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The likelihood of sampling American eelgrass and starry stonewort in Cayuga Lake varied by date, depth, and location

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ABSTRACT

Understanding the phenology of aquatic, invasive species is important from theoretical and management perspectives, particularly if phenology differs among or within waterbodies in the invaded range. Variability in the likelihood of sampling invasive starry stonewort [*Nitellopsis obtusa* (Desv.) J. Groves] and American eelgrass (*Vallisneria americana* Michx.) in Cayuga Lake, New York, was evaluated with respect to date, geographical location, and water depth. Following point-intercept methodology, 25,741 samples were collected at 22 sites among 3 locations (northern, middle, southern) from 2020 through 2022. Based on logistic regression, the likelihood of sampling both species followed quadratic relationships with increasing date and water depth. Relationships differed among locations and between species, but variability was notably greater for starry stonewort. American eelgrass was most likely to be sampled at 2.5 m of water compared to 3.5 m for starry stonewort. The likelihood of sampling American eelgrass increased from June through August, peaked in September, and declined through November and was similar among locations. Overall, the likelihood of sampling starry stonewort increased from June to peak near the end of July and was very low by November. Among locations, the date of peak likelihood of sampling starry stonewort differed by 42 d. If sampling likelihoods are positively correlated with biomass phenology, large variability in the likelihood of sampling starry stonewort due to water depth and date among locations reflects an inability to generalize the phenology of this species in Cayuga Lake. Reported regional differences in phenology further highlight challenges in generalizing this aspect of starry stonewort life history.

Key words: aquatic plant management, invasive species, macroalgae, *Nitellopsis obtusa*, *Vallisneria americana*.

INTRODUCTION

Starry stonewort (*Nitellopsis obtusa* (Desv.) J. Groves; family Characeae), an invasive charophyte native to Europe and Asia, was accidentally introduced to the Great Lakes basin in the early 1970s (Geis et al. 1981, Sleith et al. 2015). Like other charophytes, starry stonewort may outcompete native macrophytes and phytoplankton (Blindow 1992, Brainard and Schulz 2017, Ginn et al. 2021). It may limit essential nutrients for other species (Kufel and Kufel 2002), influence sediment dynamics (Pullman and Crawford 2010, Harrow-Lyle 2021), increase cyanobacterial blooms (Harrow–Lyle and Kirkwood 2020), and decrease habitat suitability for fish (Caraco and Cole 2002, Murphy et al. 2018). Dense beds of starry stonewort have the potential to interfere with recreational activities, beach quality, and water delivery systems (Chambers et al. 1999, Sleith et al. 2015, Glisson et al. 2018). Populations of starry stonewort are difficult to control with herbicides, algaecides, or mechanical harvesters (Glisson et al. 2018, Larkin et al. 2018, Ginn et al. 2021) and may even increase if other competitive, invasive species are removed through these means (Larkin et al. 2018).

Starry stonewort is a cryptic invader (Brainard and Schulz 2017): it may go unnoticed in deeper waters that are difficult to monitor and is challenging to distinguish from some native *Chara* spp. and *Nitella* spp. (Brainard and Schulz 2017, Escobar et al. 2018). Since discovery, it has spread to lakes in two Canadian provinces and seven states (Larkin et al. 2018), including Cayuga Lake in New York State (Sleith et al. 2015).

Differences in regional macrophyte phenology, a term used here to indicate seasonal changes in biomass accumulation and critical life stages (Lieth 1974), and patterns of invasion among starry stonewort populations are also evident. Phenological differences could give a competitive advantage to invasive species (Glisson et al. 2022) and influence local or regional management strategies. A study of two Minnesota lakes, for example, found that starry stonewort biomass was low in June, increased steeply in July and August, and peaked in September before declining; the biomass of native species in the same study peaked earlier in the season (Glisson et al. 2022). Some early studies in the invaded range of starry stonewort observed a similar phenology (references in Glisson et al. 2022). At the head of the Detroit River, however, starry stonewort was first observed in July, biomass increased from July to September, and remained relatively high from September through January (Nichols et al. 1988). Beyond these comparisons, the degree of regional variability in starry stonewort phenology is not known.

Although comparing the phenology of starry stonewort to other widespread, invasive macrophytes may help to

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understand aspects of multiple invasions (Glisson et al. 2022), comparing the phenology of starry stonewort to that of a common, widespread native species could provide additional perspectives. Not only would the comparison help predict outcomes of starry stonewort control measures on native species (Wersal and Madsen 2018, Glisson et al. 2022), it could also serve to highlight the local plasticity of starry stonewort life history patterns.

More information is needed to understand patterns of starry stonewort invasion. Anecdotal reports indicated that starry stonewort may invade deeper waters first before moving to shallower water (Pullman and Crawford 2010). A study in New York State, however, found that starry stonewort was more frequent in shallower, rather than deeper, water (Brainard and Schulz 2017). Discrepancies between the maximum depth at which starry stonewort is found in its native range (i.e., 31 m; Larkin et al. 2018), and the greatest depths at which it was reported in North America (i.e., 9 m; Pullman and Crawford 2010), indicate the potential for continued cryptic invasion as well as the need to understand responses of starry stonewort to local conditions.

Cayuga Lake is deeper than many freshwater lakes in the invaded range of starry stonewort ($Z_{\max} = 133$ m; Birge and Juday 1914) and offered an opportunity to explore starry stonewort phenology at littoral zone depths not commonly evaluated in this new range. Additionally, Cayuga Lake rarely freezes over (Oglesby 1978), which may result in phenological responses of starry stonewort that differ from previous reports. Starry stonewort has been present in this lake since at least 2009 (Sleith et al. 2015). Eurasian watermilfoil (*Myriophyllum spicatum* L.), another invasive species, has been present since the 1960s (Johnson et al. 2000). Hydrilla [*Hydrilla verticillata* (L.F.) Royle], an invasive species present in Cayuga Lake since 2011 (Holden et al. 2016), is another management concern. Chemical treatment of hydrilla at a few sites in Cayuga Lake could potentially influence the local presence of other submersed aquatic vegetation (SAV; Hofstra and Clayton 2001, Poovey et al. 2002). Both starry stonewort and American eelgrass (*Vallisneria americana* Michx.), a common native plant species, may initially respond to local hydrilla treatments but will regrow in a matter of weeks or months (Netherland et al. 1997, Mudge and Glomski 2012, Glisson et al. 2018, Wersal 2022).

Concern about the potential spread of hydrilla in Cayuga Lake resulted in intense monitoring efforts for aquatic invasive species following the point-intercept method (Madsen 1999). The presence or absence of native and invasive SAV species, including starry stonewort and American eelgrass, was determined at points associated with 22 sites around Cayuga Lake through tens of thousands of rake tosses conducted from 2020 through 2022. Presence/absence and the likelihood of sampling SAV using rake tosses are positively correlated with species biomass (Yin and Kreiling 2011). Our objectives here were to use point-intercept data to explore seasonal variability in the likelihood of sampling American eelgrass and starry stonewort, assumed to indicate variability in biomass due to differences in water depth and geographic location in Cayuga Lake. Demonstrable changes in the likelihood of sampling these species over the course of the season, as well as differential responses between the species, would validate using point-intercept methodology to evaluate phenology and, more generally, the use of this approach to indicate the success of management approaches among targeted species.

MATERIALS AND METHODS

Study site

Cayuga Lake, a glacially formed Laurentian lake located in central New York State, is 61 km long, 2.8 km wide, and 54.4 m deep, on average (Oglesby 1978). It has a maximum depth of 133 m (Birge and Juday 1914) and a surface area of 172.1 km^2 (Youngs and Oglesby 1972). Based on long-term water quality monitoring at five sites (Wang et al. 2020, NYSDEC 2022), Cayuga Lake is classified as mesotrophic, or moderately productive, with low water clarity (Secchi disk depth = 1.4 to 2.6 m), relatively high alkalinity (pH = 7.9 to 8.4), moderate levels of chlorophyll a (4 to 8 μg/L), and high phosphorus levels lake wide (0.015 to 0.022 mg/L). Total phosphorus and total nitrogen have increased significantly over the past 5 yr (NYSDEC 2022). Surrounding land cover primarily includes agricultural (40%) and forested areas (38%; Wang et al. 2020). The lake lies on an approximate north–south axis, with the northern end characterized by shallow mudflats and the southern end also indicated as relatively shallow (Zhu and Georgian 2014). Littoral areas along the middle portion of the lake are less extensive than those in the northern and southern locations and feature rockier, harder substrates as well as a steep increase in depth with increasing distance from shore (Oglesby 1978).

Sites sampled in Cayuga Lake ($n = 22$) are grouped here based on geography into northern, middle, and southern locations (Figure 1). Sites within a given location were likely more similar to each other in substrate type, depth, and habitat composition than to sites in other locations (Oglesby 1978, Zhu and Georgian 2014).

Point-intercept surveys

Trained personnel from the Finger Lakes Institute completed surveys of SAV using kayaks and canoes in prioritized areas of Cayuga Lake, mainly marinas and public boat launches that could potentially facilitate the spread of invasive aquatic macrophytes (Rothlisberger et al. 2010). Sampling was more regular during the years of this study, 2020 through 2022, which occurred after discoveries of hydrilla populations in Cayuga Lake, beginning in 2011. Intense monitoring and local chemical treatments were undertaken to control hydrilla infestations lake-wide; management efforts are ongoing. Because of the potential for hydrilla treatments to influence the local presence of other SAV species (Nelson et al. 1998, Hofstra and Clayton 2001, Mudge and Glomski 2012), only American eelgrass and starry stonewort were examined here. Although both species may exhibit an initial negative response to herbicide or algaecide treatments associated with hydrilla management, they tend to regrow in a matter of weeks (Mudge and Glomski 2012, Glisson et al. 2018, Wersal 2022).

Following a modified version of the point-intercept method (Madsen 1999), rake-toss surveys were regularly

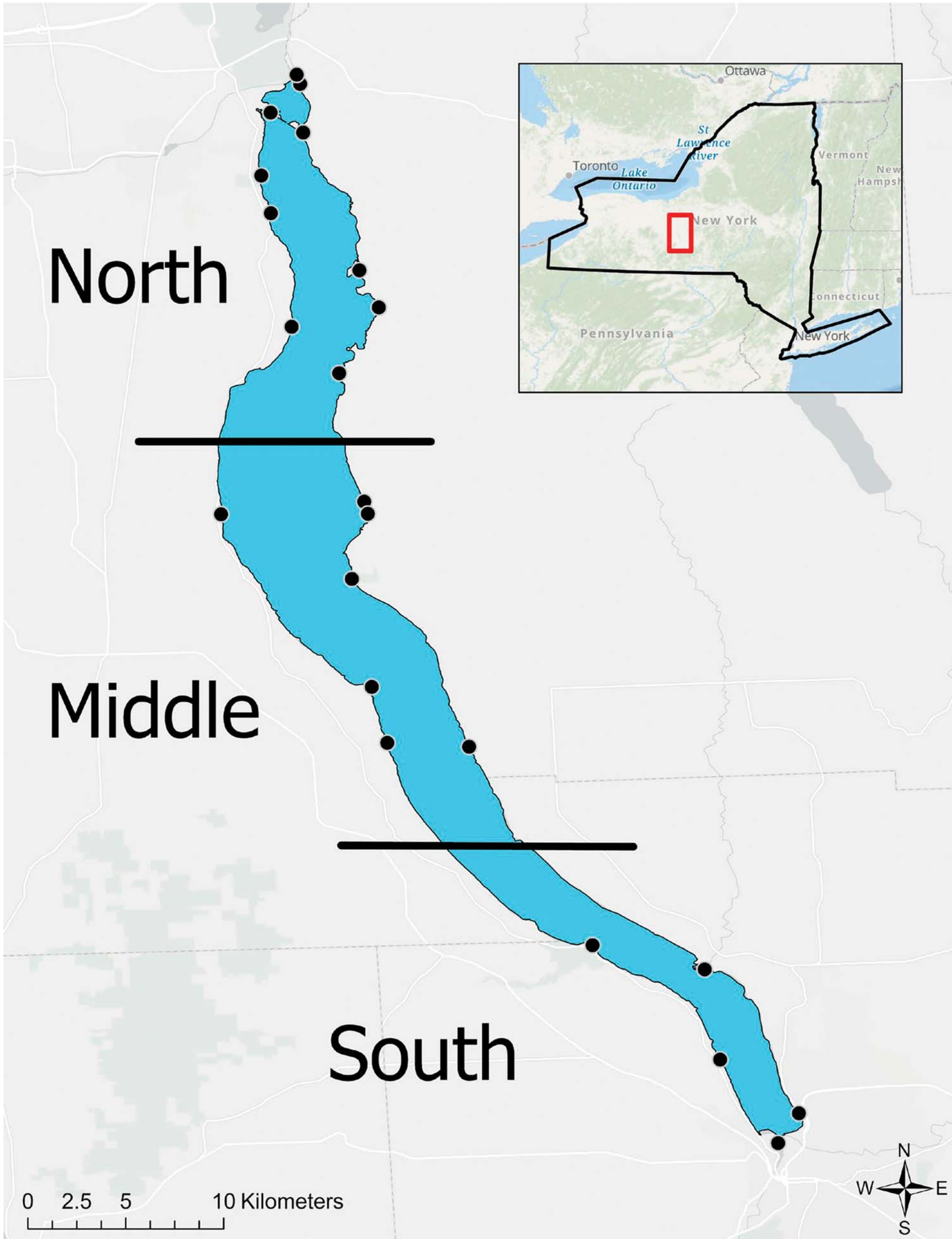

Figure 1. Cayuga Lake, in central New York State, with point-intercept sampling sites indicated for the northern, middle, and southern locations of this study. Arbitrary borders of these geographic locations are indicated with horizontal black lines. A total of 25, 741 rake tosses were conducted at these 22 sites from 2020 through 2022, inclusive.

conducted from June through November, 2020 through 2022, at sites in each of the three locations in Cayuga Lake (northern, middle, and southern). Annual data were combined to ensure adequate coverage of each location. Sampling was completed at regularly spaced points on a 25-m grid overlaid on a 500-m-radius circle centered on each site. A sampling rake consisted of a double-sided garden rake with handles removed and 9 m of rope attached. This rope length indicated the maximum depth at which sampling occurred in this study. At each grid point, a sample rake was tossed into the water, dragged along the lake bottom, and pulled up by the sampler. Sampling along the grid was concluded once water depth exceeded 9 m. In addition to date and global positioning system readings, data collected at each rake-toss location included water depth and presence/absence of American eelgrass and starry stonewort, represented as binary data. The retrospective study design presented here, including stratification of sites by location and regular sampling along a predetermined grid centered on each site, is similar to the random-systematic design of Madsen and Wersal (2017).

Data analysis

Analyses were completed with SAS software, version 9.4, 2016. The likelihood of sampling American eelgrass and

TABLE 1. THE NUMBER OF RAKE-TOSS SAMPLES COLLECTED FOR JUNE THROUGH NOVEMBER AMONG 22 SITES DISTRIBUTED AMONG THREE GEOGRAPHIC LOCATIONS (NORTH, MIDDLE, SOUTH) IN CAYUGA LAKE, NEW YORK. DATA WERE COLLECTED FROM 2020 THROUGH 2022.

Month	North rake tosses (*n*)	Middle rake tosses (*n*)	South rake tosses (*n*)	Total
June	2,390	386	932	3,708
July	1,597	767	1,858	4,222
August	4,489	2,626	2,685	9,800
September	2,373	387	1,227	3,987
October	1,836	761	330	2,927
November	448	62	587	1,097
Total	13,133	4,989	7,619	25,741

starry stonewort due to date, location, and water depth was examined with a logistic regression based on a logit transformation of the binary response variable (presence/absence) and location included as a class variable (PROC GENMOD). If there was a difference in the likelihood of sampling either species due to an effect of location in the overall model, the effect of date and depth on the likelihood of sampling both species was separately evaluated with logistic regression at each of the three locations.

Describing the response variable as the "likelihood of sampling" American eelgrass or starry stonewort due to location, date, or water depth, as we do here, is a more conservative approach than assuming that frequency of occurrence was sampled. Frequency of occurrence implies a direct correlation between the presence of each species in Cayuga Lake and the likelihood of it being collected with a rake toss; we did not follow that assumption. Changes in macrophyte phenology over the season, structural SAV characteristics, and substrate hardness, among other potential factors, influence the likelihood of sampling a given species if it is present (Capers 2000, Yin and Kreiling 2011). Although the likelihood of sampling American eelgrass and starry stonewort was likely strongly correlated with frequency of occurrence, density, and biomass we could not explicitly evaluate those relationships with our data.

RESULTS AND DISCUSSION

The distribution of samples collected at each location (northern, middle, and southern) on Cayuga Lake from June through November of 2020 through 2022, are presented in Table 1 and totaled 25,741 rake tosses.

Starry stonewort was more frequently observed in deeper water compared to American eelgrass (Figure 2). Overall, the likelihood of sampling both American eelgrass and starry stonewort exhibited strong patterns of increasing and then decreasing as water depth increased (Figure 3; Type 3 likelihood ratio statistics for depth, depth squared, and location: all chi-square > 336, all $P < 0.0001$). Lakewide, rake tosses conducted in 2.5 m of water were more likely to contain American eelgrass than tosses at other water depths. The likelihood of sampling starry stonewort was greatest in 3.5 m of water (Figure 3).

Examined separately, water depth associated with the greatest likelihood of sampling American eelgrass at each of the three locations peaked at approximately 2 to 3 m, with the northern location exhibiting the shallowest depth (1.8 m) associated with the greatest likelihood of sampling (Figure 4; Type 3 likelihood ratio statistics for depth, depth squared for each location: all chi-square > 104, all $P < 0.0001$). Similarly, the likelihood of sampling starry stonewort with increasing water depth differed among locations (Figure 5; Type 3 likelihood ratio statistics for depth, depth squared for each location: all chi-square > 65, all $P < 0.0001$), with the northern location also having the shallowest water depth (2.4 m) associated with the greatest

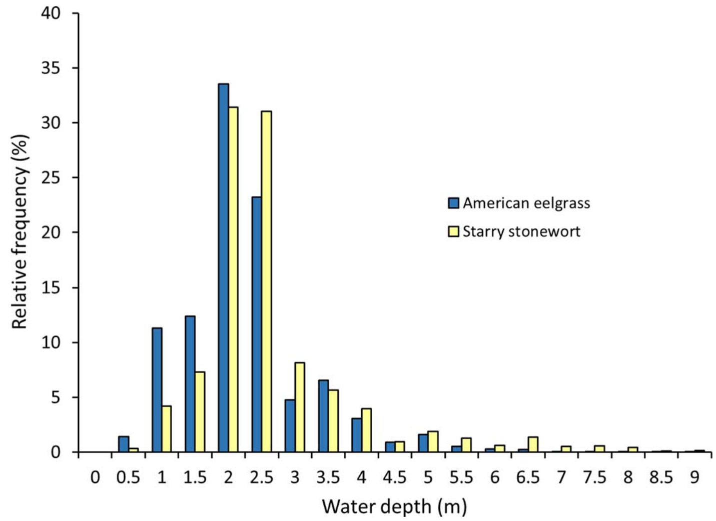

Figure 2. The relative frequency of water depth (m) at sample points that contained American eelgrass or starry stonewort in Cayuga Lake, New York. American eelgrass was found on 7,484 out of 25,741 points sampled and starry stonewort was detected on 3,768 of those points.

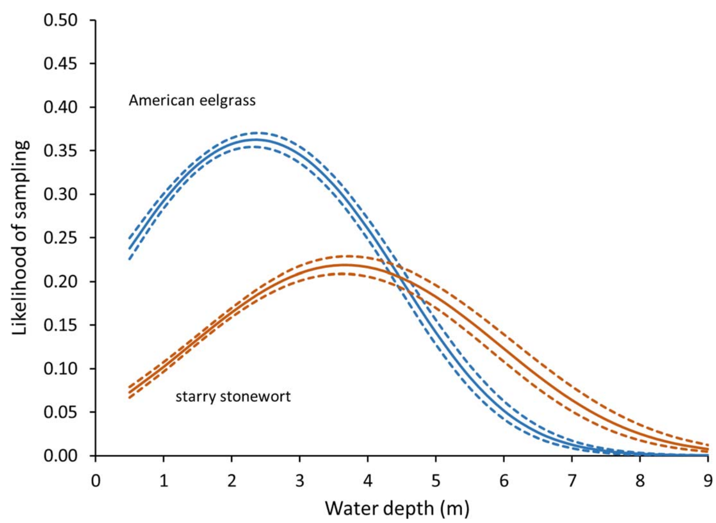

Figure 3. The likelihood of sampling American eelgrass and starry stonewort for all 25,741 points examined in Cayuga Lake, New York, exhibited a quadratic relationship with water depth (see text for statistics). Overall, American eelgrass was most likely to be sampled in 2.5 m of water and starry stonewort was most likely to be sampled in 3.5 m of water. Dashed lines represent 95% confidence intervals. Note that the likelihood of sampling and associated water depth values changed, sometimes substantially, when data from locations within the lake were examined separately (see Figures 4 and 5).

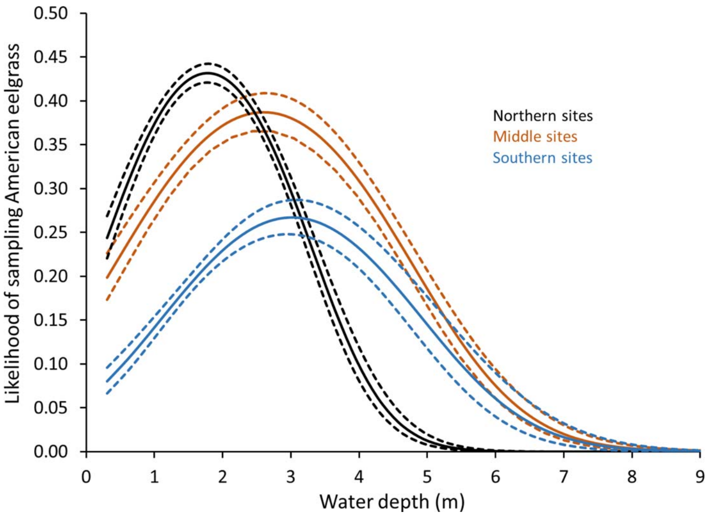

Figure 4. The likelihood of sampling American eelgrass was dependent on water depth and differed among the three geographic locations in Cayuga Lake. The relationship was quadratic in form for each location, with a peak likelihood of sampling at water depths of 1.8, 2.7, and 3.0 m in the northern, middle, and southern locations, respectively. See text for statistics. Dashed lines represent 95% confidence intervals for respective locations.

likelihood of sampling among locations. The north end of the lake was previously recognized as having more extensive mudflats and shallower water than other parts of the lake (Oglesby 1978, Zhu and Georgian 2014). Water depth associated with the peak likelihood of sampling starry stonewort varied more dramatically among locations than that of American eelgrass, differing by approximately 3.5 m, with the deepest water (5.8 m) associated with the middle location of the lake. Littoral areas in the deeper middle portion

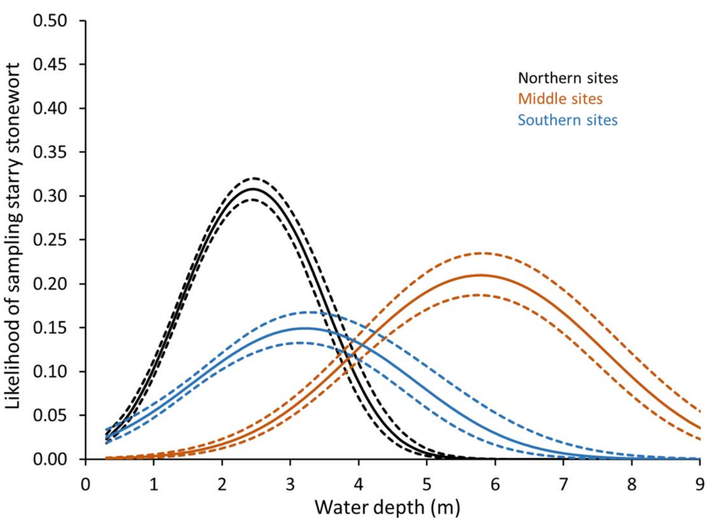

Figure 5. The likelihood of sampling starry stonewort in Cayuga Lake was dependent on water depth and varied among the three geographic locations. The relationship was quadratic in nature for each location, with peak likelihood of sampling occurring at water depths of 2.4, 5.8, and 3.3 m in northern, middle, and southern locations, respectively. See text for statistics. Dashed lines represent 95% confidence intervals.

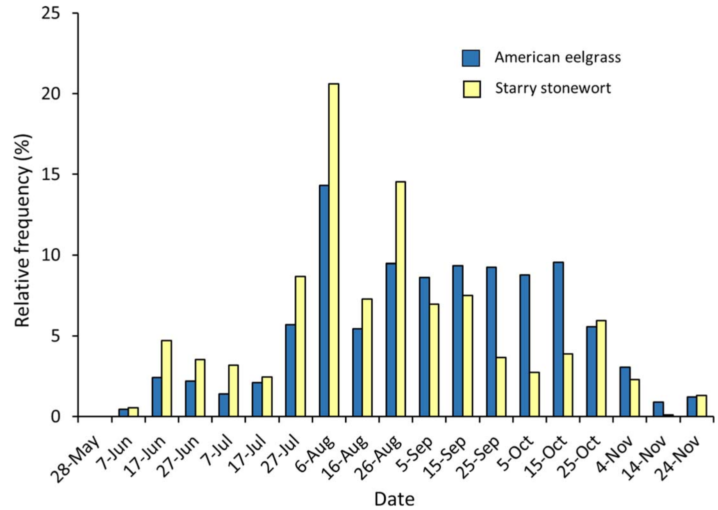

Figure 6. The distribution of sampling dates among points in Cayuga Lake, New York that contained American eelgrass or starry stonewort was approximately normal for both species. Starry stonewort exhibited a greater relative frequency at sampled points from June through August than American eelgrass, and the relative frequency of American eelgrass was greater than that of starry stonewort from September through October.

of the lake are less extensive than at the ends (Oglesby 1978).

The distribution of dates on which American eelgrass and starry stonewort were collected approximated a normal distribution for each species (Figure 6). The likelihood of sampling American eelgrass in Cayuga Lake demonstrated a quadratic relationship with date, peaking on 17 September (Figure 7; Type 3 likelihood ratio statistics for date, date squared, and location: all chi-square > 650, all $P < 0.0001$).

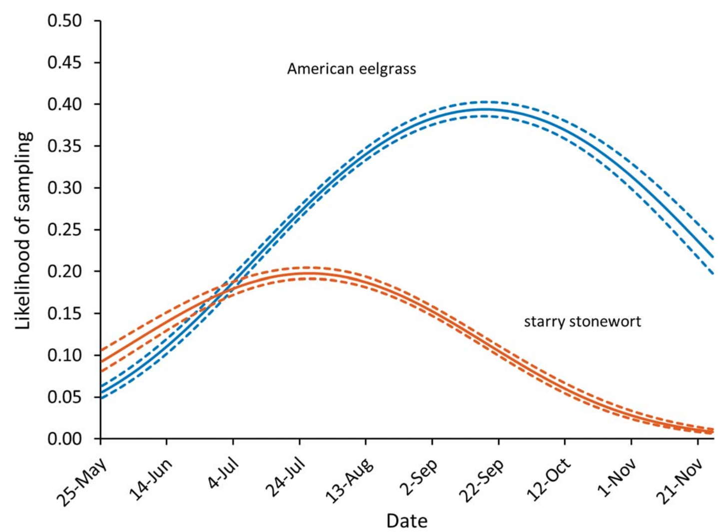

Figure 7. The likelihood of sampling American eelgrass and starry stonewort in Cayuga Lake, New York, increased and then decreased in a quadratic manner as the date of data collection increased (see text for statistics). Data are from 2020 through 2022, combined, and represent 25,741 sample points. American eelgrass was most likely to be sampled on 17 September and starry stonewort was most likely to be sampled 26 July. Dashed lines represent 95% confidence intervals. Note that these values differ from those determined from the North, Middle, and South locations examined separately (see Figures 8 and 9).

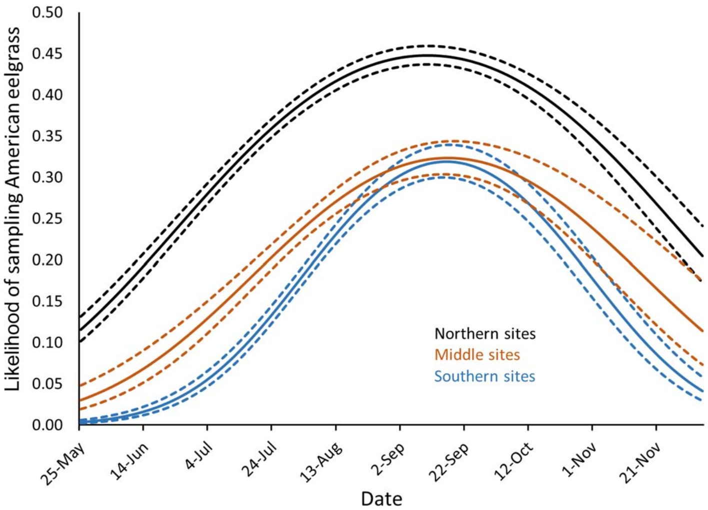

Figure 8. The likelihood of sampling American eelgrass due to sampling date differed slightly among locations in Cayuga Lake. The relationship was quadratic in form for each location, with a peak likelihood of sampling of 10 September, 17 September, and 16 September for the northern, middle, and southern locations, respectively. See text for statistics. Dashed lines represent 95% confidence intervals for respective locations.

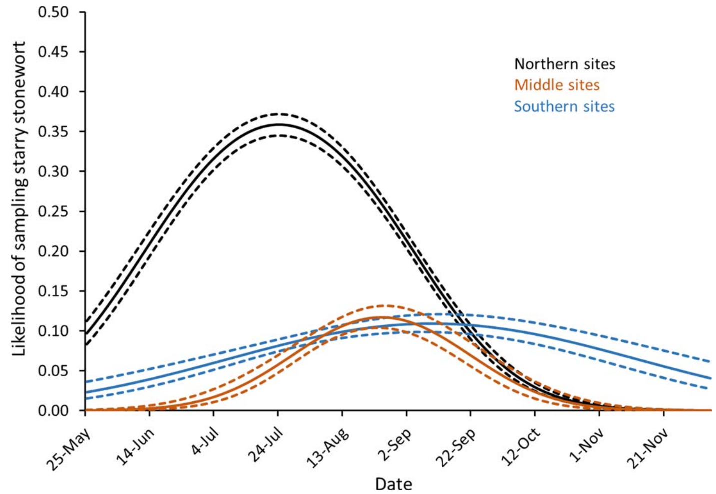

Figure 9. The likelihood of sampling starry stonewort in Cayuga Lake, New York, was dependent on date and varied among the three geographic locations. The relationship was quadratic in nature for each location, with a peak likelihood of sampling occurring on 24 July, 25 August, and 9 September for the northern, middle, and southern locations, respectively, with a maximum difference among locations of 42 d. See text for statistics. Dashed lines represent 95% confidence intervals.

The effect of date on the likelihood of sampling American eelgrass differed slightly among locations (Type 3 likelihood ratio statistics for depth, depth squared for each location: all chi-square > 63, all $P < 0.0001$); dates associated with the greatest likelihood of sampling American eelgrass at each location were within 7 d of each other (Figure 8).

The likelihood of sampling starry stonewort in Cayuga Lake also followed a quadratic relationship with date, with a lake-wide peak on 26 July, or 53 d earlier than that of American eelgrass (Figure 7; Type 3 likelihood ratio statistics for date, date squared, and location: all chi-square $>$ 447, all $P < 0.0001$). Variability among locations in dates associated with peak likelihood of sampling was, again, much greater for starry stonewort, which differed by 42 d among locations (Type 3 likelihood ratio statistics for depth, depth squared for each location: all chi-square > 38, all $P < 0.0001$), than for American eelgrass (Figure 9).

In Minnesota, starry stonewort exhibited a late-season peak in biomass phenology, a pattern that differed from other invasive or native macrophytes in the study (Glisson et al. 2022). The general phenology in Minnesota was of low biomass through June, an increase in biomass from July through August, and a peak in September. The phenology of starry stonewort in its invaded range is not well understood (Midwood et al. 2016, Brainard and Schulz 2017, Glisson et al. 2022), but some early studies reported a phenology similar to that described from Minnesota: an increase in biomass in June, accelerated biomass development in July and August, and a peak in September (references in Glisson et al. 2022).

This pattern does not generalize well, however. The overall pattern in the likelihood of sampling starry stonewort over time in Cayuga Lake, presented here as an indicator of biomass phenology, differed from that of Minnesota: the likelihood of sampling starry stonewort was low in June, peaked in late July, decreased sharply in September through October, and was very low in November. The likelihood of sampling starry stonewort in the middle location of Cayuga Lake, however, exhibited a temporal pattern similar to that described for Minnesota (see Figure 9). Starry stonewort phenologies varied among other studies. As already given, starry stonewort was first observed in July at the head of the Detroit River, biomass increased from July to September, and remained high from September through January. Biomass decreased in February at the beginning of ice breakup and starry stonewort was senescent in March (Nichols et al. 1988). Lack of freezing may delay senescence (Glisson et al. 2022). This species was not observed to senesce in the relatively shallow (3.4 m average depth) Lake Scugog, Ontario, Canada (Harrow–Lyle and Kirkwood 2021), however, and green starry stonewort was reported under the ice during winter in Minnesota (Glisson et al. 2022).

The likelihood of sampling American eelgrass in Cayuga Lake was low in June, increased through July and August, and peaked in mid-September. This general pattern in the likelihood of sampling American eelgrass was consistently followed among sites in the northern, middle, and southern locations of the lake. The phenology of American eelgrass in the Upper Mississippi River, based on production of biomass, was low early in the growing season and peaked in early September (Donnermeyer 1982). Phenology in Otsego Lake, New York, at a latitude similar to Cayuga Lake, included emergence from the substrate in mid-June, rapid growth to a maximum height in mid-September, and then decomposition (Harman 1974). A similar phenology was observed in Chenango Lake, New York (Titus and Stephens 1983). The assumption that the likelihood of sampling American eelgrass is positively correlated with biomass phenology is bolstered by these congruent findings.

Brainard and Schulz (2017) referred to starry stonewort as a "cryptic invader": the species occurs in deeper waters, where it is difficult to detect, and it also resembles the appearance of some native species. The variability associated with the likelihood of sampling starry stonewort in different water depths and on different dates in distinct locations and, presumably, habitats in Cayuga Lake reinforces this description. In its native range, starry stonewort was found in water ranging from 0.4 to 31 m in depth (Larkin et al. 2018), much greater than the maximum depth ranges reported in studies conducted in its invaded range in North America, < 10 m (Geis et al. 1981, Sleith et al. 2015). New sampling techniques may be required to search for starry stonewort in deep water (Brainard and Schulz 2017), however, especially in water that is challenging to sample with rake tosses. Charophytes generally are found at much deeper depths than vascular plants (Azzella 2014, Azzella et al. 2017).

Every major study of starry stonewort in its invaded range expressed strong concerns about the immediate and pending effects of its introduction (e.g., Brainard and Schulz 2017, Larkin et al. 2018, Ginn et al. 2021, Harrow–Lyle and Kirkwood 2021). Control of starry stonewort requires an understanding of stage of infestation, water chemistry, habitat and species associations, phenology, and sampling techniques that can inform management approaches (Brainard and Schulz 2017, Hussner et al. 2017, Larkin et al. 2018, Ginn et al. 2021, Harrow-Lyle 2021). The methods presented here, for example, could be improved by using substrate type, rather than geographical location, as a basis of sampling stratification but that information was not readily available. Given the cryptic and plastic nature of starry stonewort invasions locally and regionally, the development of site-specific, rather than region-wide, management plans seems prudent. More generally, determining the correlation between the likelihood of sampling a species with point-intercept methodology as it is commonly practiced—with one rake toss per grid point—and biomass phenology is important. If rake-toss results are highly correlated with biomass, methods and figures similar to those presented here could be important and accessible indicators of regional and local differences in phenology as well as indicators of management success. The substrate type and the growth form of the species in question may limit this application (Yin and Kreiling 2011).

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