Invasive invertebrate predator, *Bythotrephes longimanus*, reverses trophic cascade in a north-temperate lake

Jake R. Walsh 🄳,* Richard C. Lathrop, M. Jake Vander Zanden
Center for Limnology, University of Wisconsin – Madison, Madison, Wisconsin

Abstract

Trophic cascades can determine the structure of aquatic food webs, a role often used to manage water quality in lakes. However, trophic cascades are subject to multiple interacting drivers of environmental change. For example, invasive species can dramatically alter food webs, though we know less about invasive species effects on managed trophic cascades. Here, we investigate the changing food web dynamics of Lake Mendota (Wisconsin, U.S.A.) over a 40-yr time period. Piscivore stocking (biomanipulation) beginning in 1988 coupled with a 1987 die-off of cisco (the dominant zooplanktivore) led to decreased zooplanktivory that cascaded to increases in the large-bodied herbivorous zooplankton *Daphnia pulicaria* and greater water clarity. In 2009, the invasive spiny water flea *Bythotrephes longimanus* was first detected in Lake Mendota and soon reached record densities. As a result of this invasive invertebrate predator, zooplanktivory increased to 47% of the earlier cisco period. Concomitant with the spiny water flea population explosion were declines in *D. pulicaria* and water clarity as both exhibited a strong negative relationship to zooplanktivory across the 40-yr time series. We argue that the trophic cascade of 1987–1988 created an environment of high food resources and low fish planktivory that promoted the proliferation of *Bythotrephes* as it functionally replaced cisco in Lake Mendota's food web. Our results highlight how a manipulated, eutrophic lake was vulnerable to adverse impacts by invasive species, calling attention to the importance of understanding interactions among drivers of environmental change.

Food webs can be regulated by both the availability of resources (bottom-up control) or predation by higher trophic levels (top-down control), and studies have found that changes at the top of the food web can cascade all the way to primary producers (Carpenter et al. 1985; Terborgh and Estes 2010). In lakes, increasing algal biomass often degrades water quality (Carpenter et al. 1985) and efforts to manage water quality have traditionally focused on controlling nutrient inputs, which is a bottom-up approach (Bennett et al. 2001; Motew et al. 2017). In recent decades, manipulating cascading food web interactions has become an important management tool for improving water quality (e.g., Hansson et al. 1998; Motew et al. 2017). However, such efforts to manage ecosystems must increasingly consider the broader context of ongoing habitat degradation and global environmental change, such as climate change and biological invasion (Strayer 2010; Carpenter et al. 2011).

Invasive species can dramatically alter food webs (Vander Zanden et al. 1999), including cascading trophic interactions. However, relatively few studies have evaluated how invasive species affect managed trophic cascades (e.g., Kimbro et al. 2009), although invasive species have been shown to induce trophic cascades in recipient ecosystems (e.g., Courchamp et al. 2003; O'Dowd et al. 2003; Croll et al. 2005). Furthermore, food webs play an important role in ecosystem resistance to invasion, and the loss of higher-level predators can leave ecosystems vulnerable to invasion by prey or mid-level predator species (Carlsson et al. 2009; Estes et al. 2011). This is consistent with the invasion ecology paradigm that anthropogenic disturbance increases the susceptibility of ecosystems to the establishment and impact of invasive species (MacDougall and Turkington 2005; Light and Marchetti 2007; Johnson et al. 2008; Vander Zanden et al. 2016). Understanding the interactions between efforts to manage ecosystems (e.g., via manipulating food webs), and factors such as changing climate and invasive species represents a key challenge for future environmental management (Carpenter et al. 2011).

*Correspondence: jransom.walsh@gmail.com

Additional Supporting Information may be found in the online version of this article.
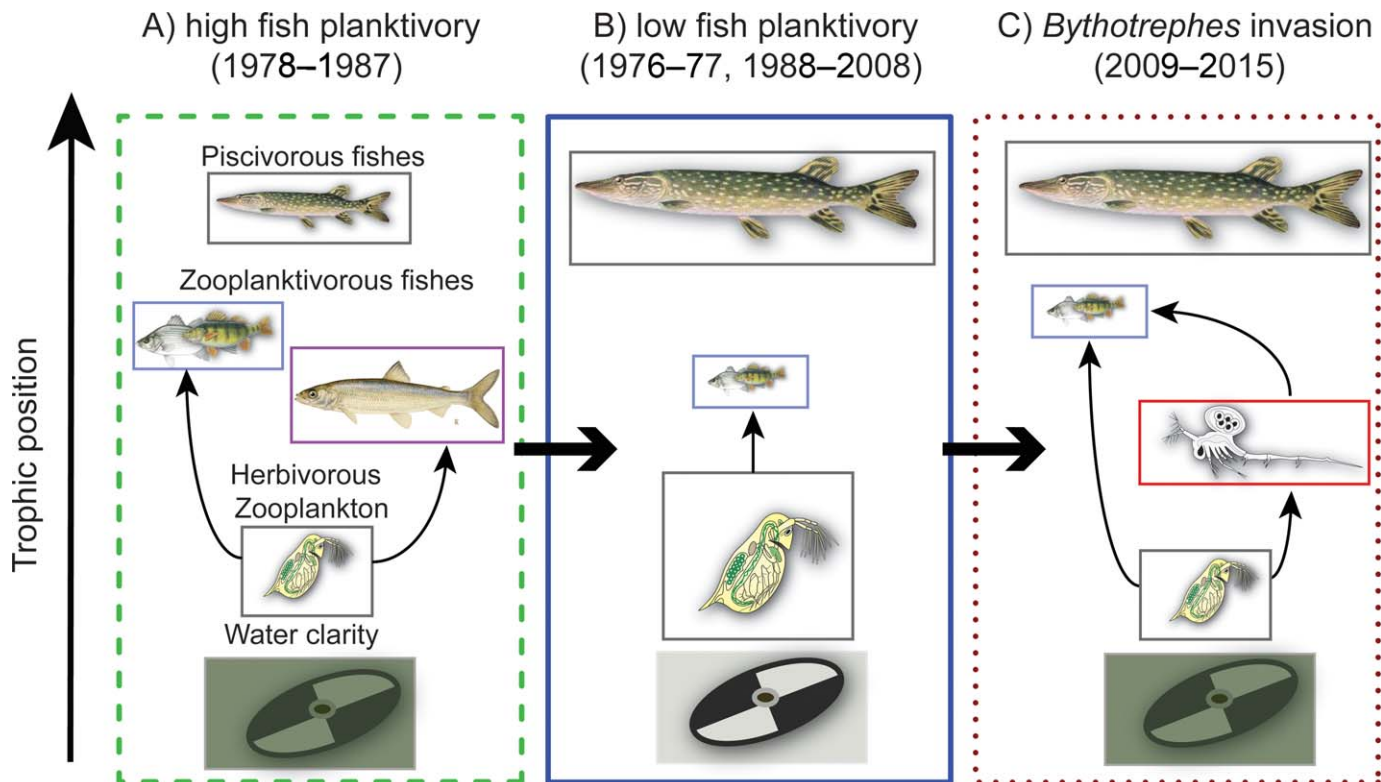
Fig. 1. Panels depict the Lake Mendota food web before (**A**) and after (**B**) the whole-lake biomanipulation and cisco die-off in 1987, as well as after the detection of *Bythotrephes* in 2009 (**C**). Arrows represent zooplanktivory on *D. pulicaria* before and after *Bythotrephes* invasion as well as zooplanktivory of native fishes on *Bythotrephes*. Species boxes change in size in response to management (**A** to **B**) and invasion (**B** to **C**) to reflect changes in biomass.

Water quality in eutrophic lakes is sometimes managed by manipulating cascading food web interactions—a process called biomanipulation—with the intent of controlling phytoplankton biomass (Fig. 1). For example, herbivorous zooplankton may be released from predation directly by the removal of zooplanktivorous fishes or indirectly through a trophic cascade induced by the addition of piscivorous fishes (Hansson et al. 1998; Bernes et al. 2015). Herbivorous zooplankton are then able to increase water clarity by reducing phytoplankton biomass. However, predatory invertebrates can interfere with the desired top-down effects of biomanipulation by dampening the strength of the cascade (Carpenter et al. 1985; MacKay and Elser 1998; Shurin et al. 2002). Accordingly, invasive invertebrate predators can interfere with cascading interactions in biomanipulated lakes as well as non-managed lakes (e.g., Ketelaars et al. 1999; Ellis et al. 2011; Walsh et al. 2016*a*).

To evaluate this concept, we present the case of the invasion of the predatory invertebrate, *Bythotrephes longimanus* (spiny water flea) into eutrophic Lake Mendota (Wisconsin, U.S.A.). Water quality in Lake Mendota has been strongly influenced by top-down cascading food web interactions. Following the die-off of planktivorous cisco (*Coregonus artedi*) in 1987, piscivores were stocked heavily in Lake Mendota in

an effort to manipulate these cascading interactions to increase water clarity (Kitchell 1992). Reduced zooplanktivory following cisco decline and piscivore stocking established *Daphnia pulicaria* as the lake's dominant grazer, improving water clarity by over 1 m (Lathrop et al. 2002). Despite decades of implementing best management practices to reduce agricultural runoff into the lake, the biomanipulation has been the single most effective tool to manage water clarity in Lake Mendota (Carpenter and Lathrop 2014).

The eruption of the predatory *Bythotrephes* from low densities in Lake Mendota in 2009 coincided with a 60% decline in *D. pulicaria*, and a nearly 1 m decline in lake water clarity, incurring economic damages estimated at over US$100 million (Walsh et al. 2016*a,b*). *Bythotrephes* is known as a voracious zooplanktivore (Bunnell et al. 2011) that selects for large-bodied herbivorous zooplankton (Schulz and Yurista 1998). However, Lake Mendota was the first report of such a strong cascading effect on water clarity (first evaluated in Strecker and Arnott 2008, also *see* Strecker et al. 2011).

Utilizing a 40-yr dataset, we examine how Lake Mendota's management history may have enhanced the cascading impact of the invasive *Bythotrephes* on the Lake Mendota food web. We evaluate the potential contribution of *Bythotrephes* to total zooplanktivory in Lake Mendota and

demonstrate the mechanism by which *Bythotrephes* reversed a trophic cascade that provided improved water clarity for two decades. Our work also highlights the possibility that eutrophic lakes that are managed through cascading trophic interactions may be uniquely vulnerable to invasive invertebrate predators such as *Bythotrephes*. Last, our study reveals how habitat degradation, management efforts, and invasions can interact to yield novel management challenges.

Methods

Study site and species

Lake Mendota (39.6 km^2 area, 25.3 m max depth, and 12.7 m mean depth) is a culturally eutrophic lake adjacent to Madison, Wisconsin (U.S.A.). To improve water clarity, managers began stocking the lake with piscivorous fishes and enacted strict regulations on their harvest in 1987 and 1988. This manipulation increased predation pressure on zooplanktivorous fishes, thus relaxing pressure on herbivorous zooplankton like *D. pulicaria*, which improve water clarity by grazing algae. Biomanipulation, coupled with a massive die-off of zooplanktivorous cisco (*C. artedi*; ∼ 90% reduction in biomass in 1987), resulted in a 76% reduction in the biomass of zooplanktivorous fishes (Fig. 1A,B; Rudstam et al. 1993; Johnson and Kitchell 1996; Lathrop et al. 2002). Prior to *Bythotrephes* detection in 2009, the *Daphnia* community was dominated by *D. pulicaria* and, to a lesser extent, *Daphnia galeata mendotae*, a smaller and less efficient grazer (Kasprzak et al. 1999).

The lake's dominant zooplanktivorous fishes are yellow perch (*Perca flavescens*), white bass (*Morone chrysops*), and cisco, though cisco have been rare in the past three decades. The diets of adult yellow perch, white bass, and cisco were found to be comprised of 77%, 74%, and 94% *Daphnia*, respectively, with no clear shifts to larger prey with age or size (Johnson and Kitchell 1996). Young-of-year cisco are large enough to consume primarily *Daphnia* by early summer, and white bass and yellow perch grow large enough to do so by late summer. The lake also has two predatory zooplankton, the invasive *Bythotrephes* (as of 2009) and the native *Leptodora kindtii*. While the predatory invertebrate *Chaoborus* is present in the lake, they have become exceedingly rare in recent decades (Lathrop 1992a,b) and have been absent from recent day-night zooplankton net hauls targeting *Bythotrephes* (Walsh unpubl.) and are, therefore, unlikely to contribute to total zooplanktivory.

Long-term data

We obtained long-term data of lake temperature profiles (1995–2015; North Temperate Lakes Long-Term Ecological Research, NSF 2015a), fish abundance (1976–1998, 2005–2015; Supporting Information Table S2; Lathrop et al. 2002; North Temperate Lakes Long-Term Ecological Research, NSF 2015b), fish lengths and weights (1981–2015; North Temperate Lakes Long-Term Ecological Research, NSF 2015c),

zooplankton abundance and length (1976–2015; Supporting Information Table S2; North Temperate Lakes Long-Term Ecological Research, NSF 2015d), and water clarity (1976–2015; Lathrop et al. 2002; North Temperate Lakes Long-Term Ecological Research, NSF 2015e) from the National Science Foundation North Temperate Lakes Long-Term Ecological Research (NTL-LTER) program database. Lake Mendota's fish community was surveyed annually. Water clarity, zooplankton, and temperature were generally sampled bi-weekly in spring and summer, monthly in fall and one to two times in winter when the lake was ice-covered. To account for differing sampling frequencies within and among years, we interpolated water clarity, zooplankton, and temperature data to daily values. We used annual geometric mean Secchi depth as a measure of water clarity in Lake Mendota, which is lognormally distributed within years. Lakewide pelagic fish density was estimated in late summer by sonar runs using an HTI Model 241 echosounder with 120 kHz split beam configuration. Signals were interpreted using HTI sounder software v. 1.0 and calibrated using gill net sampling and fish length and weight measurements, allowing for species-specific estimates of lakewide abundance and biomass (North Temperate Lakes Long-Term Ecological Research, NSF 2015b). We estimated zooplankton biomass using length to dry weight equations from the literature (McCauley 1984). Seasonality in zooplankton biomass and Secchi depth was visualized by fitting generalized additive models (GAM) of biomass or Secchi depth fitted to day of the year (Wood 2011).

We calculated volumetric density of zooplankton by dividing areal density by the sampling depth of zooplankton net tows, which was 24 m from 1976 through 1994 and 20 m from 1995 through 2015. Changes in the sampling depth of zooplankton tows may affect zooplankton biomass concentration estimates presented here. There are two cases in which this change could bias our results. First, if *Daphnia* were completely absent from the lake bottom during summer anoxia (June through early October), which is likely at the extremely low dissolved oxygen concentrations reached each summer at both 20 m and 24 m depths (< 1 mg L^{-1}), this would "dilute" the 1976–1994 zooplankton biomass concentration estimates by 16% relative to 1995–2015 concentration. While this dilution is not insignificant, it is small relative to the long-term changes presented here, which vary over orders of magnitude. Alternatively, *Daphnia* have been shown to migrate downward in the water column to avoid predation by *Bythotrephes* and fishes (Pangle and Peacor 2006; Bourdeau et al. 2015). Therefore, it is possible that sampling only 20 m into the water column would fail to capture migrating *Daphnia* during months when the hypolimnion contained enough oxygen to support *Daphnia* (e.g., before June and after October). As a result, deep vertical migration during oxygenated months in the hypolimnion could introduce a source of error in the results we present here: a decline in *Daphnia* biomass with *Bythotrephes* may be,
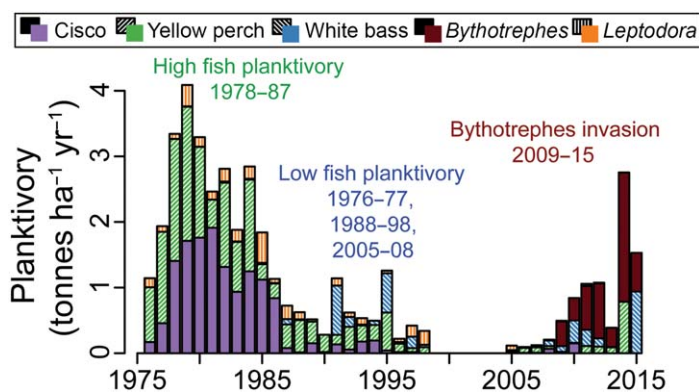
Fig. 2. Total annual zooplanktivory (tonnes ha^{-1}) in Lake Mendota in the past 40 yr (Cisco in solid light purple, yellow perch in green with northeast oriented lines, white bass in blue with northwest oriented lines, *Bythotrephes* in solid dark red, and *Leptodora* in orange with vertical lines). Note the gap in data from 1999 to 2004.

Fig. 3. Daily planktivory rates by fishes (kg ha^{-1} d^{-1}; cisco in short-dashed purple, the sum of white bass and yellow perch in long-dashed and dotted blue) and *Bythotrephes* (solid dark red) under average conditions noted by year ranges in matching colors.

in part, due to failing to capture deep-migrating *Daphnia* in midday sampling during months of adequate hypolimnetic oxygen.

Planktivory

We used allometric relationships to estimate zooplanktivory (hereafter, "planktivory") by Lake Mendota planktivores. Allometric models of ingestion rates are simpler than bioenergetics modeling, requiring fewer measurements, parameters, and assumptions. Allometric models of individual ingestion rates were derived from observed individual ingestion rates fitted to a three-quarter power function of individual body mass (individual ingestion = a*body mass^0.75; a[fishes] = 6.4, a[invertebrates] = 9.7; Yodzis and Innes 1992). For each planktivorous fish, we scaled body size (kg) and ingestion rates (kg yr^{-1}) to the population level (individuals ha^{-1}) by calculating the individual ingestion rates from the observed population weight distribution and summing across all individuals (kg ha^{-1} yr^{-1}). *Leptodora* and *Bythotrephes* dry weights were converted to wet weights by multiplying by a factor of 10 (Winberg 1971). Due to large within-year seasonal variation in zooplankton population densities, we estimated invertebrate ingestion rates at a daily time step. Annual planktivory for each invertebrate predator was then the sum of daily planktivory in each year.

Daily planktivory rates were estimated by back-calculating from estimated mean annual planktivory. To account for seasonality in lake surface temperature and its influence on planktivory, we used a temperature dependence function commonly used in bioenergetics (Kitchell et al. 1977). Here, daily planktivory rates increased with temperature to their maximum (f[temperature] = 1) when the surface temperatures of the lake were at a planktivore's optimal temperature and declined rapidly as lake temperatures increase further from optimal temperatures to a planktivore's thermal limit
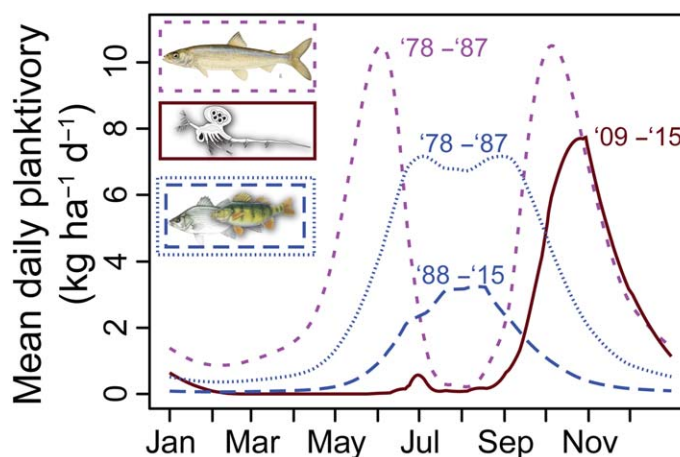
(temperature dependent parameters found in Kitchell et al. 1977; Johnson 1993; Kim and Yan 2010; Yurista et al. 2010; Bunnell et al. 2011). Notably, *Bythotrephes* and cisco are cool-water planktivores with cooler optimal temperatures (16°C and 16.8°C, respectively) than yellow perch (23°C), white bass (28.3°C), and *Leptodora* (25°C). We assumed fish zooplanktivore biomass to be constant within a year while *Bythotrephes* biomass varies as it would under an average post-2009 year (GAM seasonal model as described above with *Daphnia* and water clarity). We characterized the potential cascading relationships in the food web of Lake Mendota between zooplanktivory, *Daphnia*, and water clarity by reporting Pearson's correlation coefficients between annual means of log-transformed variables (each variable is lognormally distributed within years). All statistics and analyses were conducted in R (R Core Team 2016).

We do note that mass specific estimates of *Bythotrephes* consumption rates can vary widely and our allometric approach was purposefully chosen because of its generality. In a more detailed approach using bioenergetics, Bunnell et al. (2011) estimated *Bythotrephes* mass specific consumption rates ranging from 72.3% to 114.5% per day (i.e., mass consumed of prey per mass of predator per day). Our allometric estimates of mass specific consumption rates from Yodzis and Innes (1992) would be 84.9% per day for a *Bythotrephes* of average mass and ranged from 64% to 113% per day for the largest and smallest *Bythotrephes*—comparable to estimates from Bunnell et al. (2011).

Results

With *Bythotrephes* invasion, total planktivory increased nearly threefold (1.1 tonnes ha^{-1} yr^{-1}; 2009–2015 mean) over that during the low fish planktivory years (0.46 tonnes
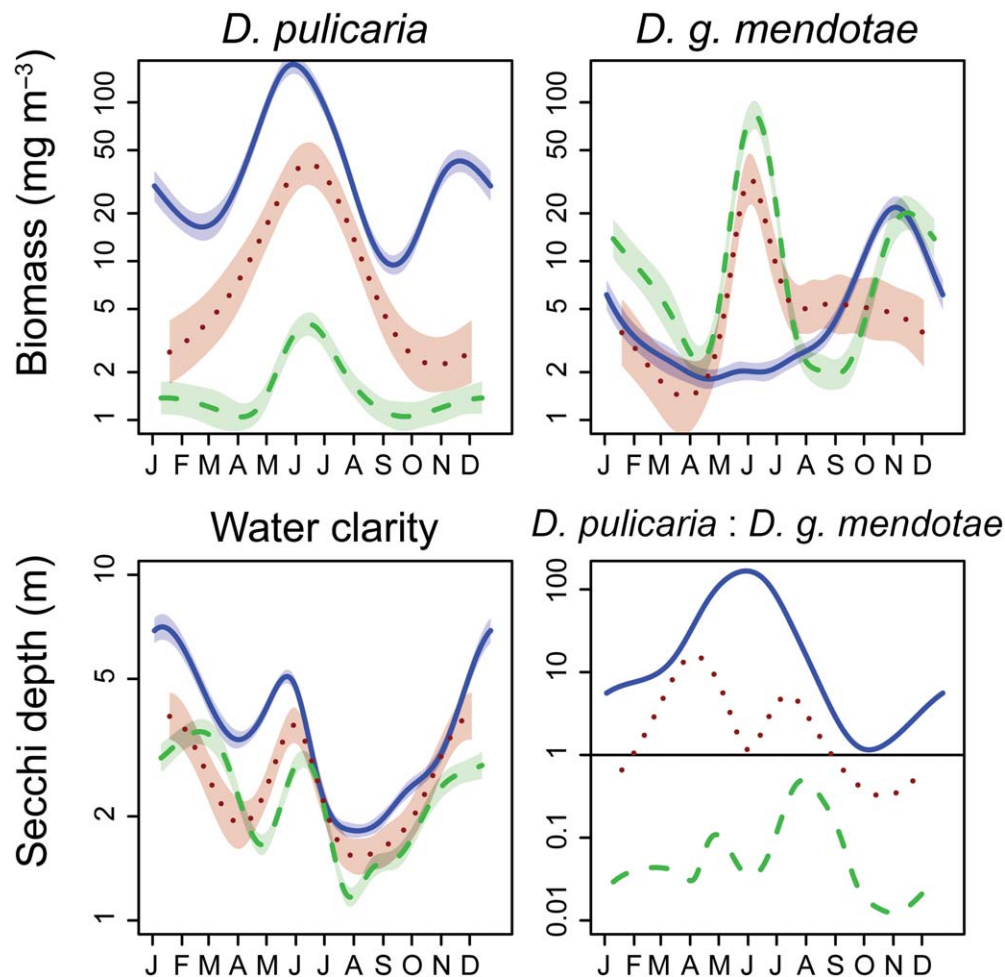
Fig. 4. Seasonality in plankton biomass and water clarity over three study time periods (solid blue = low fish planktivory years; dashed green = high fish planktivory years; dotted red = *Bythotrephes* years) is visualized by fitting zooplankton biomass (mg m^{-3}) and Secchi depth (m) to smoothed GAM of day of the year (estimates in lines ± 1 SE, shaded area). The biomass ratio of *D. pulicaria* to *D. g. mendotae* is calculated by dividing fitted GAM curves of the two species. Note that the y-axis of each panel is on a log-scale.

ha^{-1} yr^{-1}; 1988–1998, 2005–2008 mean) and reached 47% of mean planktivory during high fish planktivory, cisco years (2.4 tonnes ha^{-1} yr^{-1}; 1978–1987) (Fig. 2). Predation by *Bythotrephes* made up 62% of total planktivory from 2009 to 2015. Abundant yellow perch and *Bythotrephes* in 2014 and white bass in 2015 more than doubled planktivory over the post-2009 mean (0.77–2.1 tonnes ha^{-1} yr^{-1}). Planktivory by *Bythotrephes* was highest in the fall and nearly matched peak daily planktivory rates by cisco during the high zooplanktivory years (Fig. 3). Planktivory by cisco was highest in the spring and fall, while planktivory by white bass and yellow perch peaked in the summer (Fig. 3). There was little evidence of predator control of *Bythotrephes* planktivory by fishes (planktivory[*Bythotrephes*] = 0.89 [0.68 SE] * planktivory[fishes] + 330 [360 SE]; $R^2 = 0.25$, $p = 0.24$, $F = 1.72$ on 1 and 5 df). Finally, we found that allometric estimates of planktivory were a good predictor of

bioenergetic estimates ($R^2 = 0.90$, df = 21, $t = 13.9$, $p \ll 0.001$ for 1976–1998 bioenergetics estimates from Lathrop et al. 2002 and allometric estimates here).

D. pulicaria biomass increased from high fish planktivory years (0.05 mg m^{-3}) to low fish planktivory years (32.9 mg m^{-3}), then declined with *Bythotrephes* invasion (2.99 mg m^{-3}), particularly in the fall (Fig. 4A). Spring biomass of *D. pulicaria* declined overall (Fig. 4A), but was notably high in 2012 and 2013 (Fig. 5). Conversely, *D. g. mendotae* biomass declined from high to low fish planktivory years (6.15–1.2 mg m^{-3}), particularly in the spring after being displaced by *D. pulicaria* (Fig. 4D) as fall *D. g. mendotae* biomass remained relatively high (Fig. 4B). After *Bythotrephes* invasion, *D. g. mendotae* biomass increased overall (2.24 mg m^{-3}) but was lower than during high fish planktivory years. In particular, spring *D. g. mendotae* biomass increased from low fish planktivory years to *Bythotrephes* years, but fall biomass
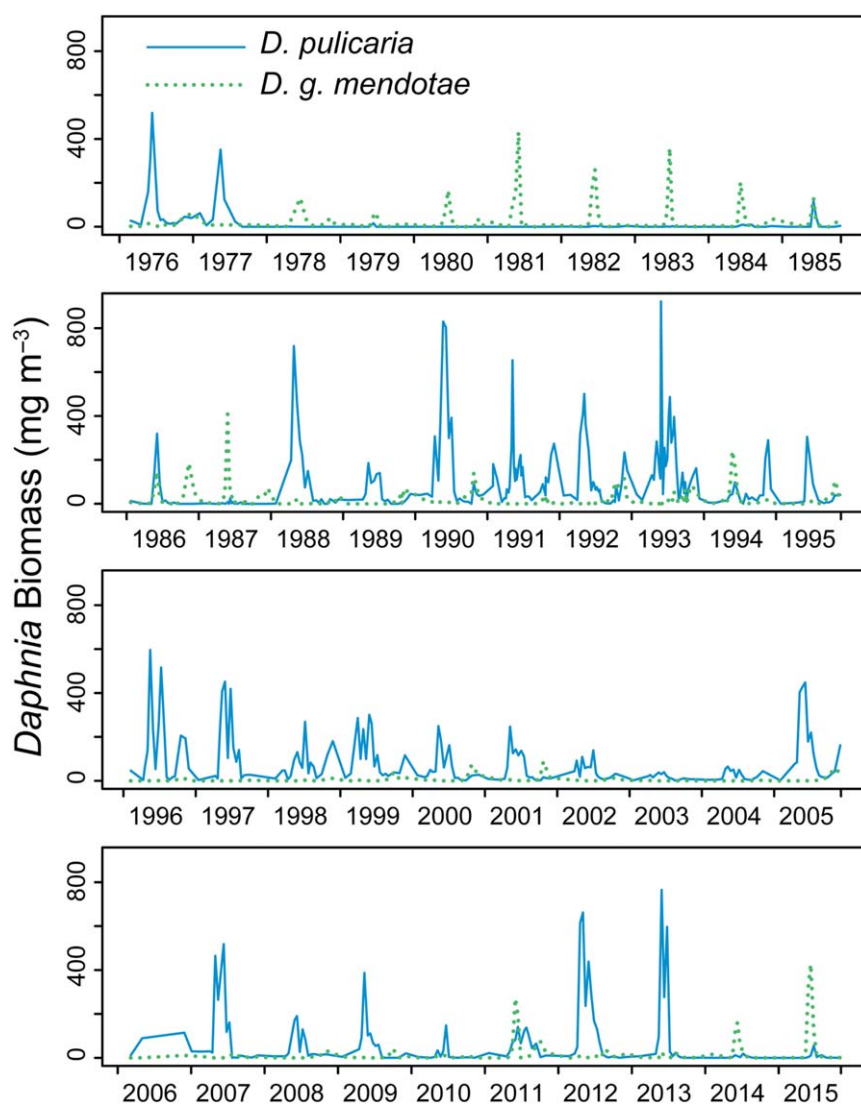
Fig. 5. Forty-year time series of *D. pulicaria* (solid blue) and *D. g. mendotae* (dotted green) biomass (mg m^{-3}). The data are not log-transformed in order to highlight spring peaks in biomass by both species.

fell nearly fivefold (Fig. 4B). Accordingly, *D. g. mendotae* dominated the plankton during high fish planktivory, switching to dominance by *D. pulicaria* during years of low fish planktivory, and shared dominance during *Bythotrephes* years (Fig. 4D).

Long-term geometric mean *Daphnia* biomass (sum of *D. pulicaria* and *D. g. mendotae* biomass) increased with lower fish planktivory from 6.9 mg m^{-3} to 43 mg m^{-3} and declined with *Bythotrephes* invasion to 11 mg m^{-3}. The lowest *Daphnia* biomass from the years of low fish planktivory was reached in 2003 and 2004 with 11 mg m^{-3} and 16 mg m^{-3} annual geometric means, respectively. Annual geometric mean *Daphnia* biomass fell to all-time lows in 2014 (5.0 mg m^{-3}) and 2015 (4.1 mg m^{-3}) (Fig. 5). Also, with *Bythotrephes* invasion, total *Daphnia* biomass fell below NTL-LTER detection limits in 2010, 2014, and 2015, with the 2014 collapse lasting 59 d, the longest collapse on record (previous high of 46 d in 1987 and a mean occurrence of 12 d per year from 1978 to 1987).

Water clarity increased after cisco die-off and biomanipulation (2.3–3.7 m, long-term mean Secchi depth) and declined after *Bythotrephes* invasion (2.7 m), particularly in winter and spring (Fig. 4C). The mean duration of the spring clear-water phase (here defined as Secchi depth measurements > 4.0 m) increased from 12 d to 53 d from high to low fish planktivory and declined to < 30 d after the 2009 *Bythotrephes* population explosion including 0 d in 2014–2015.

Cascading interactions appeared to drive relationships between planktivory, *Daphnia*, and clarity in Lake Mendota (Fig. 6). Over the 40-yr dataset, water clarity was positively
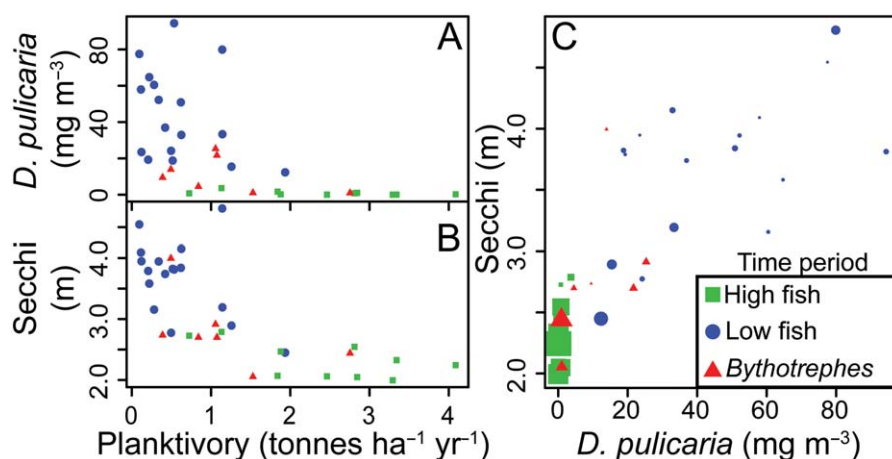
Fig. 6. Cascading relationships in Lake Mendota. Annual planktivory (tonnes ha^{-1} yr^{-1}) is negatively associated with both annual geometric mean *D. pulicaria* biomass (mg m^{-3}; **A**) and water clarity (m; **B**) over the 40-yr study time period (1978–1987 in green squares, 1976–1977 and 1988–2008 in blue circles, and 2009–2015 in red triangles). *D. pulicaria* biomass has been positively correlated with water clarity (**C**; point sizes are scaled by annual planktivory rates).

associated with *D. pulicaria* (Fig. 6C; Pearson's *r* [log Secchi Depth, log *D. pulicaria* biomass] = 0.81, *t* = 8.0, df = 32, *p* ≪ 0.001) and inversely associated with total annual planktivory (Fig. 6B; Pearson's *r* [log Secchi depth, log planktivory] = −0.78, *t* = −7.1, df = 32, *p* ≪ 0.001). Also, *D. pulicaria* biomass was inversely associated with total annual planktivory (Fig. 6A; Pearson' *r* [log *D. pulicaria* biomass, log planktivory] = −0.74, *t* = −6.3, df = 32, *p* ≪ 0.001). We also report potential nonlinearities in the cascading relationships between planktivory, *D. pulicaria* biomass, and water clarity: annual geometric mean *D. pulicaria* biomass and water clarity declined exponentially with annual planktivory and water clarity increased logarithmically with *D. pulicaria* biomass (Fig. 6, Supporting Information Fig. S1, Supporting Information Table S1).

Discussion

The invasion of Lake Mendota by *Bythotrephes* corresponded with large declines in *D. pulicaria* and water clarity (Walsh et al. 2016a)—offsetting many of the gains of the whole-lake biomanipulation beginning in 1988 following the cisco die-off in 1987 (Lathrop et al. 2002). We found that *Bythotrephes* was the largest contributor to total planktivory in the lake from 2009 to 2015. *Bythotrephes* preyed on *Daphnia* primarily in the fall, nearly matching fall daily planktivory rates by the abundant 1978–1987 cisco population. Fall predation by *Bythotrephes* complemented peak planktivory by fishes in the summer. As a result, planktivory by fishes and planktivory by *Bythotrephes* was largely additive. In addition, elevated zooplanktivory had a cascading effect on herbivorous zooplankton and water clarity. Furthermore, this cascade exacerbated the harmful effects of eutrophication, revealing multiple benefits of preventing such invasions in lakes like Mendota and reducing nutrient

loading into lakes. A key management implication of this study is that high planktivory by fishes did not control *Bythotrephes* in Lake Mendota even though some fish consumption of *Bythotrephes* occurred.

Bythotrephes dramatically elevated total planktivory in Lake Mendota compared to the low fish planktivory period (1988–2008) by extending the period of peak planktivory into the fall. Little seasonal overlap occurred between planktivory by *Bythotrephes* and planktivory by the warm-water white bass and yellow perch that consume the most zooplankton in summer (Fig. 3). This contrasted with the warm-water native predatory invertebrate *L. kindtii*; peak productivity of *L. kindtii* is more likely to overlap with peak planktivory by native warm-water fishes as both occur in the summer (Lunte and Luecke 1990). Fall planktivory by *Bythotrephes* offered *Daphnia* little to no reprieve after peak summer planktivory by yellow perch and white bass. Planktivory by *Bythotrephes* quickly succeeded peak planktivory by fishes in years with high summer fish planktivory (e.g., 2010, 2011, 2014, and 2015; Figs. 2A, 3) while *Bythotrephes* made up a significant portion of both summer and fall planktivory in years with lower summer planktivory by fishes (e.g., 2009, 2012, and 2013; Figs. 2A, 3). In this way, *Bythotrephes* "filled the gaps" left by poor fish year classes and by the natural decline in warm-water fish planktivory during the fall.

When total planktivory was high, *D. pulicaria* were rare and water clarity was low (Figs. 4, 5). These cascading relationships (e.g., Fig. 6) provide a likely mechanism for reported declines in *D. pulicaria* abundance and water clarity in Lake Mendota with *Bythotrephes*' population explosion in 2009 (Walsh et al. 2016a). Also, this cascade is consistent with the historical understanding of the role of planktivory in governing plankton dynamics and water quality in Lake Mendota (Lathrop et al. 2002). Our findings build on this

understanding and further demonstrate the contribution of invertebrate predators to total zooplanktivory and, in turn, water quality (as in Ellis et al. 2011). Additionally, due to potential nonlinearities in these cascading relationships (Supporting Information Table S1), planktivory by both fishes and *Bythotrephes* may have to be substantially reduced to see gains in *D. pulicaria* biomass or water clarity.

Planktivorous fishes also prey on *Bythotrephes* and, as a result, predation pressure on *Daphnia* from both *Bythotrephes* and planktivorous fishes may not be completely additive. *Bythotrephes* has been a key diet item of yellow perch, comprising 46% of fish diets from August of 2011–2013 and as much as 80% of diets in years of higher August *Bythotrephes* abundance (2011; Walsh unpubl.), though it should be noted that *Bythotrephes*' tail spines are cleared at a much slower rate than other diet items, biasing these proportions upward (Compton and Kerfoot 2004; Stetter et al. 2005). Further, young-of-year yellow perch and white bass may struggle to capture and handle *Bythotrephes* due to its long tail spine (Compton and Kerfoot 2004). In years of large young-of-year classes (e.g., 2014 and 2015, in which sonar data indicate a massive shift from a large population of yellow perch to a large population of white bass), high planktivory by fishes on *Daphnia* may not equate to high planktivory on *Bythotrephes* due to this gape limitation. Further, little temporal overlap within years likely limits planktivorous fishes' capacity to ease *Bythotrephes* impact on *D. pulicaria* (e.g., we reported no relationship between planktivory by fishes and planktivory by *Bythotrephes* over 2009–2015).

High planktivory rates by *Bythotrephes* and all fishes likely led to compounding negative impacts on *D. pulicaria*, but their impact on the smaller-bodied *D. g. mendotae* is less clear. *D. g. mendotae* was dominant during years of high fish planktivory by cisco. As a less abundant and less efficient grazer, this led to low water clarity (*sensu* Lathrop et al. 1996, 2002). After *Bythotrephes* invasion, *D. g. mendotae* increased in biomass in the spring, likely due to reduced competition from *D. pulicaria*. However, *D. g. mendotae* biomass declined substantially in the fall, to densities lower than either the high or low fish planktivory years (Fig. 6). *D. g. mendotae* decline was consistent with reported *Bythotrephes* impacts in other lakes. For example, Kerfoot et al. (2016) reported a spring increase, but overall decline in *D. g. mendotae* in six lakes in northern Minnesota. As a result of fall decline, *D. g. mendotae* biomass was much lower in *Bythotrephes* years than in past years of high fish planktivory. In fact, when planktivory by fishes and *Bythotrephes* were both high (e.g., 2010, 2014, and 2015), total *Daphnia* biomass declined to exceptionally low levels, such as in 2010, and historically low levels, such as in 2014 and 2015. Low *Daphnia* biomass in 2014 and 2015 is highlighted by a whole *Daphnia* community collapse from fall 2014 through early Spring 2015. Spring water clarity was exceptionally low in these years (2014 and 2015 were the 8th and 2nd lowest mean clarity,

respectively), and failed to increase past 4.0 m Secchi depth for just the second and third time in the 40-yr dataset here. Additional research should investigate the potential mechanism of *Bythotrephes*' summer and fall impact on *Daphnia* persisting into spring of the following year (e.g., effect on *Daphnia* resting egg production or effect on overwintering *Daphnia* in the water column). Further, while *D. g. mendotae* is a poor grazer relative to *D. pulicaria* (Kreutzer and Lampert 1999), it is much larger and more efficient than the small herbivorous copepods in Lake Mendota (Hansen et al. 1997).

In fact, by the same allometric relationships of ingestion rates to body size used for planktivory here, the average *D. pulicaria* in Lake Mendota "outgrazes" the average *D. g. mendotae* by a ratio of 1.6 : 1. However, the average *D. g. mendotae* outgrazes the average herbivorous copepod by a ratio of 32 : 1 (2009–2015 mean copepod length) or 3.7 : 1 (1976–2008 mean copepod length) to the average herbivorous copepod prior to *Bythotrephes* invasion. Lower copepod grazing rates are likely due to a decline in mean length of herbivorous copepods (0.97–0.23 mm) despite an overall increase in both calanoid and cyclopoid abundance (North Temperate Lakes Long-Term Ecological Research, NSF 2015*d*). Therefore, the nature of *Bythotrephes* impact on *D. g. mendotae* may have key implications for water clarity in Lake Mendota.

The dominant planktivorous fishes of Lake Mendota have not controlled *Bythotrephes*. Therefore, our findings suggest that simply increasing yellow perch or white bass populations in Lake Mendota is not likely to control *Bythotrephes* and stabilize *D. pulicaria*. However, successful examples of such efforts have been reported (e.g., Wissel et al. 2000). Notably, cool-water planktivorous fishes (e.g., cisco; Coulas et al. 1998) or fishes with more efficient feeding methods (e.g., pumpkinseed and bluegill; LeDuc and Kerfoot unpubl.) may be more successful in controlling *Bythotrephes*. However, these fishes would also prey on *D. pulicaria* and potentially harm water quality, as in the case of cisco (Johnson and Kitchell 1996).

Differing tolerance to harmful cyanobacteria toxins among (e.g., DeMott et al. 2001) and within (e.g., Ghadouani and Pinel-Alloul 2002; Sarnelle and Wilson 2005) *Daphnia* species has been recognized as a key driver in structuring *Daphnia* communities in lakes. Interestingly, extreme precipitation and flooding in Madison, WI in 2008 led to enormous nutrient loading and high in-lake phosphorus concentrations in 2008 and 2009 which lead to extremely poor summer water quality characterized by cyanobacteria blooms in 2008. Since 2010, in-lake phosphorus has actually declined by nearly 30% under the long-term mean (1995–2008; Walsh et al. 2016*a*) alongside declining cyanobacteria biomass (Walsh unpubl.) with no subsequent recovery of *D. pulicaria*. While it is possible that extremely eutrophic conditions exacerbated *D. pulicaria* decline after 2009, we conclude that *D. pulicaria* biomass since 2010 is likely driven by

planktivory in Lake Mendota rather than lake trophic state. Regardless, Lake Mendota provides an interesting case study in which to test hypotheses regarding cyanobacteria tolerance within and among *Daphnia* species in a natural system.

In the adjacent Lake Monona (connected via the Yahara River), *Bythotrephes* is much less abundant (Walsh unpubl.; North Temperate Lakes Long-Term Ecological Research, NSF 2015*d*) and exploring the factors that drive lower abundance in Lake Monona could inform *Bythotrephes* management in Lake Mendota. For example, Lake Monona has a shallower mean depth than Lake Mendota (8.3 m and 12.7 m, respectively) and is thought to have a higher littoral influence than Lake Mendota, providing habitat and refuge for zooplanktivorous fishes that selectively consume large zooplankton like *Bythotrephes*. Also, Lake Monona has been managed as a "panfish" or zooplanktivore lake in contrast to managing Lake Mendota as a "gamefish" or piscivore lake (i.e., strict regulations on harvest of piscivorous fishes that persist through present day; Lathrop et al. 2002), promoting an abundant population of bluegill. It is possible that high biomass of bluegill, a predator adapted to handle *Bythotrephes*' long tail spine (LeDuc and Kerfoot unpubl.), may be responsible for controlling *Bythotrephes* in Lake Monona. Additional research should investigate whether additional planktivory by fishes would mitigate or compound *Bythotrephes* effect on *D. pulicaria* and water clarity.

Ecological degradation is thought to increase ecosystem vulnerability to nonnative species establishment and impact (MacDougall and Turkington 2005; Light and Marchetti 2007; Johnson et al. 2008; Vander Zanden et al. 2016). For example, cultural eutrophication in Lake Mendota was managed through biomanipulation (Lathrop et al. 2002). With the biomanipulation, the biomass of planktivorous fishes declined and the biomass of large zooplankton like *D. pulicaria* increased (Johnson and Kitchell 1996). *Bythotrephes*' range expansion and establishment is limited by biological factors like predator abundance and prey availability (Young et al. 2011); as such the Lake Mendota biomanipulation may have changed the food web to favor *Bythotrephes*. Furthermore, decline of the cool-water cisco may have opened niche space for the cool-water *Bythotrephes*, as both species reach peak planktivory rates during cool-water time periods which complements existing planktivory by warm-water fishes and invertebrates (e.g., Fig. 3). *Bythotrephes* has reached higher densities in Lake Mendota than any other system in its native or invaded range (e.g., Jokela et al. 2011; Young et al. 2011). Brown et al. (2012) report a positive relationship between chlorophyll *a* (a measure of lake primary productivity) and *Bythotrephes* abundance, which partially explained elevated *Bythotrephes* densities in reservoirs over natural lakes. It is possible that the food web structure brought by biomanipulation of the highly productive Lake Mendota contributed to the establishment and elevated abundance of *Bythotrephes* (as described in Walsh et al. 2016*b*).

Furthermore, Lake Mendota is the first reported case of *Bythotrephes*' impact cascading into reduced lake water clarity (Walsh et al. 2016*a*). Walsh et al. (2016*a*) confirm that it is unlikely that this change in clarity was due to changes in nutrient loading or in-lake concentrations and that declining clarity has been due nearly entirely to increasing algal biomass (Walsh unpubl.). Prior *Bythotrephes* invasions were limited to less productive lakes that are not subject to the same degree of cultural eutrophication as Lake Mendota (Strecker and Arnott 2008). As *Bythotrephes* expands into lakes in highly agricultural watersheds, additional research should investigate the interactions among eutrophication, *D. pulicaria* grazing, and *Bythotrephes* zooplanktivory. Further, if cultural eutrophication is a key factor driving *Bythotrephes*' impact, lakes like Mendota should be targets of invasion prevention efforts to avoid such drastic and expensive impacts in the future. Likewise, efforts to reduce nutrient loading into lakes should offset *Bythotrephes* impact on water quality (Walsh et al. 2016*a*). The *Bythotrephes* invasion into eutrophic Lake Mendota highlights how food webs and nutrients interact to influence ecosystem vulnerability to biological invasion and their undesired consequences.

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Acknowledgments

Conflict of Interest

None declared.