DNR AIS R&D Grant Report

**Final report** on DNR AIS project# AEPP-365-12

**Early detection, vectors and impact of invasive spiny water flea in Wisconsin Lakes**

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This grant was awarded in spring of 2012. The project is now completed, and below we describe our objectives and our accomplishments.

**Scope of project and description of project area**

This ‘Research and Demonstration’ project focused on the Madison chain of lakes, but also included some other Wisconsin lakes known to be invaded by spiny water flea (Table 1). The Yahara Chain of lakes; lakes Mendota, Monona, Waubesa and Kegonsa of Dane County, WI comprise the original four study lakes for this project. We expanded the scope to include three additional lakes: Stormy Lake (Vilas County, WI), the Gile Flowage (Iron County, WI) and Lake Gogebic (Gogebic/Ontonagon Counties, Upper Peninsula, MI). At the time submitting the proposal, spiny water flea were limited to these seven lakes, presenting a unique opportunity to propose a project with a statewide scale encompassing a diverse range of environmental, ecological, and social interactions that strengthen the benefits of the project. Since 2012, spiny water flea have been found in several additional lakes in northern Wisconsin: Butternut (Forest County, 2014), Ike Walton (Vilas County, 2015), Star (Vilas County, 2013), and Trout (Vilas County, 2014). Spiny water flea appear to be expanding their rate of spread in northern Wisconsin. This further highlights the need for research to help understanding the ecological and economic impacts of this new player in Wisconsin’s lake communities.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Lake | Lake Area (ha) | Max Depth (m) | Mean Depth (m) | Chlorophyll-a (ug\*L-1) | Secchi Depth (m) | County, State |
| Mendota1 | 3,985 | 25.3 | 12.7 | 8.6 | 3.4 | Dane, WI |
| Monona1 | 1,326 | 22.6 | 8.3 | 8.1 | 2.4 | Dane, WI |
| Waubesa1,2 | 843 | 11.6 | 4.7 | 10 – 15 | 1.2 | Dane, WI |
| Kegonsa1,2 | 1,299 | 9.8 | 5.1 | 18 – 20 | 0.9 | Dane, WI |
| Stormy3 | 211 | 19.2 | 10.1 | NA | 8.0 | Vilas, WI |
| Gile Flowage3 | 1,369 | 8.2 | NA | NA | 1.6 | Iron, WI |
| Gogebic4 | 5,414 | 12.0 | 5.3 | NA | NA | Ontonagon & Gogebic, MI |

Table 1. Study lakes and relevant information. Lakes Gogebic, Monona, Waubesa, Kegonsa and the Gile Flowage are considered eutrophic. Lake Mendota is mesotrophic to eutrophic depending on the rate phosphorus loading into the lake and Stormy Lake is highly oligotrophic. [1] NTL-LTER; [2] Lathrop, 1988; [3] WI-DNR; [4] MI-DNR

*The Yahara Chain of Lakes* – The Yahara River flows into Lake Mendota from the north connecting it to Lakes Monona, Waubesa and Kegonsa to the south. The spiny water flea was first detected in these lakes in the summer of 2009. Lake Mendota supports the most abundant population of spiny water flea in its entire invaded or native ranges, reaching densities of over 1,500 individuals/m3. Spiny water flea is much less abundant in Lake Monona, and even less abundant in Lakes Waubesa and Kegonsa. These four lakes provide us with a diverse range of lake characteristics (morphometry, ecology, and water chemistry) while at the same time, the four lakes share a common climatic setting.

*The Lakes of Northern WI* – Stormy Lake and the Gile Flowage are located in Northern Wisconsin. The Gile Flowage was the first WI inland lake to be invaded (2003) and was monitored by Craig Roesler of the DNR from 2004 – 2008. Stormy Lake was invaded in 2007 and has since been monitored by the UW Center for Limnology Trout Lake Research station. Lake Gogebic is the largest inland lake of the Upper Peninsula and is highly trafficked by lake users. Spiny water flea was reported in the mid-late 1990s, and confirmed in 2003. The proximity of Lake Gogebic to WI lakes and the potential traffic across the border by recreational boaters makes this lake of concern to the state.

By incorporating northern and southern WI lakes into this project we hope to broaden its scientific scope and raise awareness of the spiny water flea on a statewide scale. With the growing interest in the spiny water flea from lake associations and DNR managers, we have a unique opportunity to understand and aid others in the understanding of Aquatic Invasive Species and their impacts.

**Description of problems addressed**

*Ecological Impact* - Once introduced to a lake, the predatory spiny water flea (*Bythotrephes longimanus*) can drastically impact the native zooplankton community composition and abundance (Barbiero and Rockwell 2008, Strecker and Arnott 2008, Yan and Pawson 1997, Walsh unpublished data). Impact on algae, water quality, and the fish community hinges on the impact in the zooplankton community. The spiny water flea consumes native zooplankton, thereby competing with native zooplanktivorous fishes. The spiny water flea is also a diet item of many fishes though its long tail spine deters predation by the smallest fishes (Compton and Kerfoot, 2004). If the spiny water flea reduced herbivorous zooplankton, algae could be allowed to grow unchecked.

*Identification of Transport Vectors* - The spiny water flea invaded the Laurentian Great Lakes in the 1980’s from Eastern Europe and Western Asia via transatlantic shipping vessels and spread to inland lakes in the 1990’s as a result of transport by recreational boats. The spiny water flea has spread rapidly among inland lakes in some regions, but has attracted relatively little attention (Yan et al. 2011). To better understand the transport vectors we need to examine how it manages to attach or hitchhike on recreational boats, and at the broader scale, which lakes are most likely to be source waters and the site of future invasions. Developing a basic understanding of these factors will greatly help in targeting containment efforts.

*Early Detection* – Spiny water flea are small (~10 mm), patchily distributed in space and highly seasonal. This makes detection, particularly at low densities, especially difficult. There is no widely accepted methodology for early detection of the species, and no research has been conducted to identify when, where and how we can most effectively detect spiny water flea and begin steps to contain it.

**Objectives and major findings**

The overarching goal of this work was to increase the fundamental understanding of the spiny water flea in WI. In doing so, our efforts are helping to provide guidance for future management of spiny water flea in WI and the broader region. Specifically, we have conducted work in the following thematic areas: ecological impact, early detection, and transport vectors.

*Ecological Impact* – The objective was to assess the ecological impact of spiny water flea in WI lakes with a focus on zooplankton, fish, and water clarity. Determining the impact of an invasive species requires adequate pre-invasion data to provide a before and after comparisons of invaded lakes.

The Yahara Lakes and Trout Lake are LTER study lakes, and thus provide exceptional pre-invasion limnological data for evaluating ecological impact of spiny water flea. We surveyed zooplankton communities by zooplankton tows taken weekly at the deepest points of Lake Mendota and every other week in Lakes Monona, Waubesa and Kegonsa. Targeted sampling for spiny water fleas is taken with a larger, coarser net (50 cm mouth and 250 micron mesh) alongside zooplankton community tows. Spiny water flea were at their highest levels in Lake Mendota, and occurred at lower levels in all the other lakes. Peak densities were consistently observed during fall.

We have conducted an ecological impact assessment for the spiny water flea in the Madison chain of lakes, focusing on Lake Mendota. We have evaluated the impact of spiny water flea on zooplankton, phytoplankton, water clarity, and nutrients by comparing pre- (1976 – 2009) and post-invasion (2009 – present) data using cutting edge methods such as multivariate autoregressive state space modeling (MARSS). Zooplankton communities have shifted dramatically in response to SWF invasion. The largest change is the sharp decline of *Daphnia pulicaria*. This species has long been a keystone grazer in Mendota and the Madison lakes. With the decline of Daphnia, water clarity has declined by about 1 meter, despite no overall change in Phosphorus loading to Mendota (Walsh et al. Appendix 1). Phosphorus cycling has also changed, and TP concentrations have decline by ~ 37%. This represents a tremendous change to the Lake Mendota ecosystem. We estimated that recovering the water clarity lost due to spiny water flea through additional phosphorus abatement efforts would cost approximately $175 million over a 20 year period (Walsh et al. Appendix 1).

In addition to the dramatic changes described above, zooplankton and algal communities have shifted in complex ways, which has had unexpected implications for phosphorus cycling. The many details of the seasonal and community-level shifts are being summarized in a separate scientific manuscript (Walsh et al. *in preparation*). This body of research highlights the clear need to redouble P reduction efforts in light of SWF’s powerful ecological impacts and negative effects on water clarity.

Spiny water flea are known to be consumed by plantivorous fishes. To what extent might key planktivory by zooplanktivorous fishes such as yellow perch be a factor in the dynamics of spiny water flea? Our yellow perch diet study revealed that perch prey heavily on spiny water flea when spiny water flea are abundant. Perch diets in August used to consist of 60% *Daphnia* (Johnson and Kitchell 1996). We estimate that perch diets are now comprised of less than 1% *Daphnia* and 47% spiny water flea. Despite this massive diet shift, we have observed no changes in perch condition. However, further attention must be paid to this valuable fishery. The decline of native Daphnia, a key food item for perch, may negatively affect perch. We were unable to detect any substantial changes in overall perch populations, though our fish sampling is not particularly sensitive to detecting population changes. Our work highlights the potential role of zooplanktivorous fishes such as perch that select for spiny water flea (spiny water flea is represented ~47% in diets and ~1% in zooplankton community). To what extent might fisheries management be used to help limit SWF populations? This is a key question that should be addressed in the future using bioenergetics simulations.

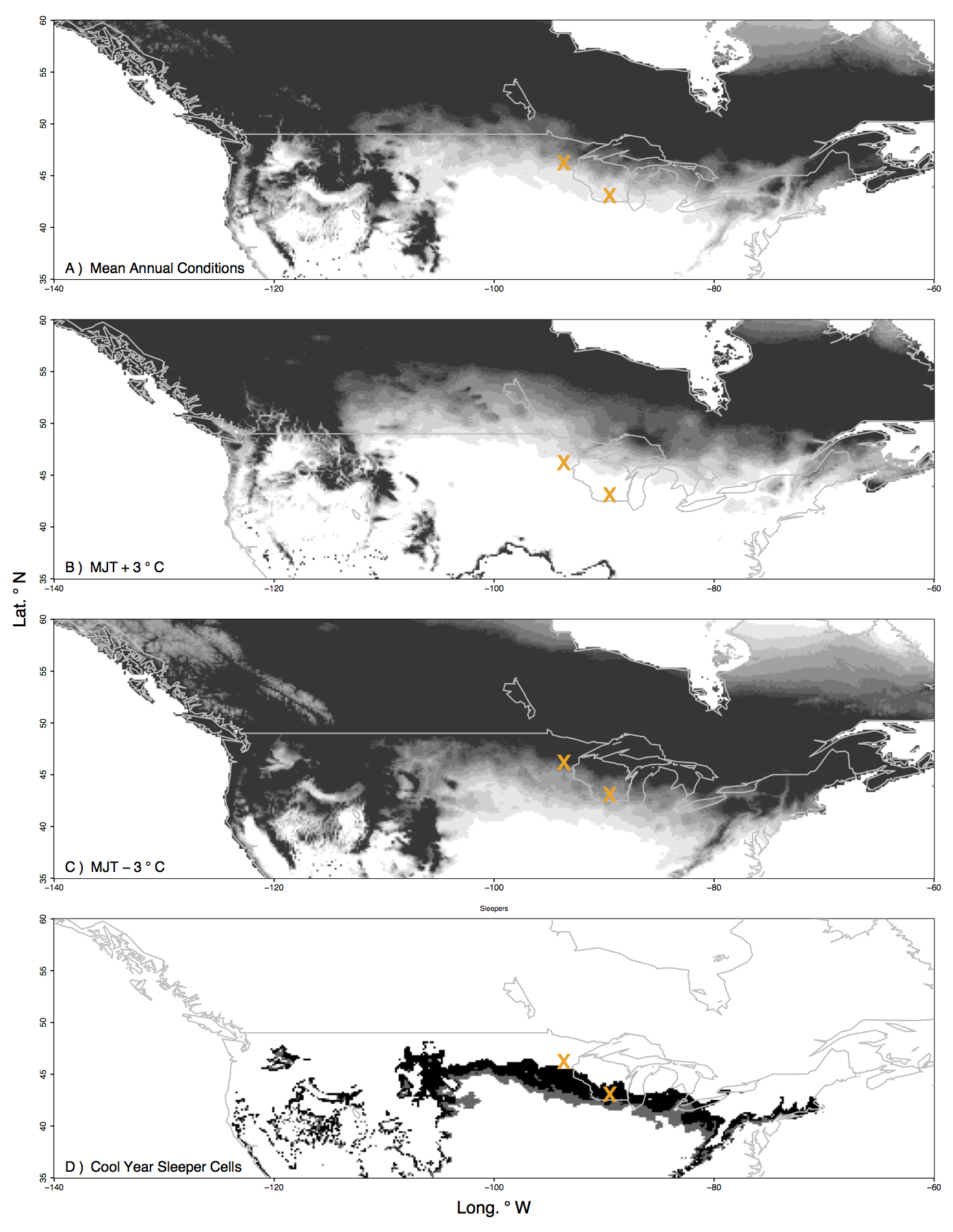


Fig. 1. Maps showing suitablility to SWF under different climate scenarios. Lake Mendota (WI) and Mille Lacs Lake (MN) and indicated by X. Spiny water flea was detected in both lakes in the cool summer of 2009. MJT = Mean July Air Temperature and is used to model lake water surface temperature.

In our efforts to understand impact, we developed a population model of SWF. The model strongly predicted the invasion of SWF in the Madison lakes in 2009. This model can be used as a mechanistic ecological niche model, and be used to make predictions of SWF invasion in other systems, and in the future under various climate change scenarios (Fig. 1). We are also developing correlative ecological niche models for spiny water flea using MAXENT models. These models have been difficult to interpret since SWF inhabit different types of lakes in different parts of their range. These models are being used to project potential habitat for this species, and strongly complement the mechanistic niche models mentioned above.

Carol Warden (WI-DNR, Trout Lake Station) was involved in regular sampling for zooplankton and limnological characteristics (temperature, dissolved oxygen profiles, secchi depth) in Stormy Lake and the Gile Flowage using the methods employed on the southern lakes. The resulting products of this monitoring can be found on our collaborators’ webpages (e.g. http://www.friendsofthegile.org/home/flowage-publications), and we worked with Whitewater Associates, Friends of the Gile Flowage, Lake Gogebic Association, and the Stormy Lake Association. Jake Walsh attended and presented at annual meetings with this set of collaborators from 2011 – 2013.



Fig 2. Seasonal abudance of SWF in Gile Flowage and Stormy Lake.

*Early Detection* – The second objective was to improve our ability to accurately and efficiently detect spiny water flea. We evaluated zooplankton tows, as well as sampling lake sediments for tail spines and resting eggs.

We found spiny water flea to exhibit large seasonal fluctuations in population density. Monitoring in both the Yahara Lakes and the northern lakes revealed highest abundance in late summer and fall (Fig. 2). This has direct bearing on our ability to detect SWF. Our detection study was conducted during low spiny water flea abundance. We varied sampling intensity, timing and tow method to test how effectively and efficiently we detect spiny water flea. We compared two methods of sampling zooplankton. The vertical haul involves dropping the net to 2 m off the bottom of the lake and pulling it vertically back to the boat. The oblique tow involves a drop to 2 m off the bottom, moving the boat a known distance horizontally, then pulling the net back to the boat. The vertical haul is the most accurate to determine the density of the spiny water flea. The vertical haul is also the easiest to process in lab. The oblique tow filters a larger amount of water, increasing the probability of detecting spiny water flea. It is much more difficult to calculate the amount of water filtered and more difficult to process in lab. We found that oblique tows detect SWF at a higher rate at low densities of the spiny water flea (Fig. 3). For simple detection, we recommend oblique tows. Since spiny water flea is most abundant in late summer and fall of all our monitored lakes, we recommend targeted sampling from June through October.



Fig. 3. Comparison of oblique tows (circles) and vertical tows (triangles). Frequency of SWF occurrence in nets tows as a function of density in Lake Mendota. Note that these are relatively low densities.

Due to these sampling issues and the seasonal cycles, our overall body of work highlights the limits of sampling in the water column, since we commonly fail to find spiny water flea in lakes where they’re known to be present. We have been developing and testing methods for detecting spines and resting eggs in lake sediments. Research carried out in 2015 evaluated 12 Wisconsin lakes, 5 from the Madison area and 7 from around the Trout Lake research station area, to span a range of population densities and dates of introduction. We used 3 different methods to sample all of the lakes, and a fourth just on Mendota. On all lakes, we have used an oblique plankton tow to sample the water column, as well as used an Ekman grab to sample both the top sediment layer and a larger, deeper portion of sediment (Fig. 4). We also collected water samples for eDNA analysis. Additionally, on Lake Mendota, we have taken sediment cores to get a picture of the timeline over which the SWF has been introduced, looking for spines of both the SWF and other species whose populations may fluctuate in response to the presence or absence of the SWF.



Fig. 4. Summary of Ekman grabs among lakes. Points represent means plus or minus 1 s.d. ME = Lake Mendota, MO = Lake Monona, WA = Lake Waubesa, KE = Lake Kegonsa, WI = Lake Wingra (no confirmed population of spiny water flea). The abundance of spiny water flea evidence in the sediment appears to correlate with the number of spiny water flea in the water column.

We are currently developing a relationship between the mean density of adult spiny water flea in the water column and the number of tail spines or resting eggs in the sediment of invaded lakes. This will provide a means for estimating mean water column abundance from sediment samples. While the work is still underway, Ekman grabs may give accurate measurements of population size and a reasonable measure of how long the species has been in the body of water. By comparing the top sediment layer in the grab to the whole sample, which can go back up to 15 years, we are able to evaluate recent population size relative to earlier years. Sediment cores appear to provide a highly accurate estimate, but it can be quite difficult to collect, and dating the cores is an expensive procedure.

*Identification of Transport Vectors* – An additional objective was to determine primary vectors of transportation among the invaded lakes of WI. Spiny water flea is spread among inland lakes by recreational boaters. By determining where on a boat we are most likely to transport spiny water flea, we can instruct boaters in how to effectively clean their boats when leaving a spiny water flea invaded lake.

We conducted a study that searched boats leaving invaded and highly trafficked Lake Mendota for spiny water flea adults and resting eggs. We sampled live wells, engines, bait buckets and ballast tanks by draining and spray washing them through a filter to collect spiny water fleas that may have been present on the boat. We also sampled anchors and anchor lines (Table 2). Our experiment evaluating spiny water flea transport vectors on recreational watercraft revealed that, despite considerable effort, they were exceptionally difficult to find being transported on boats. This led to us ultimately focusing more on the role of resting eggs in sediment. In invaded lakes such as Mendota, we found resting eggs at very high levels in the mud. Our results strong suggest that mud on anchors and anchor lines are an important vector of spiny water flea transport among lakes.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Adults | Eggs | Embryos | Tail Spines |
| **A) In Lake Mendota:**  Water column (1.4 m3 water) | 12.0 | 2.3 | 10.6 | 5.0 |
| Sediment (1 cm3) | 0 | 0.43 | 0 | 4.1 |
| **B) In simulated trip**  Anchor and anchor line | 0.33 | 0 | 0.33 | 2 |
| Live well simulation | 0.5 | 0 | 0 | 1 |
| Motor | 0.33 | 0 | 0 | 0 |
| Inside boat | 1 | 1 | 0 | 3 |

Table 2. Density in water column estimated from a single large (0.5m mouth) vertical zooplankton net tow. Density in sediment estimated from surface layer (1 cm) of sediment core. Trips occurred over 3 simulated trips in the fall of 2012. 2012 was a particularly poor year for spiny water flea population growth and abundance.

Fig. 5. Temporal variation in the number of resting eggs (/m3) in Lake Mendota during 2013.

In addition, we estimated the number of eggs per cubic meter of water in Lake Mendota 2013 (Fig. 5). Despite difficulty detecting hitchhiking spiny water flea on our simulated trips on Lake Mendota, this low density multiplied over the many boats leaving the lake could represent a significant pathway for spiny water flea invasion.

**Products and deliverables**

We have documented dramatic ecological and economic impacts in Lake Mendota, where data were available to do this. While impacts may be heterogeneous among lakes, this finding highlights the need to keep spiny water flea from spreading further, especially in southern WI lakes. We are still working on our early detection protocols, but our preliminary data indicates Ekman grabs as the most reliable tool for spiny water flea presence detection. And finally, our work strongly indicates the role of anchors and anchor lines transporting resting eggs as the main target for controlling SWF spread in the future.

Jake Walsh gave a public presentation at the North American Lakes Management Society conference on the impact of the spiny water flea in Lake Mendota. He presented at the WI lakes convention in 2014, and at the Joint Aquatic Sciences meeting in May 2014, the Ecological Society of America in August of 2015, and at the annual spiny water flea meetings organized by Whitewater Associates from 2011 - 2013. Jake Walsh provided a large amount of material and a report for Whitewater Associates. Jake Vander Zanden has presented these findings to a number of audiences, including the Clean Lakes Alliance (once in conjuction with Jake Walsh) two times. We have shared this work at regular meetings with DNR staff, AIS coordinators meetings (including Oct 2015), and other partners of the project. This work was featured in a July 26 2014 feature article in the Milwaukee Journal Sentinel (<http://m.jsonline.com/267014431.htm>), a feature in the May 14 2014 Cap Times/Wisconsin Watch (<http://wisconsinwatch.org/2014/05/water-cleaning-crustacean-devoured-by-new-predator-in-lake-mendota/>), and NBC15 in spring of 2015. Vander Zanden wrote an article for the Yahara Lakes Association newsletter. Overall, we have reached a large audience with this work, and have dramatically increased awareness of spiny water flea in Madison and elsewhere.

**Expected Publications**

1. The impact of the spiny water flea cascades into primary production in Lake Mendota (WI, USA) [intended outlet: Nature]
2. The impact of the spiny water flea on the food web dynamics and ecological processes of two eutrophic lakes. [intended outlet: Ecological Monographs]
3. Sleeper cells: environmental conditions trigger population boom of spiny water flea in Lake Mendota (WI). [intended outlet: Ecology]
4. Modeling population dynamics at the landscape level: Predicting spiny water flea abundance in susceptible lakes across North America. [intended outlet: Ecology]
5. Early detection methods for the invasive spiny water flea (*Bythotrephes longimanus*). [intended outlet: Canadian Journal of Fisheries and Aquatic Sciences]

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**Appendix 1**

**Massive ecological and economic impact of an invasive species**

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Keywords: invasive species, ecosystem services, water quality, Daphnia, Bythotrephes longimanus, spiny water flea, lake, eutrophication

In preparation for *Nature*

**Despite major advances in the global recognition of the value of ecosystem services, the direct connection between invasive species and their impacts on ecosystem goods and services is poorly characterized. This is concerning as invasive species cause enormous ecological damages and their impacts on human well-being are likely similarly large and harmful. Here we evaluate the economic impacts of an invasive species on a valuable cultural ecosystem service. The predatory zooplankton, the spiny water flea (SWF), invaded Lake Mendota (WI, USA) where it has maintained record densities. Through predation on the water-purifying algae grazer, *Daphnia pulicaria* (60% biomass loss), SWF has caused never before seen cascading effects on water clarity (0.9m decline), which has been valued at US$140M (US$640 per household) present-day value in citizens’ willingness-to-pay for 1m of water clarity. We find that clarity in Mendota is driven by *D. pulicaria* biomass, phosphorus, and seasonal surface temperature with 57% of the decline in clarity directly related to a loss in grazing. To offset these effects of SWF, we estimate it would take an 80% reduction in P-loading, costing US$175M (US$810 per household). These results highlight the ecological and economic importance of assessment and valuation of invasion impacts on ecosystem services to help inform public policy where trade-offs between the costs of invasive management and damages must be considered simultaneously.**

Despite exponential increases in global recognition of the importance of ecosystem services1, linkages between species invasions and ecosystem services remain poorly documented and poorly understood2,3. Globally, invasive species are among the primary threats to ecosystem resilience and the sustainability of ecosystem services4–6. Therefore, investing in the prevention of invasions can be considered investment in the protection of the benefits to humanity provided by ecosystem services. However, the lack of valuations of the damages to ecosystem services due to invasion leaves policymakers with little to no information by which to weigh the trade-offs of such investments7–9.

Freshwater ecosystems are a cornerstone of human society, providing drinking water, fisheries, pollution dilution, recreation, and other goods and services10. Valuation of these services is critical for public policy, but many of the services provided by freshwater ecosystems are not monetized8,11, leaving them overlooked and undervalued and thus poorly integrated into decision frameworks1,6. One such service is water quality of lakes and reservoirs which is degraded by phosphorus pollution12. *Daphnia*, a genus of freshwater zooplankton, moderate water quality by filtering out algae13. Accordingly, lakes are often managed to support large *Daphnia* populations by reducing the abundance of their predators14.

The invasive spiny water flea (SWF), *Bythotrephes longimanus*, is a voracious zooplanktivore that has the capacity to consume more zooplankton than fish and other invertebrate planktivores combined15. Despite this planktivory and large documented ecological impacts on zooplankton communities16, SWF has not been found to have cascading effects on lake primary production and water clarity17. The lack of cascading effects of SWF invasion is perhaps because the productive lakes most vulnerable to impaired water quality are thought to be relatively unsuitable for SWF establishment18,19.

SWF was detected in the well-studied urban Lake Mendota in 2009 at some of the highest densities on record (> 1500 m-3). The invasion was of immediate concern as a preferred prey of SWF, *Daphnia pulicaria*, has been the focal point of Lake Mendota’s food web management, supporting the lake’s fishery20 and maintaining clear water through grazing algae21. Lake Mendota is located within an agricultural watershed and receives large amounts of phosphorus from farm run-off, driving poor water quality by fertilizing algal growth22. This ecosystem service provided by *D. pulicaria* has provided huge economic benefits over the past 27 years, not only affecting shoreline property values on the order of millions of dollars 23,24, but also providing recreational value to citizens who have been estimated to be willing to pay US$140M present day value for 1 m of water clarity 25. Here we evaluate the ecological and economic impacts of the SWF invasion into Lake Mendota and thereby demonstrate significant economic impacts of an invasive species.

**The loss of ecosystem service**

Since the detection of SWF in 2009, water clarity in Lake Mendota has declined by 0.9 m (Fig. 1F) alongside a 60% reduction in *D. pulicaria* biomass (Fig. 1B). In addition, there was a 37% decrease in total phosphorus (TP) (Fig. 1D) despite no clear change in P-loading (Fig.1E), and a 17% increase in total zooplankton biomass (Fig. 1C; 56% increase in non-*D. pulicaria* grazers). A cascading impact of SWF has not been previously documented 17 and this is an unusually large cascading effect for an invertebrate mesopredator 26. It is also striking that water clarity declined despite favorable TP concentrations.

Though the strongest effects of SWF on *D. pulicaria* are observed in the fall, the most surprising observed changes were in the spring. We propose that *D. pulicaria* are heavily predated by SWF in the fall andstruggle to make the robust egg bank required to overwinter and re-establish zooplankton community dominance over other grazing zooplankton in the spring. The replacement of *D. pulicaria* by smaller grazers like *D. galeata mendotae* and copepods may explain why water clarity was lower at all points in the year, but was particularly low in the spring despite low TP.

These lingering effects are most obvious in the recent whole-*Daphnia* community collapse from 2 September 2014 through 12 May 2015, concurrent with exceptionally high SWF biomass in the fall. This collapse, lasting over 250 days, is the longest absence of *Daphnia* spp. in the recorded history of Lake Mendota (since 1976) 27, with previous *Daphnia* absences lasting a maximum of 14 days and the most recent of any duration occurring in 1989. This collapse led to historically low spring water clarity conditions and a weaker and later clarity maximum driven by *D. galeata mendotae*. An alarming component of the 2014 - 2015 *Daphnia* collapse is the disappearance of not only *D.* *pulicaria* but also of the smaller *D. galeata mendotae*, which had become more successful after SWF invasion in Lake Mendota. While not as efficient as a grazer as *D. pulicaria*, *D. galeata mendotae* does provide shorter, later clear water maxima and better water clarity relative to smaller, more selective grazers like copepods 21. To date, the changes in water clarity have been driven by the switch between *Daphnia* species. If *D. galeata mendotae* declines in years with high SWF biomass, the changes in water clarity could be more severe in the future.

Multivariate autoregressive state-space modeling (MARSS)28, commonly used for measuring the strength and direction of ecological interactions, revealed that higher external phosphorus loading and seasonal surface temperatures have driven lower water clarity and *D. pulicaria* biomass has driven higher water clarity over the past two decades in Lake Mendota (Fig. 2). These results are consistent with our previous understanding of the lake’s food web 21. Due to competition for the algal food source, *D. pulicaria* biomass has a negative effect on the total biomass of all other zooplankton species, which do not consume algae fast enough to have an effect on lake water clarity or on *D. pulicaria*. Therefore, the decline in *D. pulicaria* likelyexplains why total zooplankton biomass increased after the invasion of a predator.

**Ecological implications**

We predicted water clarity under high (pre-2009) and low (post-2009) *D. pulicaria* biomass (Fig. 3) and under varying P-loading scenarios (-99% to +100%) using our fitted MARSS model (Fig. 3B). To compensate for the loss of grazing and offset the impact of the SWF invasion, we estimate we would have to reduce external P-loading into the lake by 80% to return to the water clarity with higher *D. pulicaria* biomass. Fortunately, *D. pulicaria* was often less abundant in summer months and, thus, efforts to reduce P-loading into the lake will likely be effective in summer months even under the post-2009 regime (Fig. 3A). Furthermore, the water clarity benefits provided by a 50% P-load reduction goal set before 2009 are now more than likely out of reach, now requiring enormous P-load reductions.

**Economic implications**

To put these ecological implications in economic terms we consulted socio-economic literature regarding Lake Mendota and its watershed. In 2013, Strand Associates estimated the cost of reducing P-loading into Lake Mendota by 50% and 86% over the next 20 years to be US$70.3 M (US$176 per kg P diverted) and US$177 M (US$309 per kg P diverted), respectively29. Removing the least cost-efficient P-load reduction options from the maximum implementation plan (86% reduction) to reach a reduction of 80% leaves a cost of US$175M (US$810 per household in Dane County). The report was written with the understanding that *D. pulicaria* would be providing its pre-2009 level of grazing and any benefits of the reduction goals would be on top of this ecosystem service. Our estimate reveals that Madison would have to invest significantly more money to simply return to pre-invasion water clarity and any further improvements to water clarity would have to be made on top of this investment.

An additional perspective on this economic impact is offered by the results of Stumborg and others who found that citizens in the region (Dane County, WI) are willing to pay US$140M present day value (US$640 per household) for 1 m of water clarity gained by managing the lake25 - roughly equivalent in magnitude to the loss of 0.9 m by declining *D. pulicaria*. In the context of this cultural value of water clarity in Madison, US$175M is a huge price tag for a single invasion. Managers may need to consider new strategies to directly mitigate SWF’s effect on *D. pulicaria* (e.g. via managing the fishery). Additionally, preventing the spread of SWF from Lake Mendota into other lakes in the region is paramount, lest these effects be multiplied as SWF spreads.

These damages and costs highlight the severity of even a single case of invasion affecting a single ecosystem service. Furthermore, the economic efficiency of prioritizing the prevention of invasions is reported widely 9,30,31. The information reported here allows for a direct comparison of the trade-offs between preventing invasions and assuming their damages. For example, the cost to offset the SWF’s impact and the damages associated with a loss of 1 m of water clarity highlight the value of broader-scale invasion prevention efforts like closing direct access to the St. Lawrence Seaway by transatlantic shipping vessels. Allowing direct access to the seaway by these ships provides US$55M of annual savings relative to alternative methods32. The cost to offset the damages of this single secondary invasion (US$8.75M per year or 16% of those savings) alone make a strong case for preventing future invasions at this scale.

Linkages of ecological processes with economic or social benefits are needed to apply ecosystem service concepts in public policy1,33,34. We have shown that an invasive species degraded an ecosystem service, demonstrated the mechanism, and estimated the economic cost. SWF invasion has not only decreased water quality. It has also caused serious additional costs for improving water quality by directly reducing phosphorus input. Water quality targets for the lake are more difficult and expensive to achieve as a result of the invasion. Thus the value of an ecosystem service is also related to the ecological mechanism of achieving that service. Ecological mechanisms, as well as economic ones, must be analyzed together to bring ecosystem services into decision processes regarding species invasion 8.

**Methods Summary**

**Time series -** Lake Mendota is a part of the NSF North Temperate Lakes Long Term Ecological Research program. We were able to obtain fortnightly time series for water clarity (Secchi depth), zooplankton biomass35, phosphorus concentrations, and surface temperatures from the long-term database (lter.limnology.wisc.edu). Phosphorus loading data is obtained through a USGS monitoring site on the Yahara River that correlates strongly (R2 = 0.97) with total phosphorus load into the lake (usgs.gov). We visualize pre-2009 and post-2009 changes using generalized additive models fitted to day of the year36. **MARSS -** We used multivariate autoregressive state-space time series modeling28 to investigate ecological interactions in Lake Mendota and predict water clarity under varying grazing and P-loading scenarios. **Economic Information -** We obtain P-load reduction cost information from the Yahara CLEAN engineering report conducted by Strand Associates29. We update valuation of water clarity25 to present day using the Consumer Price Index Inflation Calculator (data.bls.gov) and household estimates in Dane County, WI to 2014 census information (census.gov).

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**Figure Legends**

Fig. 1 Seasonal dynamics pre- (blue; 1995 - 2007) and post-SWF (red; 2009 - 2014) of SWF (A), zooplankton grazers (B-C), phosphorus dynamics (D-E), and water clarity (F) are plotted as a smoothed GAM function of day of the year. Shaded areas represent 1 standard error.

Fig. 2 MARSS estimates of ecological interactions are shown with arrows. Red arrows are significant negative effects, black arrows are significant positive effects, and grey arrows are insignificant effects. Half circle arrows represent first-order autoregressive terms, akin to “density-dependence” in population modeling.

Fig. 3 MARSS model predictions under pre (blue) and post (red) 2009 zooplankton grazing conditions highlight the loss of the ecosystem services provided by *D. pulicaria* (A) and the cost of offsetting SWF’s impact through P-loading reductions (B). This is calculated as the P-loading reduction necessary to return the lake to pre-2009 clarity (blue filled circle) under post-2009 grazing (red filled circle).

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