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Does Macroalgae Invasion Alter Macroinvertebrate or Macrophyte Communities in Wetland Habitats?

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Does Macroalgae Invasion Alter Macroinvertebrate or Macrophyte Communities in Wetland Habitats?

by

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Abstract of Thesis

Macroinvertebrates play an important role in maintaining ecosystem functionality. Processes such as nutrient cycling, and primary productivity are directly linked to macroinvertebrates and their value as a food source for higher trophic levels is undeniable. Therefore, disruptions to co-evolutionary adaptations between macroinvertebrates and native macrophytes remain a concern. This study investigated patterns in macroinvertebrate richness, abundance, and functional feeding group representation, as well as plant richness and total biomass across five sites in upstate New York with varying dominance by the non-native macroalgae, Starry Stonewort (*Nitellopsis obtusa*).

As *N. obtusa* proportional biomass increased, other plant community biomass declined at two of the five locations. Starry Stonewort mass had no impact on macrophyte richness. Macroinvertebrate richness declined as *N. obtusa* biomass increased at two of the five sampled waterways, but increased with total vegetative biomass at one site. Functional feeding group representation differed among the sample locations, but only predators showed a significant decline as percent *N. obtusa* biomass increased. Increasing Starry Stonewort mass may facilitate *Dreissena polymorpha* expansion. These findings suggest that this non-native macroalgae may alter some, though not all, plant and macroinvertebrate community metrics.

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Chapter 1: Introduction to Starry Stonewort

Submerged aquatic vegetation (SAV) serve multiple uses for their related faunal community, being used as a direct or secondary food resource, as a hunting ground for predators, for predation refugia, or as an oviposition site for a variety of species (Diehl and Kornijów 1998). However, the extent to which taxonomic changes in SAV community structure may affect the associated macroinvertebrate assemblages is debatable, and likely based on a suite of structural, chemical, and phenological considerations (Schultz and Dibble 2012).

The "State of the Great Lakes 2019 Highlights Report" indicates that the presence and spread of invasive species throughout the basin is causing significant negative impacts to regional ecosystems (EPA and ECCC 2020). Currently 189 invasive and non-indigenous species can be found within and along the coasts of the Great Lakes, representing a diverse array of flora and fauna that are linked to an equally wide array of detrimental impacts (USGS 2012). Aquatic invasive species (AIS), in particular, have been associated with the degradation of natural habitats, disruption of food-webs, displacement of native species, and the increased occurrence of algal blooms (Rosaen 2016). Socio-economic related impacts such as a collapse of region's sport and commercial fishing industries, the increased operating cost for water treatment facilities, manufacturing hubs, and power generation plants, a loss of revenue from declining tourism and recreational opportunities, or simply the cost to manage an infestation, have tangible, far-reaching and everyday consequences (Rosaen 2016, Sturtevant and Lower 2018). It has been estimated that invasive species inflict a monetary cost upwards of $137 billion annually in the US (Lodge 2005). This nationwide financial burden is echoed in the Great Lakes, with ship-borne nonindigenous AIS causing an estimated $138 million in damages to ecosystem services every year (Rothlisberger et al. 2012). Aquatic invasive macrophytes, in particular, can radically alter the structure and functions of an ecosystem by outcompeting native species, permanently altering natural habitats, temporally modifying local abiotic conditions of the sediment and water column, destabilizing the natural food web, and decreasing overall biological diversity and abundance (Kovalenko et al. 2010, Schultz and Dibble 2012). One unique and understudied plant-like invader that has the potential to inflict many of the aforementioned consequences upon ecosystems across the Great Lakes basin is the macroalgae, *Nitellopsis obtusa* (Desv.) J. Groves (1919), more commonly known as Starry Stonewort.

Taxonomic Background

Starry Stonewort is a member of the Characeae family, a group of ancient green macroalgae that have been proposed to be one of the closest ancestors of land plants and which can be found on every continent except for Antarctica (Beilby et al. 2018, Sleith et al. 2018). Charophytes, also known as Stoneworts, of the Order Charales and Family Characeae encompass some 400 species in 6 genera (*Chara*, *Lychnothamnus*, *Tolypella*, *Nitella*, and *Nitellopsis*) (Lambert 2009). Charophytes were more genetically and ecologically diverse in the past relative to the present, with many contemporary species being considered pioneers of shallow aquatic habitats (Beilby et al. 2018).

Charophytes are algae that have a complex morphology, generally consisting of a central axis made of long unicellular internodal cells, and short multicellular nodes where whorls of branchlets originate at somewhat regular intervals (Schneider et al. 2015). Charophytes may be monoecious or dioecious and have the ability to reproduce sexually via the fertilization and deposition of oospores and asexually via bulbils and fragmentation (Urbaniak and Gabka 2014). Starry Stonewort is the only extant member of the genus *Nitellopsis,* with a contemporary Eurasian native range stretching sporadically from Western Europe to Japan, where it is often considered a rare, threatened, or endangered species (Larkin et al. 2018) (Figure 1). Apart from being the only living member of its genus, Starry Stonewort harbors some unique characteristics that set it apart from other charophytes.

Phytotomy & Ecology

Unlike other charophytes, Starry Stonewort is ecorticate, not hispid, lacking stipulodes as well as generally lacking the layer of calcium encrustation that cover many other charophytes, resulting in a bright green, almost plastic appearance (Lambert 2009). Another difference between this species and other charophytes is that it can generally grow to greater heights and at greater depths, being found to a depth of 14 m and having a maximum height of about 2 m, with an average height between 30 and 120 cm (Lambert 2009, Brenner 2018). Populations in North America are most common between a depth of 0.5 and 3 m in depth (Boissezon et al. 2018). Despite these differences, the species does maintain a physical structure like that of other macroalgae consisting of rhizoids, thallus, internodes, nodes, and branchlet whorls (4-6 irregular branchlets in Starry Stonewort). One noteworthy discrepancy relating to the reported physical characteristics of this species however, is a broad range of reported thallus width (<0.5mm, 1mm, ≤ 2mm or up to 3 mm) (Urbaniak and Gabka 2014, Alix et al. 2017, Hackett et al. 2017).

In upstate New York, Starry Stonewort generally “sprouts” in April or sometime late spring, which is followed by rapid upward growth pattern into the early summer months, eventually leading to lateral growth and entanglement upon reaching the water surface, or the structure collapses upon itself. By late summer or early fall (August / September) the species reaches peak biomass. Basal portions of plant shaded by the upper mat layers begin to senescence, turning dark black in color while generally maintaining physical integrity. As day length shortens and senesced material begins to decompose, mats of the material compress to the substrate (Johnson et al. 2002). Although the species can remain viable during winter months, including under a thick layer of snow and ice, it is more common for compressed mats to be washed into deeper waters during the onset of strong fall storms.

Due to the lack of a true root system, this species is generally limited to protected environments with little wave action, low flow rates, and a soft sediment substrate. Despite these bathymetric constraints, Starry Stonewort can tolerate eutrophic and oligotrophic conditions, variable pH, substrate conditions, and light availability and also has the ability to overwinter, albeit at lower densities (Alix et al. 2017, Brenner 2018, Larkin et al. 2018). Habitat suitability assessments suggest the likely range in North America will expand due to direct and indirect consequences of climate change (MDARD 2015, Neuman 2021), whereas the species is primarily boreal in distribution in its native range (Kato et al. 2014). The inherent risk of spread is augmented by its diverse and unique reproductive capabilities.

Reproduction

Only male specimens of Starry Stonewort have been observed in North America, although some speculation exists on whether this is truly an accurate assessment. An accurate assessment of the existing North American population is difficult when considering the cryptic nature of this species (especially in newly invaded waterways) and the low abundance of female organs under sub-optimal environmental conditions makes confirmation difficult (Larkin et al. 2018). In its native range, male and female individuals are rarely observed within the same waterbody and it is uncommon to find signs of sexual reproduction (Kato et al. 2014). However, the species ability to reproduce vegetatively via bulbil production and fragmentation has allowed it not only to successfully colonize new habitats but also sustain its populations despite major efforts to eradicate it.

Fragmentation occurs as pieces of the macroalgae are separated from the parent plant and then reform into another individual, which may be spread via human-mediated transportation (i.e. recreational watercraft), epizoochory, or wave action (Alix et al. 2017). These modes of transportation also disperse bulbils. In Starry Stonewort, bulbils are pale white, stellate, asexual structures found attached to clear filamentous rhizoids near the sediment for which the macroalgae gets its name “Starry” Stonewort. Besides these, there are also green, more circular bulbils that develop at nodes along the thallus (Sleith et al. 2015, Larkin et al. 2018). Bulbils are generally thought of as the seasonal or overwintering mechanism of the species. Once the thalli of the Starry Stonewort have senesced for the winter or have been washed away, bulbils can be found resting near the top layer of the sediment, able to form new colonies during the next growing season. While the highest numbers of bulbils are produced late in the growing season, coinciding with peak biomass, these vegetative structures can be found attached to living thalli throughout most of the year (Hackett et al. 2017). This clonal reproductive strategy has aided the species spread across N. America.

Invasion History

First discovered incidentally within the St. Lawrence River near Quebec, Canada in 1974, it is believed that the species was introduced via trans-oceanic shipping (Geis et al. 1981, Karol and Sleith 2017). Only a few years later, in 1983, Starry Stonewort had entered the Laurentian Great Lakes being documented as far west as the St. Claire – Detroit River system (Alix et al. 2017). Since that time, the species has been reported in eight states, two Canadian provinces and all the Great Lakes except for Lake Superior (Kipp 2012).

Now listed by the USGS as an aggressive invasive, Starry Stonewort remains the only known charophyte to be classified as such (Karol and Sleith 2017, Larkin et al. 2018). Generally, within its invaded range Starry Stonewort is considered a littoral invader, most often colonizing coastal habitats in the Great Lakes basin to a depth from less than one to three meters (Hackett et al. 2017). Boat launches and sites with high conductivity or general indications of human disturbance are common sites of occurrence (Midwood et al. 2016). Anthropogenic transport via boat / trailer / kayak has been suggested as the main vector of this species introduction to new waterways. Other methods of dispersal for the species may include endozoochory, epizoochory, and dispersal via wave action, the latter possibly attributing to its continual spread throughout Great Lakes coastal wetlands.

Once introduced to a waterway, Starry Stonewort will generally experience a period of cryptic expansion, intermingling with other macrophytes until it eventually becomes a nuisance by fouling boat motors and impeding swimming and fishing (Sleith et al. 2015). This process may occur rapidly (1 season) or gradually (many years), depending upon the conditions of the receiving waterbody, robustness of local macrophyte beds, and seasonal management strategies (Ginn et al. 2021). The last variable mentioned has undoubtedly received the most attention by researchers across N. America.

Numerous works have been published in peer-reviewed journals, lake association newsletters, and government reports looking into the success, cost, risk, and public perception of treatment methods (MDARD 2015, Thill 2017, Glisson et al 2018, Pokrzywinski et al. 2020). Generally, these works are conducted in areas where Starry Stonewort has already established itself as a major nuisance for the surrounding community. Unfortunately, no single or combined treatment method has been identified to eradicate infestations of the species, with chemical methods bringing concerns to water users and impacts on the environment, as well as a hefty price tag; for example, a pilot project to reduce Starry Stonewort biomass in Lake Koronis, MN cost over

$800,000 dollars for only two years of management (Wessel 2016, Pokrzywinski et al. 2020). Despite the threats brought from Starry Stonewort and invasive classifications by many state and national agencies, most work surrounding the ecological impact of Starry Stonewort is anecdotal.

Only a handful of peer-review publications have quantitatively described some of the ecological impacts caused by Starry Stonewort in North America, many of which were published in the last two years. While habitat preferences have been thoroughly addressed in existing research, the effects that this macroalgae has on contemporary macrophyte communities within North America has generally been confined to single lake studies, and investigations into it's impact on contemporary macroinvertebrate communities is almost non-existent. Accordingly, this is a knowledge gap recognized by multiple papers and by organizations such as The Starry Stonewort Collaborative (Hackett et al. 2017, Larkin et al. 2018, Kastan 2020). A proper understanding of how this species may impact these lower-level community interactions and composition dynamics is essential to comprehending ecosystem level changes that may occur throughout any given aquatic system.

Macrophytes Overview

Macrophytes are littoral zone plants that are structurally complex and are either submerged, emergent, or floating-leaved, and generally rooted. Macrophytes, including native charophytes, provide a variety of ecosystem services and act as an integral feeding ground and refugia for invertebrates, fish, and waterfowl (Alix et al. 2017, Sleith et al. 2018). Like their faunal counterparts, macrophytes require specific abiotic and biotic conditions to exist in wetland habitats.

A diverse macrophyte community can support ecological and anthropogenic processes that extend both beneath and above the surface of the water at the microscopic and macroscopic level (Rejmankova 2011). Structural habitats created by various vegetation types can influence associated organisms and restoration and conservation efforts have been directly linked to the presence of a healthy macrophyte community (Humphries 1996, Thomaz and Cunha 2010). Unfortunately, naturally occurring macrophyte communities within the Great Lakes basin have been declining due to water level regulation, sedimentation, physical disturbances such as dredging, and the influx of aggressive invasive species (Albert and Minc 2004). Studies have indicated that a shift from a diverse vegetative habitat to a dense monotypic stand of an invasive species can seriously alter aquatic ecosystem processes and community assemblages (Papas 2007, Stiers et al. 2011).

Macroinvertebrates Overview

Aquatic macroinvertebrates play an important part in maintaining proper ecosystem functioning. They are prey for fish, amphibians, and waterfowl, play a critical role in nutrient cycles, and process organic material within aquatic ecosystems (Stumpf 2009, MDNR 2021). Macroinvertebrates are often categorized in terms of their functional feeding group (FFG) based on a collective of mechanical and behavioral mechanisms that evolved to take advantage of their desired food source (Wallace and Webster 1996). Thus, each FFG has a distinct role to play in aquatic ecosystems . Common FFG’s include: predators, collector-gatherers, collector-filterers, scraper-grazers, shredders, and piecers (Barbour et al. 1999). Common macroinvertebrate predators include hemipterans, odonates, and many beetles that consume other macroinvertebrates. Scraper-grazers such as certain Trichoptera and gastropods graze on periphyton and algae from the surface of substrates. Shredders include some Diptera, Coleoptera, Trichoptera and crayfish, which commonly consume large decomposing plant material. Collector-gatherers like amphipods and isopods, as well as some Trichoptera and Diptera, feed primarily on benthic fine particulate organic matter. Collector-filterers, composed primarily of bivalves, use specialized anatomical structures to remove fine particulate matter suspended in the water column. Piecers, like some Trichoptera, pierce plants and extract desired liquids. Members of every functional feeding group are vulnerable to things such as eutrophication, anthropogenic chemical pollutants, loss of native aquatic vegetation, and, potentially, the emergence of AIS (Papas 2007).

Changes in freshwater macroinvertebrate communities may arise following AIS introductions due to alterations in complex connections among macroinvertebrates and their associated food-webs (Covich et al. 1999). Different macrophyte species typically support different assemblages of macroinvertebrates; often attributed to varying microhabitats created by the plant structural composition (Humphries 1996). The introduction of AIS has the potential to disrupt co-evolutionary adaptations between macroinvertebrates and the contemporary plants they utilize. FFG composition has been shown to vary based on plant community structure (Walker 2013). Whether invading Starry Stonewort, and its potential to alter contemporary macrophyte community structure, will lead to changes in macroinvertebrate assemblages remains to be tested.

Chapter 2: Starry Stonewort effects on macrophyte and macroinvertebrate communities

Introduction

Understanding the relationship between fauna and their floristic surroundings remains a fundamental activity for ecologists. Submerged aquatic vegetation (SAV) serves multiple uses for the macroinvertebrate community, being used as a direct or secondary food resource, as a hunting ground for predators, for predation refugia, or as an oviposition site for a variety of species (Diehl and Kornijów 1998). However, the extent to which taxonomic changes in SAV community structure may affect the associated macroinvertebrate assemblages is debatable, and likely based on a suite of structural, chemical, and phenological considerations (Schultz and Dibble 2012).

Non-native aquatic macrophytes and their impacts on native plant and macroinvertebrate communities have been a source of interest for environmental managers for decades. As resources for prevention and management of these species if often limited, it's important to quantify and prioritize the tangible effects that exotics may have on an ecosystem (Hofstra et al. 2020). While some studies have indicated that non-native macrophytes due little to change the overall composition and or richness of aquatic plant communities (Mjelde et al. 2012, Kuehne et al. 2016); others have indicated significant declines in native plant community metrics due to the introduction of exotic macrophytes (Madsen et al. 1991, Nichols 1994).

Similarly, findings regarding the impact that non-native macrophytes might have on macroinvertebrates assemblages are variable. Hogsden et al. (2007) reported macroinvertebrate abundance significantly increased when a structurally complex and or high biomass non-native macrophyte was the dominant SAV species. However, Stiers et al. (2011) suggested macroinvertebrate abundance significantly decreased when non-native macrophytes dominated the SAV community. Variability also exists as to the impact of non-native species on macroinvertebrate richness, with some data suggesting a significant positive relationship with the presence of native macrophytes (Kovalenko et al 2010), and other data displaying almost no difference as long as the invading species was structurally complex (Cheruvelil et al. 2022). When a non-native species becomes the dominant component of an aquatic ecosystem, the outcome is often attributed to the non-native species ability to outcompete its native counterparts due to advantages relating to life history, growth rate, growth structure, allelopathy, phenotypic plasticity, propagule pressure, and the presence of a disturbed habitat (Fleming and Dibble 2015).

Littoral wetland communities in the State of New York have undergone many changes over the past decades due to multiple factors, such as water level fluctuations, alterations in nutrient availability and water clarity, and the introduction of non-native aquatic species. To date, the State of New York is host to 50 non-native aquatic / riparian plant species (USGS 2022). Many of these exotic species are known to have entered the State via incidental transport during shipping practices (USGS 2022); often originating from the Eurasian sub-continent (USGS 2022). *Nitellopsis obtusa*, also of Eurasian origin, was first observed within New York waterways in the 1970's (Romero-Alvarez D. et al. 2017).

A green macroalgae, *N. obtusa*, more commonly known as Starry Stonewort is the only member of the Characeae family to be classified as invasive (Muthukrishnan et al. 2018). Found in shallow, slow moving, littoral habitats this species emerges from asexual stellate bulbils in late spring and grows rapidly upward forming thick monotypic "bushes" that can reach the water's surface. Following a phenological cycle that promotes late-season growth, this species maintains a heightened presence within infested waterbodies, until it is generally washed away following strong fall storms.

While native Characeae, such as Muskgrass (*Chara sp*.), act as a valuable food resource and structural habitat for a variety of aquatic and avian species; the excessive growth rate and pioneering nature of Starry Stonewort makes it a threat to pre-existing macrophyte communities. The threat across the Great Lakes basin may be exacerbated when taking into account the degraded nature of many coastal habitats (Cvetkovic and Chow-Fraser 2011). Unfortunately, the species presence in these highly prized, ecological, recreational, and aesthetic settings amplify its potential impacts.

Often found near boat launches and other anthropogenically disturbed habitats, the movement of clonal reproductive organs, bulbils, and fragments via watercraft is thought to be its primary means of dispersal in North America (Larkin et al. 2018). Unfortunately, this cryptic invader often remains unnoticed within invaded ecosystems until reaching nuisance levels where it begins to entangle boat motors and impede other recreational activities (Glisson et al. 2020). It is at this stage where the species has received the most research, which has been predominantly focused on treatment / management and spread prevention techniques. To date, no reported management strategy or combined approach has been successful at eradicating Starry Stonewort from an invaded waterway (Pokrzywinski et al. 2021).

While many peer-reviewed articles are available on spread control and management options, very little has been published onto the impacts that this unique macroalgae has on the ecology of habitats it invades. It is unclear how the arrival of an invasive macroalgae such as Starry Stonewort might impact the abundance and richness of macroinvertebrates that commonly inhabit contemporary stands of submerged aquatic vegetation. While some studies, have documented impacts by Starry Stonewort on contemporary macrophyte beds (Brainard and Schulz 2017, Ginn et al. 2021, Wagner 2021); there is still a need to verify these findings across a wider geographical and hydrologically diverse landscape. Thus, I will investigate the macroinvertebrate and macrophyte communities associated with the presence of Starry Stonewort in aquatic ecosystems throughout upstate New York, while paying particular attention to the richness, abundance, and FFG composition of these assemblages. I hypothesize that both macroinvertebrate and macrophyte community metrics will decrease as Starry Stonewort increases.

Methods

The influence of Starry Stonewort on macroinvertebrate and plant community metrics was assessed in five wetland locations (Figure 2), that were selected based on verification of *N. obtusa* occurrences reported on the publicly-sourced GIS-based data management system known as ‘iMapInvasives’, © [2021] NatureServe. Initial confirmation of *N. obtusa* presence was based on sites surveyed via wading and standup paddleboarding which occurred during the months of June 2021 – August 2021. Effort was made to visit relevant sites on days with low wind and mostly sunny conditions to provide for efficient and accurate preliminary surveys of *N. obtusa* at the location. Final sampling sites were selected based on three factors: 1) accessibility, 2) *N. obtusa* presence at depths of ≤ 1.5 m, and 3) the presence of *N. obtusa* across a linear distance of at least 150 m along the sediment surface. All three parameters are based on sampling guidelines set in place by the Great Lakes Coastal Wetland Monitoring Program (GLCWMP) (Uzarski 2019).

Field Sampling Protocols

Macroinvertebrate and plant sampling took place over a nine-day period from August 24th to September 3rd, 2021, at five locations across the Western and Central New York region, including Burnt Ship Creek, Braddock Bay, Cayuga Lake, Cazenovia Lake, and the southernmost portion of the Keuka Lake outlet directly bordering Keuka Lake proper. This sampling window is compliant with guidelines set forth by the GLCWMP and corresponds to the late season period of maximum *N. obtusa* biomass reported by studies within the Great Lakes watershed (Scholesser et al. 1986, Nichols et al. 1988, Glisson et al. 2022). Initially, plot locations were selected based on visual estimation of Starry Stonewort abundance, attempting to collect samples from a gradient of coverage from 0-100% *N. obtusa*, since macroalgae is documented to have high spatiotemporal variability (Boissezon et al. 2018).

Ten plant and macroinvertebrate samples were taken at each location and were located at least 15 meters apart based on the Euclidean distance between GPS coordinates logged on a GARMIN GPSMAP 78s. Individual samples provided a range of *N. obtusa* coverage from 0% to 100% among the 10 samples at a site. A paddleboard was used to access sites and to transport all the needed field equipment. It also allowed the ability to dismount the vessel delicately so as to not disturb the inhabiting macroinvertebrates.

Plant and macroinvertebrate collection followed a modified sweep-netting technique as described by Turner and Trexler (1997) and Uzarski (2019). A standard D-frame dip net (width = 30 cm, mesh = 600 μm) was passed through a one-meter sampling line moving left to right at the surface of the water column, repeating at mid-depth and again near the substrate. In total six, one-meter passes were conducted through each sample, covering the relative top, middle, and bottom of the water column twice. A sweep constitutes the six, one-meter, singular directional passes of the D-net through the water column. Once the net reached the lowest sweeping zone

(5th and 6th passes) it was bounced gently along the sediment surface to dislodge any organisms found within the water-sediment interface. During this process, passes were conducted rapidly to ensure that more mobile macroinvertebrates did not escape from the net. Following the final pass, the net mouth was turned parallel to the sky and vegetation hanging out of the sampler was clipped at the net perimeter. This was done to account for the large amounts of *N. obtusa* that can be collected during the sweeps due to the species' highly intertwined structure. Once the sample was retrieved, clipped, and field-rinsed, the contents were placed in a 3.78 L Ziploc storage bag and labeled. Collected samples were then placed in an ice-filled cooler that was moved from site to site on top of the paddleboard.

Once all ten samples were collected at a location, they remained in the cooler until returned to Buffalo State College where the samples were preserved in a 75% ethanol solution and placed in a refrigerator. This process occurred within 24 hours of each collection day. Once all 50 samples (5 sites, 10 samples per site) were collected and preserved, plant and macroinvertebrate sorting commenced.

Sample Sorting

Each sample was first placed in a sorting tray and large macroinvertebrates were removed. Next, the sample was placed in a large water-filled bowl and clumps of vegetation were vigorously shaken to dislodge attached fauna. Each clump was then held just above a 500-µm mesh sieve and rinsed thoroughly, to catch any remaining macroinvertebrates. Processed vegetation was then returned to the labeled zip-lock bag and frozen to be processed at a later date. In most cases, this process was repeated several times as it was unlikely that the entire sample could be processed in a single round. Once completed, each container used during the process was poured through the 500-µm mesh sieve and washed to remove as much of the settled detrital material and sediment as possible. Any remaining material along with macroinvertebrates was then placed into a Whirl-Pack bag and again preserved in 75% ethanol, where it could be stored until processing at a later date.

Plant Processing

Once initial sorting was completed, plant samples were removed from the freezer and gently thawed using a gentle flow of tap water as to not damage fragile species such as those found in the *Najas* or *Nitella* genus. The entire plant sample was then sorted to the lowest possible taxonomic level (often species) through the examination of physical characteristics using keys of Borman et al. (1997). Species analyzed for this project include all submersed species, as well as those emergent and floating-leaved species that may have been collected during the sweep. Once sorted, each plant species was placed into labeled aluminum weighing boats and dried at 60°C for 72 hours before recording dry mass (g).

Macroinvertebrate Processing

Macroinvertebrate samples were evenly spread across a gridded, shallow, white sorting tray (35.5 x 20 cm). Grid lines resulted in 28, 25-cm^2 subsample quadrats. A random subsample was retrieved from the tray, placed in a grided, clear petri dish (9.2 x 9.2 cm), and viewed under a dissecting scope (Olympus SZX7). All macroinvertebrates were removed and counted, and the processes was repeated until at least 150 specimens were obtained. Once a count of 150 was reached, any remaining macroinvertebrates found in a subsample were counted toward the total. The number of individuals per sample was extrapolated by 28 to obtain an estimated total of macroinvertebrates present. These subsamples were then labeled and placed in small glass shell vials containing 75% ethanol until they could be taxonomically identified at a later date.

Once all 50 samples had at least 150 macroinvertebrates selected via subsampling, specimens were then identified to the Family level (with the exception of *Hydrachnida* and *Oligochaeta*) based on keys from Peckarsky et al. (1990). Identified specimens were then returned to glass shell vials filled with 75% ethanol and labeled with site / sample information for long term storage.

Bulbil Collection & Sorting

Along with vegetation and macroinvertebrate samples collected for this project, bulbil samples were also collected at each sampling location. This collection took place over a six-day period from December 28, 2021 – January 2, 2022, at 10 random sites within the same 150-m transect used for plant and macroinvertebrate collection. Sample sites were reached via paddleboard and thin layers of ice were broken where necessary. Samples were collected by inserting a KB corer (2.5 cm diameter x 50 cm) as deep into the sediment as possible and then placing the retrieved sample into a 600-µm sieve to reduce the sediment load. The remaining sample was then placed into a zip-lock bag, returned to the lab within 24 hours, and refrigerated until they could be processed (generally within 72 hours).

In the lab, bulbil samples were vigorously rinsed through a 500-µm mesh sieve to remove any remaining sediment. Samples were then placed in a shallow tray and picked without magnification to remove the larger bulbils. The remaining material from each sample was then transferred to clear plastic, square, grided petri dish (9.2 x 9.2 cm) and viewed under magnification to remove remaining bulbils. Picked bulbils were then counted and placed in glass shell vials containing labels and 75% ethanol to facilitate long-term storage. The species produces cream-colored stellate rhizoidal bulbils and green nodal bulbils (Sleith et al. 2015, Larkin et al. 2018). Both bulbil types were counted.

Statistical Analysis

Macrophyte Communities

Total macrophyte mass per location and Stary Stonewort mass per location were compared using an analysis of variance (ANOVA), on log-transformed data to meet assumption of normality and homogeneity of variances. Starry Stonewort mass was assessed for its relationship to macrophyte species richness and biomass within each location using correlation analysis. Richness refers to the total count of unique species per sample. Results of correlation analysis were visualized using scatterplots.

Macroinvertebrate Communities

Macroinvertebrate counts were first converted to number per gram of macrophyte dry mass for each sample. Abundance (#/g) and richness estimates were compared among locations using ANOVA. Starry Stonewort mass as a predictor of macroinvertebrate abundance (#/ g plant tissue) and richness was investigated using regression analysis. Functional feeding group (FFG) counts were compared among locations using a log-linear test of independence (G-test), with categories grouped together if the count represented less than 5% of individuals in the sample. Starry Stonewort mass was assessed for its relationship to each FFG category using correlation analysis. Macroinvertebrate and macrophyte community composition was investigated by using principal component analysis (PCA) in order to visualize similarity or lack thereof across locations. Components investigated included macroinvertebrate and plant richness, macroinvertebrate abundance, non-stonewort plant biomass, Starry Stonewort biomass, and percent Starry Stonewort biomass in the sample.

Bulbil Density

Total bulbil density (#/m^2) among sites was compared using ANOVA. Counts for nodal and rhizoidal bulbils within each site were compared using a series of paired t-tests.

Data Analysis

Regression, correlation, and ANOVA methodologies were processed in IBM SPSS Statistics (Ver. 28.0.0.0), while PCA was performed in R-studio Desktop (version 2022.02.2+485) using the FactoMineR (Husson et al. 2008) and Factoextra (Kassambara and Mundt 2020) packages. For ANOVA, Shapiro-Wilk was used to test the normality of the data, and Levene's test was used to test for homogeneity of variance across the data. A log-transformation was used to meet assumptions. Multiple comparisons were made by using the Tukey post-hoc test.

Results

Starry Stonewort & Macrophyte Communities

A total of 36 macrophyte species were identified during this project, ranging from 16 species (Keuka Lake outlet) to 26 species (Burnt Ship Creek), with communities from Cayuga Lake, Cazenovia Lake, and Braddock Bay falling between these two values (Table 1). Besides *N. obtusa*, *Ceratophyllum demersum* and *Elodea canadensis* were the two most commonly encountered species, occurring in 36 of the 50 sample plots. *Myriophyllum alterniflorum*, *Nelumbo lutea*, and *Sagittaria latifolia* were the least commonly occurring species, each found in only 1 sample plot (Table 1).

There was a significant difference in total macrophyte mass among the sampled locations ($F_{(4,45)} = 8.06$, $P < 0.001$). Braddock Bay differed from all the other sites ($P < 0.05$) except for

Burnt Ship Creek (Fig. 3; Table 1). The remaining sites were not significantly different from each other. There was a significant difference ($F_{(4,45)} = 5.64$, $P < 0.001$) in total Starry Stonewort mass among the sampled locations (Fig. 4). A post-hoc Tukey test revealed that Braddock Bay was significantly different from Burnt Ship Creek ($P = 0.025$). There was a significant difference in total macrophyte richness among the sampled locations ($F_{(4,45)} = 9.21$, $p < 0.001$; Fig. 5). A post-hoc Tukey test revealed that Burnt Ship Creek was significantly different from Cayuga Lake ($P = 0.006$), Cazenovia Lake ($P = 0.012$), and Keuka Lake ($P < 0.001$). Also, Braddock Bay differed from Keuka Lake ($P = 0.011$).

Starry Stonewort dry mass (g) was negatively related to other plant dry mass (g) at Burnt Ship Creek ($r = -0.660$, $n = 10$, $P = 0.038$) and the Keuka Lake outlet ($r = -0.644$, $n = 10$, $P = 0.044$; Fig. 6). Starry Stonewort dry mass was not a correlated with other plant dry mass at the other three locations. Starry Stonewort dry mass was not a correlated with plant richness at any location ($P > 0.05$) (Fig. 7).

Macroinvertebrate Data

A total of 44 macroinvertebrate families were identified during this project, ranging from 19 (Cayuga Lake) to 29 (Keuka Lake outlet) families per location, with Braddock Bay, Burnt Ship Creek and Cazenovia Lake falling between this range (Table 3). Braddock Bay had the least abundant estimated population at (35 ± 7/g plant tissue), whereas the Keuka Lake outlet contained the largest number of estimated individuals (157 ± 23/g plant mass), with Burnt Ship Creek, Cayuga Lake, and the Cazenovia Lake falling between these estimates (Table 3).

There was a significant difference in estimated macroinvertebrate abundance (# / g plant tissue) among the sampled locations ($F_{(4,45)} = 10.44$, $P < 0.001$), with Braddock Bay different from all other locations (Fig. 8). There was no significant difference in macroinvertebrate family richness among all locations ($F_{(4,45)} = 1.78$, $P = 0.150$; Fig. 9).

Macroinvertebrate abundance (#/g plant tissue) was negatively associated with total plant dry mass at all five locations (all $P < 0.05$), but plant dry mass explained only ~20% of the variability in macroinvertebrate abundance, on average (Fig. 10). Starry Stonewort dry mass was only a predictor of estimated macroinvertebrate abundance (# / g plant tissue) at Cayuga Lake ($R^2 = 0.453$, $F_{(1, 8)} = 6.636$, $P = 0.033$), where abundance decreased with increasing stonewort mass (Fig. 11). Other plant dry mass (minus stonewort) was not a significant predictor of estimated macroinvertebrate abundance (# / g plant tissue) at any location (Fig. 12).

Starry Stonewort dry mass was a significant predictor of macroinvertebrate family richness at Braddock Bay ($R^2 = 0.701$, $F_{(1, 8)} = 18.793$, $P = 0.002$) and Cayuga Lake ($R^2 = 0.503$, $F_{(1, 8)} = 8.099$, $P = 0.022$), trending negatively across all locations (Fig. 13).

Other plant richness was only a significant predictor of estimated macroinvertebrate abundance (# / g plant tissue) within Burnt Ship Creek ($R^2 = 0.421$, $F_{(1, 8)} = 5.805$, $P = 0.043$), trending positively (Fig. 14). Similarly, other plant richness was a significant predictor of macroinvertebrate family richness at Burnt Ship Creek ($R^2 = 0.619$, $F_{(1, 8)} = 12.998$, $P = 0.007$), however, a positive trend was displayed at every location except for Braddock Bay (Fig. 15).

Overall, the FFG representation differed among the five locations ($G_{adj} = 46.72$, df = 12, $P < 0.001$; Fig. 16). Gatherer-collector (GC), scraper-grazer (SC), and predator (PR) functional feeding groups (FFG) generally were more abundant in samples across all locations and stonewort gradients than members of the filterer-collector (FC), shredder (SH), and piercer (PI) groups. At Braddock Bay, Starry Stonewort dry mass was a significant predictor of the percent of predator macroinvertebrates within a plot ($R^2 = 0.541$, $F_{(1, 8)} = 9.417$, $P = 0.015$), trending negatively (Fig. 17). Starry Stonewort did not predict any other significant changes in functional feeding group representation at Braddock Bay or any of the other locations. However, Cayuga Lake, where an infestation of zebra mussels (*Dreissena polymorpha*) elevated the percentage of filterer-collectors in the system, Starry Stonewort dry mass was a significant predictor *Dreissena* abundance ($R^2 = 0.638$, $F_{(1, 8)} = 14.090$, $P = 0.006$), trending positively (Fig. 18).

A principal component analysis revealed that there was significant overlap between all of the locations, with Braddock Bay expressing the largest within-system variability; the first two principal components accounting for 65.6% of the variability (Fig. 19). These two components likely represented percent Starry Stonewort on the first axis and Starry Stonewort mass on the second axis (Fig. 20).

Bulbil Data

The average number of bulbils per m^2, including both stellate rhizoidal type and round nodal type, did not differ among sites ($F_{(4,45)} = 0.77$, $P = 0.553$; Table 2; Figure 21), and Starry Stonewort dry mass did not correlate with bulbil density / m^2 ($r = 0.259$, $n = 5$, $P = 0.380$) (Fig. 22). There was a significant difference in the mean numbers of rhizoidal and nodal bulbils at three of the five locations ($P < 0.05$) with nodal bulbils being more prevalent than rhizoidal bulbils at every site except for Burnt Ship Creek (Table 2).

Discussion

Starry Stonewort was abundant in each of the study locations, but there was considerable variability in native SAV and macroinvertebrate community responses among the five sample locations. Total SAV mass differed among locations with Braddock Bay having about twice the total plant mass relative to the other sites (Fig. 3). Similarly, Braddock Bay had significantly more mass of stonewort than the other sites (Fig. 4). However, stonewort mass accounted for about the same percent of the total plant mass among the sites (55-60%), except for Burnt Ship Creek (~25%). As predicted, when Starry Stonewort mass increased, other SAV mass was reduced (Fig. 6). The strong relationship between stonewort mass and other SAV mass did not transfer into effects on other SAV richness. There was a significant difference in SAV richness among the sites (Fig. 5), but SAV richness did not correlate with stonewort mass.

The loss of native SAV mass as stonewort mass increases follows the pattern of macrophyte displacement displayed in other Great Lakes locations (e.g., Brainard and Schulz 2017, Harrow-Lyle 2021, Ginn et al. 2021). Although data did not show a relationship between Starry Stonewort mass and plant richness, I believe that is a result of edge sampling. I collected many samples along the edge of seemingly monotypic stands of Starry Stonewort to obtain samples with native SAV representation. This may have affected stonewort mass-SAV richness relationships.

Some commonly occurring macrophyte species identified in this study (e.g., *Elodea*, *Myriophyllum*, *Najas*, *Potamogeton*, *Vallisneria*, and *Ceratophyllum*) are susceptible to dominance by Starry Stonewort (Scholesser et al 1986, Nichols et al. 1988, Hackett et al. 2017). Unfortunately, Starry Stonewort has even been shown to outcompete other invaders such as *M. spicatum* (Ginn et al. 2021). In the most extreme cases, such as those documented in Tamarack Lake, MI, Starry Stonewort may seasonally extirpate most other submerged plant species (Aquest 2017). In addition to simply occupying all the available space, Starry Stonewort can alter water and sediment conditions to better fit its needs at the expense of other rooted macrophytes (Harrow-Lyle and Kirkwood 2020 and Harrow-Lyle 2021). High propagule pressure via bulbil production also contributes to the success of Starry Stonewort in invaded systems (Brainard 2018). Bulbil densities in this study were extremely high compared to those at other sites such as Lake Koronis, where over three years the average density (#/m^2) was found to be ~2,500 (McComas et al. 2020). Although, the reported number from Lake Koronis may have been higher if sampled later in the season, similar to this project. The large difference in the number of bulbil's being reported at other sites is likely due to only counting the cream-colored stellate bulbils. In this study, there was no difference in total bulbil density among sites, yet there was a large difference in the abundance of the two bulbil types. On average, nodal bulbils were roughly three times more common than rhizoidal bulbils at four of the locations, and the exclusion of these structures could lead to mismanagement of infestations. Surprisingly, total bulbil density overwintering in the substrate did not correlated with the later summer biomass, suggesting bulbil density may not be a good predictor of future infestation levels.

Chemical treatment of Starry Stonewort plots and the associated re-growth of the species led to a substantial increase in bulbil production (Glisson et al. 2018, Glisson et al. 2022). Whereas the mechanical removal treatment of Starry Stonewort has not been associated with increased bulbil production, incidental transportation of bulbils to other portions of a waterway is a concern; in Cayuga Lake a substantial growth of the species was found in the area adjacent to the lake harvester docking site (Glisson et al. 2018). Although individual bulbils have relatively little tolerance to a variety of desiccation methods, these structures have much higher resiliency when under slightly protected environments (Glisson et al. 2020, Gottschalk and Karol 2020, Glisson et al. 2022). The threat from bulbils in any ecosystem is extremely high and these structures will likely continue to be the primary source of introductions and population longevity in the future.

Starry Stonewort may have direct or indirect positive and negative consequences on the macroinvertebrate community by altering the richness and abundance of plant communities and the assemblages associated with them. Total abundance of invertebrates was different among the five sites (Fig. 8) with Braddock Bay having significantly fewer invertebrates per gram of plant tissue than the other sites. Braddock Bay also had the greatest overall plant mass, as well as the highest percent Starry Stonewort. Total plant mass correlated negatively with macroinvertebrate numbers; as SAV communities became more dense (higher biomass), invertebrate abundance declined. Surprisingly, this pattern was not directly mimicked when looking at Starry Stonewort mass only; as stonewort mass increased, no consistent significant impact was displayed in macroinvertebrate abundance. Total invertebrate Family richness did not differ among the sample locations (Fig. 9), even though total SAV and stonewort mass differed among sites. Collectively, these plant/invertebrate relationships suggest macroinvertebrate reliance on specific types or abundances of SAV are not particularly strong.

As the functional feeding group observations show, whereas there may not always be significant impact on overall richness in a community there may be a shift in the types of groups that comprise an assemblage. For example, rapidly reproduce taxa (such as gastropods) may respond to SAV changes more easily than taxa with relatively slow/seasonal life cycles like many predatory taxa (e.g., Odonata). While changes in proportional amphipod and isopod abundance was insignificant, perhaps sampling later in the fall would provide a significant relationship such as that noted by Hargeby (1990), where the temporal limitation in the species led to a decrease in these types of macroinvertebrates. Along with this, the increased presence of *Dreissena* associated with Starry Stonewort may only serve to exacerbate the spread and effects of these invasive mussels across the basin and beyond; along with the reported possibility of

Starry Stonewort monocultures supporting *Microcystis* blooms (Harrow-Lyle and Kirkwood 2020).

Conclusions

The impact of Starry Stonewort on existing macrophyte community abundance was clear and consistent with the findings of others across the basin. The impacts on macroinvertebrate communities was equivocal, and this may be attributed to a community shift where gastropods and chironomids dominated the communities. Although identifying macroinvertebrate specimens to a lower taxonomic level may have increased the occurrence of significant differences across a gradient of Starry Stonewort dominance, I feel that Genus level findings may have had little impact on the outcome based on preliminary findings. Future studies should compare monotypic stands of Starry Stonewort to mixed patches of vegetation where the species is absent as opposed to collecting samples with a gradient of Starry Stonewort percentage. Although co-occurring species were noted earlier in this paper, most macrophyte species were not observed directly intermingling with Starry Stonewort, but along the outer edges of infestations.

Another concerning trait observed in this species, but not studied in this project, is its highly variable habitat permanence. As noted in Hargeby (1990), certain macroinvertebrates may avoid Starry Stonewort due to its seasonal dieback. Similarly, heavy fall rains and/or fall storms that generate a lot of currents tend to wash away whole stonewort stands. As observed in Burnt Ship Creek, large swaths of the substrate were covered with 100% Starry Stonewort that was then rapidly swept away by a large spate event late in the growing season, leaving bare sediment in its place and a lack of habitat complexity for macroinvertebrates. Future studies should also take greater note of the green nodal bulbils produced by this species, both in terms of their abundance and resilience compared to rhizoidal bulbils and their role in the life history of the species.

The species direct and indirect impacts across the lower aquatic food web will likely exacerbate ecological issues already being felt across the Great Lakes basin and its large growth form will likely continue to impede recreational activities. With Starry Stonewort predicted to spread across all 50 states, in part due to climate change, the threat of this species expands far beyond the Great Lakes basin (MDARD 2015, Harrow-Lyle and Kirkwood 2020). Continuing to gain and verify basic ecological knowledge about this unique invasive macroalgae will serve to prepare communities and environmental managers for changes that may occur in their wetland ecosystems.

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Tables

Table 1. List of plant species, total dry mass (g), and percent dry mass (g) across all five locations sampled from August-September, 2021, using a modified D-net technique.

	Braddock Bay		**Burnt Ship Creek**		**Cayuga Lake**		**Cazenovia Lake**		**Keuka Lake Outlet**	
Taxa	Dry Mass	%	Dry Mass	%	Dry Mass	%	Dry Mass	%	Dry Mass	%
Brasenia schreberi	0.169	0.03	0.000	0.00	0.000	0.00	0.000	0.00	0.277	0.15
Butomus umbellatus	0.000	0.00	1.109	0.39	0.000	0.00	0.000	0.00	0.000	0.00
Ceratophyllum demersum	104.042	21.50	3.263	1.14	0.202	0.10	19.598	8.90	29.247	16.12
Chara sp.	0.000	0.00	79.041	27.51	0.004	0.00	12.977	5.90	0.000	0.00
Elatine minima	0.033	0.01	0.000	0.00	0.233	0.12	0.288	0.13	0.000	0.00
Elodea canadensis	10.771	2.23	9.530	3.32	5.909	3.02	12.757	5.80	4.384	2.42
Elodea nuttallii	1.023	0.21	1.921	0.67	0.050	0.03	1.060	0.48	0.764	0.42
Gratiola aurea	0.000	0.00	0.000	0.00	0.122	0.06	1.244	0.57	0.000	0.00
Myriophyllum alterniflorum	0.223	0.05	0.000	0.00	0.000	0.00	0.000	0.00	0.000	0.00
Myriophyllum heterophyllum	1.332	0.28	0.206	0.07	0.000	0.00	0.000	0.00	0.000	0.00
Myriophyllum sibiricum	16.772	3.47	2.503	0.87	27.310	13.97	0.130	0.06	3.754	2.07

Myriophyllum spicatum	15.994	3.30	6.274	2.18	1.969	1.01	0.000	0.00	9.497	5.23
N. flexilis / canadensis	0.770	0.16	5.928	2.06	1.470	0.75	0.923	0.42	0.000	0.00
Najas gracilima	0.106	0.02	21.441	7.46	0.186	0.10	0.353	0.16	0.026	0.01
Najas minor	0.000	0.00	18.299	6.37	0.224	0.11	0.080	0.04	0.000	0.00
Nelumbo lutea	0.000	0.00	0.000	0.00	0.000	0.00	0.264	0.12	0.000	0.00
Nitella sp.	0.000	0.00	1.079	0.38	0.000	0.00	0.000	0.00	0.000	0.00
Nitellopsis obtusa	309.343	63.91	78.406	27.29	118.772	60.77	133.243	60.53	118.610	65.36
Nuphar variegata	0.000	0.00	15.786	5.49	0.000	0.00	0.000	0.00	3.627	2.00
Nymphaea odorata	1.370	0.28	6.349	2.21	0.345	0.18	0.000	0.00	5.309	2.93
Potamogeton confervoides	0.102	0.02	0.212	0.07	0.000	0.00	0.000	0.00	0.166	0.09
Potamogeton crispus	0.000	0.00	0.000	0.00	0.000	0.00	1.292	0.59	0.000	0.00
Potamogeton diversifolius	0.496	0.10	0.000	0.00	0.000	0.00	0.000	0.00	0.018	0.01
potamogeton foliosus	3.523	0.73	0.413	0.14	0.000	0.00	0.000	0.00	0.000	0.00
Potamogeton natans	0.000	0.00	1.061	0.37	0.000	0.00	0.000	0.00	0.000	0.00
Potamogeton nodosus	0.000	0.00	5.593	1.95	0.000	0.00	0.000	0.00	5.222	2.88
Potamogeton pectinatus	1.612	0.33	1.830	0.64	1.402	0.72	2.405	1.09	0.000	0.00

Potamogeton praelongus	0.000	0.00	12.461	4.34	0.000	0.00	0.514	0.23	0.000	0.00
Potamogeton pusillus	0.000	0.00	1.544	0.54	0.000	0.00	0.000	0.00	0.014	0.01
Potamogeton richardsonii	0.000	0.00	0.000	0.00	0.000	0.00	2.590	1.18	0.000	0.00
Potamogeton zosteriformis	7.921	1.64	0.000	0.00	1.130	0.58	24.000	10.90	0.415	0.23
Sagittaria latifolia	0.000	0.00	0.674	0.23	0.000	0.00	0.000	0.00	0.000	0.00
Scirpus subterminalis	0.000	0.00	0.062	0.02	0.133	0.07	0.000	0.00	0.000	0.00
Ultricularia vulgaris	0.000	0.00	11.044	3.84	0.000	0.00	2.528	1.15	0.133	0.07
Vallisneria americana	8.021	1.66	1.265	0.44	18.473	9.45	2.201	1.00	0.000	0.00
Zosterella dubia	0.396	0.08	0.000	0.00	17.514	8.96	1.669	0.76	0.000	0.00
Total Dry Mass	484.019		287.294		195.448		220.116		181.463	
Mass / Sweep (se)	48.528 (7.123)		28.729 (2.06)		19.549 (2.885)		22.012 (4.169)		18.146 (2.485)	
Richness	20		26		18		20		16	

Table 2. List of mean bulbil densities per m^2, for both nodal and rhizoidal type bulbils. Samples taken from December–January, 2021/2022 using a standard KB corer.

	Braddock Bay		**Burnt Ship Creek**		**Cayuga Lake**		**Cazenovia Lake**		**Keuka Lake Outlet**	
	Rhizoidal	Nodal	Rhizoidal	Nodal	Rhizoidal	Nodal	Rhizoidal	Nodal	Rhizoidal	Nodal
x̄ **(se)**	1271 (452)	6786 (1860)	6575 (4102)	4309 (1179)	2707 (1163)	6354 (1918)	2983 (747)	7182 (2418)	4586 (985)	10608 (2752)
t	-3.660		0.963		-2.677		-1.916		-2.445	
P	**0.005**		0.361		**0.025**		0.088		**0.037**	

Table 3. List of macroinvertebrate Family taxa, including the total counted specimens from 10 replicate sweeps per location (150 individual minimum), estimated abundance per sweep, estimated number of individuals per (g) of plant tissue, and functional feeding group classification based on EPA Bioassessment Protocols manual. Samples gathered from 5 locations using modified D-net sweep techniques between August–September, 2021.

Family:	**Braddock Bay**	**Burnt Ship Creek**	**Cayuga Lake**	**Cazenovia Lake**	**Keuka Lake Outlet**	**FFG**
Arachnida						
Trombidiformes	54	28	19	17	36	PR
Bivalvia						
Corbiculidae	0	0	0	0	1	FC
Dreissenidae	1	0	94	1	0	FC
Sphariidae	0	22	0	21	9	FC
Clitellata						
Glossiphoniidae	11	15	0	8	20	PR
Piscicolidae	1	0	0	0	2	PR

Crustacea						
Asellidae	2	35	0	28	19	GC
Gammaridae	21	20	0	13	1	GC
Talitridae	214	69	12	23	84	GC
Gastropoda						
Ancylidae	0	0	8	0	0	SC
Bithyniidae	0	72	0	0	0	SC
Hydrobiidae	427	19	231	279	155	SC
Lymnaeidae	0	1	4	1	0	SC
Physinae	54	141	30	14	16	SC
Planorbidae	68	496	310	114	108	SC
Valvatidae	40	77	167	102	27	SC
Viviparidae	0	0	0	1	5	SC
Insecta						
Aeshnidae	0	0	0	0	1	PR
Baetidae	0	0	0	0	3	GC
Brachycentridae	0	0	1	0	0	FC
Caenidae	166	3	18	107	150	GC
Ceratopogonidae	10	5	0	3	1	PR
Chironomidae	95	443	396	650	425	GC
Chrysomelidae	4	0	0	2	2	SH
Coenagrionidae	37	8	3	39	178	PR
Corduliidae	0	0	0	1	6	PR
Corixidae	0	149	0	0	0	PR
Ephyridae	2	38	0	0	0	GC
Gomphidae	0	0	0	0	2	PR
Haliplidae	0	46	4	6	66	SH
Hebridae	0	62	0	0	0	PR
Hydrophiliidae	2	1	0	3	7	PR
Hydroptilidae	40	2	105	45	22	PI
Leptoceridae	306	7	286	35	140	GC

Lestidae	0	0	1	1	2	PR
Libellulidae	1	0	0	4	14	PR
Limnichidae	1	0	0	4	0	GC
Mesoveliidae	65	1	0	0	0	PR
Pleidae	15	12	0	0	0	PR
Simuliidae	0	1	15	0	0	FC
Tabanidae	2	0	0	1	0	PR
Veliidae	5	0	0	0	0	PR
Oligochaeta						
Oligochaeta	30	43	30	36	117	GC
Total Count:	1,674	1,816	1,734	1,559	1,619	
x̄ (se) # per sweep	1,565 (221)	4,052 (441)	2,184 (230)	1,532 (331)	2,615 (445)	
# / g plant tissue (se)	35.0 (7.08)	144.8 (17.01)	122.5 (11.4)	76.6 (10.31)	157.3 (22.78)	
Family richness:	27	27	19	28	29	

Figures

Figure 1. Map of Starry Stonewort's reported native and non-native range based on currently available literature. *Note: It's unknown if the species is native to Ireland*.

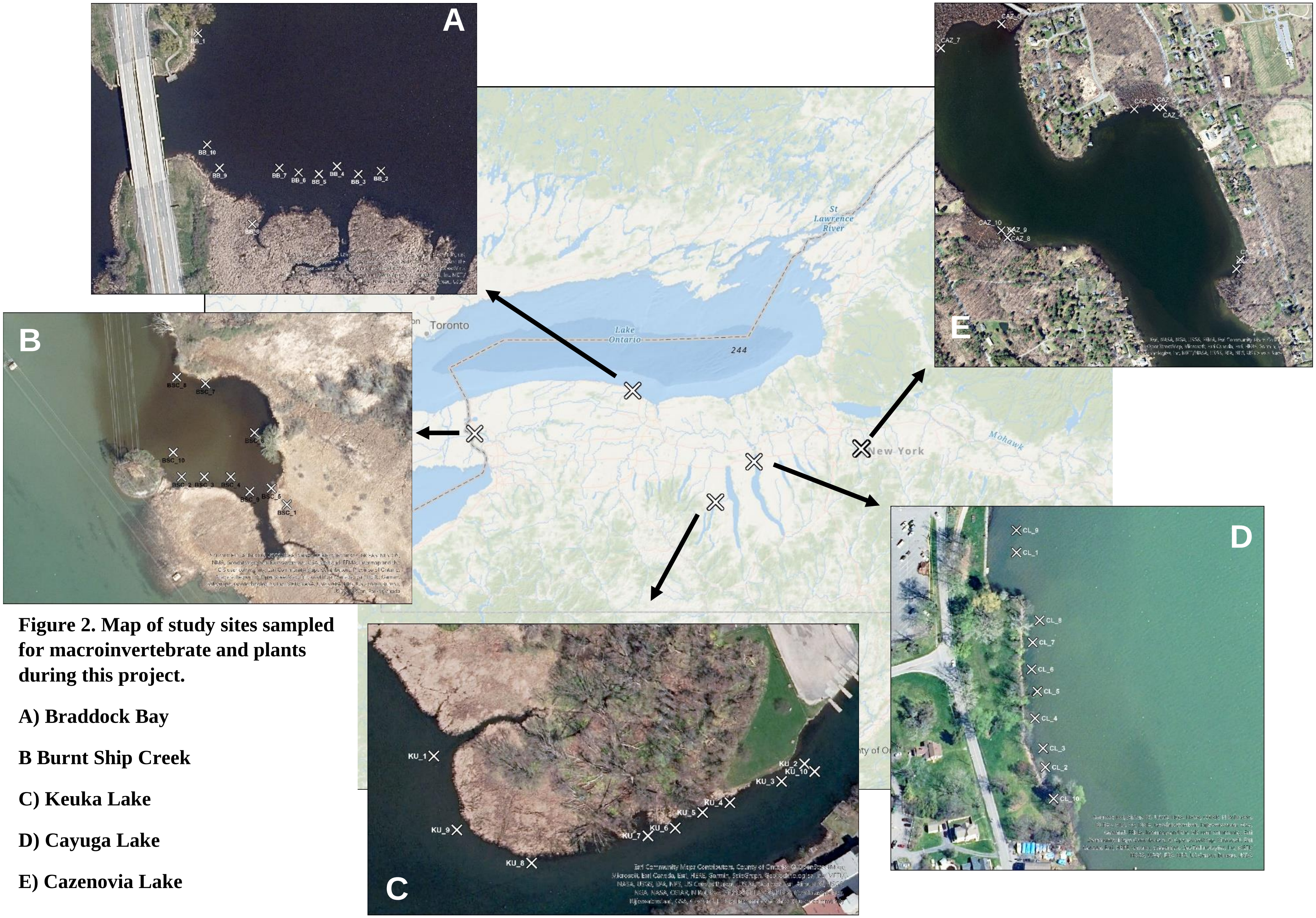


Figure 2. Map of study sites sampled for macroinvertebrate and plants during this project.

A) Braddock Bay

B Burnt Ship Creek

C) Keuka Lake

D) Cayuga Lake

E) Cazenovia Lake

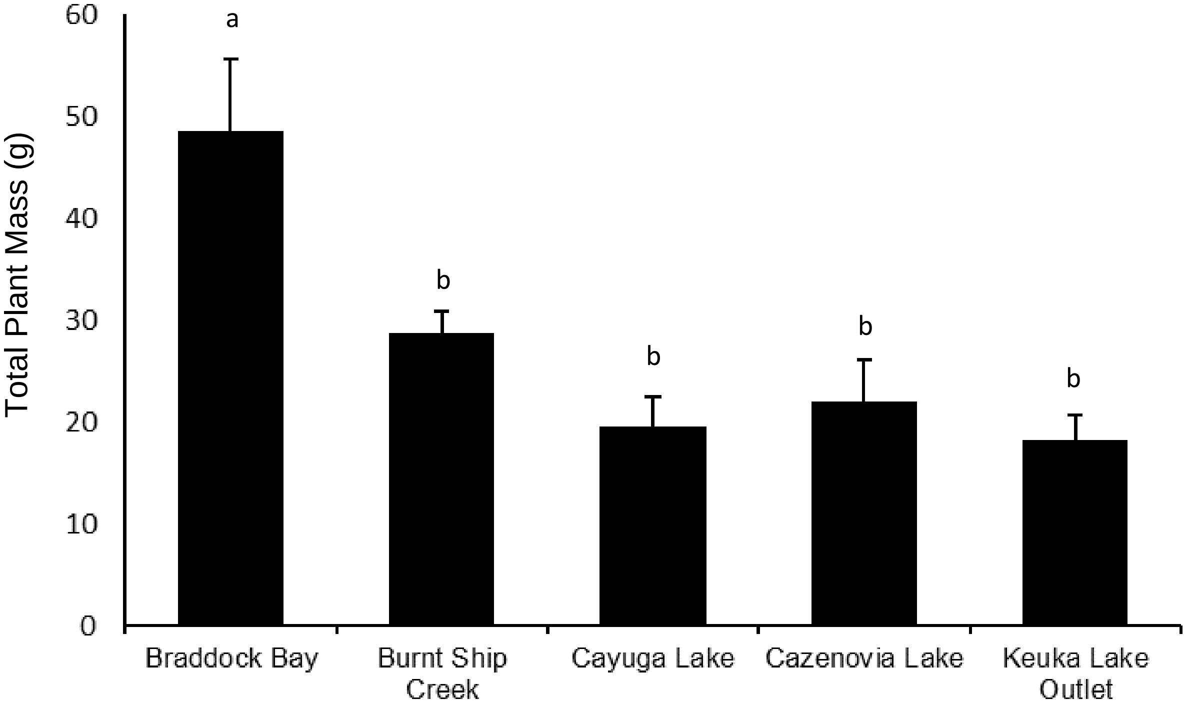


Figure 3. Total macrophyte mass among sampled locations, with error bars representing standard error. Same letter indicates no differences between means based on Tukey post-hoc tests.

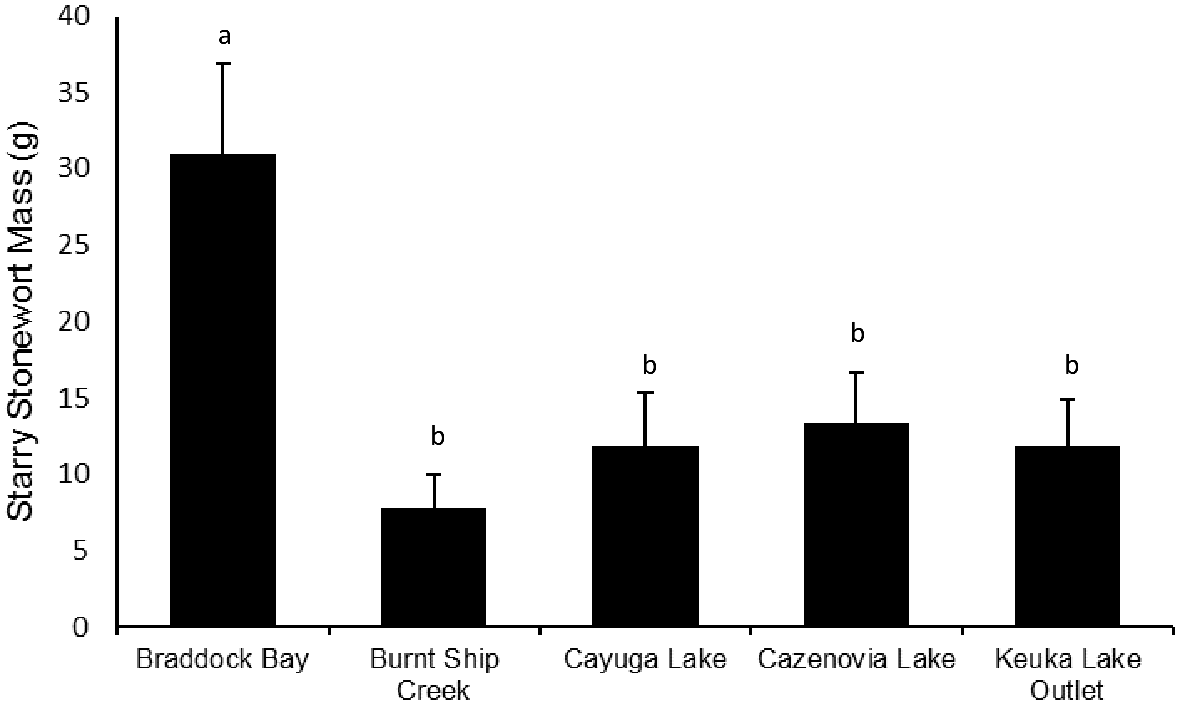


Figure 4. Total Starry Stonewort mass among sampled locations, with error bars representing standard error. Same letter indicates no differences between means based on Tukey post-hoc tests.

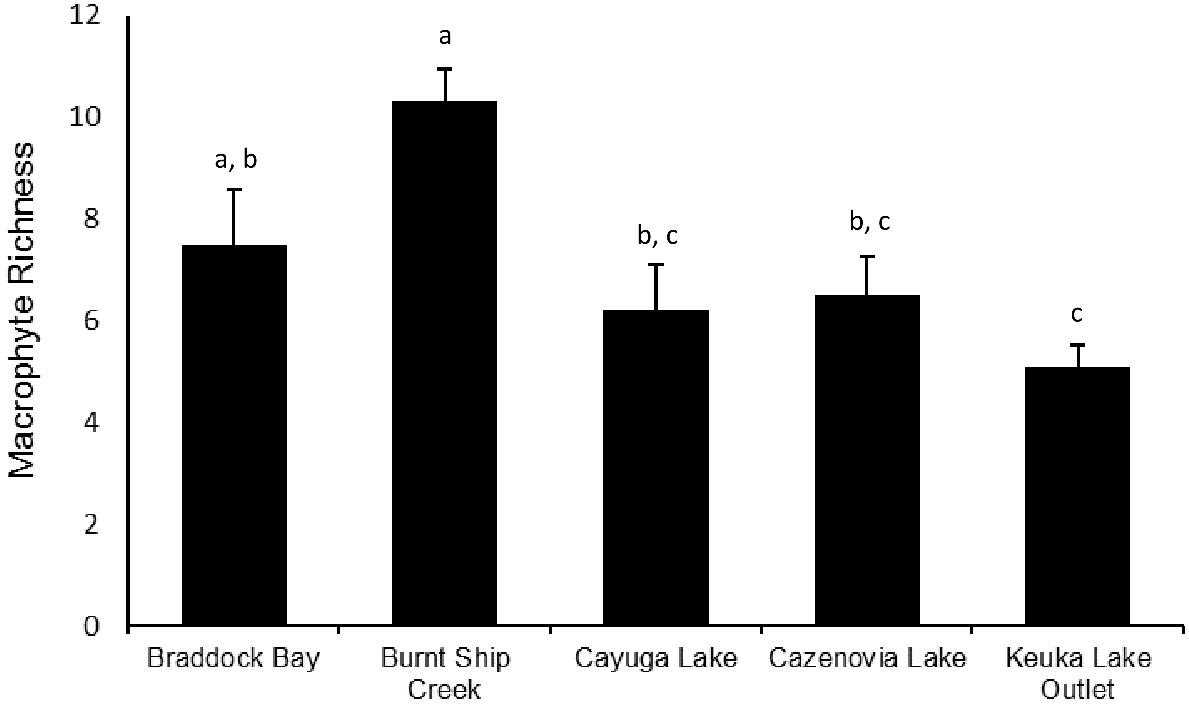


Figure 5. Total macrophyte richness among sampled locations, with error bars representing standard error. Same letter indicates no differences between means based on Tukey post-hoc tests.

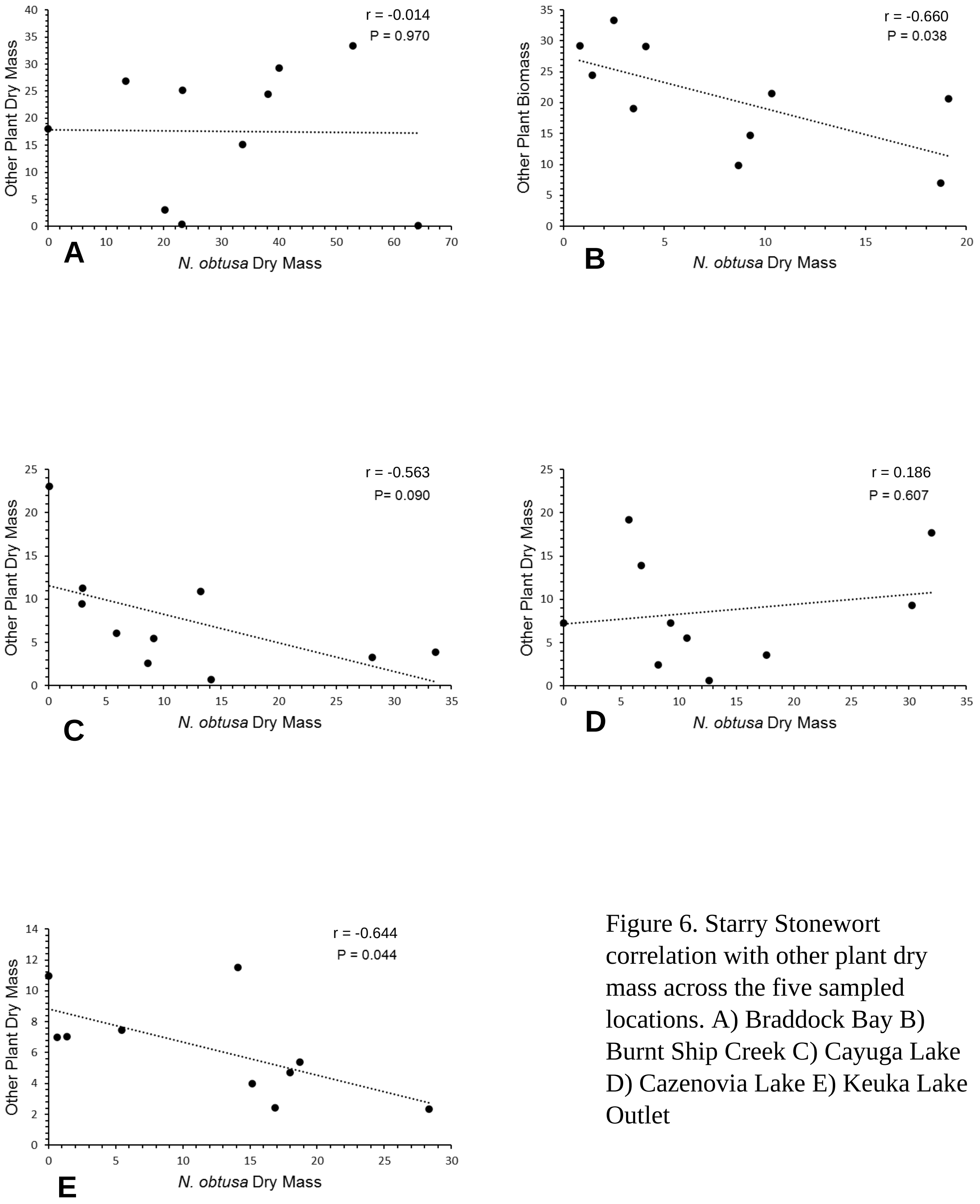


Figure 6. Starry Stonewort correlation with other plant dry mass across the five sampled locations. A) Braddock Bay B) Burnt Ship Creek C) Cayuga Lake D) Cazenovia Lake E) Keuka Lake Outlet

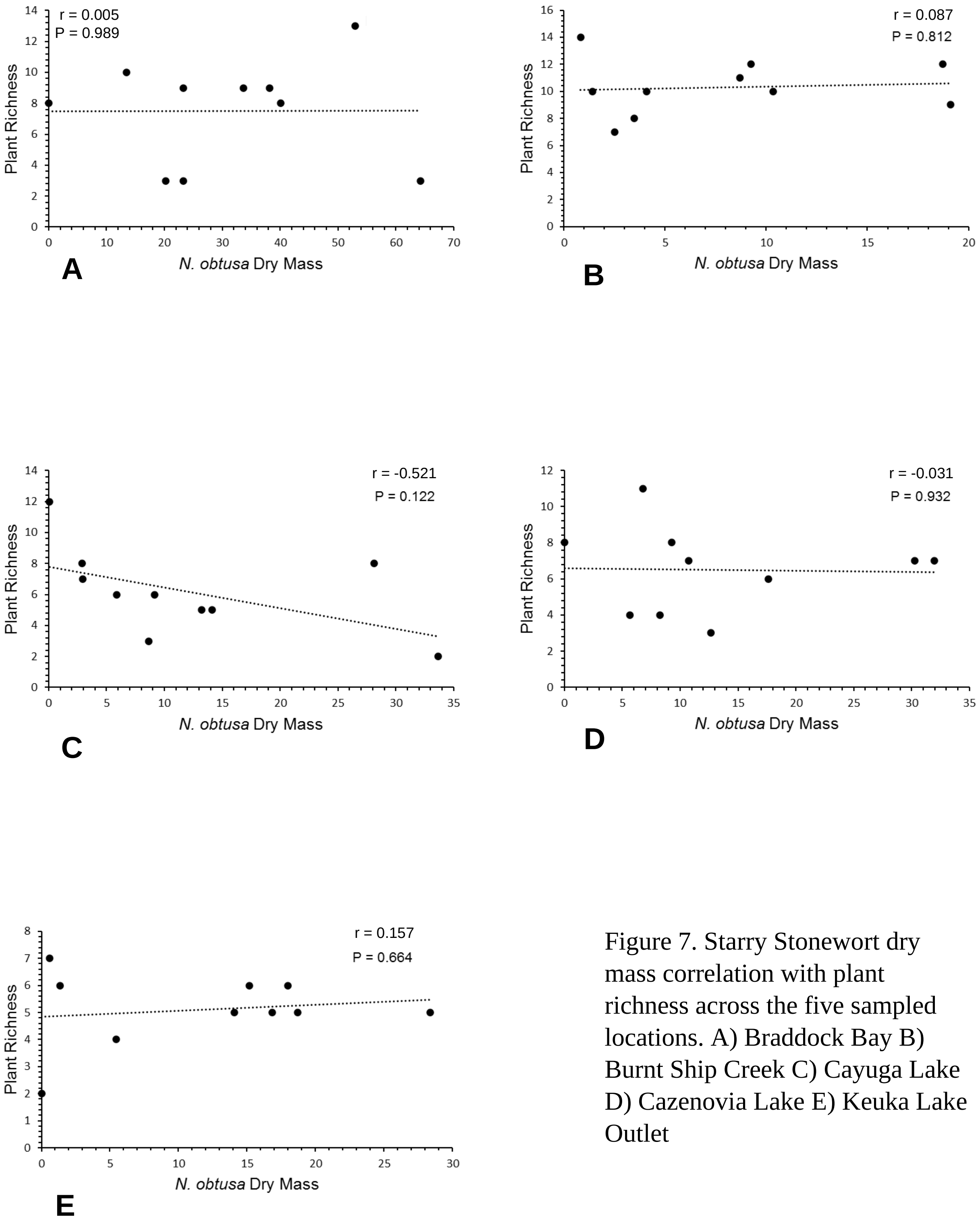


Figure 7. Starry Stonewort dry mass correlation with plant richness across the five sampled locations. A) Braddock Bay B) Burnt Ship Creek C) Cayuga Lake D) Cazenovia Lake E) Keuka Lake Outlet

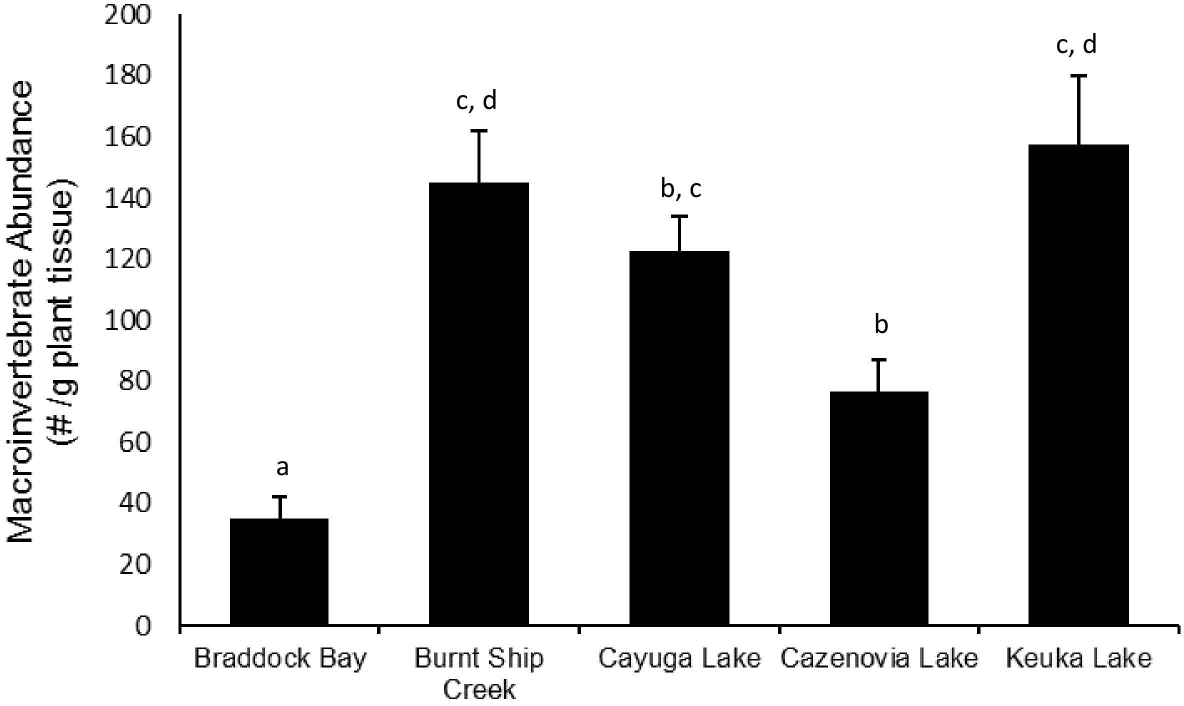


Figure 8. Macroinvertebrate abundance (# / g plant tissue) among sampled locations, with error bars representing standard error. Same letter indicates no differences between means based on Tukey post-hoc tests.

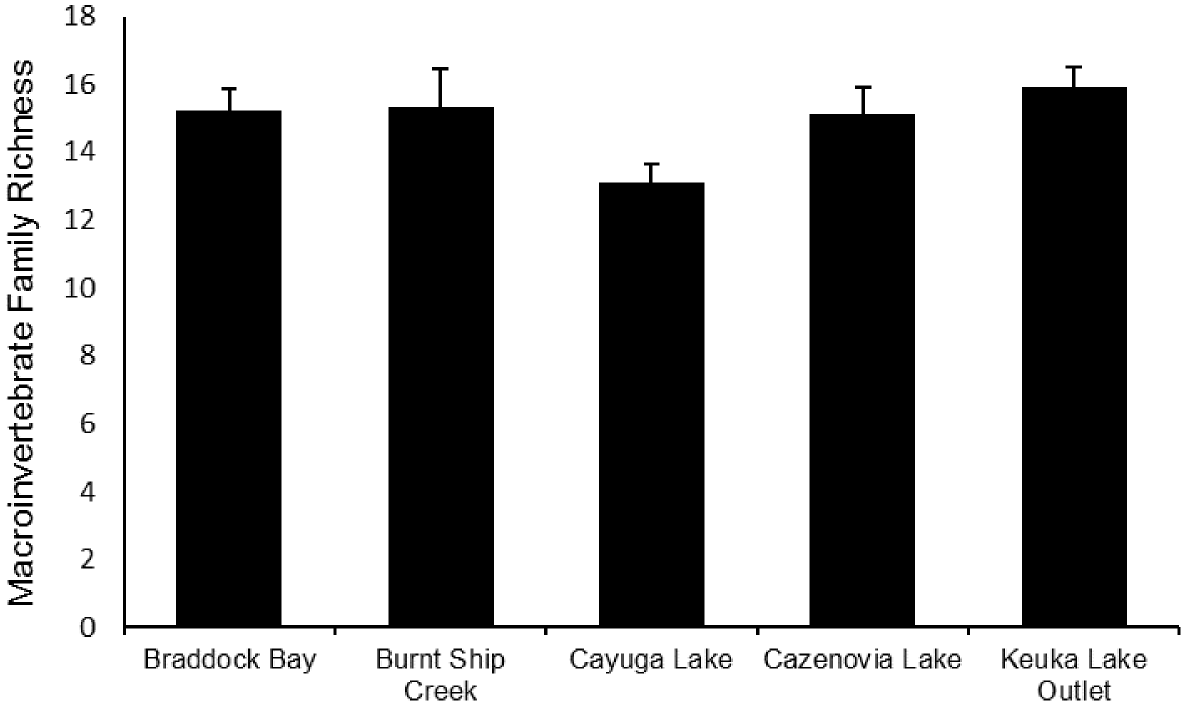
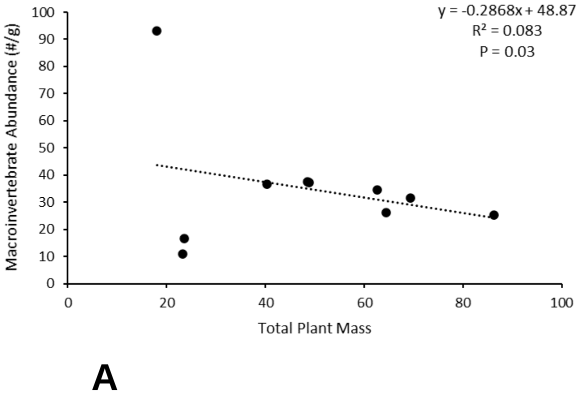
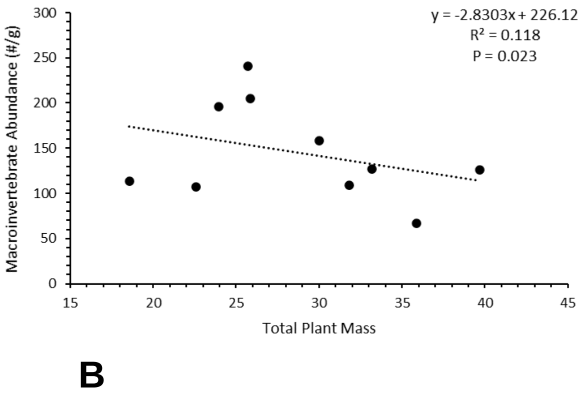
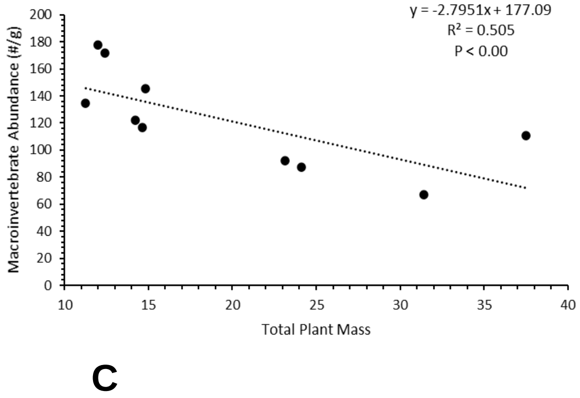
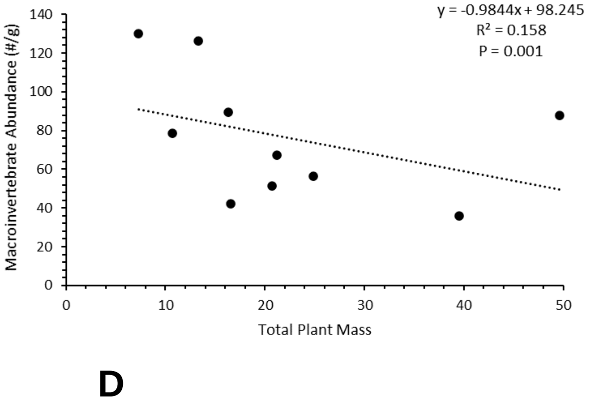


Figure 9. Macroinvertebrate family richness among sampled locations, with error bars representing standard error.









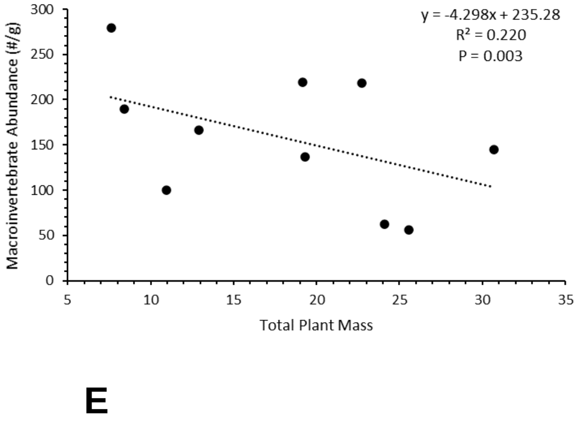


Figure 10. Total plant mass as a predictor of macroinvertebrate abundance (#/g plant tissue) across the five sampled locations. A) Braddock Bay B) Burnt Ship Creek C) Cayuga Lake D) Cazenovia Lake E) Keuka Lake Outlet

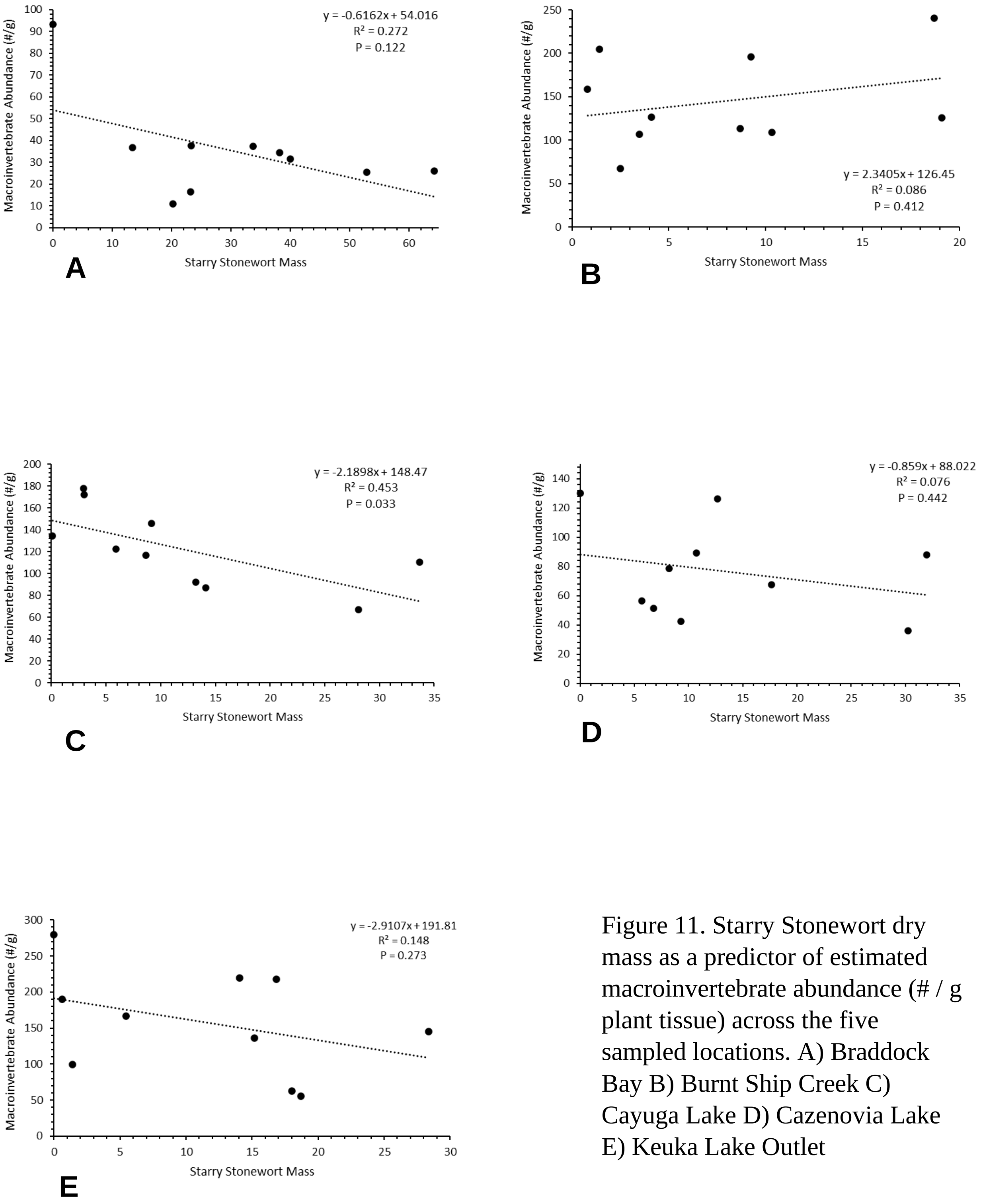
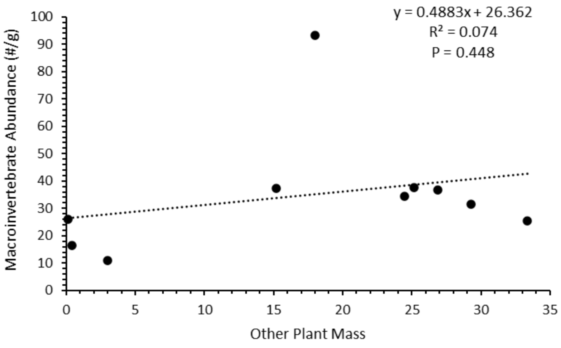
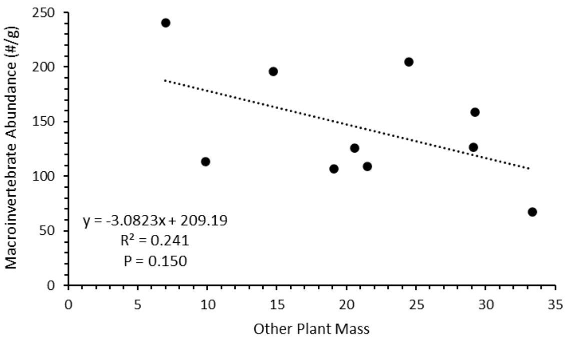


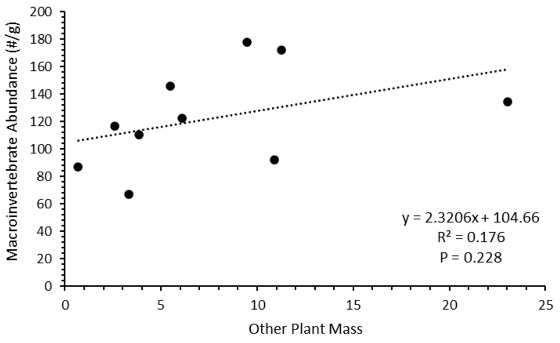
Figure 11. Starry Stonewort dry mass as a predictor of estimated macroinvertebrate abundance (# / g plant tissue) across the five sampled locations. A) Braddock Bay B) Burnt Ship Creek C) Cayuga Lake D) Cazenovia Lake E) Keuka Lake Outlet



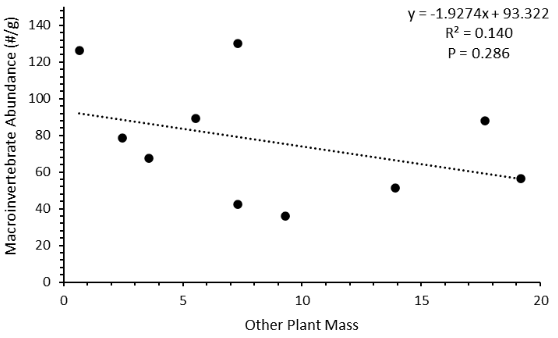
A



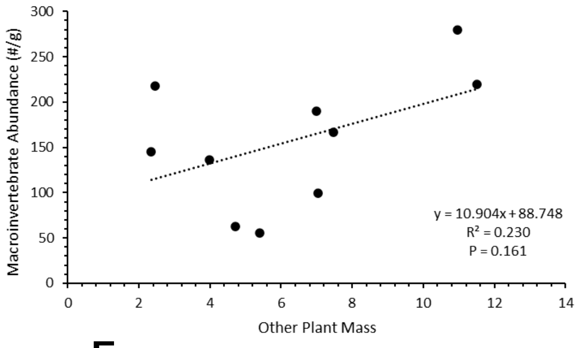
B



C

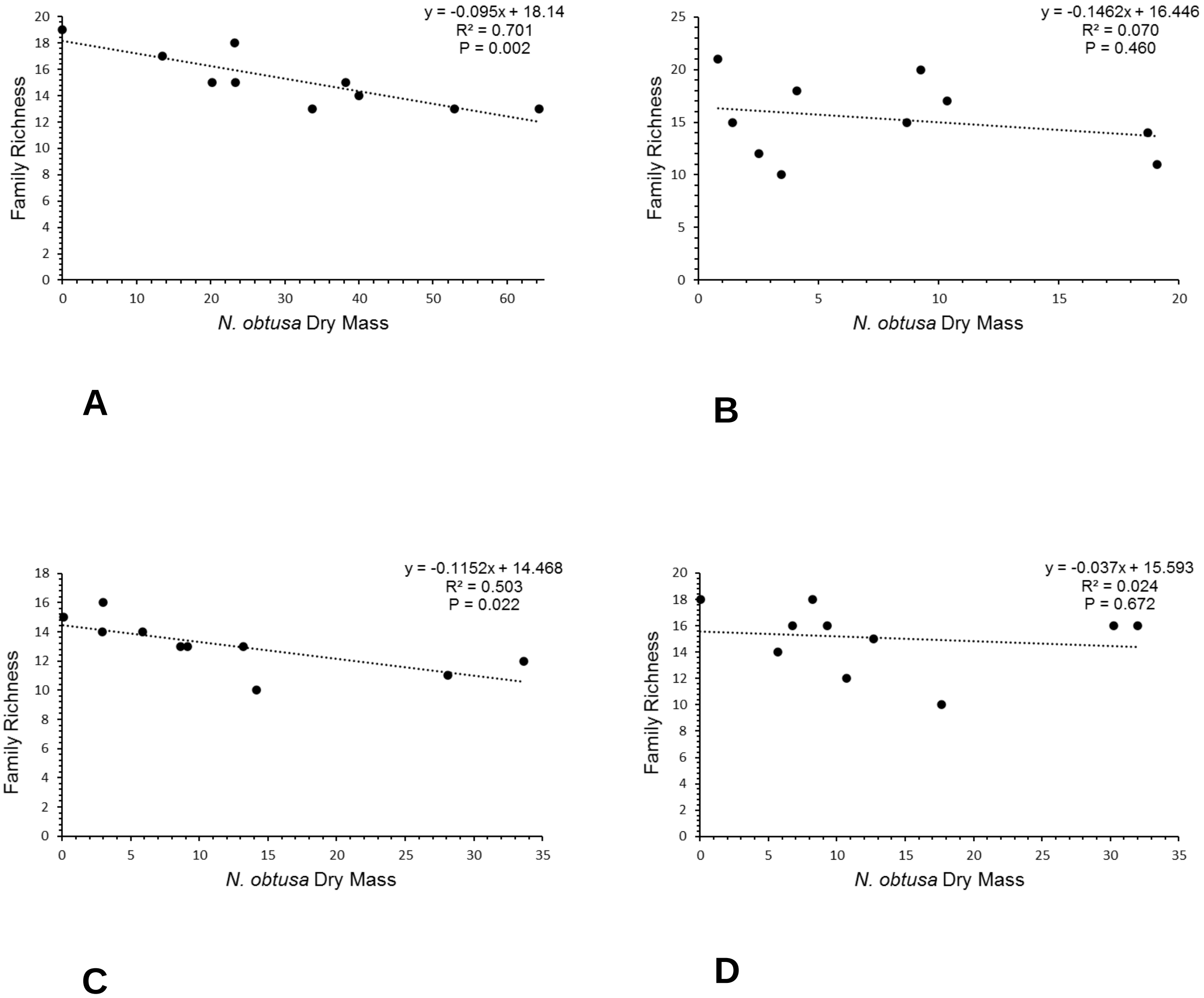


D



E

Figure 12. Other plant dry mass as a predictor of estimated macroinvertebrate abundance (# / g plant tissue) across the five sampled locations. A) Braddock Bay B) Burnt Ship Creek C) Cayuga Lake D) Cazenovia Lake E) Keuka Lake Outlet



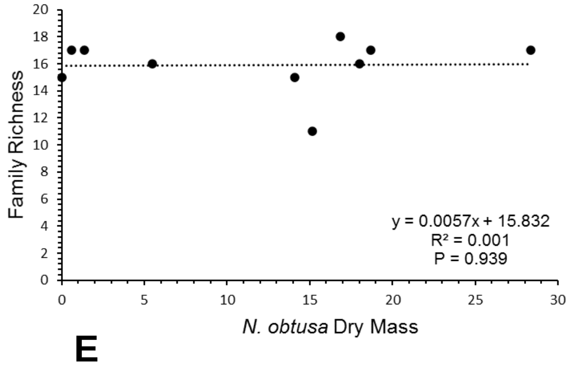
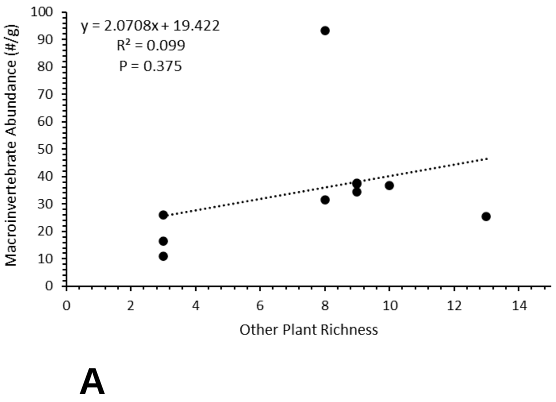
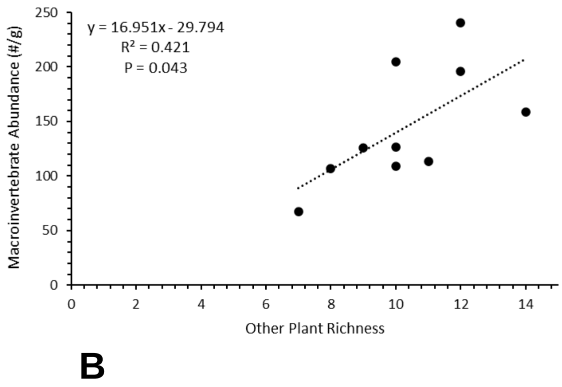
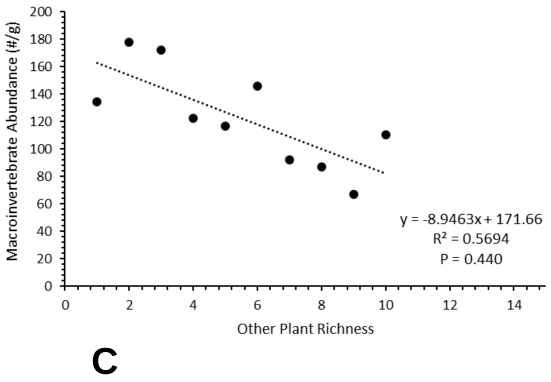
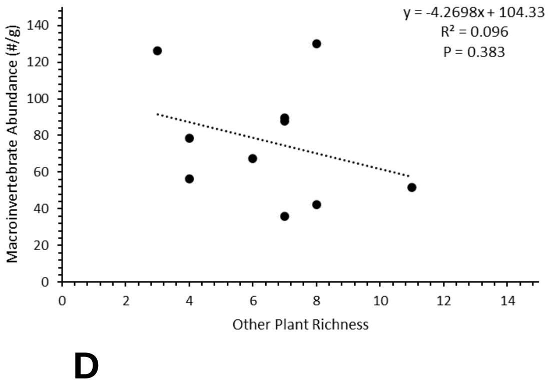


Figure 13. Starry Stonewort dry mass as a predictor of macroinvertebrate family richness across the five sampled locations. A) Braddock Bay B) Burnt Ship Creek C) Cayuga Lake D) Cazenovia Lake E) Keuka Lake Outlet









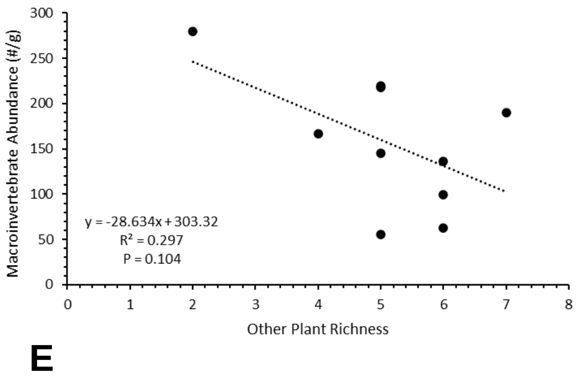
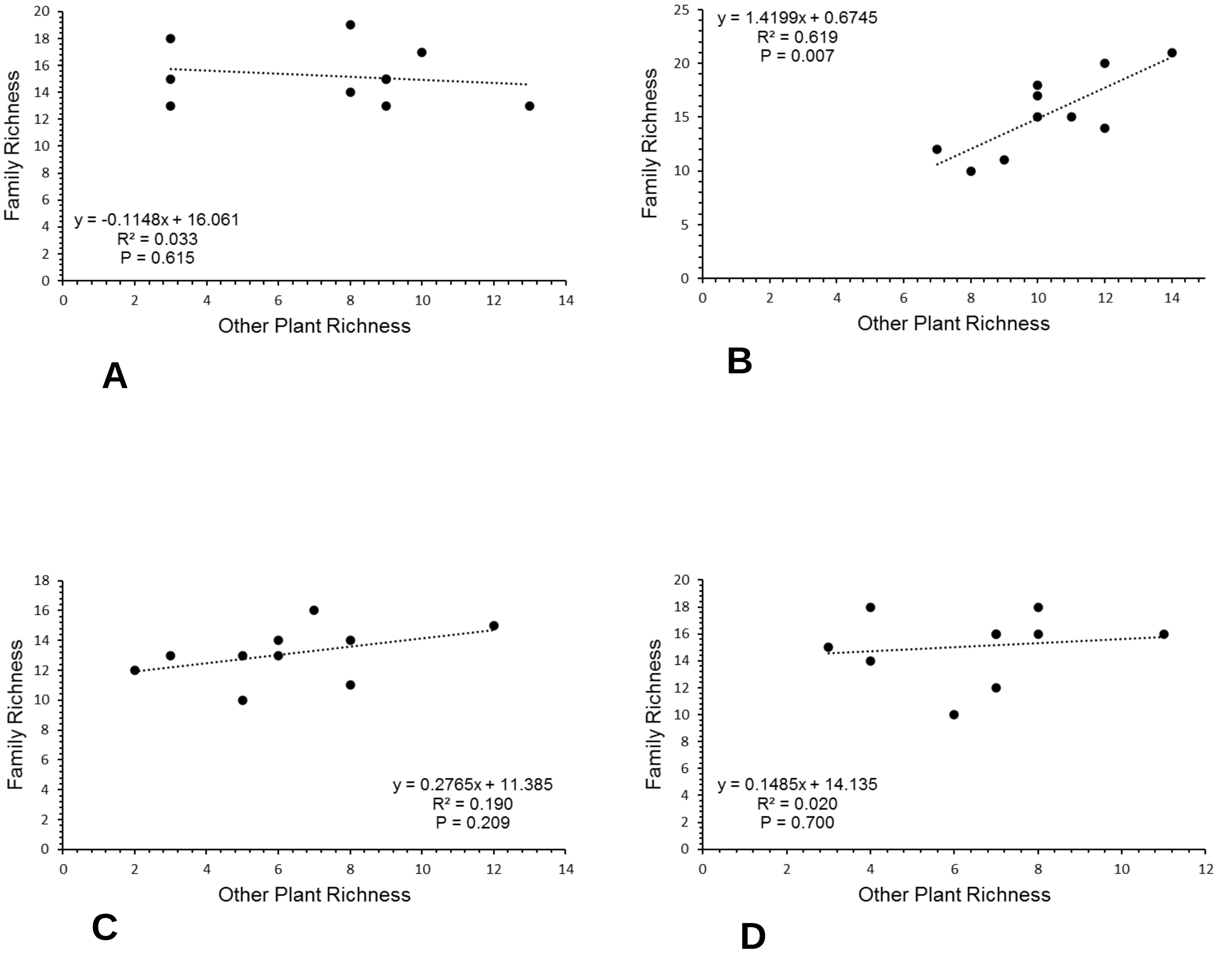


Figure 14. Other plant richness as a predictor of estimated macroinvertebrate abundance (# / g plant tissue) across the five sampled locations. A) Braddock Bay B) Burnt Ship Creek C) Cayuga Lake D) Cazenovia Lake E) Keuka Lake Outlet



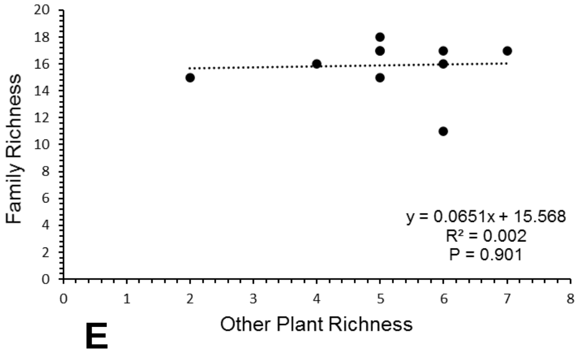


Figure 15. Other plant richness as a predictor of macroinvertebrate family richness across the five sampled locations. A) Braddock Bay B) Burnt Ship Creek C) Cayuga Lake D) Cazenovia Lake E) Keuka Lake Outlet

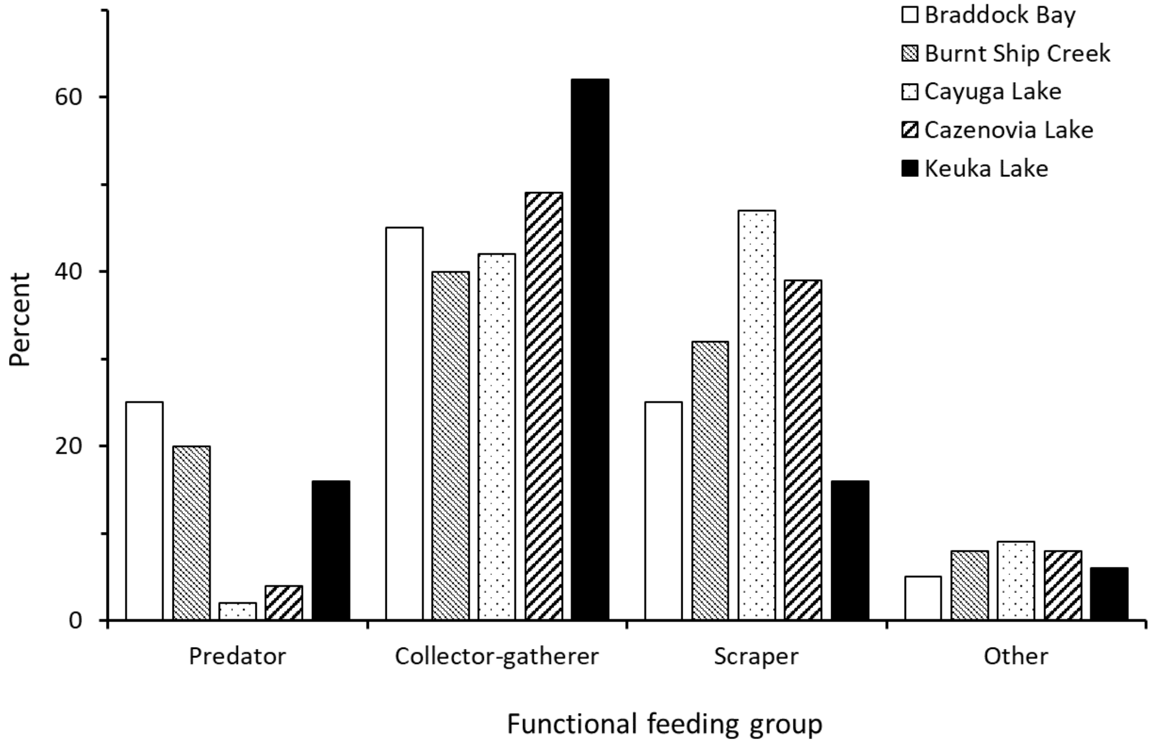


Figure 16. Functional feeding group representation among the five sample locations.

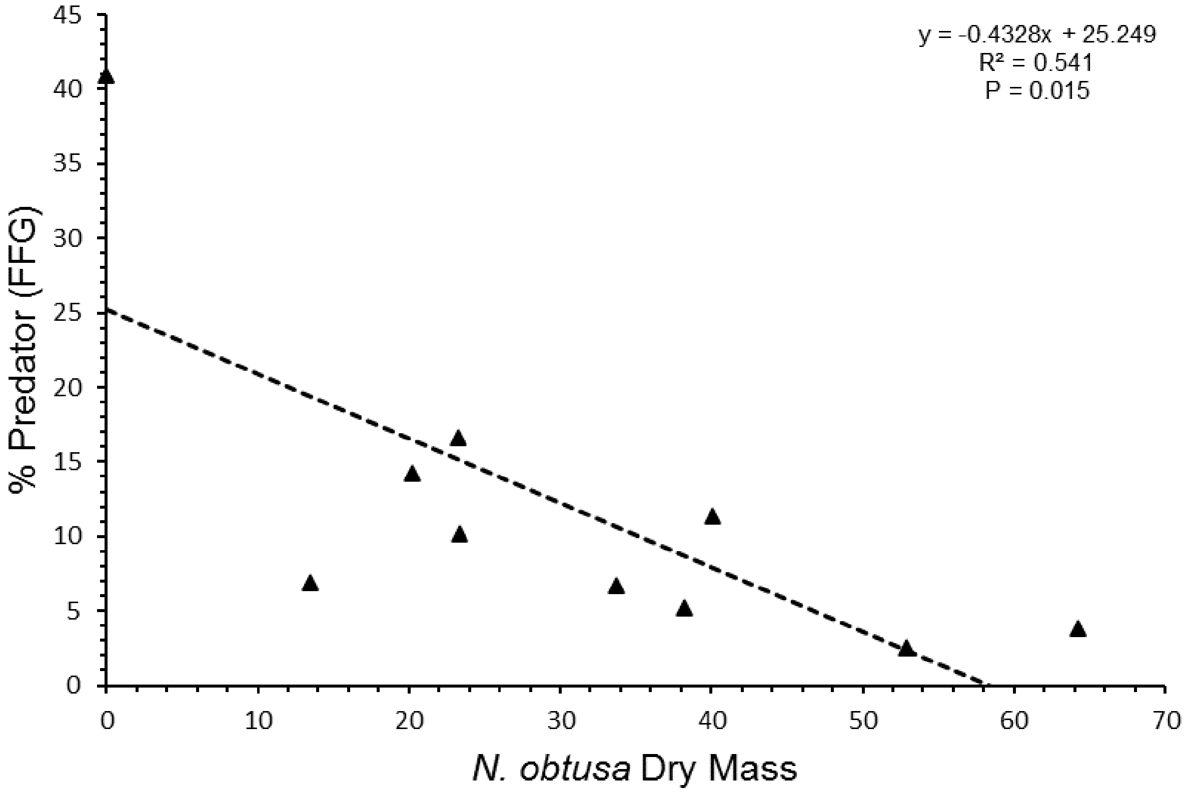


Figure 17. Starry Stonewort dry mass as a predictor of percent functional feeding group representation at Braddock Bay. Predator (PR)

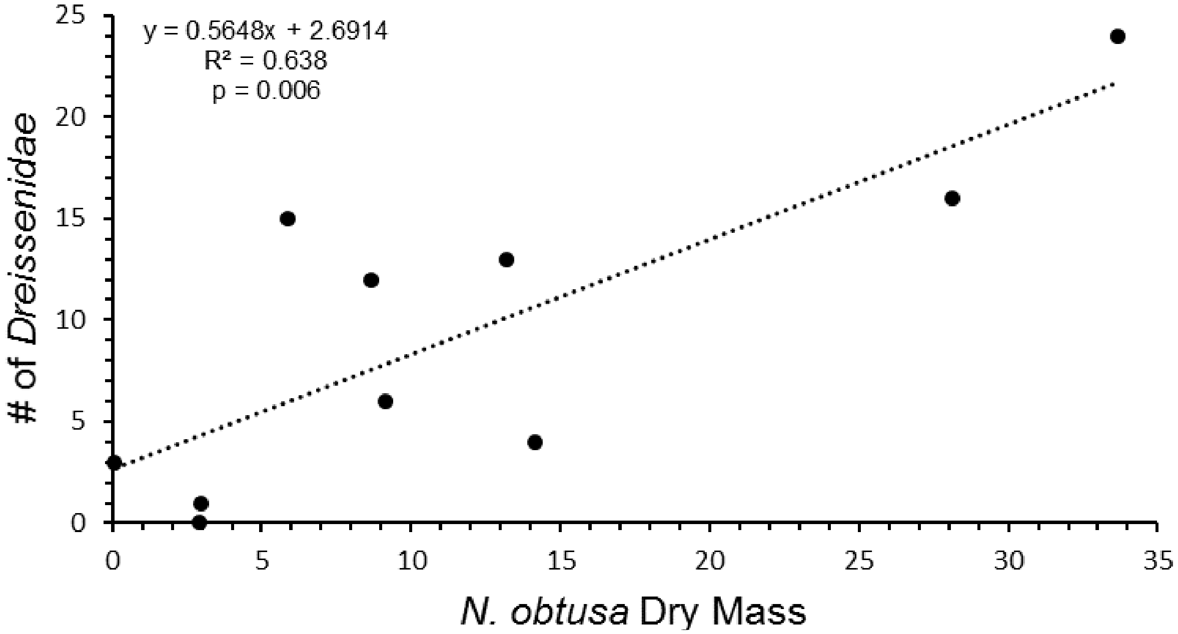


Figure 18. Starry Stonewort dry mass as a predictor of *Dreissenidae* abundance at Cayuga Lake.

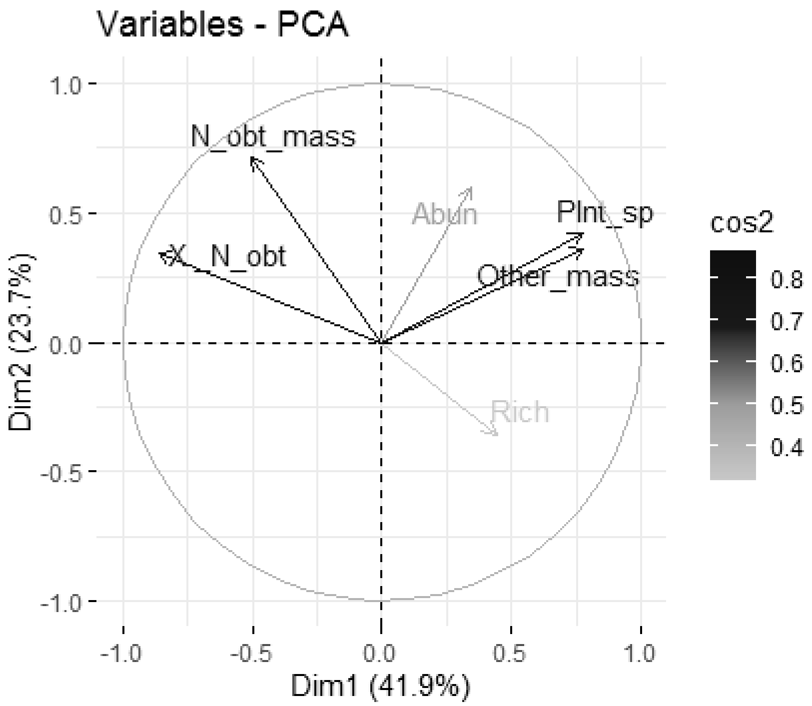


Figure 19. PCA loading plot representing Percent Starry Stonewort (X_N_obt), Starry Stonewort Mass (N_obt_mass), Other Plant Mass (Other_mass), Plant Richness (Plnt_sp), Macroinvertebrate Estimated Abundance (Abun), and Macroinvertebrate Family Richness (Rich).

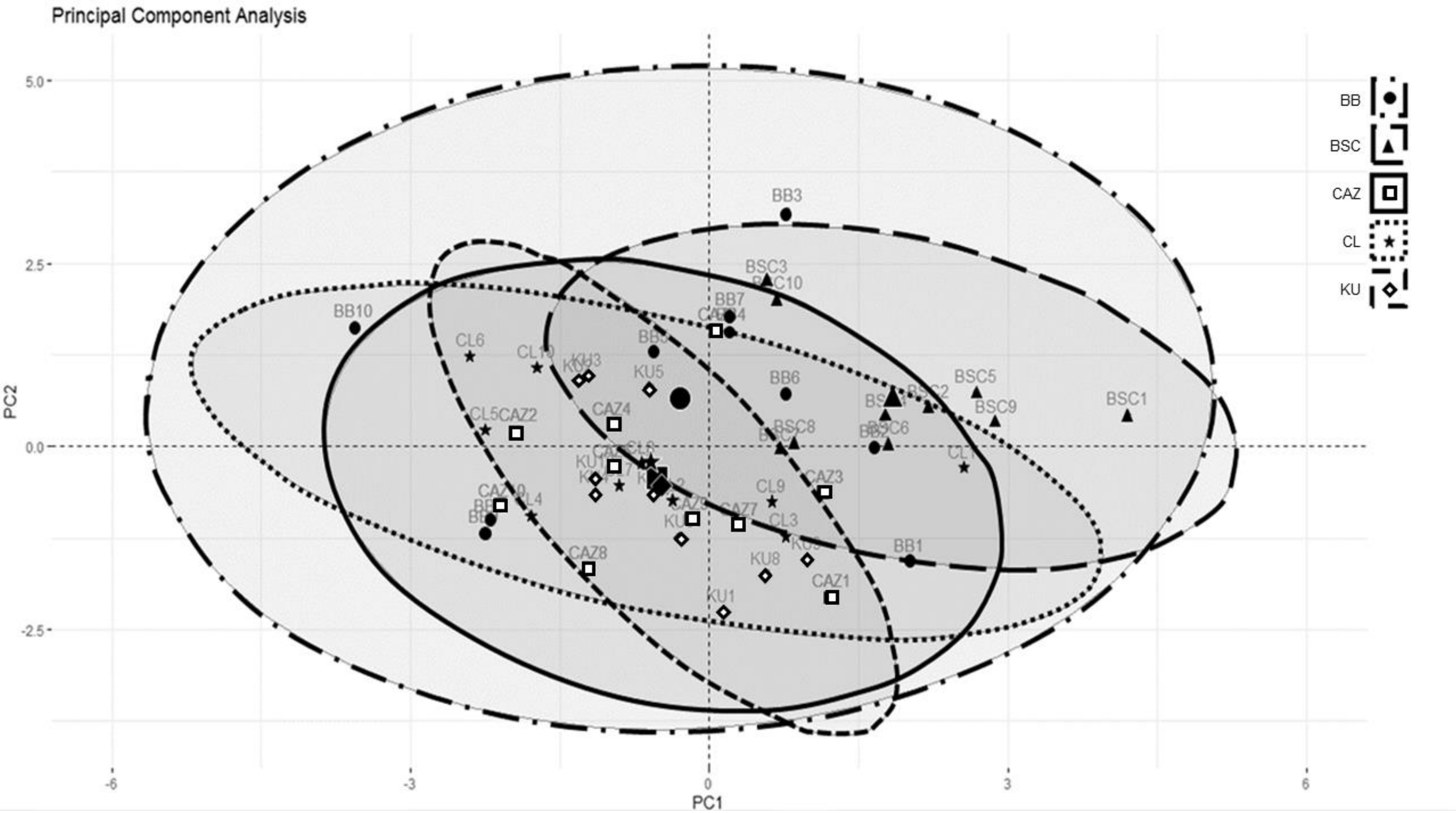


Figure 20. Principal Component Analysis with Representative Ellipses: Burnt Ship Creek (BSC), Braddock Bay (BB), Cayuga Lake (CL), Cazenovia Lake (CAZ), Keuka Lake Outlet (KU). PCA variables include macroinvertebrate and macrophyte variables. Ellipsoid center represented by larger symbols.

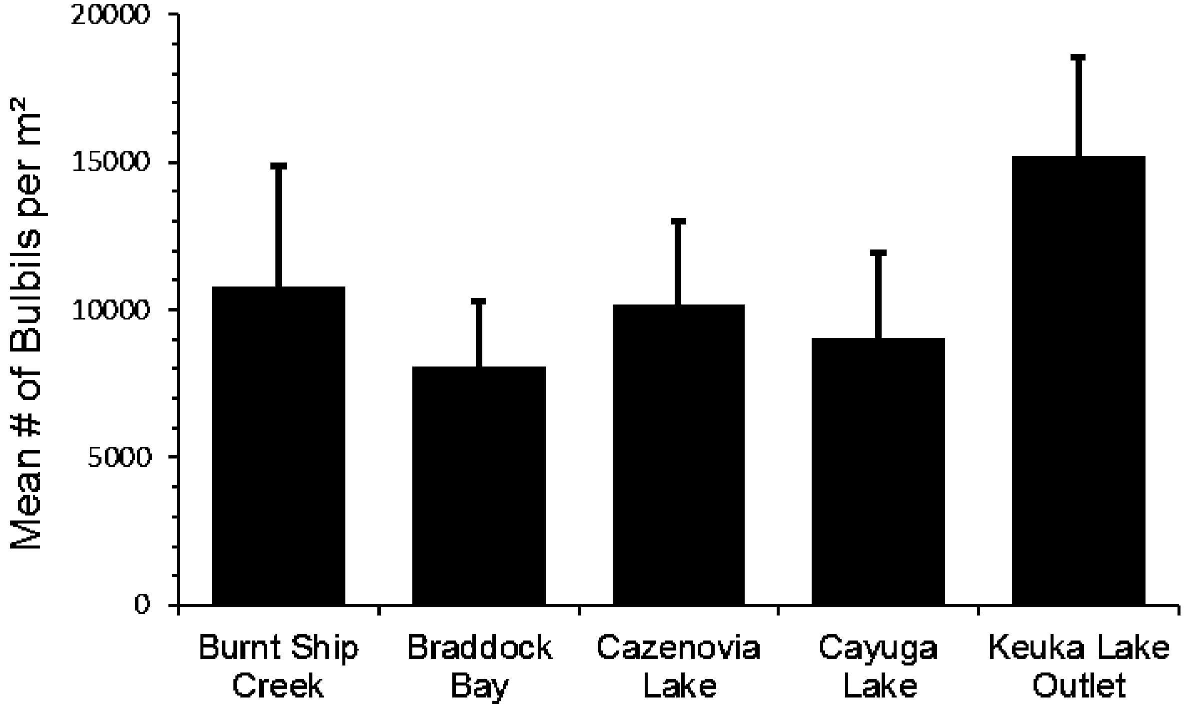


Figure 21. Mean number of bulbils (combined rhizoidal and nodal) per m^2 across the five sampled locations.

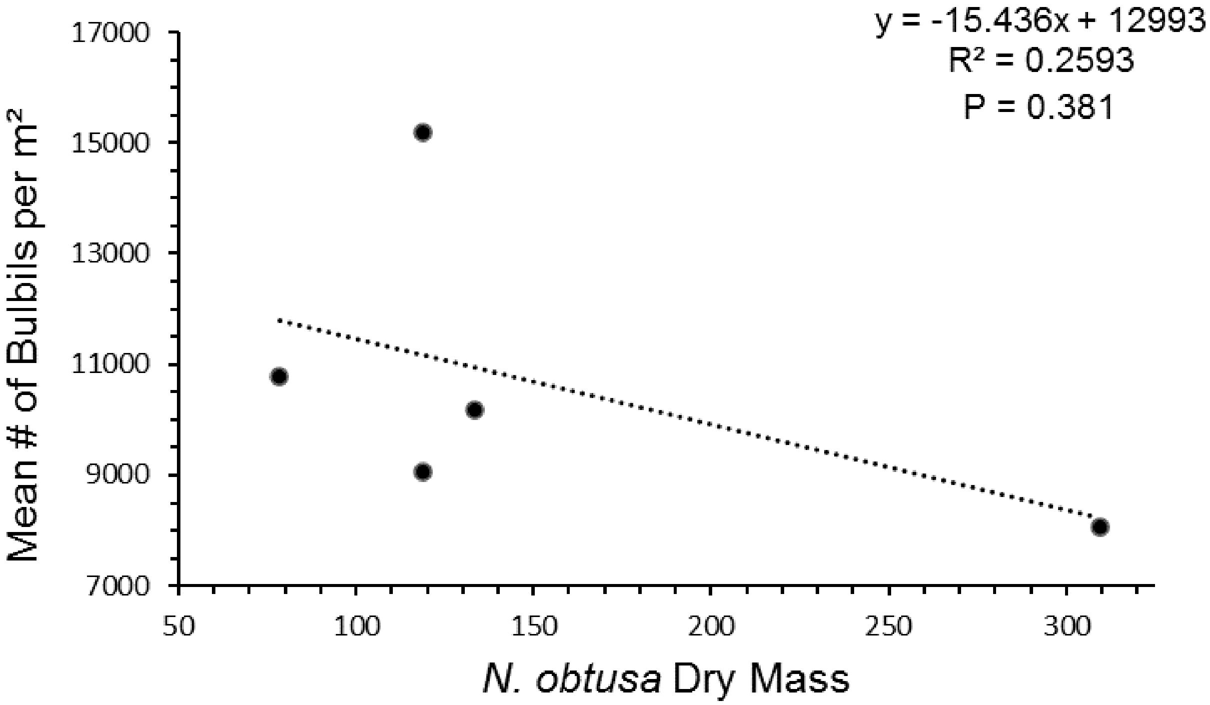


Figure 23. Starry Stonewort dry mass as a predictor of bulbil density at the five sampled locations.