

Network analysis to inform invasive species spread among lakes

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Abstract Often facilitated by human-mediated pathways, aquatic invasive species are a threat to the health and biodiversity of global ecosystems. We present a novel approach incorporating survey data of watercraft movement in a social network analysis to reconstruct potential pathways of aquatic invasive species spread between lakes. As an example, we use the green alga *Nitellopsis obtusa*, also known as starry stonewort, an aquatic invasive species affecting the Great Lakes region in the United States and Canada. The movement of algal fragments via human-mediated pathways (i.e., watercraft) has been hypothesized as the primary driver of starry stonewort invasion. We used survey data collected at boat ramps during the 2013 and 2014 open-water seasons to describe the flow of watercraft from Lake Koronis, where *N. obtusa* was first detected in Minnesota, to other lakes in the state. Our results suggest that the risk of *N. obtusa* expansion is not highly constrained by geographic proximity and management efforts should consider highly connected lakes. Estimating human movement via network analysis may help to explain past and future routes of aquatic invasive species infestation between lakes and can improve evidence-based prevention and control efforts.

Keyword: *Nitellopsis obtusa*; starry stonewort; lake; network; invasion

1 INTRODUCTION

Aquatic invasive species are a threat to the health and biodiversity of global ecosystems, with the potential to cause harm to the ecology and/or economy in invaded regions (Lockwood et al., 2007). Unintentional human-mediated translocation of species has been associated with many invasion events and is consequently a significant focus for management (Strayer, 2009). Estimating human movement between lakes may help to reconstruct past invasions and predict future routes of aquatic invasive species infestation. We explore the potential for human movement information to elucidate the pathways of the potential aquatic invasive spread between lakes. As a case study we use the green macroalga *Nitellopsis obtusa*, also known as starry stonewort, from the Characeae family, which is an invasive species in the United States albeit vulnerable,

near threatened, and endangered in the United Kingdom, the Baltic Sea, and Japan respectively (Joint Nature Conservation Committee, 2010; HELCOM, 2013; Kato et al., 2014). In some areas of its invasive range, *N. obtusa* has been reported to outcompete native vegetation, and impair the recreational use of lakes (Hackett et al., 2014; Sleith et al., 2015; Brainard and Schulz, 2017). It could also be associated with reduced habitat quality for fish, although this hypothesis still needs experimental confirmation (Pullman and Crawford, 2010). Consequently, this species has been identified by many organizations, including the Minnesota Aquatic Invasive Species Research Center (<http://www.maisrc.umn.edu/>), the Minnesota Department of Natural Resources (<https://goo.gl/5dIqC1>), and the

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U.S. Geological Survey (<https://goo.gl/7rS981>) as an important non-indigenous aquatic invasive species.

Nitellopsis obtusa was reported in North America 40 years ago (Geis et al., 1981; MISIN, 2015); since then, it has spread and established in lakes in Michigan, Wisconsin, Indiana, New York, and Vermont in the United States and in Ontario and Quebec in Canada (Pullman and Crawford, 2010; Sleith et al., 2015; Midwood et al., 2016). In 2015, *N. obtusa* was reported for the first time in Minnesota, in Lake Koronis (longitude 94.711 6°W, latitude 45.334 85°N; Fig.1) (DNR, 2015).

Nitellopsis obtusa is a dioecious species, with separate male and female individuals; however, only male individuals have been identified in invasive populations in North America (Sleith et al., 2015). This suggests that the spread of *N. obtusa* is driven by asexual reproduction via movement of viable bulbils and fragments. Human movement of bulbils and fragments via watercraft is considered to be the most likely factor for *N. obtusa* spread in North America (Pullman and Crawford, 2010; Sleith et al., 2015; Midwood et al., 2016). Thus, characterizing pathways for human-mediated translocation of *N. obtusa* via watercraft movement between lakes may be an effective means for prioritizing intervention strategies. As a proof-of-concept, we used a network analysis approach to understand lake connectivity for Lake Koronis, the first lake invaded by *N. obtusa* in Minnesota.

2 MATERIAL AND METHOD

We used survey data of watercraft movement, previously collected by the Koronis Lake Association (<http://koronislakeassociation.org/>). Lake Koronis is within the North Fork Crow River Watershed in Minnesota and has an area of ~1 220 ha and a maximum depth of ~40 m. The in-person survey was performed at the Lake Koronis public boat access during the Summer months of 2013 and 2014. All types of watercraft were included in the study with surveys developed on a daily basis during the hours of more activity (~8:00–16:00). The primary question of interest for this study was “What was the most recent lake visited and what is the next lake you plan to visit with your watercraft?” To identify and visualize lake connectivity, we used ArcGIS software (v.10.3.1) including a raster file of Minnesota lakes from the U.S. Geological Survey for the geolocalization of lakes (NASA and USGS, 2014). We estimated in-degree values (i.e., amount of watercraft flow arriving



Fig.1 *Nitellopsis obtusa* reaching the water surface in Lake Koronis in Minnesota (September 2015)

Insert: star-shaped bulbils (arrow) are thought to be key propagules for the spread (Photos: DJ Larkin).

at a specific lake) to represent connectivity among lakes according to the interviews.

3 RESULT

A total of 5 742 surveys were conducted, with a 67.6% ($n=3,882$) response rate to the question of interest (i.e., past and future lakes to be visited); from these, most reports corresponded to past and future visit to the same lake (i.e., Koronis) so that no connections were estimated for these reports. We found that network analysis successfully classified in-degree values enabling identification of “super receiver” lakes—defined here as a destination receiving $\geq 25\%$ of connections from a single source. Here, the super receiver lake was Rice Lake, which has a direct hydrologic connection to Lake Koronis and accounted for 25.7% of watercraft movement from Lake Koronis (Fig.2). Mean values of watercraft movement revealed that Rice, Horseshoe (8.3% of connections), and Clearwater (6.3% of connections) Lakes in Stearns County, and Green Lake (8.8% of connections) in Kandiyohi County, would have the highest risk for *N. obtusa* translocation from Lake Koronis. Also of note, Lake Mille Lacs is at considerable distance from Lake Koronis (12 km), but the lakes are well-connected in terms of watercraft movement ($>5\%$ of connections).

4 DISCUSSION

Network analyses have been used to reconstruct the translocation of infectious diseases at fine (VanderWaal et al., 2016) and coarse scales (Brockmann and Helbing, 2013). Network analysis can also help to describe the flow of people and

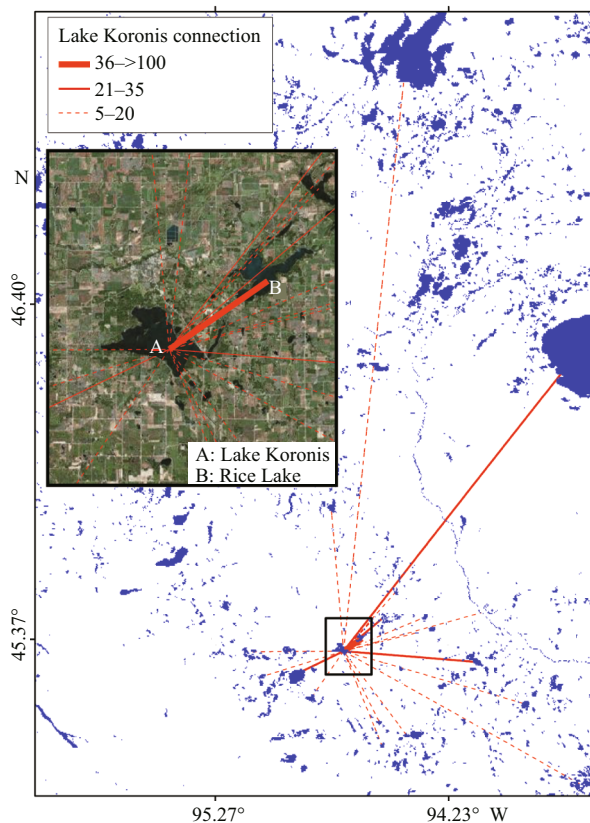


Fig.2 The connection of *Nitellopsis obtusa*-infested and non-infested lakes in Minnesota

Watercraft movement, between Lake Koronis, currently infested with *N. obtusa* (node) and other lakes in Minnesota, was determined based on surveys of the origin and intentions of future destination of boats to identify lakes with high (thick red line), mid (thin red line), and low (dashed red line) risk of *N. obtusa* translocation. Inset a zoom of Lake Koronis (black square) showing that the highest connection is with Rice Lake.

products between waterbodies, and their potential to translocate invasive species, which has been explored at coarse scales via global shipping networks (Keller et al., 2011). However, the application of network analysis to understand fine-scale translocation of invasive species (e.g., between lakes) is in its infancy. One of the main challenges of network analysis applications in invasion ecology is data availability (How many samples are enough? What are the effects of sampling bias?). Here, we explore the use of fine-scale network analysis based on between-lake boater movement or intention of movement, to untangle the connection between invaded and uninvaded lakes with *N. obtusa*. Interestingly, Brainard and Schulz (2017) recently reported an invasion pattern matching our proposed mechanism for *N. obtusa* invasion in lakes with high boat traffic as compared to lakes with low boat traffic. Similarly, Sleith et al. (2015) found

N. obtusa populations in lakes with high access and absence of the species in lakes with minimal access. Here, the risk was defined as levels of connection between the invaded lake and non-invaded lakes. We identified lakes with high, mid, and low risk, as compared with other—not connected—lakes. That is, low-risk lakes still receive boat traffic from infested lakes and translocation of *N. obtusa* is plausible, especially in scenarios of translocation of a high amount of propagules in a single visit.

Nitellopsis obtusa is an aquatic invasive species for which there are concerns about effects on recreation and native biological communities (Hackett et al., 2014; Sleith et al., 2015; Brainard and Schulz, 2017). Strikingly, its geographic spread is still active and by April 2018 ten lakes in Minnesota were confirmed by authorities to be infested with *N. obtusa* (Cass, Grand, Koronis, Minnewaska, Moose, Rice, Turtle, Upper Red, West Sylvia, Winnibigoshish) (MNDNR, 2018). In addition, efforts to control *N. obtusa* have proven to be challenging and expensive (Pullman and Crawford, 2010; Hackett et al., 2014; Sleith et al., 2015; Midwood et al., 2016). Thus, methods to prioritize allocation of spread prevention efforts are justified. Our results suggest that boater movement surveys can inform understanding of lake connectivity in a manner that geographic proximity alone cannot characterize. Furthermore, highly connected lakes could be subject to increased early detection efforts for this and other cryptic invaders that can be easily missed at early stages of infestation (Pullman and Crawford 2010; Hackett et al., 2014; Midwood et al., 2016).

We note that even when the number of interviews may seem statistically representative ($n=5\,742$), the number of lakes surveyed may be an underrepresentation of the boat traffic in the study area. Increasing the number of lakes in which surveys are conducted may help to reduce the uncertainty of lake connections captured here. Identification of candidate lakes to be surveyed could be facilitated by information related to the number of parking spaces at public accesses at each lake. This is based on the assumption that parking spaces serve as a proxy for popularity (high boat traffic), traditionally difficult information to estimate. This would improve data collection efficiency. Additionally, other study design components that deserve exploration include data collection strategies to obtain a representative sample (e.g., identification of seasons, weekdays, hours in which the data should be collected) and methodologies

to increase the rates of responses. That is, future research should aim to determine the minimum amount of effort necessary to capture representative patterns of watercraft movement among lakes. This information may vary by season and geographic area so that sampling strategies should be a factor of critical evaluation.

An important limitation of this study is accuracy on the response. For example, our dataset included oral interviews of previous and future visits to lakes by boat owners; this source of information may include incorrect reports from past or future boater movements (e.g., unjustified fear of punishment due to previous visits to infested lakes or visitation of a different lake than was originally intended). That is, we recorded past movement and intention for future boat movement, which may not be as accurate as tracking individual boats across time. Errors of information in the survey may add noise to the final estimation of watercraft flow among lakes. Additionally, we focused the survey on the first reported lake to be invaded by *N. obtusa* in the most active season of boater movement; however, including more lakes (invaded and not invaded) and seasons may be a more informative—but expensive—strategy to account for potential sampling bias in the capture of patterns of boat movement among lakes.

5 CONCLUSION

This exploration suggests that using fine-scale network analysis from boater movement data may help to anticipate invasions at the lake level and can reconstruct potential routes of aquatic invasive species spread. Our approach can be a tool to determine high-risk lakes to develop early warning systems and guide prevention and management efforts. Challenges still exist in the study design to collect data under representative areas and seasons. Our ongoing work includes the estimation of lake connectivity based on geographic distance, boat movement, and lake-river connections to identify network scenarios that can best reconstruct past aquatic invasions in the Great Lakes region of North America using invasive plants, animals, and pathogens as model species.

6 DATA AVAILABILITY STATEMENT

All data generated or analyzed during this study are included in this published article and the Appendix.

7 ACKNOWLEDGMENT

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APPENDIX

A number of boats moving from Lake Koronis to other lakes, based on self-reported boater surveys.

Lake_ori	Lat_Ori	Lon_Ori	Lake_dest	County_dest	Y2013	Y2014	Annual average	Lat_Des	Lon_Des
Koronis	45.329 84	-94.698 6	Big	Stearns	9	11	10	45.423 17	-94.575 3
Koronis	45.329 84	-94.698 6	Big Fish	Stearns	0	14	14	45.517 25	-94.463 4
Koronis	45.329 84	-94.698 6	Buffalo	Wright	0	11	11	45.164 85	-93.892 6
Koronis	45.329 84	-94.698 6	Clearwater	Stearns/Wright	14	35	24.5	45.296 19	-94.106 7
Koronis	45.329 84	-94.698 6	Diamond	Kandiyohi	14	24	19	45.182 86	-94.842 8
Koronis	45.329 84	-94.698 6	Florida	Kandiyohi	0	10	10	45.251 01	-95.058 2
Koronis	45.329 84	-94.698 6	Goodners	Stearns	0	7	7	45.387 48	-94.374 3
Koronis	45.329 84	-94.698 6	Grand	Stearns	0	8	8	45.435 91	-94.339 0
Koronis	45.329 84	-94.698 6	Green	Kandiyohi	25	44	34.5	45.260 10	-94.903 5
Koronis	45.329 84	-94.698 6	Horseshoe	Stearns	25	40	32.5	45.429 63	-94.531 4
Koronis	45.329 84	-94.698 6	Leech	Cass	0	14	14	47.148 66	-94.420 7
Koronis	45.329 84	-94.698 6	Mille Lacs	Mille Lacs	19	22	20.5	46.252 98	-93.660 5
Koronis	45.329 84	-94.698 6	Minnetonka	Hennepin	20	9	14.5	44.907 34	-93.634 4
Koronis	45.329 84	-94.698 6	Minnie-Belle	Meeker	0	12	12	45.034 19	-94.527 7
Koronis	45.329 84	-94.698 6	Mississippi River	Sherburne	0	17	17	45.449 74	-94.088 6
Koronis	45.329 84	-94.698 6	Norway	Kandiyohi	8	0	8	45.327 99	-95.125 0
Koronis	45.329 84	-94.698 6	Rice	Stearns	58	143	100.5	45.369 58	-94.617 3
Koronis	45.329 84	-94.698 6	Ripley	Meeker	9	0	9	45.108 58	-94.539 5
Koronis	45.329 84	-94.698 6	Stella	Meeker	0	16	16	45.066 53	-94.418 3
Koronis	45.329 84	-94.698 6	Big Birch	Stearns	9	0	9	45.779 13	-94.754 3

Lake_ori: site of the departure of boats (i.e., Lake Koronis); Lat_Ori: geographic latitude of the site of origin; Lon_Ori: geographic longitude of the site of origin; Lake_dest: final destination of the boat; County_dest: county of destination; Y2013: data obtained in the year 2013; Y2014: data obtained in the year 2014; annual average: an average of years; Lat_Des: geographic latitude of the site of destination; Lon_Des: geographic longitude of the site of destination.