Pathways of Invasion: Developing models to predict recreational boater activity, aquatic invasive species distributions, and landscape level connectivity to inform aquatic invasive species management across New York State

Report to the New York State Department of Environmental Conservation

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Adirondack Watershed Institute

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Executive Summary

The Paul Smith's College Adirondack Watershed Institute (AWI) has worked to protect water quality in the Adirondacks and northern New York state since 1989. Its flagship Stewardship Program is the primary vehicle for aquatic invasive species spread prevention, achieved through direct engagement with recreational boaters. Since 2017, more than 100 watershed stewards at boat launches throughout the region inspect incoming and outgoing vessels and collect vital data from the recreational boating community. The long history of AWI and the Stewardship Program, together with the regional partnerships that have developed coordinated survey methodologies across this large geography, have resulted in a wealth of data that can inform the prevention, introduction, spread, management, and ecology of invasive species in our region and elsewhere. We used these data to broaden our understanding of the current distribution of AIS in the Adirondack ecosystem, the role of recreational boating activity in their dispersal across the landscape, the connections among waterways that result in a range of invasion risk among Adirondack waters, and the means by which our understanding can provide tools and recommendations for efficient deployment of limited financial resources for AIS prevention and management in other areas of the State.

Our project goal was to *help managers to allocate AIS spread prevention resources efficiently by quantifying the axes of invasion risk and potential pathways of distribution in the Adirondacks and Northern New York and by developing a generalizable model that can be applied to prioritize management actions throughout New York State and other regions.* Our objectives were to: (1) *model the spatial pattern and intensity of recreational boating activity in the Adirondack landscape,* (2) *model the abundance and distribution of aquatic invasive species in Adirondack waters,* (3) *identify and predict connections and most likely pathways of spread between established AIS populations and additional waterways*, and (4) *disseminate findings, demonstrate uses and applicability, and encourage their adoption to inform landscape level AIS management across New York State*.

We used data from the Watercraft Inspection Steward Program Application (WISPA) to summarize aquatic recreation patterns for 2015-2020 and compiled data on individual lake characteristics representing physical/geographic, aesthetic/impairment, and social/amenities with potential influences on boat traffic. Watershed stewards interacted with more than 475,000 launching vessels during this period, with motorboats making up the largest proportion (72%) of launching boats. The majority of influential covariates related to motorized boat use were social/amenity characteristics of lakes, while for non-motorized craft, characteristics of aesthetics/impairment and physical/geographic descriptors were also important. Numbers of motorboats/day predicted for a given lake was best described by lake area, proximity to interstate, and presence of a marina. We identified basic spatiotemporal patterns of use which provide information for the design of aquatic invasive species spread prevention efforts and also help inform other aquatic recreation concerns in the Adirondack Park.

We also explored the factors that influence the successful establishment of AIS once they have arrived in freshwater ecosystems, and which therefore determine the risk of new or increasing invasions. We built on previous efforts to model the distribution and abundance of AIS in Adirondack waters by taking advantage of aquatic plant survey data collected by AWI, combined with available spatial data for characterizing geographic and landscape characteristics of lakes, and lake chemistry information from long-term water quality monitoring. We modeled Eurasian watermilfoil and variable leaf milfoil and found that they were best predicted by disparate lake characteristics, with distribution of Eurasian watermilfoil most closely related to longitude, number of upstream invaded waterways, native plant community richness, and connected waters while variable leaf milfoil was best predicted by number of upstream invaded waters, amenities, native plant community richness, connected waters, and predicted motorboat use. In both cases, inclusion of water chemistry data improved predictability for these species including alkalinity, dissolved calcium and pH. Though, as expected, factors influencing the distribution of the invasive milfoils differed between the two species, the importance of hydrologic connections and the characteristics of native plant communities across lakes were highlighted.

Finally, we used the information gained from these efforts to identify important vulnerabilities and potential pathways of connection between invaded and uninvaded lakes. We used a network analysis to examine the underlying structure of known lake connections based on information collection by boat launch stewards on previous waterbodies visited by recreational boaters. Combining information on risk from boat traffic with known connectedness identified from the network model, we identified several lakes as important invasion spread hubs and others as potential linkage waterways based on their centrality in the network, confirming many of the earlier findings of Johnstone et al. (2014) in the Adirondack landscape. Our analysis revealed that several lake attributes show strong associations with centrality measures and may be helpful in predicting lake importance in other regions where previous waterbody information is unavailable and actual lake connections are unknown. Our individual regression models can be applied and tested in other regions where information on predictor variables is available to highlight potential risk from propagule pressure and invasibility. Where data are not available, our findings suggest that prioritizing large lakes and especially those with hydrologic or navigable connections to other waters will go far toward identifying the lakes most likely to have high motorboat use, most likely to already harbor AIS, and most likely to function as critical nodes within a network of recreational boat traffic.

Introduction

Invasive species are second only to habitat destruction among the causes of species extinction (Wilson 2002). In addition to biodiversity loss, invasive species contribute to enormous economic losses and result in negative impacts to human health and ecosystem services. New York State has more than 7,600 freshwater lakes, ponds and reservoirs, 70,000 miles of rivers and streams, and borders two of the five Great Lakes. These aquatic resources are vital to the economy and ecology of the state and require significant investments of time and resources for detection, management, and prevention of aquatic invasive species (AIS). The magnitude of the threat, and the cost of mitigating or removing AIS once established, are such that preventive measures will always be the most cost-effective action available to combat the spread of AIS. The number of waterbodies in need of protection is very large, however, and available financial resources are inadequate to provide for 100% detection and prevention of AIS. No state is likely to have adequate resources to fully address the potential threat of AIS, given competing needs and the exacerbating effect that climate change is likely to have on this and other natural resource issues (Rahel and Olden 2008). Given these circumstances, new methods and decision support tools are needed to aid managers in distributing limited resources for maximum protection.

Since 1989, the Paul Smith's College Adirondack Watershed Institute (AWI) has worked to protect water quality in the Adirondacks and northern New York state. Combatting the establishment and spread of invasive species is a vital component of AWI's mission and is achieved by education, research, and outreach. These efforts are realized through AWI's full suite of activities including water quality monitoring, aquatic invasive species monitoring, AIS infestation management and rapid response, environmental science and data analysis, and broad public outreach and education. The AWI's flagship Stewardship Program is the primary vehicle for spread prevention, achieved through direct engagement with recreational boaters. These efforts include the annual employment of 100+ watershed stewards at boat launches throughout the region who inspect incoming and outgoing vessels and collect vital data from the recreational boating community, as well as the deployment and staffing of decontamination stations at strategic locations. This work is highly collaborative and involves longstanding partnerships with the New York State Department of Environmental Conservation (NYSDEC), the Department of Transportation (NYSDOT), Lake Champlain Basin Program, Adirondack Park Invasive Plant Program (APIPP), the Adirondack Lake Alliance, numerous municipalities, as well as the Nature Conservancy and partners engaged in the 2 regional Partnerships for Regional Invasive Species Management (PRISMs; Adirondack and St. Lawrence/Eastern Lake Ontario) that encompass the northern part of the State. These annual efforts are resource intensive, with deployment of resources based on data and expert judgement.

AWI began implementing AIS spread prevention monitoring and control programs on various Adirondack regional waterways in 2000. Since then, AWI has educated over 900,000 members of the public, intercepted and prevented more than 14,000 aquatic invasive organisms from further spread, conducted detailed aquatic plant surveys of more than 100 waterbodies, and removed more than 200,000 pounds of invasive plants from Adirondack lakes. AWI has also conducted field studies of AIS management (Kelting and Laxson 2010) and laboratory studies on desiccation tolerance of Eurasian watermilfoil in support of AIS prevention efforts (Evans et al. 2011). Stewards have also collected innumerable data that characterize the types, intensities, and patterns of recreational use in Adirondack waters. The long history of AWI and the Stewardship Program, together with the regional partnerships that have developed coordinated survey methodologies across this large geography, have resulted in a wealth of long-term and broad-scale data that can be used to better understand the prevention, introduction, spread, management, and ecology of invasive species. These data provide an opportunity to broaden our understanding of the current distribution and abundance of AIS in the Adirondack ecosystem, the ways in which they are moved around and dispersed by recreational boating activity in the landscape, the specific pathways that link these two systems and result in a range of invasion risk among Adirondack waters, and the means by which our understanding can provide tools and recommendations for efficient deployment of limited financial resources for AIS prevention and management in other areas of the State.

The goal of this project is to *help managers to allocate AIS spread prevention resources efficiently by quantifying the axes of invasion risk and potential pathways of distribution in the Adirondacks and Northern New York and by developing a generalizable model that can be applied to prioritize management actions throughout New York State and other regions.*

Objectives

Biological invasions are multistage processes that involve both dispersal and establishment in new locations. As such, it is important to understand the factors that influence both the ability of invasive species to reach new areas (propagule pressure) and those which influence the likelihood of their successful establishment (invasibility; Leung and Mandrak 2007). Efforts to control the arrival and spread of invasive species are often described as a combination of offensive and defensive options and actions (Drury and Rothlisberger 2008, Stewart-Kostler et al. 2015). Offensive actions contain the invader at source areas by preventing their departure from these locations, while defensive actions are aimed at preventing the arrival of invasive species at uninvaded locations. Many factors influence the potential effectiveness of either strategy including available resources for combating AIS, as well as the degree to which the invasion process has progressed in a given location. Knowledge of the characteristics of locations which support already established populations of AIS can inform where offensive actions should be directed to contain those species, and knowledge of factors influencing propagule pressure can inform the prioritization of defensive actions to prevent new invasions. Our efforts were aimed at enhancing the understanding of both components of the invasion process, as well as to directly link them by identifying the most likely pathways of invasion in this landscape, such that multiple aspects of risk can be understood and planned for in this and other regions. Our objectives were to: (1) *model the spatial pattern and intensity of recreational boating activity in the Adirondack landscape,* (2) *model the abundance and distribution of aquatic invasive species in Adirondack waters,* (3) *identify and predict connections and most likely pathways of spread between established AIS populations and* *additional waterways*, and (4) *disseminate findings, demonstrate uses and applicability, and encourage their adoption to inform landscape level AIS management across New York State*.

Recreational boating patterns

Though other means of dispersal are possible and likely to occur, recreational boating is thought to represent the primary means by which aquatic invasive species are dispersed and spread among inland waterways (Johnson et al. 2001, Leung et al. 2006, Rothlisberger et al. 2010). Overland transport via recreational vessels has been implicated in the spread of invasive mollusks such as zebra mussel (*Dreissena polymorpha*; Leung and Mandrak 2007), zooplankton including spiny waterflea (*Bythotrephes longimanus*; Muirhead and MacIsaac 2005), and aquatic vegetation including fanwort (*Cabomba caroliniana*; Jacobs and MacIsaac 2009) and Eurasian watermilfoil (*Myriophyllum spicatum*; Johnstone et al. 1985, Buchan and Padilla 2009). All are among species that are known to exist in and have been encountered by AWI boat launch stewards in the Northern New York region.

Efforts have been made to model recreational boat usage in many places and for many reasons (e.g. protection of coastal resources, Sidman and Fik 2005; evaluating carrying capacity, Falk et al. 1992), including risk of transporting AIS (Leung et al. 2006, Stewart-Koster et al. 2015). Such efforts in New York state have been limited to the large coastal regions of the Great Lakes and Long Island. Because northern NY is a region in which abundance of lakes and therefore boater choice is relatively high, we can reason that both physical and sociological factors combine to determine where boaters choose to go in this landscape (Reed-Andersen et al. 2000). Past research suggests that a suite of factors that may influence boater choice, among them physical characteristics such as lake location and size (Leung et al. 2006), home location, access, and waterway intersections (Sidman and Fik 2005), recreational facilities, and distance to highways and population centers (Reed-Andersen et al. 2000). Social factors may also influence boating activity levels including perception of good fishing, boat density (Reed-Andersen et al. 2000), favorite activities, willingness to travel (Sidman and Fik 2005), and awareness and attractiveness of individual lakes (Purdue 1987). Though data on preferences of recreational boaters are unlikely to be broadly available, data on the physical characteristics of lakes, the associated transportation network, and recreational facilities are often readily available and, in several cases, have been found to be useful indicators of boater activity levels (Reed-Andersen et al. 2000, Leung et al. 2006).

Approach

We used data from the Watercraft Inspection Steward Program Application (WISPA; NY iMapInvasives 2021) to summarize aquatic recreation patterns. Partnerships for Regional Invasive Species Management (PRISMs) throughout New York State coordinate invasive species management actions and data acquisition is conducted via WISPA, allowing for the collection of real-time data on invasive species via stewards stationed at boat launches. The WISPA project is a collaborative effort of several public and private agencies and the database contains information collected in the field by watershed stewards including records of all launching and retrieving vessels, numbers and types of organisms detected via boat inspection, and information provided voluntarily by boaters on the last waterbody visited, awareness of aquatic invasive species, and actions taken to prevent their spread. Boat launches are generally staffed from 8am to 4pm from approximately Memorial Day to Labor Day, with additional hours added at busy launches. Stewards are allocated according to the programmatic goal of maximum coverage on as many launches as possible during highest-traffic days; those with high boat traffic are often staffed by two stewards. All launches are staffed Thursday through Monday and many have 7-day coverage.

We compiled WISPA data collected from 2015–2020 by the Adirondack Watershed Institute and two partner programs, the Lake Champlain Basin Program and the Lake George Park Commission, at a total of 114 launches distributed across 64 lakes in northern New York State. We subset the full data to a set of lakes for which we considered the data to be adequate for analysis and considered a lake to be sampled adequately if data were collected on at least 30 days during the months of June, July, and August for at least 2 of the 6 years between 2015 and 2020. This resulted in a set of 39 lakes for analysis and boat encounter data for a total of 35,101 sampling days. The number of sample days exceeds the number of potential calendar days for the 6-year period because several lakes have multiple launches. For each of the 39 selected lakes, we calculated total boats/day for all vessel types, group size, and times, dates, and days of week for launching boats. Additionally, we summarized dates of launching for boats found to be carrying harmful aquatic invasive species to determine if launching patterns for these boats differed from all boats as a group.

We compiled data on 36 individual lake characteristics representing physical/geographic, aesthetic/impairment, and social/amenities factors that we considered to be potential influences on boat traffic. We obtained information on physical characteristics of lakes from existing GIS datasets and from lake attribute information compiled by Olivero-Sheldon and Anderson (2016) including latitude, longitude, area, perimeter, elevation, depth, trophic status, alkalinity, temperature, and connectedness to other lakes (i.e., part of a navigable lake chain). We compiled social/amenity information for individual lakes primarily from NYSDEC online boating information resources (NYSDEC 2021a) and these variables included presence and/or number of features such as marina, boat rental, campsites, campground, launches, and whether the lake was a NYSDEC recommended fishing lake. We consulted ebook editions of Sportsman's Connection Fishing Map Guides for New York (Sportsman's Connection 2016a, 2016b, 2016c) for information on presence of individual game fish species. Distance to nearest town and road were calculated in ArcMap 10.6.1 and relevant to the nearest population center or road, regardless of size, while distance to interstate and city restricted to class 1 roads and cities within a 200 km radius of the park center. We also collated aesthetic or impairment characteristics of lakes which may influence their attractiveness to boaters including presence of known AIS within lakes, obtained from AWI aquatic plant survey data and from the Adirondack Park Invasive Plant Program, number of dams and proportion of unprotected private land within 500m of the shoreline obtained from Olivero-Sheldon and Anderson (2016), recent reported harmful algal bloom occurrence (HAB; NYSDEC 2021b) or existing fish consumption advisory (NYSDOH 2021), and a mean Index of Ecological Integrity value summarized at lake level from McGarigal et al. (2018).

We found that there was no significant effect of year on mean boats/day among the 6 years of study, and therefore combined information across years into a single mean for 2015–2020 of boats/day for each lake. We fit negative binomial regression models (glm.nb; R - MASS package; Venables and Ripley 2002, R Development Core Team 2008) to investigate the influence of physical, aesthetic, and social characteristics of lakes on mean counts of boats/day for 2015–2020. We modeled only motorboats, personal watercraft (PWC), kayaks, and canoes as these vessels represented most boat types recorded at launches. We reduced the initial set of covariates to a smaller set of 18 (Table 1) from which we constructed single-covariate models for each vessel type. Subsequently, we constructed multivariate models using combinations of significant predictors from the single-variable model set, restricting multivariate models to no more than 3 predictors and confirming the fit of top models with chi square. We modeled both weekday and weekend boats but found that the best predictors of use did not differ between weekdays and weekends; reported findings represent weekend boat use. We projected top models to the largest 100 lakes in the Adirondack Park to explore patterns of boat traffic across the region.

We independently examined the extent to which the lakes in our dataset were representative of the larger set of lakes across the Adirondacks that have public boat access. We compared characteristics of our set of modeled lakes to these additional lakes including latitude, longitude, elevation, area, perimeter, depth, amount of private land within 500m of the shoreline, mean lake IEI (McGarigal et al. 2018), and number of launches.

Findings: General patterns

Watershed stewards interacted with more than 475,000 launching vessels between 2015 and 2020, with motorboats making up the largest proportion (72%) of launching boats, followed by kayaks (13%), PWC (8%), and canoes (5%). Barges, docks, rowboats, sailboats, stand-up paddleboards, and windsurfers together made up less than 2% of logged vessels. Boat use demonstrated a pattern of increase over time for some of the most observed vessel types, with particularly high levels in 2020, though there was no significant effect of year on observed boat use (Table 2). The spatial distribution of use was extremely similar for weekdays and weekends, but boats were approximately twice as abundant on weekends. Across all years, the mean number of launching boats/day on weekend days was highest for motorboats (24.4 per lake), with smaller numbers of kayaks (5.1), PWC (3.4), and canoes (1.4).

Table 1. Predictors included in negative binomial generalized linear models to investigate the influence of physical, aesthetic, and social characteristics of lakes on mean counts of boats/day on Adirondack Lakes, 2015–2020.

Factor	Covariate	Explanation
Physical	Area (ha)	Lake size, numeric
Physical	Connected	Part of a navigable lake chain, y/n
Physical	Depth (m)	Depth, numeric
Social	Marina	Marina present, y/n
Social	Boat rental	Boat rental available, y/n
Social	Campsites	Campsites available, y/n
Social	Campground	Campground present, y/n
Social	Total amenities	Total of 4 previous amenities present, numeric
Social	Launches	Number of known public launches, numeric
Social	DECrecomfish	Recommended fishing lake, NYSDEC, y/n
Social	Gamefish	Total of 7 individual gamefish present, numeric
Social	Dist. Interstate (km)	Distance to interstate road, numeric
Social	Dist. City (km)	Distance to major metropolitan area, numeric
Aesthetic	AIS	Aquatic invasive species present, y/n
Aesthetic	Unprotected500 (%)	Unprotected private land within 500m of lakeshore, numeric
Aesthetic	Mean lake IEI	Index of Ecological Integrity, numeric
Aesthetic	Recent HAB	Harmful algal bloom reported in last 5 years, y/n
Aesthetic	Fish advisory	Fish consumption advisory in place, y/n

Saturdays and Sundays were the busiest launch days, followed by Fridays, with mean number of launches relatively similar Mondays–Thursdays (Figure 1). Motorboats, kayaks, and canoes launched most frequently between 11am and 12pm, while PWC launches peaked between 12 and 1pm (Figure 1) at AWI launches. Programs on Lake George and Lake Champlain are sometimes staffed earlier and later in the day, especially if fishing tournaments are scheduled. We observed a distinct peak in boats launching both before 8am and after 5pm on these 2 lakes as compared to other lakes (Figure 2).

Table 2. Total number of documented boats launching on 39 lakes in the Adirondack Park, May–September 2015–2020.

Type	2015	2016	2017	2018	2019	2020
Motorboat	42,271	47,437	60,551	58,830	61,982	72,865
Kayak	5,494	7,448	11,819	10,049	10,651	16,556
PWC	4,443	5,086	7,153	7,611	5,623	8,633
Canoe	2,880	3,168	4,244	3,950	3,559	4,413
Stand Up Paddleboard	234	283	538	462	598	1,295
Sailboat	591	516	658	702	399	401
Rowboat	151	168	256	225	183	360
Dock	37	24	67	45	106	146
Barge	17	17	11	68	20	22
Windsurfer	0	0	0	38	21	44

Through the course of the season, the highest numbers of launching motorboats were observed in July, followed closely by May, while launches were also high in August for kayaks and canoes (Figure 1). The proportion of total launching boats found to be carrying AIS rose steadily through the early part of the season, peaking in the month of July and then declining, as did the proportion of boats found to be carrying any organisms of any kind; these patterns were similar to those for all boats (Figure 3). Mean group size was highest for canoes (2.8), followed by motorboats (2.4), kayaks (2.3), and PWC (1.8).

Findings: Predictors of Use

When modeling each of the predictor variables individually, we could identify a top model ($\Delta AIC \leq 2.0$) that contained 72% or more of the total model weight for each of the primary vessel types (Table 3). Motorboats were best predicted by lake area while PWC and kayaks were best predicted by the number of launches per lake and canoes were best predicted by presence of campsites. The majority of influential covariates related to motorized boat use were social/amenity characteristics of lakes, while for non-motorized craft, characteristics of aesthetics/impairment and physical/geographic descriptors were also important (Table 3). In multivariate models, the best model for motorboats included lake area (β = 1.21, SE = 0.17, z = 7.31, $P < 0.0001$) distance to interstate (β = −0.02, SE = 0.004, z = −4.24, $P < 0.0001$), and presence of a marina (β = 0.65, SE = 0.21, z = 3.05, $P < 0.002$; Figure 4). PWC were best predicted by the total number of launches per lake (β = 4.48, SE = 0.67, z = 6.74, $P < 0.0001$) in combination with the amount of private land within 500m of the shore (β = 2.10, SE = 0.74, z = 2.84, $P < 0.005$). Additional predictors did not improve model fit over the single variable model for kayaks. Canoes were best predicted by presence of campsites (β = 0.90, SE = 0.36, z = 2.54, $P < 0.02$) and shoreline private land (β = −1.02, SE = 0.68, z = −1.50, P = 0.13) but, in contrast to PWC, canoes had a negative association with private land and were more abundant on lakes with higher proportions of protected shoreline. Across the park, highest use by motorboats is predicted in Lake Champlain, Lake George, Great Sacandaga Lake, Indian Lake, and Schroon Lake when accounting for lake area, distance to interstate, and presence of marinas (Figure 5).

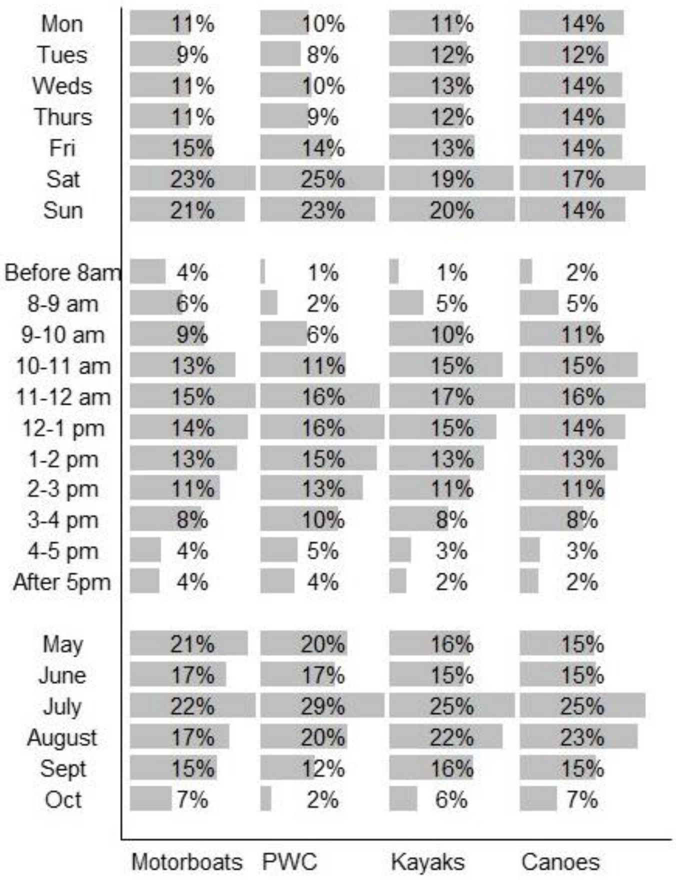

Figure 1. Daily, hourly, and monthly patterns of watercraft launches on Adirondack lakes, 2015–2020.

Table 3. Parameter estimate from negative binomial regression models predicting mean boats/day on Adirondack lakes, 2015–2020. Covariates exhibiting a significant influence ($P < 0.05$) on boat numbers are shown.

Response	Predictor	Estimate (SE)	Z value	P	AIC	ΔAIC	Weight
Motorboat	Area	1.64 (0.20)	8.20	<0.001	279.41	0	99%
	Launches	4.61 (0.66)	7.03	<0.001	288.48	9.07	1%
	Depth	4.10 (0.71)	5.80	<0.001	299.24	19.83	<1%
	Gamefish	0.31 (0.06)	5.32	<0.001	301.13	21.72	<1%
	Marina	1.99 (0.32)	6.32	<0.001	301.56	22.15	<1%
	Amenities	0.74 (0.14)	5.21	<0.001	305.19	25.78	<1%
	Dist. city	−0.03 (0.01)	−4.62	<0.001	307.89	28.48	<1%
	Dist. interstate	−0.03 (0.01)	−4.77	<0.001	307.92	28.51	<1%
	Unprotected500	2.85 (0.68)	4.19	<0.001	314.96	35.55	<1%
	AIS	1.51 (0.41)	3.71	<0.001	318.56	39.15	<1%
	DECrecomfish	2.21 (0.61)	3.62	<0.001	320.49	41.08	<1%
	Campground	1.02 (0.38)	2.67	<0.01	322.26	42.85	<1%
	Boat rental	0.90 (0.40)	2.27	<0.01	324.11	44.70	<1%
	Connected	−0.01 (0.44)	−2.31	<0.05	324.28	44.87	<1%
PWC	Launches	5.32 (0.75)	7.10	<0.001	134.71	0	95%
	Area	1.56 (0.31)	5.08	<0.001	141.32	6.61	3%
	Depth	4.40 (0.95)	4.61	<0.001	143.38	8.67	1%
	Gamefish	0.35 (0.08)	4.24	<0.001	148.54	13.83	<1%
	Marina	1.97 (0.47)	4.18	<0.001	150.93	16.22	<1%
	Dist. city	−0.04 (0.01)	−4.15	<0.001	151.64	16.93	<1%
	Dist. interstate	−0.04 (0.01)	−4.09	<0.001	151.97	17.26	<1%
	Unprotected500	3.65 (0.92)	3.96	<0.001	152.28	17.57	<1%
	Campground	1.56 (0.48)	3.24	<0.01	156.49	21.78	<1%
	Amenities	0.63 (0.22)	2.86	<0.01	157.17	22.46	<1%
	AIS	1.58 (0.61)	2.57	<0.01	159.90	25.19	<1%
Kayaks	Launches	1.64 (0.59)	2.78	<0.05	192.58	0	78%
	Area	0.46 (0.22)	2.09	<0.05	197.03	4.45	8%
	Recent HAB	0.66 (0.31)	2.16	<0.05	199.35	6.77	3%
Canoes	Campsites	1.07 (0.33)	3.23	<0.005	113.92	0	72%
	Unprotected500	−1.62 (0.67)	−2.41	<0.05	118.12	4.2	9%

In a comparison of study lakes to the broader set of Adirondack lakes with known public launches, we found that lakes in our dataset had longer perimeters (mean 47.8 vs. 8.2 km, $F = 6.78$, $P < 0.011$), were deeper (mean 8.8 vs. 3.2 m, $F = 34.84$, $P < 0.0001$), and had a larger proportion of private land within 500m of the shoreline (mean 57.9 vs. 29.4%, $F = 15.85$, $P < 0.0001$). They also tended to have more launches per lake (mean 2.0 vs. 1.1, $F = 17.64$, $P < 0.10$) and be at lower elevations (mean 411 vs. 470 m, $F = 3.91$, $P < 0.10$).

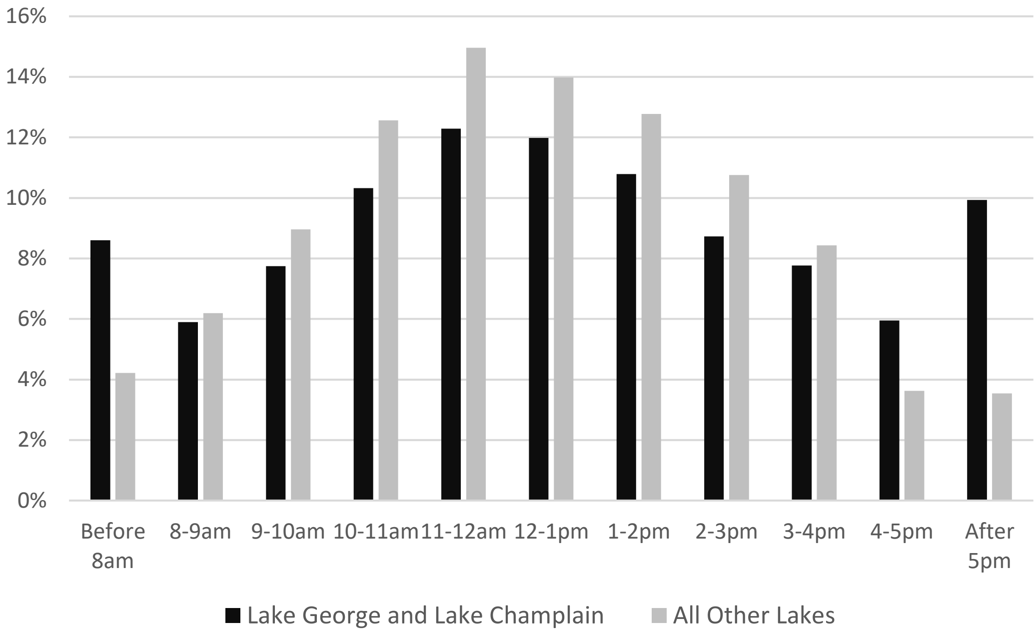

Figure 2. Proportion of boats launching by time of day on Lake George and Lake Champlain in comparison to other Adirondack study lakes, 2015–2020.

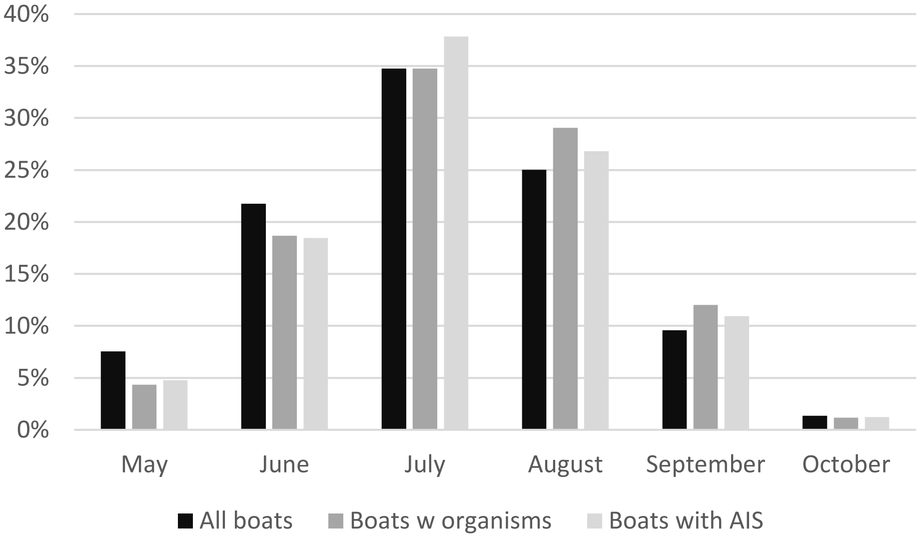

Figure 3. Temporal patterns of boats found to be carrying organisms and/or aquatic invasive species as compared to all boats on Adirondack study lakes, 2015–2020.

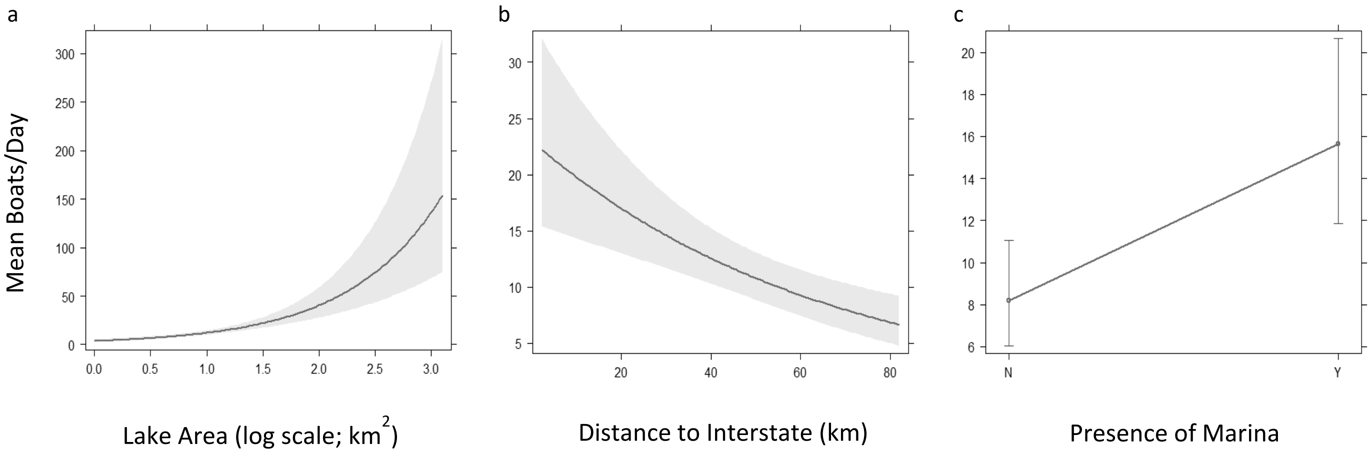

Figure 4. Effect of lake area, distance to interstate, and presence of a marina on mean number of launching motorboats per day.

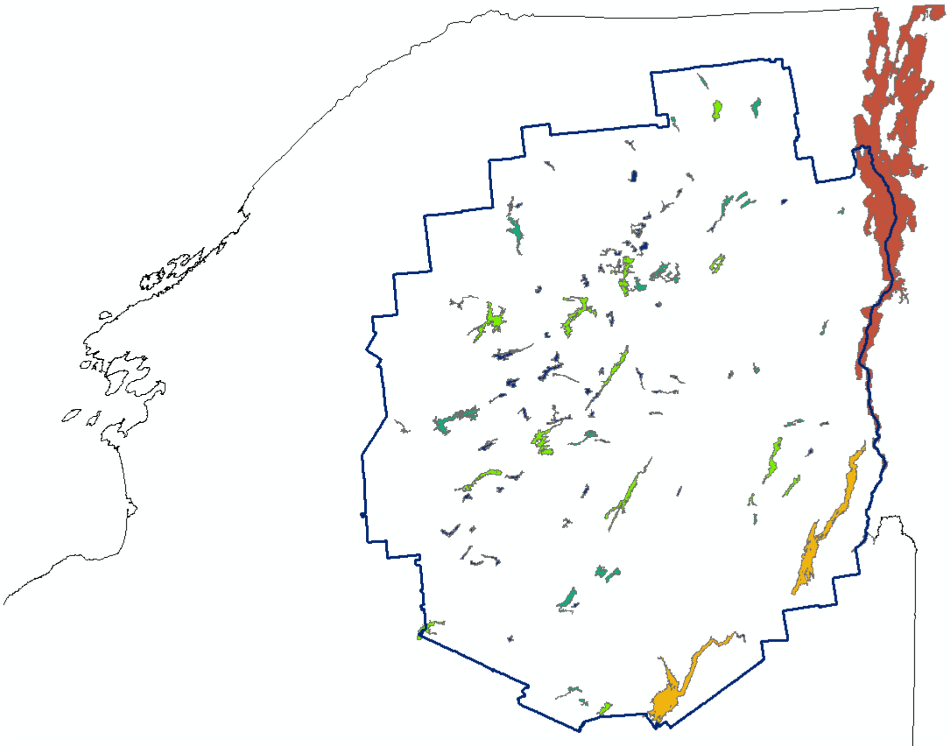

Figure 5. Graduated color map of predicted number of launching motorboats per day on largest lakes in the Adirondack Park, accounting for those on which motorboats are prohibited (n = 7); warmer colors = higher boat traffic.

Distribution of AIS

Understanding recreational boating patterns across the park helps to identify important drivers of propagule pressure in Adirondack lakes. Additionally, it is critical to understand the factors that influence the successful establishment of AIS once they have arrived in freshwater ecosystems, and which therefore determine the risk of new or increasing invasions. Previous efforts have been made to understand and predict invasion of AIS in Adirondack watersheds. In an unpublished study, Regalado and Kelting (2019) found that the number of upstream invaded lakes, watershed location, distance to urban center, and alkalinity were significant predictors of Eurasian watermilfoil (EWM) presence in Adirondack lakes, while the number of upstream invaded lakes, lake area, and road density were significant predictors of variable leaf milfoil (VLM) presence. Shaker et al. (2017) examined the distribution of aquatic invasive species richness in 125 lakes in the Adirondack region, comparing the combined occurrence of 11 different species of potential aquatic invaders to a total of 31 lake and landscape characteristics obtained primarily from public sources. Urban land cover, lake elevation, relative patch richness, and abundance of game fish were found to be the strongest predictors, with models explaining between 54 and 67% of the variation in AIS richness. This project built on these efforts by examining additional potential sources of information to explain the occurrence of AIS including recreational use levels, amenities, launch types, lake chemistry and native plant community characteristics hypothesized to provide additional explanatory power. Efforts to model the distribution of invasive species in other regions have found support for the influence of watershed level forest cover, presence and types of boat launches (Buchan and Padilla 2000), pH, temperature, dissolved calcium (Jacobs and MacIsaac 2009), distance to nearest infestation, boater traffic, hydrologic connectvity (Kanankege et al. 2018), availability of hard substrate (Ramcharen et al. 1997), watershed area, and lake depth (Stewart-Kostler et al. 2015) on occurrence of aquatic invasive animals and plants.

Approach

We built on previous efforts to model the distribution and abundance of AIS in Adirondack waters by taking advantage of the native and invasive aquatic plant dataset collected by AWI, available spatial data for characterizing geographic and landscape characteristics of lakes as well as access characteristics including those compiled under Objective 1, AWI recreational activity data derived from modeling under Objective 1, and lake chemistry data resulting from AWI's long-term monitoring efforts. The Adirondack Lake Assessment Program (ALAP) is a collaboration between AWI and Protect the Adirondacks and has worked since 1998 to develop a long-term water quality database for Adirondack lakes and ponds and document trends in limnological condition (Laxson et al. 2018). A citizen science effort, ALAP volunteers are trained in standard limnological sampling methods and record information on secchi transparency, as well as collecting surface water samples which are analyzed in the AWI Environmental Research Lab. In total, the long-term ALAP dataset provides information on transparency, chlorophyll-a, phosphorus, color, pH, alkalinity, nitrate, sodium, chloride, calcium, conductivity, and trophic status for participating lakes.

In an approach parallel to that used for modeling recreational boat use, we reviewed the literature to develop an initial set of predictor variables with the potential to influence establishment of AIS in Adirondack waterways and compiled information on known distributions of AIS from aquatic plant survey data collected by AWI in partnership with APIPP. We established a set of lakes to use for modeling from those for which aquatic plant survey data were available. Between 2012 and 2017, AWI conducted complete littoral zone surveys on 153 Adirondack waterbodies. Survey methods used a combination of visual surveys, rake tosses, and snorkeling and are described in Regalado et al. (2017). Aquatic plant beds were found by paddling in a serpentine pattern from the shore to the edge of the littoral zone. Boundaries of aquatic plant beds were estimated using rake tosses and a handheld depth sounder and marked by GPS. Percent cover estimates were taken for each plant species and taxonomic ID of aquatic plants followed Crow and Hellquist (2000). This dataset provides information on the distribution and abundance for a total of four invasive plant species including Eurasian watermilfoil (EWM), variable-leaf milfoil (VLM; *Myriophyllum heterophyllum*), curly-leaf pondweed (*Potemogeton crispus*), and European water chestnut (*Trapa natans*), as well as 3 invasive animal species, the spiny waterflea, Asian clam (*Corbicula fluminea*, and zebra mussel. Beginning in 2018, aquatic plant surveys were conducted by Adirondack Research, LLC. Compilation of aquatic plant survey data for 2012-2017 resulted in 166 total lakes available for modeling. For lakes that were surveyed more than once during the 2012-2017 period, we used the most recent aquatic plant data.

We compiled attribute data for each of the aquatic plant survey lakes within several broad categories (e.g., physical/geographic, human impact/access, AIS proximity; Table 4), drawing on many of the same resources as those used in Objective 1 to do so including Olivero-Sheldon and Anderson (2016), McGarigal et al. (2018), and Sportsman's Connection (2016a, 2016b, 2016c). Native plant community information from aquatic plant survey data included richness of native aquatic plants and the percentage of the lake surface area occupied by plant beds. AWI collected this information in 2012-2017 but subsequent plant surveys do not comprehensively survey the native plant community and are focused primarily on AIS detection and overall biovolume of vegetation (Schwartzberg et al. 2018). For those lakes surveyed in 2018 only, we replaced missing information on native plant community richness and aquatic plant bed area with the means across all other lakes. We also compiled water chemistry data for 3 parameters hypothesized to have potential influence on the distribution of aquatic invasive species including alkalinity, dissolved calcium, and pH. Water chemistry data were obtained from long-term monitoring conducted by AWI as part of our Adirondack Lake Assessment Program (ALAP) and calculated from averages of the most recent 5 years of sampling data. ALAP methods are described in Kelting et al. (2012).

Table 4. Covariates included in logistic regression models to predict probability of occurrence of Eurasian watermilfoil and variable-leaf milfoil in Adirondack Lakes.

Factor	Covariate	Explanation
Physical	Area (ha)	Lake size, numeric
Physical	Perimeter (km)	Perimeter, numeric
Physical	ShorelineD	Shoreline sinuosity index, numeric
Physical	Depth (m)	Depth, numeric
Physical	Latitude	Location, numeric
Physical	Longitude	Location, numeric
Physical	Elevation (m)	Elevation, numeric
Physical	Connected	Part of a navigable lake chain, y/n
Physical	NativeRich	Richness of native plant community, numeric
Physical	Bed%Lk (%)	Proportion of lake occupied by aquatic plant beds
Physical	Trophic	Trophic class, categorical
Physical	Alkalinity	Alkalinity class, categorical
Physical	Temp	Temperature class, categorical
Human impact	Dist. Interstate (km)	Distance to interstate road, numeric
Human impact	Dist. Rd (km)	Distance to any road, numeric
Human impact	Unprotected500 (%)	Unprotected private land within 500m of lakeshore, numeric
Human impact	Mean lake IEI	Index of Ecological Integrity, numeric
Human impact	Total amenities	Total of marina, boat rental, campsites, campground, numeric
Human impact	PredictWKND	Predicted number of motorboats/day, numeric
AIS proximity	Ups_EWM/VLM	Number of upstream invaded waters (EWM or VLM), numeric
AIS proximity	distEWM/VLM	Distance to nearest infestation (EWM or VLM), numeric
Chemical	ALK	Alkalinity
Chemical	Ca	Dissolved calcium
Chemical	pH	pH

We used logistic regression to build models predicting occurrence of AIS from compiled lake attributes. Four aquatic invasive species were recorded in the aquatic plant survey data including Eurasian watermilfoil, variable leaf milfoil, curly-leaf pondweed, and spiny waterflea. Among these, occurrences of curly-leaf pondweed and spiny waterflea were too few to model (i.e., documented in 8 or fewer of the lakes in the dataset). Although other aquatic invasive species are known to exist in Adirondack waters (Johnstone et al. 2014), they are few within the set of lakes for which aquatic plant community data were available. Several species are confined to the larger lakes on the periphery of the park (e.g., Asian clam, zebra mussel, water chestnut) and still others are nearby but have not yet reached interior waterways (e.g., hydrilla, *Hydrilla verticillata*). We concentrated modeling efforts on the 2 milfoil species and ran single variable logistic regression models followed by multivariate models constructed from combinations of the best uncorrelated predictor variables from the initial models. Because lake chemistry data were not available for all of the lakes in our aquatic plant survey dataset (n = 50 of 166), we ran a third model set on the smaller set of lakes for which chemistry data were available, using information on alkalinity, pH, and dissolved calcium in combination with best predictors from prior models to determine if the addition of water chemistry information improved the power of logistic regression models for EWM and VLM. We applied top models from the larger set for each species to the 100 largest lakes across the park to examine patterns of occurrence probability across the region.

Findings

From single covariate logistic regression models, several lake attributes were found to be significant predictors of EWM and VLM. For EWM, longitude was the top variable associated with its occurrence but several other variables were also important including number of upstream invaded waterways, richness of the native plant community, distance to interstate, connected waterways, and elevation (Table 5). Similarly, for VLM, a single top model contained 99% of the model weight and in this case the number of upstream invaded waters was the most important predictor for this species, but other variables were also significantly associated with its occurrence including perimeter of the lake, shoreline sinuosity, number of amenities, connected waters, lake area, and native plant community richness (Table 5). Best multivariate models constructed for EWM from uncorrelated predictor variables contained longitude, number of upstream waterways, native plant community richness, and connected waterways while those for VLM contained number of upstream invaded waters, number of amenities, native plant community richness, connected waters, and predicted motorboat use. In both cases, inclusion of water chemistry data improved top models with alkalinity and dissolved calcium improving predictability for EWM and pH and alkalinity improving predictability for VLM (Table 6). For EWM, alkalinity and calcium were positive predictors of occurrence, while VLM was negatively associated with both alkalinity and pH. The discrepancies in best predictor variables between the two milfoil species, coupled with the lack of broad

Table 5. Parameter estimate from single covariate logistic regression models predicting EWM and VLM occurrence on Adirondack lakes. Covariates exhibiting a significant influence ($P < 0.05$) are shown.

Response	Predictor	Estimate (SE)	Z value	P	AIC	ΔAIC	Weight
EWM	Longitude	48.93 (9.61)	5.09	<0.001	145.42	0	99%
	Ups_EWM	0.49 (0.16)	3.13	<0.01	158.38	12.96	<1%
	NativeRich	0.12 (0.03)	3.78	<0.001	166.38	20.96	<1%
	Dist. Interstate	-0.03 (0.01)	-3.71	<0.001	168.18	22.76	<1%
	Connected	1.56 (0.44)	3.54	<0.001	170.34	24.92	<1%
	Elevation	-0.01 (0.001)	-3.36	<0.001	170.78	25.36	<1%
	PredictWKND	0.12 (0.04)	2.99	<0.01	171.28	25.86	<1%
	Dist. Rd.	-0.21 (0.08)	-2.53	<0.001	172.83	27.41	<1%
	Total amenities	0.37 (0.17)	2.18	<0.001	177.98	32.56	<1%
	Mean lake IEI	-1.44 (0.72)	-1.99	<0.001	178.59	33.17	<1%
VLM	Ups_VLM	0.84 (0.20)	4.25	<0.001	117.02	0	>99%
	Perimeter	2.60 (0.59)	4.44	<0.001	155.92	38.9	<1%
	ShorelineD	0.60 (0.14)	4.31	<0.001	158.55	41.53	<1%
	Total amenities	0.82 (0.19)	4.34	<0.001	159.19	42.17	<1%
	Connected	1.81 (0.44)	4.06	<0.001	163.76	46.74	<1%
	Area	1.23 (0.34)	3.61	<0.001	165	47.98	<1%
	NativeRich	0.11 (0.03)	3.58	<0.001	165.82	48.8	<1%
	Depth	0.17 (0.05)	3.06	<0.01	170.48	53.46	<1%
	Mean lake IEI	1.79 (0.79)	2.27	<0.05	174.6	57.58	<1%
	Dist. Interstate	0.02 (0.01)	2.01	<0.05	175.65	58.63	<1%
	Longitude	-13.5 (6.76)	-2.00	<0.05	176.03	59.01	<1%

available data for some lake attributes reveals the challenge in predicting invasibility for aquatic invasive species as compared to predicting propagule pressure resulting from boat traffic.

Table 6. Top multivariate models predicting EWM and VLM in Adirondack waters; top models (cumulative model weight > 90%) shown with significance values for included predictors (P). Subset models were run on a smaller set of lakes with chemistry data available (n = 50); AIC values therefore not comparable with models above.

Spp	Model	AIC	ΔAIC	Wt	P1	P2	P3	P4
EWM	Longitude + Ups_EWM + NativeRich	115.74	0	49%	0.001	0.01	0.05	
	Longitude + Ups_EWM + Connected	116.23	0.49	38%	0.001	0.01	0.01	
	Longitude + Ups_EWM	120.92	5.18	<1%	0.001	0.001		
[subset]	Longitude + Ups_EWM + NativeRich + ALK	39.45	0	47%	0.05			
	Longitude + Ups_EWM + Connected + ALK	41.32	1.87	18%	0.05	0.05		
	Longitude + Ups_EWM + NativeRich + Ca	41.85	2.40	14%	0.05			0.05
	Longitude + Ups_EWM + Connected + Ca	42.89	3.45	8%	0.05	0.05		0.05
	Longitude + Ups_EWM + Connected	44.64	5.19	3%	0.01	0.05		
VLM	Ups_VLM + Amenities + NativeRich	88.47	0	55%	0.001	0.001	0.05	
	Ups_VLM + Amenities + Connected	90.01	1.54	26%	0.001	0.001	0.05	
	Ups_VLM + Amenities + PredictWK	91.60	3.13	12%	0.001	0.001		
[subset]	Ups_VLM + Amenities + NativeRich + pH	35.61	0	52%	0.05	0.01	0.05	0.05
	Ups_VLM + Amenities + Connected + pH	36.69	1.08	30%	0.05	0.01		0.05
	Ups_VLM + Amenities + NativeRich + ALK	39.86	4.25	6%		0.05	0.05	
	Ups_VLM + Amenities + Connected + ALK	40.44	4.83	5%		0.05		0.05

Pathways and connections

Modeling efforts associated with Objectives 1 and 2 served to identify the most important influences on both boat traffic and occurrence of invasive milfoil species in Adirondack lakes. The final step of the process undertaken here was to use the information gained from these efforts to identify important vulnerabilities and potential pathways of connection between invaded and uninvaded lakes. We approached the identification of connections among lakes and potential pathways of AIS transfer using several steps. First, we constructed a network graph using iGraph in R (Csardi and Nepusz 2006) to examine the underlying structure of known lake connections based on information collection by boat launch stewards on previous waterbodies visited by recreational boaters. A graph represents a landscape of habitat patches as a set of “nodes” (points), connected to varying degrees by “edges.” Graph theory has a long history in computer science and transportation modeling but is increasingly utilized in ecological studies, particularly those concerned with landscape connectivity (Urban and Keitt 2001, Galpern et al. 2011). An edge between two nodes implies some ecological flux between them such as propagule dispersal or material flow (Urban and Keitt 2001). Graph theoretical approaches allow for the exploration of a number of questions of importance to invasion biology and potential management and network centrality measures are useful for quantifying the connectedness of individual nodes and their importance within the network. Nodes in a network that are more central than others have more ties to other nodes, can reach other nodes faster, and control the flow of information or materials between other nodes (Kvistad et al. 2019). Subsequent to using network analysis to identify underlying structural characteristics of the network and importance of individual nodes, we used correlation analysis to determine if previously identified predictors of propagule pressure from modeled boat traffic could be used to predict network centrality measures. Last, in order to understand the degree to which identified network patterns persist and to confirm previously identified subnetworks, we used a community detection algorithm in iGraph to attempt to identify subnetworks.

Approach

In order to create a network graph, we extracted previous waterbody information for a set of 38 lakes that were used to model boat traffic under Objective 1. These data come directly from boat launch stewards who ask each boater with whom they interact to identify the lake their boat was in most recently prior to the current location. Graphs require two input files that identify the set of nodes to be mapped – in this case 38 individual lakes – and the edges between them, or the known connectivity from each lake to every other lake. Identification of edges resulted in 866 total connections representing all from- and to- links between the 39 focal lakes. Though graphs can be constructed with any number of nodes, they rapidly become very large and complicated, making both calculations and plotting more challenging. We therefore restricted the network analysis to the subset of lakes for which we had already compiled additional lake attribute information that could be used to inform node weights and understand potential connections. We extracted previous waterbody information from combined data for 2015 – 2018.

Following the approach of Kvistad et al. (2019), who used network centrality measures to prioritize invasive species surveillance efforts at Great Lakes shipping ports, we calculated 5 of the main centrality measures for each node in the network including total (Freeman's) degree, in degree, out degree, betweenness, and eigenvector centrality. Total, in, and out degree centrality measures describe the connectivity of each lake in terms of the total number of connections, and the total incoming and outgoing connections from each. The maximum in- or out-degree node score would therefore be 37 for any given lake; a lake with an in-degree score of 37, for example, would be a receiving body for every other lake in the network. Betweenness scores, in contrast, arise from the identification of the shortest paths between nodes in a network and are based on the positions of lakes within the whole. Lakes with high betweenness scores are those which act as a bridge along the shortest path between other lakes. Last, eigenvector scores are dependent on scores of other nodes within the network and identify lakes that rapidly saturate the network because these well- connected lakes are connected to other highly connected lakes (Kvistad et al. 2019). We used the resulting information to identify lakes that scored high on several centrality measures and therefore may serve as priorities within the network. We then explored the relationship between lake characteristics and centrality scores to determine which attributes of lakes are most influential on their centrality within the network. Such information may be useful in other regions where previous waterbody connections are unknown but basic information about lake characteristics could be used to identify their importance in invasive species spread prevention efforts.

Last, we applied a community detection algorithm in iGraph to identify subnetworks within the overall network. We were primarily interested in knowing whether the subnetworks previously suggested by Johnstone et al. (2014) in the Adirondack landscape could be confirmed with a network analysis. There are more than 10 clustering algorithms available in iGraph and previous researchers have attempted to provide guidance on approaches, while acknowledging that community detection in networks is an ill-defined problem and there are no clear-cut means of assessing the performance of different algorithms and comparing among them (Fortunato and Hric 2016, Labatut and Balasque 2012). Though it is but one of many potential methods, we found that the cluster_fast_greedy algorithm, which detects communities by optimizing modularity scores of subnetworks, resulted in the separation of lakes into 3 primary subgroups.

Findings

Network analysis revealed several lakes that consistently score high on centrality measures and are likely to be central players in the transport of AIS within the network (Figure 6, Table 7).

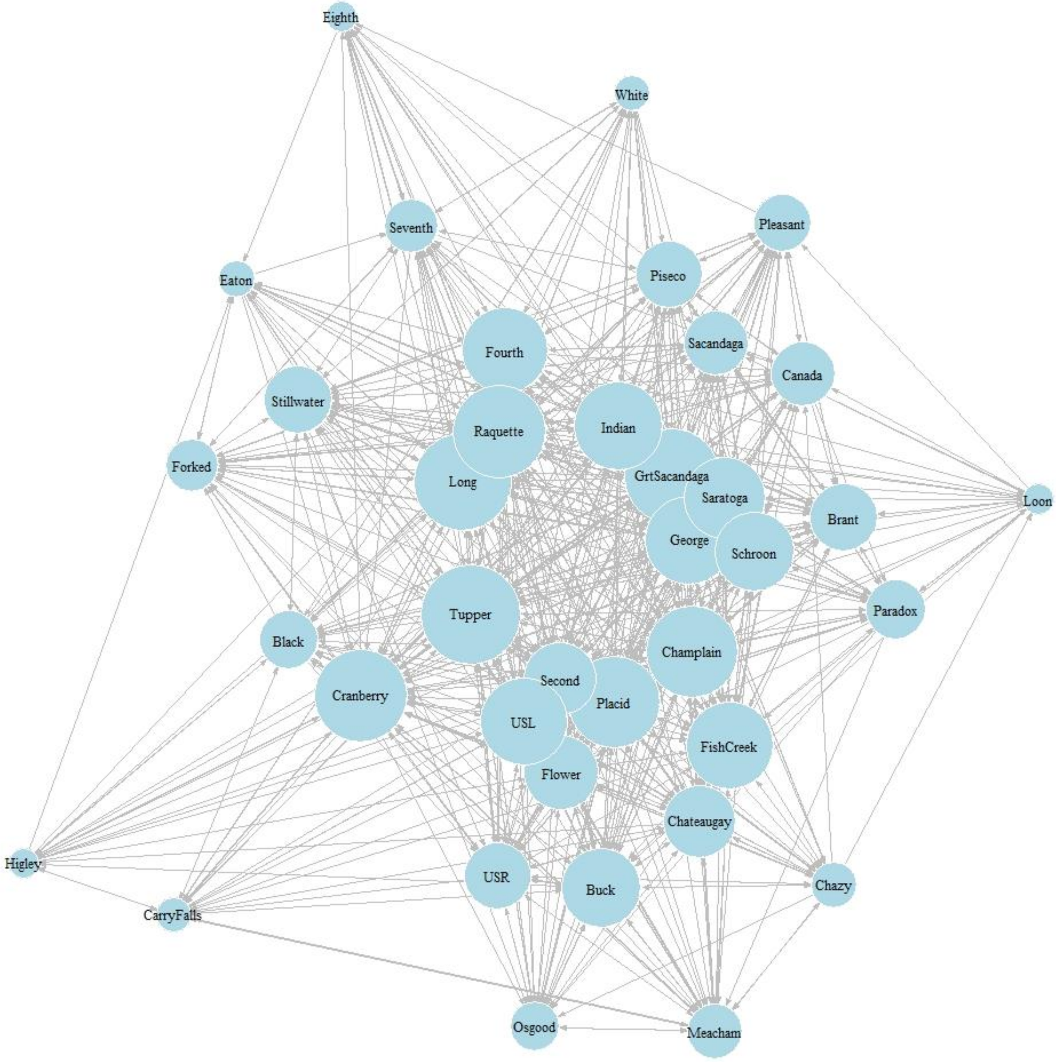

Figure 6. Network graph for 38 Adirondack lakes; nodes weighted by total degree.

Table 7. Centrality measures arising from network analysis of 38 lakes monitored by the AWI Aquatic Invasive Species Spread Prevention Program.

Lake	Degree (Total)	Degree (In)	Degree (Out)	Betweenness	Eigenvector
Black Lake	39	15	24	14.0	0.41
Brant Lake	45	24	21	8.5	0.69
Canada Lake	43	23	20	6.4	0.70
Carry Falls Reservoir	23	11	12	2.8	0.33
Chateaugay Lake	48	23	25	18.4	0.72
Chazy Lake	31	14	17	4.1	0.48
Cranberry Lake	62	30	32	48	0.89
Eighth Lake	21	10	11	0.9	0.32
Fish Creek Ponds	58	30	28	18.7	0.91
Forked Lake	35	18	19	4.6	0.55
Fourth Lake	57	28	29	27	0.79
Great Sacandaga Lake	63	31	32	30.3	0.86
Higley Falls Reservoir	20	5	15	1.6	0.13
Indian Lake	59	29	30	25.2	0.84
Lake Champlain	61	30	31	23.9	0.85
Lake Eaton	25	11	14	1.8	0.31
Lake Flower	50	27	23	12.9	0.81
Lake George	59	32	27	19.1	0.87
Lake Placid	61	33	28	24.5	0.93
Lake Pleasant	38	18	20	4.3	0.56
Long Lake	65	33	32	35.2	0.92
Loon Lake	21	6	15	1.4	0.17
Meacham Lake	37	20	17	5.7	0.62
Osgood Pond	33	20	13	1.5	0.65
Paradox Lake	40	17	23	5.7	0.56
Piseco Lake	44	22	22	5.9	0.67
Rainbow Lake (Buck)	53	26	27	26.3	0.77
Raquette Lake	62	30	32	27.2	0.85
Sacandaga Lake	43	24	19	9.0	0.73
Saratoga Lake	54	22	32	14.2	0.66
Schroon Lake	53	26	27	11.3	0.75
Second Pond	48	36	12	8.9	1.00
Seventh Lake	36	20	16	8.9	0.61
Stillwater Reservoir	45	21	24	12.9	0.63
Tupper Lake	66	33	33	38.5	0.96
Upper Saranac Lake (USL)	58	31	27	24.3	0.90
Upper St. Regis Lake (USR)	44	24	20	10.3	0.75
White Lake	24	9	15	1.8	0.26

The following lakes score among the highest for one or more of the centrality measures: Cranberry Lake, Fish Creek Ponds, Fourth Lake, Great Sacandaga Lake, Indian Lake, Lake Champlain, Lake George, Lake Placid, Long Lake, Rainbow Lake, Raquette Lake, Saratoga Lake, Second Pond, Tupper Lake, and Upper Saranac Lake. All but Rainbow Lake are known to be invaded by at least one invasive species. Floerl et al (2009) highlighted the fact that infestations can spread rapidly within networks from both “quiet” and “busy” nodes and also stressed the importance of “hub” nodes, defined as those with high volume and high connectivity.

Combining information on risk from boat traffic with known out degree connectedness, we can identify Great Sacandaga Lake, Lake Champlain, Lake George, Saratoga Lake, Schroon Lake, Black Lake, Chateaugay Lake, and Fourth Lake as potential hubs, most of which were also identified as preliminary invasion spread hubs by Johnstone et al. (2014). Similarly, Johnstone et al. (2014) identified preliminary linkage waterways of Long Lake, Tupper Lake, and Lake Champlain. Two of these – Long Lake and Tupper Lake – also score among the highest for betweenness centrality, a measure which is most analogous to the linkage waterway concept identified by Johnstone et al. (2014). Additional lakes which score high on betweenness centrality and may function as important bridges in the Adirondack network include Cranberry Lake, Fourth Lake, Great Sacandaga Lake, and Raquette Lake.

Correlation analysis revealed that several lake attributes show strong associations with centrality measures and may be helpful in predicting lake importance in other regions where previous waterbody information is unavailable and actual lake connections are unknown. Lake area, perimeter, number of amenities, number of game fish species present, and number of boats per day were all significant predictors of multiple centrality measures (Table 8).

Table 8. Lake attributes and their correlation with centrality measures resulting from network analysis of 38 lakes in the Adirondack region; significance levels denoted as P < 0.0001 (***), P < 0.001 (**), P < 0.05(*).

Lake attribute	Degree (Total)	Degree (In)	Degree (Out)	Betweenness	Eigenvector
Area	0.61***	0.51**	0.62***	0.58***	0.58***
Perimeter	0.64***	0.55***	0.64***	0.65***	0.50**
Total amenities	0.66***	0.61***	0.61***	0.61***	0.54***
Number of gamefish	0.45*	0.34*	0.50**	NS	0.35*
Total number of boats/day	0.42*	0.35*	0.42*	NS	NS

Identification of subnetworks via the central_fast_greedy algorithm identified 3 primary subnetworks of lakes within the Adirondack system (Figure 7). Although there are many ways to identify communities within graphs and the current analysis is based on a larger number of lakes, these subnetworks align roughly with those previously identified by Johnstone et al. (2014) as the High Peaks, Fulton Chain, and Northway networks. Examination of previous waterbody information for all of 2015-2020 revealed high consistency among the lakes that are reported most often as the most recent lake visited by recreational boaters and suggests that connections among lakes are relatively stable from year to year. Our network analysis focused only on waterbodies within the Adirondack geography but the following represent the top 10 previous reported waterbodies for 2015-2020: Hudson River, Saratoga Lake, Lake Champlain, Lake George, Great South Bay, Atlantic Ocean, Schroon Lake, St. Lawrence River, Upper Saranac Lake, and Lake Ontario. Although the majority of boaters report having been in the same lake previously and therefore represent low risk of AIS transport, more than 1500 waterbodies have been identified in the geography of lakes connected to Adirondack waters. Several of the most prevalent among them are large waterbodies outside of the Adirondack Park, highlighting the critical and ongoing need for AIS spread prevention measures.

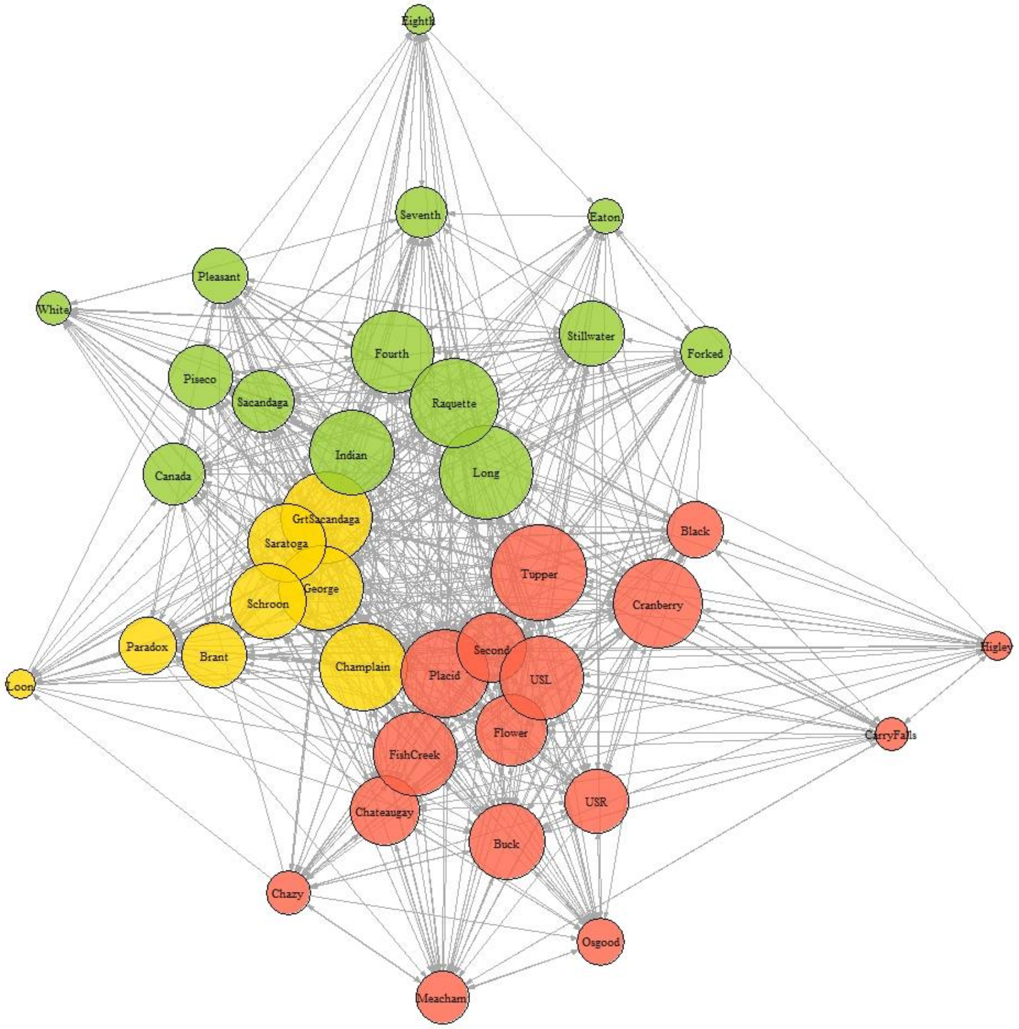

Figure 7. Subnetworks identified by greedy optimization of modularity in a network analysis of 38 Adirondack lakes.

Conclusions

Our project focused on identifying important predictors of risk to lakes from AIS arising from both propagule pressure and invasibility. Because overland transport via recreational watercraft is believed to be a primary mechanism of AIS movement within landscapes, we focused efforts related to propagule pressure on identifying drivers of recreational use of waterbodies across the Adirondack landscape. Basic spatiotemporal patterns of use provide information for the design of aquatic invasive species spread prevention efforts. Observed temporal patterns suggest that efforts to control the spread of AIS that are based on boat inspections and face-to-face communication with boaters should dedicate the highest efforts on weekends, throughout the summer but especially during July and August, and especially during the midday hours. It is also apparent, however, that on very large lakes and those that host regular fishing tournaments, a significant number of boats are launching in the early morning and in the evening, outside of the period in which the majority of spread prevention programs operate. It may be particularly beneficial to dedicate extra effort to early morning and evening hours in these locations and, where possible, to ensure that spread prevention efforts continue through the month of September.

Spatial patterns of use for motorized craft predict that the largest numbers of boats will be found on large lakes with multiple launch locations and that, in general, the number and type of amenity features available on these lakes (e.g., boat rental, marina, campground) are highly influential and probably outweigh potential indicators of impairment (e.g., presence of AIS, recent HAB) that might deter lake use. Such information – lake size, proximity to major roadways, available amenities – is generally readily available and can be used to identify relative risk to lakes from boat traffic in other regions.

We also investigated the risk to lakes from invasibility, or the likelihood of establishment of AIS once they have arrived in new locations. In contrast to recreational boating patterns, predicting the probability of establishment of AIS is more challenging and our efforts demonstrated that, as expected, primary drivers differ among species. We were able to model only 2 – Eurasian watermilfoil and variable leaf milfoil – and although these were predicted by different combinations of lake attributes, probability of occurrence for both was related to native plant community richness and the number of upstream invaded waterways. Native aquatic plant survey data are unlikely to be available for most lakes but hydrologic connections to other waterways should be readily determined and represent important risks. In the absence of additional information that may help predict establishment of AIS such as lake substrate or water chemistry information, lessons from this work suggest that in other regions it may be strategic to ensure that the largest lakes in a system are critical foci for spread prevention efforts. The Adirondack region is characterized by a skewed distribution of lake sizes with a small number of very large lakes and a multitude of smaller waterbodies; it is unknown the extent to which waterbodies in other regions match this distribution. Nonetheless, area was associated with several other lake attributes and was a strong and important driver of several aspects of risk in the Adirondack landscape.

The Adirondack region benefits from a long history of aquatic invasive species spread prevention efforts and information provided by boaters in this landscape allowed us to use known connections between lakes to create a network model and examine the importance of individual lakes within the network based on their centrality. Combined information from identified motorboat use with network centrality measures suggest that Great Sacandaga Lake, Lake Champlain, Lake George, Saratoga Lake, Schroon Lake, Black Lake, Chateaugay Lake, and Fourth Lake are potential spread hubs, while Long Lake, Tupper Lake, Cranberry Lake, Fourth Lake, and Raquette Lake are linkage waterways. Lake Champlain and Great Sacandaga Lake may function as both. We found that centrality measures for individual lakes were associated with several lake attributes and most closely with characteristics of lake size and available amenities. The closer association between lake size, rather than boat traffic, with connectedness of individual lakes suggests that quieter lakes in the network can also play important roles in AIS transport within the system.

Our individual regression models can be applied and tested in other regions where information on predictor variables is available to highlight potential risk from propagule pressure and invasibility. Where data are not available, our findings suggest that prioritizing large lakes and especially those with hydrologic or navigable connections to other waters will go far toward identifying the lakes most likely to have high motorboat use, most likely to already harbor AIS, and most likely to function as critical nodes within a network of recreational boat traffic.

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