of study reach and sampling stations along the Allegheny River. Star on inset map of Pennsylvania denotes the approximate location of Kinzua Dam.

(Garton et al. 1993; Barnhisel and Harvey 1995; Compton and Kerfoot 2004). As a result, evidence suggests that the spiny water flea can exert both top-down and bottom-up control of predator and prey populations (MacIsaac et al. 2004; Brown et al. 2012; Kelly et al. 2013).

Because of its ability to disrupt aquatic ecosystems, the spread of this species has been of concern to state and federal regulatory agencies in the United States. While the movement of *B. longimanus* among lakes has been well documented (Colautti et al. 2005), few studies have examined the fate of this species in lotic systems. Previous studies indicate that impoundments can provide suitable sites for colonization (Johnson et al. 2008; Brown et al. 2012), as recreational boaters move among systems – often unknowingly from infested to pristine waters.

The discharge of water from a reservoir colonized by *B. longimanus* could allow for downstream movement of the species. While downstream dispersal has been documented for some invasive zooplankters (e.g. *Daphnia lumholtzi*; Shurin and Havel 2002), we were unable to find studies that detailed the potential extent of downstream movement in *B. longimanus*. For this study we had three main objectives: 1) to document the presence of *B. longimanus* in the Allegheny River; 2) to describe the longitudinal distribution of spiny water fleas from the tailrace of Kinzua Dam (KD), which forms the Allegheny Reservoir (AR), to its farthest extent downstream; and 3) to determine the relative abundance of *B. longimanus* in the zooplankton assemblage.

Methods

Study location

In 1965, the U.S. Army Corps of Engineers (USACE) completed construction of one of its largest flood control structures near the Pennsylvania/New York border, Kinzua Dam (KD) (Figure 1). Designed to regulate discharge on the Allegheny River, KD created the nearly 86 km^2 AR (Cowell and Stoudt 2007). From the reservoir, water discharged through KD flows another 300 km west and south to its Pittsburgh confluence with the Monongahela River to form the Ohio River. Approximately 195 km downstream

Table 1. Allegheny River sampling stations. Geo-referenced locations are given in decimal degrees. Corresponding station location map is presented in Figure 1.

Stations	Distance from KD (km)	Latitude	Longitude
Kinzua Dam	0	41.83845	-79.00373
Warren	11	41.83859	-79.14512
Betts Park	16	41.83317	-79.17362
Starbrick	21	41.83731	-79.21445
Buckaloons Recreation Area	24	41.83827	-79.25358
Tionesta	65	41.50359	-79.45665
Oil City	100	41.42799	-79.72218

of KD is the first of a series of eight navigational lock and dam structures and their attendant pools. The AR, in addition to flood control, provides hydroelectric power and a variety of recreational benefits to the region. Because of its proximity to the Great Lakes and availability to boat access (Leung et al. 2006), it is logical to think that the spiny water flea would eventually be documented here (R. Hoskin U.S. Army Corps of Engineers, personal communication). However, because sluice gates on KD remain open during periods of low and high flow (median flow $85m^3/s$), the potential also exists for this invader to move directly into the AR system in Pennsylvania. Our study reach extended from the tailrace of KD to an area 2 km downstream of the AR's confluence with Oil Creek, a distance of approximately 100 km (Figure 1, Table 1). Within this reach we established seven sampling stations.

Sampling protocol and analysis

As part of our sampling protocol to collect larval paddlefish (*Polyodon spathula* Walbaum, 1792), we deployed paired 1000 µm mesh ichthyoplankton drift nets between May and June 2013, at mid-water (approximately 1–2 m deep) and benthic locations (up to 4 m deep) (Figure 1), as described by Braaten et al. (2009). Samples were taken under varying flow and temperature regimes, from 42 to 255 m^3/s and from 9 to 16°C, respectively (USGS 2013b); however, we did not attempt to quantify zooplankton in relation to flow or temperature as neither were recorded coincident with each sampling event. Tailrace sampling locations below KD were passively fished for 10 minutes. Here, we anchored our boat at fixed points and deployed the nets in a stationary fashion. However, because stations farther downstream did not provide the needed current to fish these nets, we switched to an active sampling method by towing the paired-drift nets through the water column for 10 minutes. Collected material was retrieved and stored in 10% formalin for post-processing. Due to the large mesh size of our nets, it is likely that many small zooplankters (e.g., *Bosmina* spp. and other Daphnids) were excluded from our samples.

In the laboratory, zooplankton and ichthyoplankton were identified to the lowest practicable taxonomic level and enumerated. Here, we report the zooplankton results. The relative abundance of zooplankton species at each station was determined from three replicate samples collected at each of the seven sampling stations. From each sample, we enumerated all individuals found in a series of subsamples until the coefficient of variation for each species fell below 30%. Subsamples were collected using a Hensen-Stempel pipette with a minimum of four 5–10 ml subsamples, from each sample. *B. longimanus* individuals were counted by eye in gridded petri dishes, while all other specimens were examined and enumerated under a dissecting microscope (~25–40× magnification). In addition, we took a subsample of 100 spiny water fleas from each station to determine life cycle stage (Instar I, II, or III). All collected organisms were identified according to Hebert (1995), Therriault et al. (2002), and Haney et al. (2013). We used Analysis of Variance (ANOVA) to determine if significant differences in proportional species and developmental stage composition existed among sampling locations. Prior to conducting the ANOVA, data were tested for normality using a Shapiro-Wilks test. In order to meet the assumption of normality, the proportional species data were arcsine square root transformed. If differences were detected in the ANOVAs, we employed a Tukey test (p-value<0.05), to ascertain statistical significance.

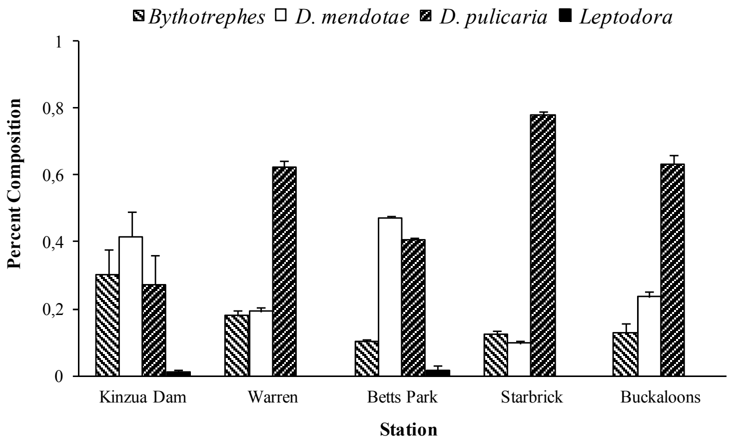

Figure 2. Mean percent community composition of zooplankton taxa among the five sampling stations. Error bars denote standard deviation about the mean.

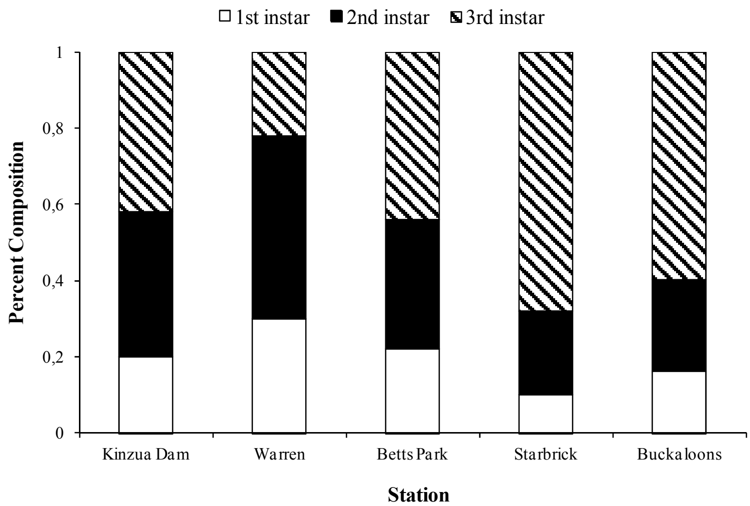

Figure 3. Percent composition of *Bythotrephes* developmental stages among all sampling stations where present

Results

The relative abundance of spiny water fleas was significantly higher in samples collected closer to the tailrace of KD (Figure 2; Tukey Test. P-value < 0.05). Our station at Warren (nearly 11 km downstream from KD) appeared to represent the initial point of a downstream decline in the relative abundance of *B. longimanus*, which comprised 18% of the sample here. The discharge from Conewango Creek (from 113 to 395 m^3/s) may have produced some dilution of the zooplankton assemblage at this station. Densities of the spiny water flea downstream of Betts Park were not significantly different (Tukey Test, p-value>0.05) from stations at Starbrick and Buckaloons, with spiny water fleas comprising about 10% of the total community composition (Figure 2). Instars I, II, and III were present (Figure 3) with the majority occurring as Instar III (Tukey Test. p-value < 0.05). Gravid females carrying developing embryos were also present. No zooplankton taxa were detected from stations at Tionesta or Oil City, 65 and 100 km downstream from KD, respectively.

In addition to the spiny water flea, we collected three other zooplankton species: *Daphnia pulicaria* Forbes, 1893, *Daphnia mendotae* Birge, 1918, and *Leptodora kindtii* (Focke, 1844) (Figure 1). *Daphnia* spp. were the dominant taxa collected, comprising over 80% of the total zooplankton abundance among four of our five sampling locations (Figure 2). By contrast, *L. kindtii* was collected from only two locations, below KD and at Betts Park, comprising < 2% of the total abundance at these stations (Figure 2). Proportional differences were detected among taxa across sampling stations (ANOVA, p-value = 0.016). Most of the *B. longimanus* (~80–90%) appeared to be in excellent condition when examined under the microscope. The remaining 10–20% had broken tail spines and other damage typically found upon examination of samples collected by plankton nets.

Discussion

Our results suggest that *B. longimanus* is present in the AR, at least 24 km downstream from KD. However, samples collected farther from KD contained fewer *B. longimanus* in relation to the native *Daphnia* species. There are at least two possible explanations for this result. First, *B. longimanus* may not have established in the Allegheny River, but may be present due to downstream movement from the AR. Mortality and dilution along the course of the river may then account for their decrease in relation to *Daphnia*. Alternatively, *B. longimanus* may have established in the Allegheny River, but changing environmental conditions along the course of the river may have favored *Daphnia*. Unfortunately, the condition of *B. longimanus* individuals in our samples did not allow us to differentiate between downstream movement and successful establishment. Most individuals examined under the microscope appeared to be in excellent condition, many carried brood pouches with developing embryos, and all three instars of *B. longimanus* were represented in our samples (Figure 3). More study will be needed to determine if spiny water fleas have actually established a self-sustaining population in the river.

As Johnson et al. (2008) suggest, reservoir construction and the conversion of lotic to lentic waters may ultimately facilitate the spread of invasive species across the landscape. The presence of *B. longimanus* in areas downstream of KD appears to support Johnson et al. (2008). However, the impact that this species has on the local fauna remains unknown. As other authors have reported, this invader can cause major shifts in zooplankton, phytoplankton, and macroinvertebrate community composition in introduced waters (Yan et al. 2002; Foster and Sprules 2009; Strecker et al. 2011). Of immediate concern is the potential for this invader to cause ecological shifts at higher trophic levels. Gill net surveys performed concurrently with zooplankton surveys yielded 22 fish species (Argent and Kimmel 2013). Among these were paddlefish, a "Species of Special Concern" in Pennsylvania, which is an obligate planktivore during portions of its life cycle (Jennings and Zigler 2009; Phelps et al. 2009). As Pegg et al. (2009) report, the spiny water flea is established in waters known to contain paddlefish and may pose a threat to their preferred forage.

A review of the literature reveals a paucity of information regarding the exploitation of the spiny water flea as a forage base by native Allegheny River fishes (see Argent and Kimmel (2013) for a list of native fishes). It is likely that larval resident fishes, if not gape limited, would utilize all zooplankton species with varying degrees of preference. However, as previous studies have demonstrated, *B. longimanus* can reduce the richness, diversity, and abundance of zooplankton in an invaded system (Yan et al. 2001, 2002; Strecker et al. 2006). If zooplankton assemblages respond similarly in the Allegheny River, resident fish populations could be negatively impacted.

We believe this study documents for the first time, the presence of the spiny water flea in the Allegheny River, an inland river system. The potential for this aquatic invader to facilitate an ecological shift exists in the areas below KD. Future studies should attempt to quantify this species' seasonal responses to varying flow regimes and its impacts on the riverine food web. Toward that end, more sampling effort should target the reach between Buckaloons and Tionesta, as well as downstream of Tionesta Reservoir, as this impoundment may serve as another inland source of expansion for the spiny water flea in the AR. Our farthest downstream locations (Tionesta and Oil City; Figure 1) did not yield any zooplankton taxa, which may be an artifact of the high flow conditions experienced during sampling events.

With the implementation of an appropriate sampling design and gear, more precise estimates of zooplankton density and species composition can be derived. Perhaps most important is the need to determine not only the linear extent of the spiny water flea, but how its presence alters the resident zooplankton assemblage of the AR. Over the lifespan of the spiny water flea (several days to a few weeks) and the flows experienced during this collection period, it is reasonable to conclude that these organisms may have traversed the entire 24km reach below the reservoir; however, it is also possible that reproduction occurred over downstream passage (as evidenced by the presence of all life cycle stages) and descendants arrived at the farthest documented downstream point. If the spiny water flea can maintain self-sustaining populations over long distances in a free-flowing river as this study suggests, it may eventually utilize the downstream series of Lock and Dam navigational pools on the AR to extend its range into the Monongahela and Ohio rivers.

Acknowledgements

We thank the State Wildlife Grants Program (SWG T2-10-R-1) and Pennsylvania Fish and Boat Commission, for their financial support. California University of Pennsylvania provided funding for zooplankton processing equipment. In addition we thank A. Stemko for assistance with sorting and identifying plankton samples and two anonymous reviewers for their comments on earlier drafts of the manuscript.

References

Amtstaetter F (2000) Lake trout and Lake Whitefish summer diet study, 1999. Ontario Ministry of Natural Resources Lake Simcoe Fisheries Assessment Unit Update No. 2000–1

Argent DG, Kimmel WG (2013) Update on the status of Paddlefish in Pennsylvania. State Wildlife Grant Interim Report. SWG T2-10-R-1: Phase III

Barnhisel DR, Harvey HA (1995) Size-specific fish avoidance of the spined crustacean *Bythotrephes*: field support for laboratory predictions. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 2111–2125

Berg DJ, Garton DW (1988) Seasonal abundance of the exotic predatory cladoceran, *Bythotrephes cederstroemi*, in western Lake Erie. *Journal of Great Lakes Research* 14: 479–488, http://dx.doi.org/10.1016/S0380-1330(88)71580-4

Berg DJ, Garton DW, MacIsaac HJ, Panov VE, Telesh IV (2002) Changes in genetic structure of North American *Bythotrephes* populations following invasion from Lake Ladoga, Russia. *Freshwater Biology* 47: 275–282, http://dx.doi.org/10.1046/j.1365-2427.2002.00805.x

Braaten PJ, Fuller DB, Lott RD (2009) Spawning migrations and reproductive dynamics of Paddlefish in the upper Missouri River basin, Montana and North Dakota. In: Paukert C, Scholten G (eds), Paddlefish Management, Propagation, and Conservation in the 21st Century: Building From 20 Years of Research and Management. American Fisheries Society Special Symposium 66, Bethesda, Maryland, pp 103–122

Branstrator DK (2005) Contrasting life histories of the predatory cladocerans *Leptodora kindtii* and *Bythotrephes longimanus*. *Journal of Plankton Research* 27: 569–585, http://dx.doi.org/10.1093/plankt/fbi033

Branstrator DK, Brown ME, Shannon LJ, Thabes M, Heimgartner K (2006) Range expansion of *Bythotrephes longimanus* in North America: evaluating habitat characteristic in the spread of an exotic zooplankter. *Biological Invasions* 8: 1367–1379, http://dx.doi.org/10.1007/s10530-005-5278-7

Branstrator DK, Lehman JT (1996) Evidence for predation by young-of-the-year Alewife and Bloater Chub on *Bythotrephes cederstroemi* in Lake Michigan. *Journal of Great Lakes Research* 22: 917–924, http://dx.doi.org/10.1016/S0380-1330(96)71012-2

Brown ME, Branstrator DK, Shannon LJ (2012) Population regulation of the spiny water flea (*Bythotrephes longimanus*) in a reservoir: Implications for invasion. *Journal of Limnology and Oceanography* 57: 251–271

Bur MT, Klarer DM, Krieger KA (1986) First records of a European cladoceran, *Bythotrephes cederstroemi*, in Lakes Erie and Huron. *Journal of Great Lakes Research* 12: 144–146, http://dx.doi.org/10.1016/S0380-1330(86)71711-5

Colautti RI, Manca M, Viljanen M, Ketelaars HA, Bürgi H, Macisaac HJ, Heath DD (2005) Invasion genetics of the Eurasian spiny waterflea: evidence for bottlenecks and gene flow using microsatellites. *Molecular Ecology* 14: 1869–1879, http://dx.doi.org/10.1111/j.1365-294X.2005.02565.x

Compton JA, Kerfoot WC (2004) Colonizing inland lakes: Consequences of YOY fish ingesting the spiny cladoceran (*Bythotrephes cederstroemi*). *Journal of Great Lakes Research* 30 (Suppl. 1): 315–326, http://dx.doi.org/10.1016/S0380-1330(04)70394-9

Coulas RA, MacIsaac HJ, Dunlop W (1998) Selective predation on an introduced zooplankter (*Bythotrephes cederstroemi*) by lake herring (*Coregonus artedii*) in Harp Lake, Ontario. *Freshwater Biology* 40: 343–355, http://dx.doi.org/10.1046/j.1365-2427.1998.00340.x

Cowell CM, Stoudt RT (2007) Dam-induced modifications to upper Allegheny River streamflow patterns and their biodiversity implications. *Journal of the American Water Resources Association* 38(1): 187–196, http://dx.doi.org/10.1111/j.1752-1688.2002.tb01545.x

Cullis KI, Johnson GE (1988) First evidence of the cladoceran *Bythotrephes cederstroemi* Schoedler in Lake Superior. *Journal of Great Lakes Research* 14: 524–525, http://dx.doi.org/10.1016/S0380-1330(88)71584-1

Evans MS (1988) *Bythotrephes cederstroemi*: its new appearance in Lake Michigan. *Journal of Great Lakes Research* 14: 234–240, http://dx.doi.org/10.1016/S0380-1330(88)71552-X

Foster SE, Sprules WG (2009) Effects of the *Bythotrephes* invasion on native predatory invertebrates. *Limnology and Oceanography* 54: 757–769, http://dx.doi.org/10.4319/lo.2009.54.3.0757

Garton DW, Berg DJ, Stoeckmann AM, Haag WR (1993) Biology of recent invertebrate invading species in the Great Lakes: the spiny water flea, *B. cederstroemi*, and the zebra mussel (*D. polymorpha*). In: McKnight NN (ed), Biological pollution: the control and impact of invasive exotic species. Indianapolis (IN): Indiana Academy Science, pp 63–84

Haney JF, Aliberti MA, Allan E, Allard S, Bauer DJ, Beagen W, Bradt SR, Carlson B, Carlson SC, Doan UM, Dufresne J, Godkin WT, Greene S, Kaplan A, Maroni E, Melillo S, Murby AL, Smith (Nowak) JL, Ortman B, Quist JE, Reed S, Rowin T, Schmuck M, Stemberger RS, Travers B (2013) An image-based key to the zooplankton of North America. University of New Hampshire Center for Freshwater Biology. http://www.cfb.unh.edu (Accessed 24 December 2013)

Hebert PD (1995) The Daphnia of North America: an Illustrated Fauna. CD-ROM version 1

Jennings CA, Zigler SJ (2009) Biology and life history of paddlefish in North America: an update. In: Paukert C, Scholten G (eds), Paddlefish Management, Propagation, and Conservation in the 21st Century: Building From 20 Years of Research and Management. American Fisheries Society Special Symposium 66, Bethesda, Maryland, pp 1–22

Johnson PTJ, Olden JD, Vander Zanden MJ (2008) Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology* 6: 357–363, http://dx.doi.org/10.1890/070156

Kelly NE, Young JD, Winter JG, Yan ND (2013) Dynamics of the invasive spiny water flea, *Bythotrephes longimanus*, in Lake Simcoe, Ontario, Canada. *Inland Waters* 3: 75–92

Lange C, Cap R (1986) *Bythotrephes cederstroemi* (Schoedler) (Cercopagidae: Cladocera): A new record for Lake Ontario. *Journal of Great Lakes Research* 12: 142–143, http://dx.doi.org/10.1016/S0380-1330(86)71710-3

Lehman JT, Cáceres CE (1993) Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. *Journal of Limnology and Oceanography* 38: 879–891, http://dx.doi.org/10.4319/lo.1993.38.4.0879

Leung B, Bossenbroek JM, Lodge DM (2006) Boats, pathways, and aquatic biological invasions: estimating dispersal potential with gravity models. *Biological Invasions* 8: 241–54, http://dx.doi.org/10.1007/s10530-004-5573-8

MacIsaac HJ, Borbely JVM, Muirhead JR, Graniero PA (2004) Backcasting and forecasting biological invasions of inland lakes. *Ecological Applications* 14: 773–778, http://dx.doi.org/10.1890/02-5377

MacIsaac HJ, Ketelaars HAM, Grigorovich IA, Ramcharan CW, Yan ND (2000) Modeling *Bythotrephes longimauns* invasions in the Great Lakes basin based on its European distribution. *Archiv für Hydrobiologie* 59: 1245–1256

Makarewicz JC, Jones HD (1990) Occurrence of *Bythotrephes cederstroemi* in Lake Ontario offshore waters. *Journal of Great Lakes Research* 16: 143–147, http://dx.doi.org/10.1016/S0380-1330(90)71407-4

MacRae P (2001) The status of Lake Trout (*Salvelinus namaycush*) in Lake Simcoe. Ontario Ministry of Natural Resources Lake Simcoe Fisheries Assessment Unit Report No. 2001–2

Nilsson NA (1979) Food and habitat of the fish community of the offshore region of lake Vanern, Sweden. *Report of the Institute for Freshwater Research, Drottningholm* 58: 126–139

Pegg MA, Chick JH, Pracheil BM (2009) Potential effect of invasive species on paddlefish. In: Paukert C, Scholten G (eds), Paddlefish Management, Propagation, and Conservation in the 21st Century: Building From 20 Years of Research and Management. American Fisheries Society Special Symposium 66, Bethesda, Maryland, pp 185–201

Phelps QE, Tripp SJ, Garvey JE, Herzog DP, Ostendorf DE, Ridings JW, Crites JW, Hrabik RA (2009) Ecology and habitat use of age-0 paddlefish in the unimpounded middle Mississippi River. In: Paukert C, Scholten G (eds), Paddlefish Management, Propagation, and Conservation in the 21st Century: Building From 20 Years of Research and Management. American Fisheries Society Special Symposium 66, Bethesda, Maryland, pp 423–440

Shurin JB, Havel JE (2002) Hydrologic connections and overland dispersal in an exotic freshwater crustacean. *Biological Invasions* 4: 431–439, http://dx.doi.org/10.1023/A:1023692730400

Sprules WG, Riessen HP, Jin EH (1990) Dynamics of the *Bythotrephes* invasion of the St. Lawrence Great Lakes. *Journal of Great Lakes Research* 16: 346–351, http://dx.doi.org/10.1016/S0380-1330(90)71429-3

Strecker AL, Arnott SE, Yan ND, Girard R (2006) Variation in the response of crustacean zooplankton species richness and composition to the invasive predator *Bythotrephes longimanus*. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 2126–2136, http://dx.doi.org/10.1139/f06-105

Strecker AL, Beisner BE, Arnott SE, Paterson AM, Winter JG, Johannsson OE, Yan ND (2011) Direct and indirect effects of an invasive planktonic predator on pelagic food webs. *Journal of Limnology and Oceanography* 56: 179–192, http://dx.doi.org/10.4319/lo.2011.56.1.0179

Therriault TW, Grigorovich IA, Cristescu ME, Ketelaars HAM, Viljanen M, Heath DD, Macisaac HJ (2002) Taxonomic resolution of the genus *Bythotrephes leydig* using molecular markers and re-evaluation of its global distribution. *Diversity and Distributions* 8: 67–84, http://dx.doi.org/10.1046/j.1472-4642.2002.00129.x

U.S. Geological Survey (USGS) (2013a) Nonindigenous Aquatic Species Database. Gainesville, Florida. http://nas.er.usgs.gov/ (Accessed 14 August 2013)

U.S. Geological Survey (USGS) (2013b) USGS Waterflow Data for Pennsylvania. http://waterdata.usgs.gov/pa/nwis/current (Accessed 15 December 2013)

Vanderploeg HA, Liebig JR, Omair M (1993) *Bythotrephes* predation on Great Lakes zooplankton measured by an in situ method: implications for zooplankton community structure. *Archiv für Hydrobiologie* 127: 1–8

Yan ND, Blukacz A, Sprules WG, Kindy PK, Hackett D, Girard RE, Clark BJ (2001) Changes in zooplankton and the phenology of the spiny water flea, *Bythotrephes*, following its invasion of Harp Lake, Ontario, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 2341–2350, http://dx.doi.org/10.1139/f01-171

Yan ND, Girard R, Boudreau S (2002) An introduced invertebrate predator (*Bythotrephes*) reduces zooplankton species richness. *Ecology Letters* 5: 481–485, http://dx.doi.org/10.1046/j.1461-0248.2002.00348.x

Yan ND, Leung B, Lewis MA, Peacor SD (2011) The spread, establishment, and impacts of the spiny water flea, *Bythotrephes longimanus*, in temperate North America: a synopsis of the special issue. *Biological Invasions* 13: 2423–2432, http://dx.doi.org/10.1007/s10530-011-0069-9